SOCIAL–ECOLOGICAL CAUSES AND CONSEQUENCES OF LANDCOVER CHANGE IN LANDSCAPES OF NEBRASKA, U.S.A.

by

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SOCIAL–ECOLOGICAL CAUSES AND CONSEQUENCES OF LANDCOVER CHANGE IN LANDSCAPES OF NEBRASKA, U.S.A.

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Landcover change is an important global change process affecting social–ecological system(s) (SES) worldwide. Human activities may directly and indirectly drive landcover change, and human populations may be directly and indirectly affected by it. Although uncertainties exist about the future of landcover change, uncertainties can be engaged strategically in the context of SESs thinking. One such means of strategic engagement involves evaluating and comparing case studies of regional human-driven landcover change—past, present, and potential future—in order to obtain a more holistic and place-based understanding of its social–ecological trajectories, causes, and consequences. Improved understanding of these aspects of regional landcover change could inform decisions and actions that increase the resilience of SESs to landcover change and related global change processes.

In this dissertation, I assess trajectories, causes, and consequences of past, present, and potential future landcover change in landscapes of Nebraska, U.S.A. in the context of SESs thinking. In these case studies, a variety of methodological approaches—notably historical literature review, statistical modeling, machine learning, graph theory, and cellular automata—are utilized to improve understanding of past, present, and potential future human-driven landcover change in Nebraska landscapes, the direct and indirect

relationships between landcover change and people, and the social–ecological tradeoffs associated with alternative landcover change trajectories.

Individually, the findings of the chapters of this dissertation are useful for increasing understanding of landscape- and SES-specific landcover change effects and for informing current and future landscape management. In such SES-specific contexts, emphasis on the short- and long-term effects of landcover change for human populations and ecosystems, as well as increasing awareness of their interdependencies, could assist decision-making through the consideration of the social–ecological tradeoffs associated with alternative landcover-based decisions and actions. In a broader sense, the utility of this dissertation's findings lies in the promotion and illustration of the engagement of social–ecological challenges like landcover change—and uncertainties about them—through the lens of SESs thinking.

DEDICATION

To Annika again and now Samara, too.

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TABLE OF CONTENTS

LIST OF TABLES xii

LIST OF FIGURES xx

CHAPTER 1: INTRODUCTION 1

DISSERTATION OVERVIEW 6

LITERATURE CITED 8

TABLES AND FIGURES 15

CHAPTER 2: LANDCOVER, FUEL, AND SOCIAL–ECOLOGICAL TRANSFORMATION IN NINETEENTH CENTURY LANDSCAPES OF THE AMERICAN GREAT PLAINS 17

ABSTRACT 17

INTRODUCTION 19

HERBACEOUS BIOMASS 21

Utilization 21

Renewability 23

Geographic distribution 24

WOODY BIOMASS 28

Utilization 28

Renewability 31

Geographic distribution 36

BUFFALO CHIPS 49

Utilization 49

Renewability 50

Geographic distribution 51

DISCUSSION 51

LITERATURE CITED 55

FIGURES 67

CHAPTER 3: COMPARISONS OF LONG-TERM AVIAN ABUNDANCES AND CROPLAND PROPORTIONS IN SEVEN NEBRASKA, U.S.A. COUNTIES 72

ABSTRACT 72

INTRODUCTION 74

METHODS 76

Study areas 76

Data 76

Statistical models 77

RESULTS 80

DISCUSSION 81

LITERATURE CITED 85

TABLES AND FIGURES 91

CHAPTER 4: DISTURBANCE REGIME ALTERATION, TREE SPECIES DISTRIBUTIONS, AND OAK CONSERVATION IN THE MISSOURI RIVER BLUFFS OF SOUTHEAST NEBRASKA, U.S.A. 113

ABSTRACT 113

INTRODUCTION 115

METHODS 122

Study area 122

Data collection 123

Species distribution models 126

RESULTS 137

DISCUSSION 142

LITERATURE CITED 150

TABLES AND FIGURES 171

CHAPTER 5: FUNCTIONAL CONNECTIVITY OF WETLANDS FOR HERPETOFAUNA IN THREE CENTRAL NEBRASKA, U.S.A. LANDSCAPES 211

ABSTRACT 211

INTRODUCTION 213

METHODS 216

Study areas 216

Data sources 218

Functional connectivity evaluations 220

Wetland functional connectivity 224

Wetland spatial distributions 225

Dispersal distance connectivity thresholds 226

Node contributions to connectivity 226

DISCUSSION 227

LITERATURE CITED 233

CHAPTER 6: A LANDCOVER CHANGE-BASED ADPATIVE INVASIVE SPECIES DISTRIBUTION MODEL FOR AN AQUATIC SNAIL IN NEBRASKA, U.S.A. 267

ABSTRACT 267

INTRODUCTION 269

METHODS 270

Framework implementation 270

RESULTS 277

DISCUSSION 278

LITERATURE CITED 281

TABLES AND FIGURES 287

CHAPTER 7: LANDUSE AND LANDCOVER CHANGE SCENARIOS AND SIMULATIONS FOR A NORTHWEST NEBRASKA, U.S.A. LANDSCAPE 295
ABSTRACT 295
INTRODUCTION 297
METHODS 300
Study area 300
Storyline development 301
Landcover change simulations 303
Further refinement 307
RESULTS 307
Scenario 1: Roadside Development 307
Scenario 2: High and Dry 312
Scenario 3: Wood commodities 317
DISCUSSION 322
LITERATURE CITED 328
TABLES AND FIGURES 339
CHAPTER 8: SUMMARY AND SYNTHESIS 360
Future research 367
LITERATURE CITED 370

LIST OF TABLES

Chapter 1

Table 1. Methodological approaches utilized in this dissertation in assessing the social–ecological causes and consequences of landcover change in past, present, and future Nebraska, U.S.A. landscapes. 15

Chapter 3

Table 1. Selected Nebraska, U.S.A. county names with their corresponding areas (i.e., hectares) and Breeding Bird Survey (BBS) routes. 91

Table 2. Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent in seven Nebraska, U.S.A. counties, based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011). 92

Table 3. Overall mean abundances (i.e., counts) for western meadowlarks (*Sturnella neglecta*), brown-headed cowbirds (*Molothrus ater*), dickcissels (*Spiza americana*), and eastern kingbirds (*Tyrannus tyrannus*) along the Petersburg, Johnstown, Kearney, Sumner, Julian, Seward, and Irvington Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 93

Table 4. Overall mean proportions of area enrolled in cropland in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.. 94

Table 5. Marginal and conditional pseudo-R^2 values for generalized linear mixed model(s) (GLMM) explaining variability in brown-headed cowbird (*Molothrus ater*), dickcissel (*Spiza americana*), eastern kingbird (*Tyrannus tyrannus*), and western meadowlark (*Sturnella neglecta*) abundances along seven Breeding Bird Survey routes in seven Nebraska, U.S.A. counties 95

Table 6. Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in dickcissel (*Spiza americana*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 96

Table 7. Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in western meadowlark (*Sturnella neglecta*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007 97

Table 8. Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in eastern kingbird (*Tyrannus tyrannus*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007 98

Table 9. Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in brown-headed cowbird (*Molothrus ater*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007 99

Table 10. Generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between brown-headed cowbird (*Molothrus ater*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 100

Table 11. Table of generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between western meadowlark (*Sturnella neglecta*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007 101

Table 12. Table of generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between dickcissel (*Spiza *americana*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 102

Table 13. Table of generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between eastern kingbird (*Tyrannus tyrannus*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 103

Chapter 4

Table 1. Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent in Indian Cave State Park of southeast Nebraska, U.S.A., based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011)............................... 171

Table 2. Constituent models of model ensembles for large [≥ 30 cm diameter at breast height (dbh)] individuals of 14 ICSP tree species. Modeling techniques included in ensembles were generalized linear model(s) (GLM), generalized additive model(s) (GAM), boosted regression trees (BRT), and random forests (RF). 172

Table 3. Expected, observed and standard deviation in Moran's I values, which indicate levels of spatial autocorrelation in the global generalized linear model (GLM) and autologistic regression model (ARM) residuals for large [≥ 30 centimeters diameter-at-breast-height (dbh)] individuals of 14 tree species in Indian Cave State Park.. 173

Table 4. Expected, observed and standard deviation in Moran's I values, which indicate levels of spatial autocorrelation in the global generalized additive model (GAM) residuals for large (≥ 30 centimeters diameter-at-breast-height) individuals of 14 tree species in Indian Cave State Park............ 175

Table 5. Expected, observed and standard deviation in Moran's I values, which indicate levels of spatial autocorrelation in the boosted regression tree (BRT) residuals for large (≥ 30 centimeters diameter-at-breast-height) individuals of 11 tree species in Indian Cave State Park. 177

Table 6. Area under the curve (AUC) statistics for the best supported generalized linear model(s) (GLM) for 10 tree species and autologistic regression model(s) (ARM) for three tree species within Indian Cave State Park. . 179

Table 7. Area under the curve (AUC) statistics for the best supported generalized additive model(s) (GAM) for 14 tree species within Indian Cave State Park. AUC statistics were obtained through 10-fold cross-validation.... 180

Table 8. Area under the curve (AUC) statistics for the optimal boosted regression tree (BRT) model for 11 tree species within Indian Cave State Park. AUC statistics were obtained through 10-fold cross-validation. 181

Table 9. Area under the curve (AUC) statistics for the best supported random forests (RF) for 16 tree species within Indian Cave State Park. 182

Table 10. Relative influences of predictor variables within boosted regression tree (BRT) models for predicting the occurrence likelihoods of 11 tree species in Indian Cave State Park of southeast Nebraska, U.S.A. 183

Table 11. Predictor variable importance values within random forests models for predicting the occurrence likelihoods of 16 tree species in Indian Cave State Park of southeast Nebraska, U.S.A., where importance is defined as the mean decrease in accuracy that accompanies the removal of the parameter across all classification trees composing the random forest. . 185

Table 12. Predictor variable coefficient estimates, standard errors, and 95% confidence interval estimates for the best-supported generalized linear models for predicting presence/absence of 10 tree species in Indian Cave State Park of southeast Nebraska, U.S.A. 187

Table 13. Predictor variable coefficient estimates, standard errors, number of smoothers for the best-supported generalized additive models for predicting presence/absence of 14 tree species in Indian Cave State Park of southeast Nebraska, U.S.A. 188

Table 14. Predictor variable coefficients, standard errors, and 95% confidence interval estimates for the best-supported autologistic regression models for predicting presence/absence of three tree species in Indian Cave State Park of southeast Nebraska, U.S.A. 190

Chapter 5

Table 1. Anuran species with the potential to rely on wetland habitats in the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) biologically unique landscapes, according to Fogell (2010). 243

Table 2. Aquatic turtle species with the potential to rely on wetland habitats in the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) biologically unique landscapes, according to Fogell (2010).. 244

Table 3. Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent in the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) Biologically Unique Landscapes, based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011).............................. 245

Table 4. Results of nearest neighbor analysis for the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) biologically unique landscapes. 246

Chapter 6

Table 1. Mean area, road density, and Euclidian distance to the City of Lincoln for 13 water bodies in Lancaster County, Nebraska, U.S.A. surveyed for Chinese mystery snails (*Bellamya chinensis*) in 2011–2013. 287

Table 2. Predictor variable importance values in the random forests model explaining variability in Chinese mystery snail (*Bellamya chinensis*) presence/absence in Lancaster County of Nebraska, U.S.A., where importance is defined as the mean decrease in accuracy that accompanies the removal of the parameter across all classification trees composing the random forest. 288

Chapter 7

Table 1. Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent the Pine Ridge Biologically Unique Landscape of southeast Nebraska, U.S.A., based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011). 339

Table 2. Internal factors listed by participants in the Pine Ridge scenario planning exercise to be potentially important drivers of change in the Pine Ridge Biologically Unique Landscape in the coming 30 years. 340

Table 3. External factors listed by participants in the Pine Ridge scenario planning exercise to be potentially important drivers of change in the Pine Ridge Biologically Unique Landscape in the coming 30 years. 341

Table 4. Changes in landcover class area (hectares) from 2015–2045 under the Roadside Development Scenario. 342

Table 5. Changes in landcover class area (hectares) from 2015–2045 under the High and Dry Scenario.. 343

Table 6. Changes in landcover class area (hectares) from 2015–2045 under the Wood Commodities Scenario. 344

LIST OF FIGURES

Chapter 1

Figure 1. Thirty-nine biologically unique landscape(s) (BUL) within the State of Nebraska, U.S.A., as delineated in the Nebraska Natural Legacy Project (Schneider et al. 2011). 16

Chapter 2

Figure 1. Omaha village with earth lodges and tipis, surrounded by depleted herbaceous vegetation.. 67

Figure 2. The steamboat Montana, which operated on the Missouri River in the late 19th century. 68

Figure 3. Men sitting on a wood pile used to fuel a Union Pacific locomotive. 69

Figure 4. Andy Owens with his family and sawmill along Plum Creek, east of present-day Pine Canyon Dam, in Brown County, Nebraska. 70

Figure 5. Polly Ann McColl collecting buffalo chips in 1893, in Kearny County, Kansas. 71

Chapter 3

Figure 1. Locations of selected counties and Breeding Bird Survey (BBS) Routes within the State of Nebraska, U.S.A., where relationships between avian abundances and the proportion of county areas enrolled in cropland were evaluated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. . 104

Figure 2. Nebraska, U.S.A. reclassified 2010 landcover (Bishop et al. 2011), counties, and Breeding Bird Survey (BBS) routes in which avian abundances from the BBS were compared with metrics of cropland conversion from the U.S. Census of Agriculture in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 105

Figure 3. Distributions of brown-headed cowbird (*Molothrus ater*) abundances (i.e., counts) along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 106

Figure 4. Distributions of dickcissel (*Spiza americana*) abundances (i.e., counts) along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone

County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 107

Figure 5. Distributions of eastern kingbird (*Tyrannus tyrannus*) abundances along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 108

Figure 6. Distributions of western meadowlark (*Sturnella neglecta*) abundances along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 109

Figure 7. Distributions of proportions of area in cropland in Boone County, Brown County, Buffalo County, Dawson County, Otoe County, Seward County, and Washington County in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 110

Figure 8. Distributions of proportions of area in cropland in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007 in Boone County, Brown County, Buffalo County, Dawson County, Otoe County, Seward County, and Washington County of Nebraska, U.S.A. 111

Figure 9. Generalized linear mixed model predictions of relationships between a) brown-headed cowbird (Molothrus ater), b) dickcissel (Spiza americana), c) eastern kingbird (Tyrannus tyrannus), and d) western meadowlark (Sturnella neglecta) abundances and the proportion of land area in cropland in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. 112

Chapter 4

Figure 1. Reclassified landcover of Indian Cave State Park in southeast Nebraska, U.S.A., from the 2010 landcover layer of the Rainwater Basin Joint Venture (Bishop et al. 2011). 191

Figure 2. Predictor variables with which predictions of tree species occurrence likelihood and presence/absence were made with generalized linear models, generalized additive models, boosted regression tree models, and random forest models consisted of: a) elevation, b) slope, c) northness, d) longitude, and e) latitude.. 192

Figure 3. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for American basswood (*Tilia americana*) within Indian Cave State Park. 193

Figure 4. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for red oak (*Quercus rubra*) within Indian Cave State Park. 194

Figure 5. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for chinkapin oak (*Quercus muehlenbergii*) within Indian Cave State Park. 195

Figure 6. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for black oak (*Quercus velutina*) within Indian Cave State Park. 196

Figure 7. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for bur oak (*Quercus macrocarpa*) within Indian Cave State Park. 197

Figure 8. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for ash (*Fraxinus* spp.) within Indian Cave State Park. 198

Figure 9. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for bitternut hickory (*Carya cordiformis*) within Indian Cave State Park... 199

Figure 10. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for black walnut (*Juglans nigra*) within Indian Cave State Park... 200

Figure 11. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for elm (*Ulmus* spp.) within Indian Cave State Park... 201

Figure 12. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for hackberry (*Celtis occidentalis*) within Indian Cave State Park... 202

Figure 13. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for honeylocust (*Gleditsia triacanthos*) within Indian Cave State Park... 203

Figure 14. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for Kentucky coffeetree (*Gymnocladus dioicus*) within Indian Cave State Park. 204

Figure 15. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for mulberry (*Morus* spp.) within Indian Cave State Park. 205

Figure 16. Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for shagbark hickory (*Carya ovata*) within Indian Cave State Park. 206

Figure 17. Maps of a) occurrence likelihood and b) presence/absence for American sycamore (*Platanus occidentalis*) within Indian Cave State Park, based a random forests model. Continuous occurrence likelihood predictions were converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960). 207

Figure 18. Maps of a) occurrence likelihood and b) presence/absence for eastern cottonwood (*Populus deltoides*) within Indian Cave State Park, based a random forests model. 208

Figure 19. Areas for which all ensemble models predicted a) oak species presence, including b) areas where all models predict presence of more than one oak species. 209

Figure 20. Examples of fish-eye lens photographs of the forest canopy in ICSP in locations where burning and/or thinning management actions have (a) and have not (b) been implemented. 210

Chapter 5

Figure 1. Locations of the a) Cherry County Wetlands, b) Central Loess Hills and c) Rainwater Basin biologically unique landscape(s) (BUL) in north-central, central, and south-central Nebraska, U.S.A., respectively. 247

Figure 2. Wetland centroids in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL) of Nebraska, U.S.A. 248

Figure 3. Reclassified Nebraska, U.S.A. landcover within the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011). 249

Figure 4. Example of wetland connectivity network, where wetland centroids constitute nodes and Euclidian (i.e., straight-line) distances between centroids constitute edges. 250

Figure 5. Mean wetland degree within the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. 251

Figure 6. Total number of wetland clusters within the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. 252

Figure 7. Mean number of wetlands per wetland cluster in the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers.. 253

Figure 8. Network-level modularity for the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. 254

Figure 9. Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 0.50 kilometers. 255

Figure 10. Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.00 kilometers. 256

Figure 11. Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater

Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.50 kilometers. 257

Figure 12. Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 2.00 kilometers. 258

Figure 13. Percentages of total network wetlands within the single largest wetland cluster in the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. 259

Figure 14. Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 0.50 kilometers. 260

Figure 15. Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.00 kilometers. 261

Figure 16. Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.50 kilometers. 262

Figure 17. Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 2.00 kilometers. 263

Figure 18. 2012 aerial imagery of the portion of the Cherry County Wetlands BUL with particularly high levels of functional wetland connectivity for herpetofauna, assuming a maximum dispersal distance of 0.50 kilometers. 264

Figure 19. 2012 aerial imagery of the portion of the Central Loess Hills BUL with particularly high levels of functional wetland connectivity for herpetofauna, assuming a maximum dispersal distance of 0.50 kilometers. 265

Figure 20. 2012 aerial imagery of the portion of the Rainwater Basin BUL with particularly high levels of functional wetland connectivity for herpetofauna, assuming a maximum dispersal distance of 0.50 kilometers. 266

Chapter 6

Figure 1. Generalized example of the adaptive invasive species distribution model (iSDM) framework, with an emphasis on the practice of adaptive inference within it. 289

Figure 2. A detailed explanation of the framework for development of adaptive invasive species distribution models (iSDM), where newly-acquired information related to invasive species distributions is used for subsequent model improvements.. 290

Figure 3. Chinese mystery snail (*Bellamya chinensis*) occurrence records in water bodies of Lancaster County, Nebraska, U.S.A. 291

Figure 4. Road density in Lancaster County, Nebraska, U.S.A., measured in kilometers (km) per km^2. 292

Figure 5. Euclidian (i.e., straight-line) distance to the City of Lincoln, Nebraska, U.S.A... 293

Figure 6. Predicted Chinese mystery snail presence/absence in water bodies of Lancaster County, Nebraska, U.S.A. 294

Chapter 7

Figure 1. Reclassified landcover (Bishop et al. 2011) in and around the Pine Ridge Biologically Unique Landscape (BUL) of northwest Nebraska, U.S.A. 345

Figure 2. Iterative process used to conduct the scenario planning exercise in the Pine Ridge Biologically Unique Landscape. 346

Figure 3. Maps of a) conservation properties and b) areas that have experienced wildfire since the mid-20th century in the Pine Ridge Biologically Unique Landscape (BUL).. 347

Figure 4. Maps of a) elevation, b) percent slope, c) aspect, and d) National Resource Conservation Service Land Capability Classes in the Pine Ridge Biologically Unique Landscape (BUL). 348

Figure 5. Euclidian (i.e., straight-line) distance from a) Highway 385, b) all roads, c) City of Chadron, and d) pine trees in the Pine Ridge Biologically Unique Landscape (BUL). 349

Figure 6. Representations of a) neighborhood and b) random (i.e., stochastic) effects introduced into cellular automata models of landcover change............. 350

Figure 7. Drivers of landcover change in the Pine Ridge Biologically Unique Landscape under the Roadside Development Scenario. 351

Figure 8. Landcover in the Pine Ridge Biologically Unique Landscape (BUL) under the Roadside Development Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045.. 352

Figure 9. Major landcover class areas (log-transformed hectares) under the Roadside Development Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. 353

Figure 10. Drivers of landcover change in the Pine Ridge Biologically Unique Landscape under the High and Dry Scenario. 354

Figure 11. Landcover in the Pine Ridge Biologically Unique Landscape (BUL) under the High and Dry Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045.. 355

Figure 12. Major landcover class areas (log-transformed hectares) under the High and Dry Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. 356

Figure 13. Drivers of landcover change in the Pine Ridge Biologically Unique Landscape under the Wood Commodities Scenario. Landcover changes are listed in red-colored font. 357

Figure 14. Landcover in the Pine Ridge Biologically Unique Landscape (BUL) under the Wood Commodities Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. 358

Figure 15. Major landcover class areas (log-transformed hectares) under the Wood Commodities Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. 359

CHAPTER 1: INTRODUCTION

In social–ecological system(s) (SES), human populations and ecosystems are inextricably linked through reciprocal influences and interdependencies (Berkes & Folke 1998; Levin et al. 2013; McGinnis & Ostrom 2014), which means that changes in ecosystems have consequences for human societies, and *vice versa*. Landuse change and landcover change are important global change processes affecting SESs worldwide (Lambin et al. 2006; Lindenmayer & Fischer 2013); however, future changes in landuse and landcover and their effects are largely uncertain (Muller et al. 2014). Strategically addressing such uncertainties in the context of SESs thinking could increase understanding about trajectories of landcover change within SESs, and could also increase the resiliencies and adaptabilities of SESs (Craig 2010) under the pressures of landcover change and related global change processes. One such means of strategic engagement involves evaluating and comparing case studies of regional landcover change—past, present, and potential future—in order to obtain a more holistic and place-based understanding of the social–ecological trajectories, causes, and consequences of landcover change in focal landscapes.

Landuse is differentiated from landcover by the intentionality of humans in utilizing biophysical attributes of the Earth's surface (i.e., landcover) for given purposes. However, in practice, definitively distinguishing between landuse and landcover change may be difficult because of issues such as the global pervasiveness of human influences (McKibben 2006), the impossibility of ascertaining human intention from remotely sensed imagery, the fact that a single landcover class can have multiple landuses (Giri

2012), and the challenges of classification (De Gregorio 2016). For example, landuse change occurs as grasslands are converted to pastures for livestock production and to rowcrop fields for grain production. At the spatial scale of hectares, grassland-to-rowcrop transitions constitute landcover change, but grassland-to-pasture conversions may or may not, depending on management practices and classification schemes. Landcover change also unfolds as grasslands transition from grassland to woodland via woody plant encroachment—a phenomenon widely driven by human fire suppression (Bowman et al. 2011; Lasslop et al. 2016). If a transitioning grassland is managed as a pasture, the replacement of grass by trees may eventually preclude grazing; however, an open-canopied woodland with a grassy understory may be utilized as pasture. Consideration of the relationships between landuse change and landcover change could help frame landcover change in the context of SESs thinking, which recognizes human activities as drivers of landscape change (Ellis et al. 2015).

Landcover change may have diverse direct and indirect social–ecological causes and consequences. For instance, landcover change in forested landscapes may be driven by changes in—and complex interactions among—various biophysical (e.g., drought frequency), economic (e.g., timber market growth), technological (e.g., degree of mechanization), demographic (e.g., immigration), institutional (e.g., land zoning), cultural (e.g., attitudes toward fire), and spatial (e.g., distance to roads) factors (Rudel et al. 2005; Geist et al. 2006; Babigumira et al. 2008; Lambin & Meyfroidt 2011; Graesser et al. 2015). Landcover change may be socially and/or ecologically beneficial or detrimental, depending on the type of change that occurs, the context in which it occurs, and the temporal scale over which it is observed (DeFries et al. 2004; Foley et al. 2005; Chhabra et al. 2006). Although the futures of human decision-making, landuse, and landcover are largely uncertain, landcover change is expected to continue affecting atmospheric conditions, biodiversity, soil quality, hydrology, and ecosystem and human health at multiple spatial and temporal scales. Climate change, in particular, will continue to interact with and potentially amplify landcover change and its effects (Chhabra et al. 2006; Jantz et al. 2015; Mantyka-Pringle et al. 2015).

There are often tradeoffs between short-term social benefits and long-term ecological costs in regard to landuse decisions and associated landcover changes (Foley et al. 2005; Walker & Salt 2006). For example, although the conversion of grasslands and wetlands to rowcrop fields increases food and energy production for human populations, it decreases habitat quality and quantity for grassland- and wetland-dependent species (Samson et al. 2004; Wright & Wimberly 2013; Johnston 2014). Decreases in habitat can create and contribute to conservation concerns, especially when they occur over long time periods and/or large spatial extents. These concerns have spurred the enactment of conservation measures, such as State Wildlife Action Plans in the U.S.A. In the State of Nebraska, U.S.A., the Nebraska Natural Legacy Project (Schneider et al. 2011) serves as the State Wildlife Action Plan. The overarching objectives of the Nebraska Natural Legacy Project are to conserve the flora, fauna, and natural habitats of the state. To achieve these objectives, management actions are focused in 39 biologically unique landscape(s) (BUL) across the state (Figure 1), which collectively offer opportunities for conserving the full array of the state’s biodiversity.

In this dissertation, my primary objective was to assess the trajectories, causes, and consequences of past, present, and potential future landcover change in landscapes of Nebraska, U.S.A. in the context of SESs thinking. In these case studies, a variety of methodological approaches—notably historical literature review, statistical modeling, machine learning, graph theory, and cellular automata (Table 1)—are utilized to improve understanding of past, present, and potential future landcover change in Nebraska landscapes, the direct and indirect relationships between landcover change and people, and the social–ecological tradeoffs associated with alternative landcover change trajectories. Major landcover classes affected by landcover change in case studies include oak (*Quercus* spp.)–hickory (*Carya* spp.) woodlands and forests, croplands, grasslands, and pine (*Pinus ponderosa*) woodlands and forests. Individually, chapter results may inform current and future decisions and actions related to specific forms of landcover change in Nebraska landscapes. Collectively, results promote the engagement of questions about landcover change and the uncertainties associated with it through the lens of SESs thinking, which may help increase the resilience, adaptability, and transformability of SESs amidst landcover change and related global change processes.

First-hand descriptions of North American landscapes and SESs—including those of present-day Nebraska—in the centuries prior to European and Euro-American exploration and resettlement are rare, although information about them can be gleaned from archaeological records (Bamforth 2011), oral traditions (Echo-Hawk 2000), and ecological legacies (Whitney 1994). It has been assumed that Europeans and Euro-Americans encountered static SESs composed of Native Americans in ancient balance with their environments; however, it is more likely that Native American societies were continually responding to and modifying their dynamic environments, just as immigrating Euro-Americans were influencing and being influenced by theirs—albeit via the adoption of different strategies (West 1998; Krech 1999; Binnema 2001; Cunfer 2005). Over the course of the 19th century, the predominant human influences on Nebraska landscapes shifted from Native Americans to Euro-Americans, though Native Americans themselves persisted (Wishart 1994, 2016). This process of colonization continues to directly and indirectly affect SES states, landuse, and landcover in Nebraska.

Within landscapes and SESs of Nebraska, landcover change has been directly and indirectly driven by people. One important form of directly human-driven landcover change is land conversion—evidenced in the large-scale transformation of grasslands and wetlands to croplands in the late 19th and early 20th centuries (Cunfer 2005). Social–ecological tradeoffs associated with conversions to cropland include increased food and energy production for human populations with corresponding decreases in habitat quality and quantity for grassland- and wetland-dependent species (Samson et al. 2004; Johnston 2014). In contrast, one form of indirectly human-driven landcover change is human manipulation of disturbance regimes. For example, Native American societies increased the frequency of fire beyond what would have occurred in their absence, but the direction of this effect was rapidly reversed through Euro-American fire suppression efforts (Courtwright 2011). This, in turn, led to the decoupling of patchy spatiotemporal interactions between fire and grazers [e.g., bison (*Bison bison*)] (Fuhlendorf et al. 2009), the encroachment of woody plants into prairies (Twidwell et al. 2013; Meneguzzo &

Liknes 2015), and the increased dominance of shade-tolerant woody species in formerly open-canopied savannas, woodlands, and forests (Abrams 1986; Rogers & Russell 2014). Future landcover changes and their effects are largely uncertain, yet are still likely to have important implications for Nebraska landscapes and SESs.

DISSERTATION OVERVIEW

Landcover change is an important global change process affecting social-ecological system(s) (SES) worldwide. Although substantial uncertainties exist about the future of landcover change and its effects, uncertainties can be engaged strategically in the context of SESs thinking. One such means of strategic engagement involves evaluating and comparing case studies of regional landcover change—past, present, and potential future—in order to obtain a more holistic and place-based understanding of the social–ecological causes and consequences of landcover change in focal landscapes. This improved understanding of past, present, and potential future landcover change trajectories could inform thinking and actions that increase resilience and facilitate adaptation and/or transformation in SESs under the influences of landcover change and related global change processes.

This dissertation is chronologically organized in eight chapters, in which I consider case studies of landcover change in the State of Nebraska, U.S.A. in the context of SESs thinking and with a diverse set of methodological approaches. This first chapter provides a review of information on landuse and landcover change pertinent to subsequent chapters. In Chapter 2, I conduct a historical literature review on landcover and human fuel procurement in 19th century landscapes of the American Great Plains—including present-day Nebraska—emphasizing the role of humans in simultaneously shaping and responding to their environments. In Chapter 3, I consider the long-term ecological effects of land conversion—particularly conversion to cropland—by statistically comparing proportions of cropland in seven Nebraska counties and counts of breeding birds along seven survey routes in those counties in seven years between 1969 and 2007. In Chapter 4, I develop ensembles of species distribution models for mature individuals of 14 tree species in Indian Cave State Park, along the Missouri River bluffs of southeast Nebraska, where more than a century of fire suppression has transformed open-canopied oak (*Quercus* spp.) savannas and woodlands to closed-canopied forests increasingly dominated by more shade-tolerant woody species. In Chapter 5, I explore relationships between landcover change intensity and the degree of functional wetland connectivity for herpetofauna in three central Nebraska landscapes, and then speculate on the quality of wetland habitats for herpetofauna in highly connected portions of networks. In Chapter 6, I develop an adaptive invasive species distribution model for a large, aquatic Chinese mystery snail (*Bellamya chinensis*) in water bodies of Lancaster County, Nebraska, paying special attention to the role of landcover change in facilitating snail spread among water bodies. In Chapter 7, I develop storylines and conduct simulations of alternative, plausible scenarios of future landcover change in the Pine Ridge landscape of northwest Nebraska, in order to strategically address the collective future uncertainties of landscape managers. In the eighth and final chapter, I synthesize and summarize dissertation results and implications and recommend future study directions.

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TABLES AND FIGURES

Table 1: Methodological approaches utilized in this dissertation in assessing the social–ecological causes and consequences of landcover change in past, present, and future Nebraska, U.S.A. landscapes.

Method	**Chapter**	**Landcover application**
Historical literature review	2	Human energy utilization
Generalized linear mixed models	3	Effects on bird abundances
Generalized linear models	4	Tree species distribution models
Generalized additive models	4	Tree species distribution models
Boosted regression trees	4	Tree species distribution models
Random forests	4	Tree species distribution models
Ensemble modeling	4	Tree species distribution models
Graph theory	5	Wetland functional connectivity
Random forests	6	Invasive species distribution models
Cellular automata	7	Landcover change simulations

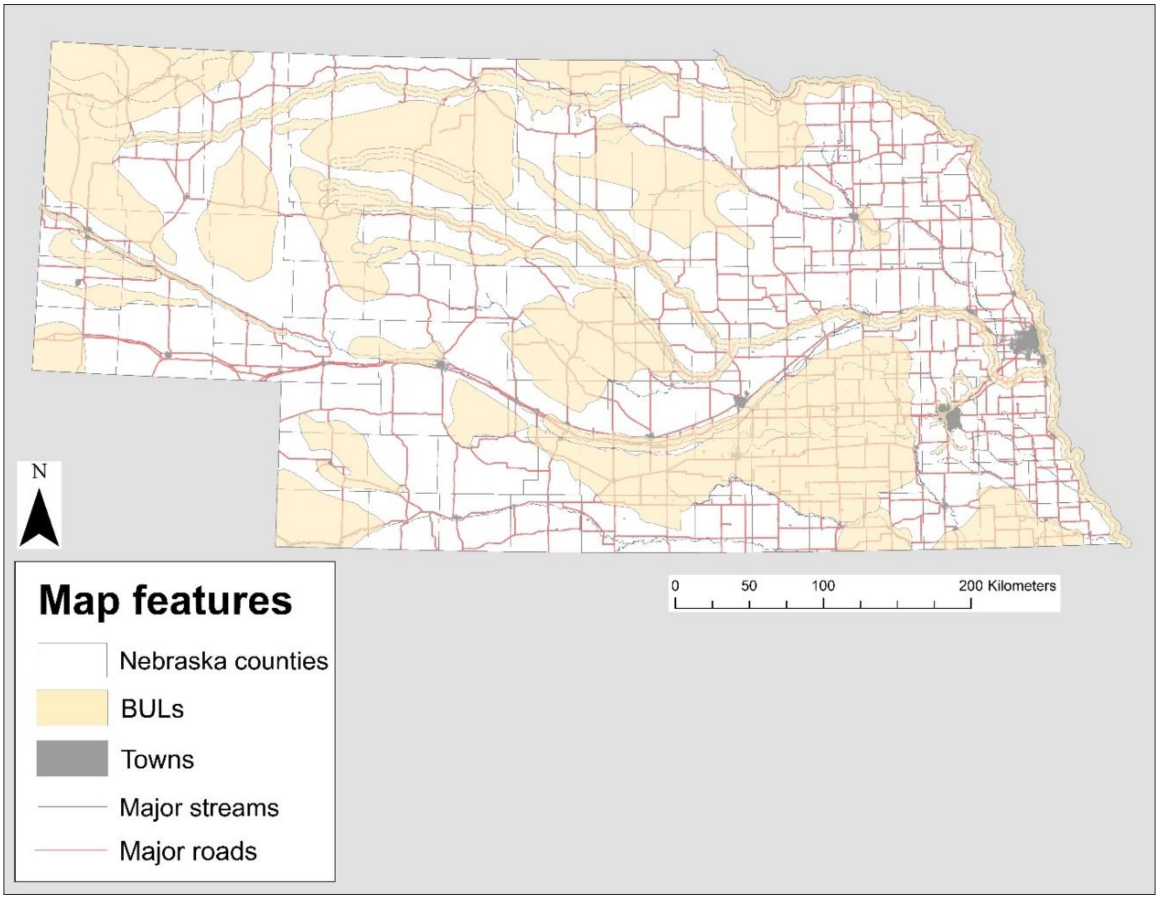
N
Map features
Nebraska counties
BULs
Towns
Major streams
Major roads
0
50
100
200 Kilometers

Figure 1: Thirty-nine biologically unique landscape(s) (BUL) within the State of Nebraska, U.S.A., as delineated in the Nebraska Natural Legacy Project (Schneider et al. 2011).

CHAPTER 2: LANDCOVER, FUEL, AND SOCIAL–ECOLOGICAL TRANSFORMATION IN NINETEENTH CENTURY LANDSCAPES OF THE AMERICAN GREAT PLAINS

ABSTRACT

Within social–ecological system(s) (SES), harnessing energy for activities like cooking, heating, and travel is a fundamental human requirement. Prior to fossil fuel adoption, much of this energy (i.e., fuel) was derived from local landscape elements, and this landuse affected landcover. In this chapter, I draw on 19th century accounts of human energy procurement in landscapes of the Central and Northern Great Plains—including those of present-day Nebraska, U.S.A.—focusing on the utility, renewability, and geographic distributions of important organic fuels, excluding coal. Native and Euro-Americans relied on herbaceous biomass, woody biomass, and ruminant dung [i.e., buffalo (*Bison bison*) and cow (*Bos taurus*) chips] for energy—which although variable in availability and co-occurrence with other essential landscape elements (e.g., water and shelter)—could regenerate on timescales shorter than the human lifespan. The ubiquity of herbaceous biomass was a defining regional characteristic, as tallgrass and shortgrass prairie species dominated vegetation in the east and west, respectively. Woody biomass was a relatively rare fuel that, in general, was restricted to lowlands and decreased from east to west. Buffalo and cow chips were common throughout the western plains, in wooded wintering areas, and along transportation routes. Amidst the social–ecological transformations of European colonization, prevailing tactics for increasing energy access,

such as rotational use and setting fire, were supplanted by strategies of resource storage and importation. The geographic distributions of herbaceous biomass, woody biomass, and buffalo chips ebbed and flowed over the course of the 19th century as a result of changes in and interactions among various factors, including environmental conditions, human harvest, and human disturbance regime manipulation. In other words, landcover changes in 19th century SESs of present-day Nebraska and the surrounding Great Plains were both directly and indirectly human-driven and occurred as Native and Euro-Americans simultaneously shaped and responded to their environments. However, differences in these responses across cultures, time, and space set Great Plains SESs on alternative trajectories characterized by unique short-term and long-term landcover-based tradeoffs that extend to present-day.

INTRODUCTION

In social–ecological system(s) (SES) thinking, human populations and the ecosystems they interact with are inextricably linked through reciprocal influences and interdependencies (Berkes & Folke 1998; Liu et al. 2007; McGinnis & Ostrom 2014). Energy (i.e., fuel) is essential for human societies, and people derive it—at different scales, in different forms, and by different means—from their environments. The scale of human energy use has greatly increased over the past several centuries (Odum 2007), with corresponding shifts in landuse, landcover, and SES states (Klein Goldewijk 2001; Chhabra et al. 2006; Fischer-Kowalski & Haberl 2007). Excellent examples of landuse change and landcover change are provided in 19th century landscapes of the American Great Plains, where Native American and Euro-American societies increasingly required fuel in the form of local landscape elements amidst the social–ecological transformations of colonization (West 1998; Cunfer 2005).

First-hand descriptions of Great Plains landscapes in the centuries prior to large-scale European exploration are rare (Wedel 1963), although second-hand information can be derived from various alternative sources (Echo-Hawk 2000; Bamforth 2011). Nineteenth century Native American societies were actively responding to and modifying their dynamic Great Plains environments, as well as responding to a number of European-based frontiers, which included: 1) horses (*Equus caballus*); 2) guns; 3) diseases; and 4) resettlement (West 1998; Binnema 2001; Alchon 2003; Wishart 2016). Immigrating Euro-Americans were also responding to and modifying their newfound Great Plains environments (Cunfer 2005), which from their perspective, were extreme and variable in weather and resource availability (Webb 1931; Malin 1956). Therefore, both Native and Euro-American cultures actively adjusted to life on the Great Plains; however, they developed and adopted different strategies—with unique social–ecological consequences—in doing so. The procurement of energy (i.e., fuel) was at the core of these adaptations (West 1998; Cunfer 2005).

With the exception of coal—which is excluded from this assessment because of its widespread availability and adoption only in the waning decades of the 19th century—human inhabitants of the Great Plains derived a large proportion of energy for accomplishing daily tasks (e.g., cooking, heating, and travel) from local landscape elements that are today considered clean and renewable energy sources, including herbaceous biomass, woody biomass, dried dung [i.e., buffalo (*Bison bison*) and cow (*Bos taurus*) chips], wind, and water. The energy production potential per unit mass (i.e., energy densities) of these fuels—excluding wind and water—was greatest in woody biomass, then herbaceous biomass, and buffalo chips (Smil 1994). Human utilization of woody and herbaceous fuels—a form of landuse—can produce landcover change within SESs. In this review of 19th century organic fuels of the Central and Northern Great Plains, I assess the importance of herbaceous biomass, woody biomass, and buffalo chips as fuel sources, according to their utilization, renewability, and geographic distributions. I also consider the effects of the social–ecological transformations of colonization in driving changes in these fuel characteristics—and associated landcover—over the course of the century. Results could be useful for improving understanding of contemporary and future landcover changes and increasing the resilience of SESs in Nebraska landscapes to landcover change and other global change processes.

HERBACEOUS BIOMASS

Utilization

Following the 16–18th century reintroduction and domestication of horses in the Great Plains, they, with other livestock, became prized for their utility in activities like travel, hunting, and drafting (Moore 1987; West 1998; Binnema 2001; Hamalainen 2003). In their energetic efficiencies (i.e., ratio of energy input to output), horses rivaled steam engines (Greene 2008). However, the benefits associated with these animal adoptions were accompanied by a requirement to continually procure food for them. Herbaceous biomass (i.e., grasses and other non-woody plants) was the primary food of plains horses and livestock, and as such, became important for human populations.

Among Native Americans, horse ownership increased the ease of travel associated with hunting and raiding, and translated into wealth. Horses provided a direct connection to the immense, ubiquitous stores of energy housed in prairie grasses, which dogs (*Canis lupus*)—the previous beast of burden—could only access indirectly via meat consumption (West 1998). Furthermore, horses did not compete directly with people or dogs for food, which diversified the energy sources on which societies relied.

There were, however, energy-related inconveniences associated with horse ownership, one of which was an inability to congregate in one location for extended time periods, due to the outpacing of local vegetative growth by herd consumption (Figure 1;

White 1982). Furthermore, in the absence of hay storage—a practice not adopted by Native Americans until at least the 1860s—feed had to be procured from landscapes year-round. Local grass scarcities were especially problematic in northern climates, where growing seasons were shorter (Ewers 1969; Courtwright 2011). One example of local herbaceous biomass exhaustion comes from the journals of the German explorer and naturalist, Prince Maximilian, who in 1833, described the prairie surrounding Fort McKenzie, in present-day Chouteau County, Montana, as “barren and dry, trampled down by men and horses, and grazed bare. Everywhere one saw Indians and bunches of grazing horses, guarded and herded by Indian boys on horseback” (Witte & Gallagher 2010:359). In other instances, travelers and horses were kept off of the grass around forts (West 1998).

For semi-nomadic peoples, who farmed and hunted bison (e.g., Pawnees and Poncas), semi-annual hunts provided a partial solution to the complication of vegetation shortages by promoting frequent movement among hunting camps (Wedel 1963)—essentially rotating the locations and broadening the spatial scale of energy procurement. For example, the Reverend John Dunbar, a Presbyterian missionary to the Pawnees, accompanied the tribe on their 1834 and 1835 summer and winter bison hunts, and recorded total hunt travel distances of 300–600 kilometers (Wishart 1994). In the 1830s, the Pawnees were grazing horses—which they owned 6,000–8,000 of at that time—on mature prairie cordgrass (*Spartina pectinata*) each autumn, prior to the winter bison hunt, on Grand Island, along the Platte River, in present-day south-central Nebraska (Wishart 1994). In fully-nomadic societies (e.g., Cheyennes and Lakotas), who did not farm, securing horse forage became a secondary, even primary, driver of movement (Moore 1987; West 1998; Hamalainen 2003).

Euro-American farmers also actively converted the energy stored within herbaceous biomass into alternative forms via horses, mules, and oxen (i.e., cattle), as evidenced by the millions of hectares of lowland and upland prairie overturned with draft animals, beginning around 1870 (Cunfer 2005). Draft animals were also powered with corn and other grains that farmers raised—largely through animal labor. Besides 1–5 kilograms of grain, the average 450-kilogram draft horse required 5–6 kilograms of roughage (i.e., herbaceous biomass) each day, depending on activity (Vogel 1996; Cunfer 2005). Hay and grain storage helped ensure that these demands could be met year-round (West 1998). As a food source, cattle—like bison—made energy in prairie grasses accessible to human metabolism.

Renewability

Grasses and other prairie plants are characterized by high degrees of renewability, which stem from their capacities to regenerate following disturbances like drought, grazing, and fire in less than a decade, typically within a year. For instance, grazed tallgrass, mixedgrass, and shortgrass prairies of the plains produce, on average, 1.66, 1.09 and 0.74 metric tons (mT) of live biomass per hectare per year, respectively (Sims et al. 1978). The resilience of grasslands to—even dependence of them upon—disturbances is attributed to plant characteristics like perennial growth, protected buds, extensive root systems, and phenotypic responses to disturbances (e.g., dormancy during drought), as well as heterogeneous and continually-shifting species compositions (Weaver 1954, 1968). Recognizing the patterns driven by these processes, Native Americans used fire to advance the onset and increase the vigor of spring herbaceous growth in and around their villages and hunting grounds, thereby increasing their access to energy from herbaceous—although not woody—biomass the following spring (Custer 1962; C.T. Moore 1972; J.H. Moore 1987; Sauer 1975; Binnema 2001; Pyne 1982; White 1982; Courtwright 2011).

Geographic distribution

In general, herbaceous biomass was readily available wherever it had not been temporarily removed by grazing, fire, drought, or soil disturbance. One of the best-documented characteristics of the plains was its domination by grass. Despite its widespread availability, to be useful to human populations and their animals, it was necessary for herbaceous biomass to co-occur with other essential landscape elements—notably water in the summer and shelter and wood in the winter (West 1998).

Because of differences in soils and moisture availability, lowlands tended to produce more aboveground vegetation than uplands, even when trees were absent. For instance, in 1833, in the Missouri River bottomlands, near the town of Bellevue, Nebraska, Maximilian wrote, “Beautiful, low prairie hills surrounded us, and before them flat alluvial land with a beautiful growth of grass…very favorable for raising livestock” (Witte & Gallagher 2010:80). In the same vicinity 14 years later, Andrew Dawson of the American Fur Company noted passing through an area that was “flat swampy and mostly covered with a long rank grass reaching over our heads when on horseback" (Wischmann & Dawson 2013:177). Further upriver, at Dakota City, Nebraska, in 1868, the British immigrant and Omaha businessman Joseph Barker Jr. stated that 6–8 tons of hay was required to raise a calf to an age of four years, and that much of it could be obtained by grazing the tall grasses of the Missouri River bottoms (Snoddy et al. 2004).

At Cottonwood Canyon (later Fort McPherson), near the North Platte–South Platte confluence at the present-day town of North Platte, Nebraska, United States Army Captain Eugene Ware (1994:44–45) described lush grass growth on river islands in 1864: "The valley here was several miles wide. There was a large island in the river of several thousand acres, upon which grew the finest grass to be found in the country". West of the town of North Platte, Joseph Barker recounted that the five-to-six-mile-wide South Platte River valley was "Covered with much the same grass as arround [*sic*] Omaha but generally not so thick or rich – But plenty sufficient & [*sic*] good for all purposes" (Snoddy et al. 2004:515). However, Barker was unimpressed by the quality and quantity of grass outside river and stream valleys west of the town of Sidney or in the Sandhills ecoregion. What he is likely to have observed in these drier uplands were shortgrass species [e.g., buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*)] and blackroot sedge (*Carex elynoides*), which actually serve as excellent forage year-round, in contrast to tallgrass species, which lose forage value late in the growing season via decreasing leaf-to-stem ratios (Nelson & Moser 1994; Binnema 2001). R.S. Elliot (1874:254–255), an industrial agent for the Kansas Pacific Railway, expanded upon the unapparent value of buffalo grass as forage, arguing that although "to the untaught observer this is a worthless-looking grass", it is "unsurpassed in nutritive qualities", and "dries to a natural hay, and it retains its nutritive properties all winter." United States Army General George Custer (1962:7–8) echoed this assertion in the late 1860s, writing:

> Nearly all graminivorous animals inhabiting the Plains, except the elk and some species of the deer, prefer the buffalo grass to that of the lowland; and it is probable that even these exceptions would not prove good if it were not for the timber on the bottom land, which affords good cover to both the elk and deer. Both are often found in large herds grazing upon the uplands, although the grass is far more luxuriant and plentiful on the lowlands. Our domestic animals invariably choose the buffalo grass, and experience demonstrates beyond question that it is the most nutritious of all varieties of wild grass.

Shortgrasses were indeed the preferred forage of bison on the northwestern plains, especially in winter (Binnema 2001). Andrew Dawson wrote the following in 1853, at Fort Clark, near the Mandan villages, in what is now central North Dakota, "the grass of the prairies in general is not over 4 inches long is very thin and is no impediment at all to walking or running" (Wischmann & Dawson 2013:252).

R.S. Elliot (1874:254–255) described a shift in the geographic distribution of buffalo grass throughout Kansas in the late 19th century, presumably due to increased anthropogenic soil disturbance:

> As the settlements of Kansas extend westward, the buffalograss disappears…Twenty years ago, as stated by reliable authority, the

> buffalograss covered much of the country about Manhattan; but it has since almost entirely disappeared to Ellsworth, a distance of one hundred miles farther west. Taller grasses take its place…Wherever the surface soil of the Plains is broken, whether by the wagon road, the railway cut, or by the plow, taller herbage takes the place of the shorter grasses.

It is important to note that as a railroad agent, Elliot may have taken liberties in these descriptions, in order to increase the appeal of Great Plains landscapes to prospective Euro-American settlers, who may have perceived the tallgrasses as superior to the shortgrasses. The historian Geoff Cunfer (2005:49) suggests an alternative, or perhaps complementary, driver of these shifts in grass communities—release from the constraints of grazing—writing: “As late as 1880 there were just over 2 million cattle in the region, on land that had supported some 28 million bison. For a decade grass biomass increased dramatically across the plains. Without bison to hold them in check, midsize and tall grasses overtook short grasses.” Buffalo grass, in particular, thrives under moderate to heavy grazing and is capable of withstanding successive years of drought (Albertson et al. 1957; Weaver 1968). Therefore, it is likely that interactions between weather, soil disturbance, grazing, and other factors (e.g., fire or the lack thereof)—many of which carried a clear human signature—produced shifts in the geographic distributions of these grassland species and communities.

Despite its widespread distribution and abundance in uplands, herbaceous biomass became scant there at times too. The Baptist missionary Isaac McCoy documented especially dry conditions that were accompanied by an autumn prairie fire in present-day north-central Kansas in 1830, writing: “Grass for our horses, is every day becoming more scarce. The season is remarkably dry. The whole country around us, has burned over today,” and later, “The grass is so poor for our horses, which are fast failing for want of food, that we deemed it indispensable to move on, in hope of reaching the Republican fork of Kanza [*Kansas River*], where we hope to find better food” (Barnes 1936:364, 366–368). In the winter of 1846–1847, United States Army Lieutenant James Abert (1966:87–89) described a similar situation near Big Sandy Creek in what is now eastern Colorado, writing, “All around our camp the prairies had been burnt…no pasture, no buffalo, 3 days starved.”

WOODY BIOMASS

Utilization

Woody biomass was another important energy source in Great Plains SESs, where it was used to produce heat, power steam engines, and feed horse herds. Although rarer than herbaceous biomass, it was energetically denser, which increased its appeal as a fuel. The majority of wood fed to horses consisted of cottonwood (*Populus* spp.) bark and twigs from timbered lowlands, which served as temporary winter camps on the western plains. Cottonwood brush on river islands also served as food for the horse herds of traveling Native Americans (Ware 1994). Maximilian also described a bush—possibly a willow species—that the Hidatsas fed their horses in winter along the Wind (i.e., Bighorn) River, in present-day south-central Montana (Witte & Gallagher 2010, 2012). Lowland cottonwood bark and twigs were especially important as an emergency horse food during harsh winter conditions (Moore 1987), when the availability of grass in uplands was limited or travel became treacherous. These refuges also attracted food for humans (i.e., bison) in winter (Moulton 2003). General Custer (1962:7) penned the following concerning the use of cottonwood as horse food, “Although not affording anything like the amount of nutriment which either hay or grain does, yet our horses invariably preferred the bark to either, probably on account of its freshness.” In general, timber stands were used by Native Americans seasonally, not year-round.

Over the course of the 19th century, the fur trade, military operations, mining, and resettlement brought numerous steamboats up the Missouri River each year, distributing trade items and supplies, taking on furs, and carrying passengers (Figure 2). Wood was the primary fuel used to power steamboats, and the average daily quantity required to do so depended on boat size and wood properties. Because of space and weight limitations, steamboats could only carry a one-day supply of wood and typically stopped twice each day to restock (Hunter 1969). Lass (2005) cites an average daily (i.e., 12-hour) steamboat demand of 15 cords of wood on the Upper Missouri in 1867–1868. When aggregated across boats and years, the quantity of wood burned by steamboats is staggering. For example, the 19 steamboats on the Upper Missouri in 1880 together burned approximately 31,394 cords of wood (Purdy 1880), which equates to 348,822 tree trunks 10 inches (25 centimeters) in diameter and 40 feet (12 meters) long (Oderwald & Johnson 2009). Other years had up to twice as many steamboats in operation. In more densely-populated reaches of the Missouri, wood was piled along the river banks ahead of time, so that boats could quickly stop to purchase and load it, whereas further upriver, beyond the resettlement frontier, woodcutters had to leave ships in search of fuel. Even abandoned trading posts were used for fuel, at times (Wishart 1992). In 1856, Lieutenant G.K. Warren pinpointed the mouth of the Niobrara River as the point above which steamboat crews on the Missouri began cutting their own wood (Schubert 1981). This was also the location specified by the early plant ecologists Roscoe Pound and Frederic Clements (1900) as a transition point in Missouri River forest communities.

Cottonwood and cedar (*Juniperus* spp.) were common fuels for powering steamboat engines on the Missouri, and over time, entire forested islands of these species were cleared for this purpose. It is initially unclear why other species with greater energy densities [e.g., ash (*Fraxinus* spp.) and oak (*Quercus* spp.)] were not more popular, but perhaps strong reliance on cottonwood and cedar stemmed from their greater availability along the river banks. Unlike dry cottonwood, green cottonwood was only a desirable fuel on the Upper Missouri. Maximilian relayed an interesting and apparently prevailing hypothesis for why this was so near the grave of the Omaha Chief Blackbird, in the vicinity of present-day Onowa, Iowa: “Here on the steamboats, green cottonwood is primarily burned; it gives off more heat here than farther downstream, because the ground here is far drier and the wood has less sap.” Indeed, at Morgan’s Island, three miles (five kilometers) below the mouth of the Little Nemaha River in now southeast Nebraska, he had previously written, “Our woodcutters and hunters went ashore but did not bring anything back, since the forest consists of nothing but cottonwoods” (Witte & Gallagher 2010:63, 90). Meanwhile, eastern redcedar was considered good fuel because it yielded much steam. Because of its low moisture and high resin content, cedar could be burned green, although this was likely not preferable (Ode 2004).

Native Americans similarly used different tree species for different seasons and purposes, according to their energetic densities. For example, the Cheyenne used poplar (*Populus* spp.) and cottonwood for summer cooking, but oak and other hardwoods for winter cooking and heating (Moore 1987). The Hidatsa preferred species other than cottonwood for firewood; however, it was the most abundant and available woody species (Wilson 2014). In addition to fuel, trees were used by Native Americans as beams in earth lodges and poles in tipis.

Steam engines in some of the first Great Plains locomotives were wood-powered (Figure 3). In fact, roads for transporting wood between railroad stations and privately-owned timber groves along the Platte River were documented by surveyors near Fort Kearny, in present-day south-central Nebraska, in the 1850s and 1860s. In several instances, this trespassing led to armed conflict between settlers and railroad employees (Richardson 1968; Johnson & Boettcher 2000). Timber-related disputes also occurred between Native and Euro-Americans. For instance, fuel-desperate settlers were on several occasions observed stealing large quantities of timber from the reservations of the Otoe-Missourias and Pawnees during harsh winters of the 1860s (Wishart 1994).

Renewability

Woody biomass was renewable on relatively short timeframes (e.g., decades), but could not recover as quickly as herbaceous plants. Regenerative potential also differed among species. For example, cycles of disturbance and recovery caused spatial differentiation in the composition of Missouri River forests, as early successional species [e.g., cottonwood and willow (*Salix* spp.)] were common along river banks and later successional species [e.g., boxelder (*Acer negundo*) and oak] were relegated to higher terraces (Johnson et al. 1976), due at least partly to the ability of cottonwood and willow to quickly regrow after being sheared off by flowing water and ice. Although some willow species [e.g., peach-leaf willow (*Salix amygdaloides*)] could grow into relatively large trees, other shrubbier species [e.g., sandbar willow (*Salix exigua*)] could not, which likely affected their usefulness as fuel. In the absence of fire, eastern red-cedar can spread and transform open prairies into closed-canopy forests in fewer than 40 years (Briggs et al. 2002), with spread occurring faster in lowlands than in uplands (Ratajczak et al. 2016). Thus, it is reasonable to assume that fast-growing trees could regenerate in decadal-long breaks between disturbance events. Slower-growing trees could also accumulate substantial growth during breaks, but took longer to fully mature.

Despite regeneration potential and rotational human use, timber depletion generally outpaced timber growth in the middle 19th century, and by 1860, many wooded stands were diminished or stressed. Factors that contributed to depletion include increased horse ownership among Native Americans, increased Euro-American travel, harsh winters, and droughts (West 1998). Although he was confident that sufficient wood supplies existed for the near term, Lieutenant Warren contemplated future shortages along the Missouri River, as he noted that steamboats were experiencing greater wind interference above Council Bluffs in 1856 than they had in years prior, due to the fact that riverside timber windbreaks—which Maximilian had described two decades earlier as “a band of tall forest” (Witte & Gallagher 2010:86)—had been severely reduced (Schubert 1981). Joseph Barker similarly depicted timber as dear and scarce in Omaha in 1866, as he observed high prices for hardwood, cottonwood lumber, and imported pine (*Pinus* spp.) lumber; settlers scrambling westward to take out Homestead and Preemption Act settlements in wooded valleys; and the construction of portable sawmills (Figure 4) for capturing and processing driftwood on the banks of the Missouri. Barker noted an average of three to four steamboats in the wharf at Omaha each day in 1866, which by 1868, had increased to between four and five (Snoddy et al. 2004). Temporary timber shortages caused sharp price spikes in local fuel and construction markets before railroad completion stabilized wood supplies.

During the latter half of the 19th century, Great Plains residents bought wood from large-scale lumber distribution networks headquartered in Minneapolis and Chicago, which imported wood into the plains from the Great Lakes region (Hudson 1985; Cronon 1991). It was common for towns to build a lumber yard near the railroad tracks for wood processing. This demand for wood in the Great Plains and other regions drove the decimating harvest of white pine (*Pinus strobus*) forests in the Great Lakes region. At the same time, global demand for bison products pushed the ungulate—one of the most important energy sources for human metabolism in Great Plains landscapes (West 1998)—to the brink of extinction. Chicago’s role as a major hub in wood and bison imports and exports was largely facilitated by the construction of the railroad in the Great

Plains (Cronon 1991). Therefore, like mounted bison hunts, the railroad increased the geographic extent of human energy procurement in SESs.

Local timber exhaustion was a problem for Euro-American forts, where soldiers were often tasked with guarding nearby trees and collecting wood from the surrounding countryside (West 1998; Witte & Gallagher 2012). The annual wood requirement for 100 soldiers was estimated to result in the clear-cutting of approximately 7–30 acres (3–12 hectares) of deciduous woodland (Moore 1987). At Fort Kearny in 1848, the ethnologist George Gibbs wrote, “No wood is to be had except the soft cottonwood found on the islands of the Platte, which is brought up with difficulty and not fit for building when obtained” (Settle 1989:299). At Fort Union, on the Missouri River, near what is now the Montana–North Dakota border, Maximilian mused that the fort’s horses were kept outside all winter, and in snowy conditions, made their way down to forested portions of the river to eat cottonwood bark.

In the years preceding resettlement, the impending mismatch between timber availability and demand in the plains was foreseen by a number of individuals. Chief Big Elk of the Omaha recognized the potential for discrepancies in uplands, as he professed to members of the Long Expedition in 1820:

> Some think, my father, that you have brought all these warriors here to take our land from us, but I do not believe it. For although I am but a poor, simple Indian, yet I know that this land will not suit your farmers; if I even thought your hearts were bad enough to take the land, I would not fear it, as I know there is not enough wood on it for the use of whites. You might

> settle along this river, where timber is to be found; but we can always get wood enough in our country to make our little fires" (James 1823:176).

Several years earlier, the Scottish botanist John Bradbury (1817:272) made a similar acknowledgement regarding the inability of plains landscapes to supply the amount of timber to which Euro-American settlers were acclimated—yet was confident of its eventual resettlement—as he penned:

> Accustomed, as they are, to a profusion of timber, for buildings, fuel, and fences, they are not aware of the small quantity of that article that may be dispensed with, in a country abounding in another substance for fuel…My own opinion is, that it can be cultivated; and that, in process of time, it will not only be peopled and cultivated, but that it will be one of the most beautiful countries in the world."

This concurs with the perspective of the historian James Malin (1984), who saw 19th century Great Plains landscapes as entirely sufficient for habitation by Euro-Americans, who gradually adjusted—albeit sloppily—to their new environments.

Native American cultures were also prone to overusing wood resources, especially in timbered winter refuges of the western plains (West 1998). For example, the Big Timbers on the Arkansas River—near present-day La Junta, CO—which stretched for 60 miles (97 kilometers) in 1805 (Hart & Hulbert 1972), had shrunken to half that size by the 1840s, and experienced additional depletion in subsequent decades (Moore 1987; West 1998). This site was used only by Native Americans, and indeed offered good supplies of grass, wood, and water (Abert 1966), with cottonwood being nearly the only tree species present (Hart & Hulbert 1972). Timber depletions were even greater at sites that experienced Native and Euro-American use, such as the Central and North Platte River valleys, where an estimated 300,000 people and 1.5 million domesticated animals traveled the Great Platte River Road in the mid-19th century (Mattes 1969; West 1998). During the same time, Native and Euro-American use greatly diminished timber further south, along the Arkansas River, and by 1864, most timbered lowlands along the Platte and Arkansas were effectively eliminated.

Geographic distribution

With the exception of elevated portions of the western plains, such as escarpments like the Pine Ridge and Black Hills, timber was primarily restricted to river valleys and other lowlands. As R.S. Elliott (1874:254) put it, “Except fringes and groves along the streams, the Plains are treeless.” Timber was also more plentiful in the eastern than western plains. A description of this east-to-west gradient of timber decrease is found in the journal of General Custer (1962:6), who wrote, “As you proceed west from the Missouri, the size of the trees diminishes as well as the number of kinds…the only trees to be seen being scattered along the banks of streams, these becoming smaller and more rare, finally disappearing altogether and giving place to a few scattered willows and oisers.” According to the Kansas State Board of Agriculture’s (1874) statewide timber assessment, the Kansas counties with the greatest proportion of timbered land area were Wyandotte (25%), Doniphan (16%), and Leavenworth (16%) in the northeastern corner of the state. Meanwhile, 18 counties further southwest were only 1% timbered. Indeed, the 99th and 100th parallels had been previously specified by Lieutenant W.H. Emory (1848) and Lieutenant Warren (Schubert 1981) as longitudinal thresholds, west of which the richness and abundance of riparian forest communities in the central plains decreased.

Spatial settlement and resettlement patterns provide additional indicators of tree distributions. To ensure consistent water and timber access, Native Americans situated their villages on river terraces, periodically shifting locations as local timber supplies were exhausted. In 1811, for example, John Bradbury (1817) noticed that all the trees on one bank of the Platte River near an Otoe-Missouria village had been cut, as did John Dunbar (Jensen 2010) at another location in 1834. In 1848, Andrew Dawson documented the Hidatsas near Fort Berthold, in what is now western North Dakota, erecting winter villages upriver and downriver from their main village, in order to access timber and shelter. This is understandable, given that he went on to describe timber in the vicinity of the fort as “only of a norrow [*sic*] stripe along the bed of the Mo [*Missouri*]” (Wischmann & Dawson 2013:200). The ethnographer Gilbert Wilson (1917, 2014) similarly documented the importance of wood availability in the historical siting of Hidatsa villages.

Timber distributions may also be inferred from Native American wintering sites. Although Pawnee movements were predominantly westward, they at times traveled east to winter in the timbered bottomlands of the Missouri River (James 1823). The Omahas were also wintering along the Missouri by the 1830s, in response to increasingly frequent and dangerous Lakota raids during winter bison hunts (Wishart 1994). In the western plains, approximately 55 kilometers east of Bent’s Fort and the town of La Junta in present-day eastern Colorado, three sites known as the Big Timbers served as common wintering grounds for the Cheyennes, Arapahoes, and Kioways (Emory 1848). The Big Timbers on the Republican River, in particular, were described by Captain Ware (1994) in 1864 as stretching for 14 miles (23 kilometers) and containing only cottonwood trees that averaged 2 feet (0.3 meters) in diameter. Other important High Plains wintering sites were situated along Lodgepole Creek, Sand Creek, Summit Springs, the Purgatoire River, the Upper South Platte River, the Republican River, the north side of the Cimarron River, near Freedom, Oklahoma, and along the Smoky Hill River in Kansas (Moore 1987; West 1998).

Lands along wooded streams were consistently occupied before uplands by Euro-American settlers. Original land surveys from 1855–1866 show the distribution of timber in riparian and adjacent uplands in the eastern half of present-day Nebraska to be sparse, spotty, and decreasing in frequency from southeast to northwest, supporting moisture availability as a factor limiting tree growth (Richardson 1968). This assessment echoes prior regional timber descriptions from Isaac McCoy (Barnes 1936), John Bradbury (1817), Lieutenant Warren (Schubert 1981), Lieutenant Franklin (Schubert 1979), and Joseph Barker (Snoddy et al. 2004). Despite overall scarcity, the operation of steam- or hydro-powered sawmills and timber sales indicates the presence of at least some trees in various locations, such as the town of Niobrara, Nebraska (Wishart 1994).

Changes in human occupancy and activity are hypothesized to have contributed to short- and long-term fluctuations in timber availability. Before resettlement, Native American timber harvest and prairie fires are likely to have restricted trees to isolated areas. In one of several examples, Maximilian described the aftermath of a fire near Mill Creek, in present-day Omaha: “One saw whole stretches of black, dead cottonwoods; the Indians set fire to the prairie and in this way also burn the trees. The dark spots of the hills were also burned forest… The burned forest had tall, completely black trees; here and there individual trees were a most beautiful green” (Witte & Gallagher 2010:81). Just a few years earlier, in the midst of an 1830 autumn prairie fire in present-day north-central Kansas, Isaac McCoy had mused: In a day the whole country put on its black and dismal dress…The fires around us were sublime—the long lines and the flame ascending ten, fifteen, and sometimes twenty feet high. On seeing these prairies on fire in such a dry time as this we cease to wonder that the wood does not increase faster—we only wonder what a vestige of wood is left” (Barnes 1936:364, 366). Finally, along the South Platte in 1842, United States Army Captain John C. Fremont (1845:24–25) penned the following east of the mouth of Lodgepole Creek, in now western Nebraska: “There were but few trees, a kind of long-leaved willow, standing; and numerous trunks of large trees were scattered about on the ground. In many similar places I had occasion to remark an apparent progressive decay in the timber.”

It is, therefore, plausible that the cessation of tree harvest and burning that accompanied Native American dispossession allowed timber in some areas to increase temporarily, after which it was reduced by incoming Euro-American settlers, until tree-planting and fire suppression once again promoted its increase (Bessey 1899; Moore 1972; Binnema 2001; Courtwright 2011). By 1895, there were approximately 200,000 acres of artificial forest in Kansas (Kansas State Board of Agriculture 1896), much of which can be attributed to the implementation of the Timber-Culture Act of 1873, the purpose of which was to increase timber on the Great Plains, and in doing so, even alter the climate (Wishart 2013). Regardless of exactly when and how distributional changes occurred, timber constituted a rare and valuable fuel in Great Plains SESs. For illustrative purposes, I provide additional details on timber distributions in the Missouri and Platte River valleys, sorting observations by upstream movement (i.e., mouth-to-headwater).

The Missouri River

Nineteenth century timber distributions in the Missouri River valley were spatially and temporally heterogeneous. Although observations from before the year 1800 are limited, information rapidly accumulated as the river became a major transportation route in subsequent decades. Tree species abundance and richness appear to have decreased with upstream movement and with the passage of time.

Maximilian paid careful attention to riverine forests, or the lack thereof, while traveling up and down the Missouri by steamboat in 1833–1834. At McKissock Island, in present-day Nemaha County, Nebraska, he provided an impressively detailed account of the forest makeup. With the disclaimer that “the number of species of trees that make up the forests on the bank in this region of the Missouri has already greatly decreased”, he documented the presence of the following species: black oak (*Quercus velutina*), black walnut (*Juglans nigra*), boxelder, cottonwood, hackberry (*Celtis occidentalis*), hickory (*Carya* spp.), honey locust (*Gleditsia triacanthos*), ironwood (*Ostrya virginiana*), pawpaw (*Asimina triloba*), red elm (*Ulmus rubra*), red mulberry (*Morus rubra*), red oak

(*Quercus rubra*), redbud (*Cercis canadensis*), American sycamore (*Platanus occidentalis*), and willow. Further upriver, in now Otoe County, Nebraska, where Weeping Water Creek empties in to the Missouri, he noted "very tall, luxurious forest with dense understory" (Witte & Gallagher 2010:68, 74).

Above the mouth of the Platte, Maximillian's Missouri River timber descriptions were increasingly dominated by stands of cottonwood and willow that were "in some places also mixed with other forest trees" (Witte & Gallagher 2010:88). In 1811, John Bradbury had described this stretch of the river valley as "partly prairie, but interspersed with clumps of the finest trees, through the intervals of which could be seen the majestic but muddy Missouri" (Bradbury 1817:50). By the early 1850s, the eastern side of the river below Council Bluffs was intensively settled and deforested, to the point that settlers were constructing dwellings from prairie sod (Oehler & Smith 1914). Fifty years earlier, William Clark had described the riverine forest at Council Bluffs as containing "tall timber, principally Willow Cotton wood some Mulberry elm Sycamore & ash…walnit [*Walnut*] coffenut [*Kentucky coffeetree*] & Oake [*sic*] in addition & [*sic*] Hickory & Lynn [*Linden*]" (Moulton 2003:33). Above the Missouri–Vermillion River confluence, near present-day Vermillion, South Dakota, Maximilian began to document less forest and more prairie, which "extended endlessly" beyond his river valley view (Witte & Gallagher 2010:101). On his return trip, he reiterated the significance of the mouth of the Vermillion as where "the tall forests, so characteristic of the lower Missouri, begin" (Witte & Gallagher 2012:299).

Maximilian used the grave of Chief Blackbird of the Omaha, near present-day Onowa, Iowa, as a landmark for where he first observed deciduous and coniferous trees co-occurring (Witte & Gallagher 2010). Further upriver, in 1856, Lieutenant Warren documented tall cedars growing in the Missouri bottomlands at 43°N latitude, north of present-day Lynch, Nebraska, noting that they tended to decrease in size and frequency in uplands and at more northern latitudes (Shubert 1981). Maximilian had previously observed 40–50 foot (12–15 meter) cedars and 40 foot oaks in the same vicinity, and from there upriver, increasingly noted the use of cedar for steamboat fuel. Little Cedar Island, upriver from present-day Yankton, South Dakota, was covered at its tips with cottonwoods and at its center with slender cedars of height 60 feet (18 meters) or greater (Witte & Gallagher 2010). Approximately two decades earlier, Little Cedar Island, as well as Great Cedar Island (i.e., American Island), had been described by John Bradbury (1817:79) as being "covered with the finest cedar." Upstream, in present-day Lyman County, South Dakota, there was another cedar-, cottonwood-, and willow-covered island by the name of Cedar Island, also known as Dorion Island Number 1. From here and a neighboring island, Dorion Island Number 2, traders Edward T. Latta and F.W. Johnson sold wood to passing steamboats (Lass 2005).

At Fort Pierre, in present-day central South Dakota, Maximilian stated that timber was rare and had to be imported from 40–60 miles (64–97 kilometers) upriver; however, on his return trip, he somewhat confusingly described "a beautiful, wild forest of one-and-a-half-foot-thick cedars growing in wild disorder" six miles (10 kilometers) below the fort (Witte & Gallagher 2012:292). The Lewis and Clark Expedition spent the winter of 1804–1805 at Fort Mandan, in present-day central North Dakota, where isolated groves of cottonwood, cedar, and ash were among the few trees dotting the flat, grass-dominated river valley (de Casa Calvo 1952). At an Arikara village on the Upper Missouri in 1795, the explorer Jean Baptiste Truteau (1952) and his crew searched 15 days for a large enough tree from which to construct a boat, but were unsuccessful, as only sparsely distributed stands of small cottonwood and willow were available on the river for some 200 kilometers above or below the village. This regional assessment coincides with the one offered by Maximilian some 30 years later, where he wrote that although thickets of willow, cottonwood, dogwood (*Cornus* spp.), ash, and elm were present in a far-extending forest, “There was little old wood left.” He also noticed that the wood being fed into the fire by Hidatsa children at their great buffalo medicine festival consisted primarily of small willow branches, that the nearby forest was “very much culled out, and there are only a few big trees left” (Witte & Gallagher 2012:79, 93). Although some cottonwood, elm, boxelder, and ash were present several miles upriver at Fort Clark in the mid-1800s (Wischmann & Dawson 2013), wood was especially scarce during the winter of 1833–1834, when the fort’s woodcutters only brought in driftwood. Throughout the winter, Mandan women were continually observed by Maximilian carrying and dragging firewood across the frozen river—even breaking the ice and wading—back to their dwellings. Likewise, fort employees pulled timber across the river on sleds. When river ice broke the following April, an ice drift carried tree trunks downriver, which the Mandans advantageously harvested for days.

Further upriver from the Mandan villages, the most commonly-observed conifers transitioned from eastern red-cedar to Rocky Mountain juniper (*Juniperus scopulorum*) and prostrate juniper (*Juniperus horizontalis*). At Fort Union, near the Yellowstone–Missouri River confluence, in present-day western North Dakota, Maximilian stated that the only timber available for use as construction material was cottonwood. Both Maximilian and Truteau (1952) observed the Upper Cheyenne and Lower Yellowstone Rivers to be well-wooded; however, here, as in other places on the Upper Missouri, deciduous trees were generally rare outside of the river valley. In a portion of present-day Phillips County, Montana that is now likely inundated by Fort Peck Reservoir, Maximilian noted 30–40 foot (9–12 meter) tall Ponderosa pine (*Pinus ponderosa*) trees in the ravines and uplands along the river. Ponderosa pine occurrence increased with movement into rougher terrain, eventually becoming common on the river's upper reaches. Substantial stands of timber, including cottonwood and boxelder, appear to have been present on islands in the vicinity of Fort McKenzie in what is currently Chouteau County, Montana. Although sufficient wood was apparently available to construct the fort in 1832, by the time of Maximilian's 1833 visit, there was not even enough hardwood for the construction of an ax handle, an assertion supported by the fact that the hickory oars of his party's keelboat were sawed up for that purpose (Witte & Gallagher 2010). Just upriver, at Fort Benton, the last steamboat stop on the Upper Missouri, Andrew Dawson and his American Fur Company colleagues stockpiled wood from nearby forests in preparation for winter, and even transported it 10 miles (16 kilometers) downriver for steamboats (Wischmann & Dawson 2013).

The Platte River

The historical distribution of timber in the Platte River valley has been the subject of lively debate. The perception of the Platte as having nearly treeless banks with cottonwood and willow covered islands is supported by: Williams (1978), who forwards several hypotheses for the scarcity of trees on the river banks; Eschner et al. (1981), who emphasize the roles of water availability and human harvest in shaping timber distributions; and Johnson and Boettcher (2000), who cite numerous early accounts of the banks and islands of the Platte being initially wooded and subsequently deforested by the hundreds of thousands of travelers, settlers, and railroad workers that passed through the river valley during the mid-19th century (Mattes 1969; West 1998). In a counter-argument, Currier and Davis (2000) use many of the same historical references as Johnson and Boettcher (2000), along with historical species occurrence data, to characterize the Platte as a sparsely-wooded, prairie river, without heavily-wooded banks or islands. It is of course possible that differing viewpoints represent timber distributions from different points in time with some degree of accuracy. This seems plausible, given the immense pressure that Euro-American travelers undoubtedly exerted on timber resources that were already being actively used by Native Americans.

As along the Missouri, timber distributions of the Platte were spatially variable. For instance, W.C. Johnson (1994), referencing the notes of the General Land Survey, suggests that trees grew on both the banks and islands of the Platte River east of present-day Kearney, Nebraska; that they were primarily restricted to islands on the Platte west of

Kearney; and that they became extremely sparse-to-absent west of the South Platte–North Platte confluence. The most frequently-observed tree species in the survey were cottonwood, willow, and elm; however, given the evidence of human timber utilization along the river, it is possible that later successional species like ash and boxelder were more common earlier.

In the 1830s, the banks of the Platte were described by John Dunbar (Jensen 2010) as relatively treeless, although he did note robust stands of timber on many river islands. In 1835, near the eastern end of Grand Island, in present-day south-central Nebraska, United States Army Captain Lemuel Ford (1934:250) stated:

> The fact that all these islands are covered with a thick and heavy growth of timber, is a conclusive proof that nothing but the annual fires, which sweep over these immense prairies prevents them from being timbered also. It is nonsense to suppose, as some have asserted, that timber cannot be made to grow on land like this. Prevent the fire from running over these prairies but for twenty years, and instead of millions and millions of acres of rich land without a stick of timber large enough for a riding switch, you would see one dense and beautiful forest of oak, hickory and ash, upon the highlands, and the majestic cotton-wood, and evergreen cedar upon the bottom lands, bordering on the great rivers.

The Platte was also described as treeless—with the exception of wooded islands—by Captain Fremont (1845) in 1842 and the Moravian missionaries Gottlieb Oehler and David Smith (1914) in 1851. As settlers filed into the river valley during the 1850s, the geologist Ferdinand Vandeever Hayden stated that the river valley contained “sufficient timber for all economic purposes,” and what Lieutenant Warren described as “fine cottonwoods” were present along the banks of the Platte between its mouth and Fort Kearny (Schubert 1981:43, 107).

In 1864, Lieutenant Ware (1994:41–42) offered the following description of the Platte River valley, upstream from Fort Kearny:

> Beautiful valleys were seen, narrow and deep, full of enormous cedar trees, box elders, hackberry, plum trees, and shrubbery…We rode along this plain, over these beautiful valleys, for fully ten miles…There had never been an axe put into these canyons, except a little at their openings near the river. The cedar trees were as straight as arrows, very numerous, and all sizes up to two feet in diameter. They grew mostly from the bottom of the canyon, yet no tree-tops were seen rising above the level of the plain.

Lieutenant Warren also noted cedars in ravines near the confluence of the North and South Platte. At Brady’s Island, not far from the confluence, Captain Fremont (1845:21) observed, “some timber, apparently pine” growing in the ravines, although it is reasonable to assume that these too were cedars. Another description of timber near the confluence was provided by Major Osborne Cross in 1849, who wrote, “The river here is nearly three miles wide [and] interspersed with islands, some of which are thinly covered with very small cottonwood and willow. In many instances they are entirely bare” (Settle 1989:67). Nearby Moran Canyon was filled with cedar trees in 1864 (Ware 1994). In fact, there were five cedar-filled canyons in the vicinity of Fort McPherson, from which a local settler, Jack Morrow, cut and sold 5,000 trees. Alternatively, in the vicinity of the town of North Platte, in the late 1860s, Joseph Barker characterized the river bluffs as "generally treeless" and noted that the river itself contained "numerous sandbars but no timber" (Snoddy et al. 2004:515).

Captain Fremont (1843:36) described a large driftwood deposit in the valley of the North Platte River in 1843, stating, "The plain between Scott's Bluffs and Chimney Rock was almost entirely covered with drift wood, consisting principally of cedar, which, we were informed, had been supplied from the Black Hills, in a flood five or six years since." Although the origin of this wood in the Black Hills, as defined today, was unlikely, the account highlights the potential for woody fuels to be deposited far downstream of their origin. The diary of United States Army Major Osborne Cross (Settle 1989:93) in 1849 includes a similar description of a wood deposit at Scott's Bluff: "Wood as usual was very scarce, but we obtained enough in the valley for our use. It had been swept from the hills by the heavy rains which frequently fall during the summer. What was found consisted principally of dwarf cedar and pine." Another potential source of this timber could be the Wildcat Hills escarpment, which lies to the south of Scott's Bluff.

Further northwest, at Fort Laramie, which was situated at the confluence of the Laramie and North Platte Rivers, Major Cross noted in 1849, "Wood is scarce immediately in the vicinity of the fort, but pine and cedar may be procured on the hills across the Platte about eight miles above here" (Settle 1989:98). Cross went on to describe the scarcity of wood over the entire High Plains, writing, “Wood is not to be procured from the time you leave Fort Kearny until you arrive at this place. Nothing is to be seen but the naked valley and boundless prairies in whatever direction the eye is turned” (Settle 1989:99). Indeed, in 1864, the nearest trees to Julesburg, in present-day northeast Colorado, were purported to be at Ash Hollow, near now Lewellen, Nebraska, a straight-line distance of 30 miles (48 kilometers) (Ware 1994).

BUFFALO CHIPS

Utilization

In areas of the plains where wood was scarce, buffalo chips were burned by both Native and Euro-Americans, in combination with various forms of herbaceous biomass like sage and corn cobs, for cooking and heating, earning it the nickname plains oak (Figure 5; Welsh 2004). Holland (1984) determined that 1.4 tons (8.9 cubic meters) of buffalo chips are required to equal the energy contained in an average cord of cottonwood. Because of the great volume of chips required to produce sustained heat, supplemental fuels are likely to have been especially important during winter; however, these were often scarce in the western plains (Wishart 2013). For example, Major Osborne Cross wrote from near the North Platte–South Platte confluence, upriver from Fort Kearney, in 1849:

> The command stood greatly in need of wood, for we had reached a region of country entirely destitute of it, where a tree might be look on as a curiosity. We were therefore compelled to resort to the *vache de bois*

> [buffalo chips], which is a fine substitute when you get used to it. It is always used by hunters, who never think of the scarcity of wood when this can be obtained" (Settle 1989:71).

Renewability

Like the herbaceous biomass they were derived from, buffalo chips were renewable on relatively short timeframes; however, their availability and utility were contingent on the presence of the ruminants to deposit them and a drying period to prepare them for burning. Plains bison are estimated to have numbered in the tens of millions in the early 19th century (Flores 1991), and given that bison cows between the ages of 3 and 18 years generally gave birth to a single calf each year (Green & Rothstein 1991; Isenberg 2000), they were capable of recovering from population losses, but not quickly. As bison herds dwindled during the latter half of the 19th century, they were replaced by the cattle of Euro-American settlers, a new source of chips. R.S. Elliot (1874:258) described this impending transition in 1873, writing:

> Our plains are the native land of the bovine race, and will continue to sustain it. We only make a slight change when we substitute domestic cattle for the buffalo. The latter, under the persecutions of Indians, hunters and sportsmen, will in a few years be extinct. The former will multiply indefinitely. The railway is fatal to the buffalo, but fosters the domestic herd.

Indeed, by the turn of the 20th century, bison were extirpated from the plains, with livestock taking their place.

Geographic distribution

The distribution of ruminants and the chips they left behind was influenced by various factors, two of which are likely to have been forage availability and winter shelter. For example, timbered groves that attracted bison during harsh winters had high chip densities. Chips may also have been more common in the northern and western plains, where bison densities were high because of the transition from C4 to C3 prairie grasses and favorable carbon-to-protein ratios in shortgrasses (Johnson 1951; Binnema 2001). Maximilian described a bison hunting scene near Fort Union, on the present-day Montana–North Dakota border, where no wood, only bison dung and fat, were used as fire fuel (Witte & Gallagher 2012). Chips left behind by cattle and livestock were likely clustered along trails. The continual harvest of chips by travelers, in combination with bison exclusion, would have decreased chip abundance in these areas, unless new depositions by livestock counterbalanced harvest.

DISCUSSION

Three important organic fuels in 19th century SESs of the Central and Northern Great Plains were herbaceous biomass, woody biomass, and ruminant dung. These fuels were derived from local landscape elements (i.e., grass, trees, and bison) and could regenerate over relatively short timeframes. Their geographic distributions varied spatially and temporally over the course of the 19th century, as they were shaped by changes in and interactions among various factors, including environmental conditions, human harvest, and human disturbance regime manipulation. In other words, landcover changes in 19th century landscapes of the Great Plains were directly and indirectly driven by people.

In general, herbaceous biomass was ubiquitous, with tallgrass and shortgrass prairie species dominating vegetation in the east and west, respectively. Woody biomass was rarer than herbaceous biomass and was primarily restricted to lowlands. In addition, the richness, abundance, and size of trees tended to decrease from east to west. Buffalo chips were associated with bison occupancy, which meant they were present throughout the Great Plains, but were likely especially prevalent in the northwestern plains and in wooded winter refuges. Cow chips, on the other hand, were likely most common along transportation routes. In addition to being available, it was necessary for these fuels to co-occur with other essential landscape elements—namely water in summer and shelter in winter—to be useful to people.

European colonization produced a number of frontiers that initiated social–ecological transformations in Great Plains landscapes, with effects on energy procurement, landuse, and landcover. Among the most important of these frontiers, from the perspective of human energy procurement and use, were the horse and resettlement. Influxes of horses and Euro-American travelers and settlers increased human energetic requirements. Both grass (i.e., herbaceous biomass) and tree (i.e., woody biomass) supplies were stressed by increased human use, especially in lowlands, toward which human habitation and travel were biased. Timber—which regenerated more slowly and was more limited geographically than grass—was noticeably diminished over the middle 19th century, as Native Americans with growing horse herds continued to rely on wooded lowlands for winter refuge, fuel, and horse forage. A series of harsh winters and droughts further contributed to these depletions, as did use by Euro-American travelers and settlers in certain areas (e.g., Platte and Arkansas River valleys). Prevailing Native American strategies for improving access to fuels, such as rotational use and fire setting, were ineffective for maintaining resource bases under these increasing energetic demands.

As resettlement progressed, Native American strategies for increasing fuel availability were largely replaced by Euro-American strategies of resource storage and importation. Native American dispossession, bison extirpation, and fire suppression likely interacted to increase grass and timber growth in the latter decades of the 19th century, especially as wood was imported from distant regions (e.g., the Great Lakes) and coal—an energetically denser, yet non-renewable, fuel—began to replace wood. Therefore, humans directly and indirectly drove landcover change as they simultaneously shaped and responded to their environments; however, differences in these responses set SESs on alternative trajectories with unique landcover-based tradeoffs that extend to the present. For example, after more than a century of fire suppression and heavy reliance on fossil fuels, Great Plains grasslands are transitioning to woodland and forest (Meneguzzo & Liknes 2015), which makes them less suitable for cattle crazing and as habitat for grassland-dependent species.

Proposed avenues for increasing sustainability in human–environment interactions—particularly regarding energy—include the production of energy for human metabolism (Jackson 2011) and internal combustion engines (Mitchell et al. 2016; Schmer et al. 2013; Moore et al. 2014) from prairie species instead of fossil fuels. These landuse changes would certainly affect landcover; however, the direction of effects (e.g., positive, neutral, or negative) are likely to depend on the landcover classes that conversions occur between and the contexts they occur in (Uden et al. 2013, 2015). Additional assessments of the trajectories, causes, and consequences of human-driven landcover change in regional SESs of the past, present, and future could assist with the evaluation of the social–ecological tradeoffs associated with novel changes in landcover. For instance, this chapter focused on historical energy-based landcover change; similar assessments could be performed for food-based landcover change in the past, present, and potential future.

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FIGURES

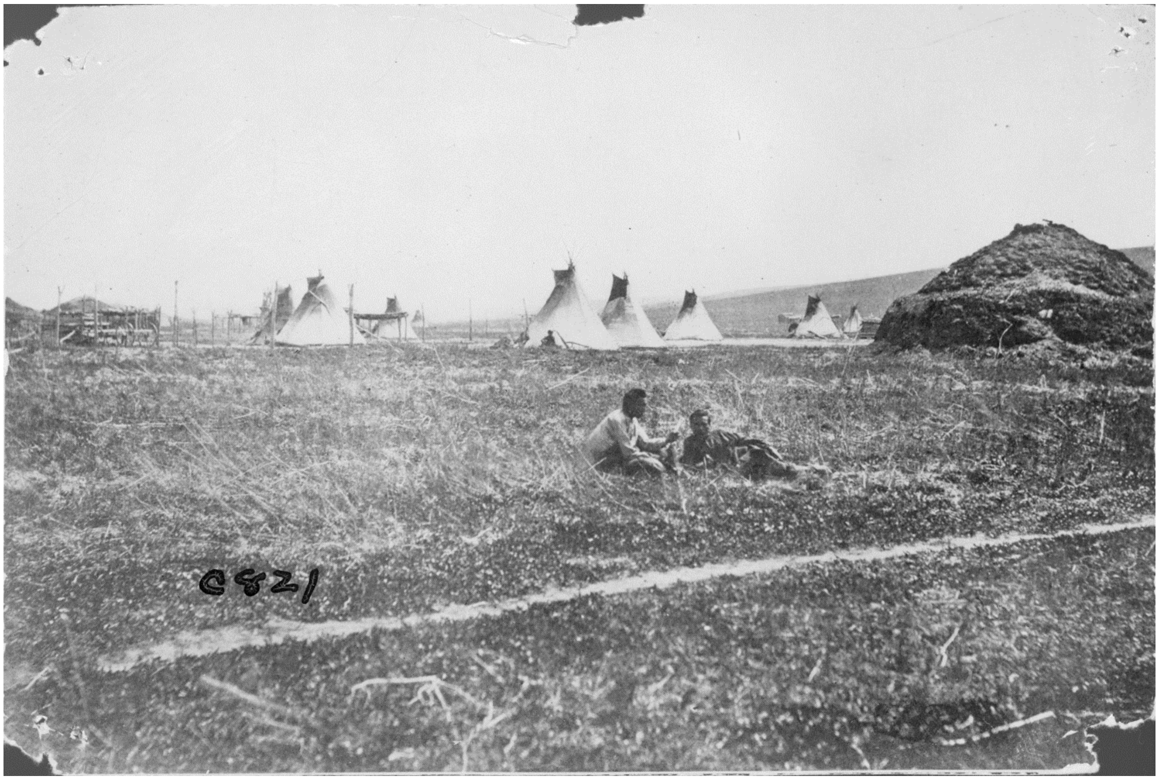

Figure 1: Omaha village with earth lodges and tipis, surrounded by depleted herbaceous vegetation. Credit: Nebraska State Historical Society.

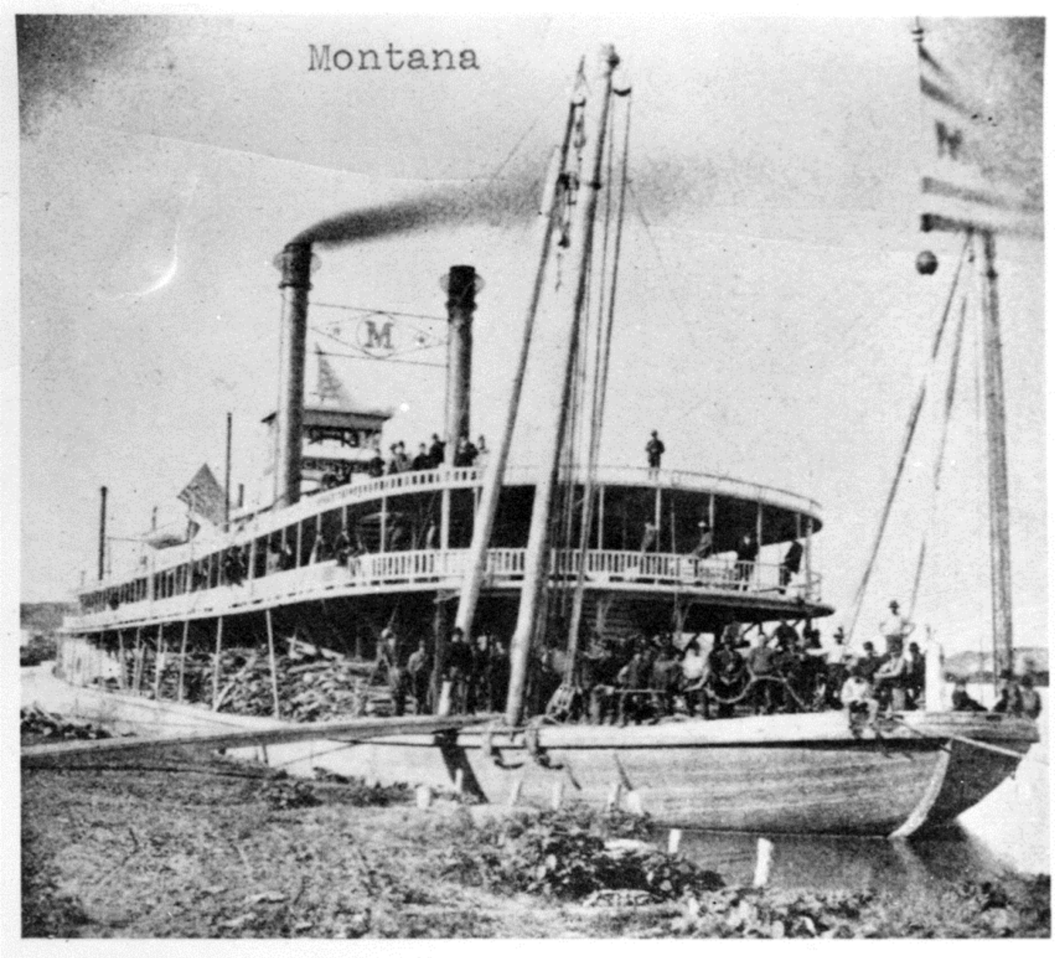

Figure 2: The steamboat Montana, which operated on the Missouri River in the late 19th century. Credit: Nebraska State Historical Society.

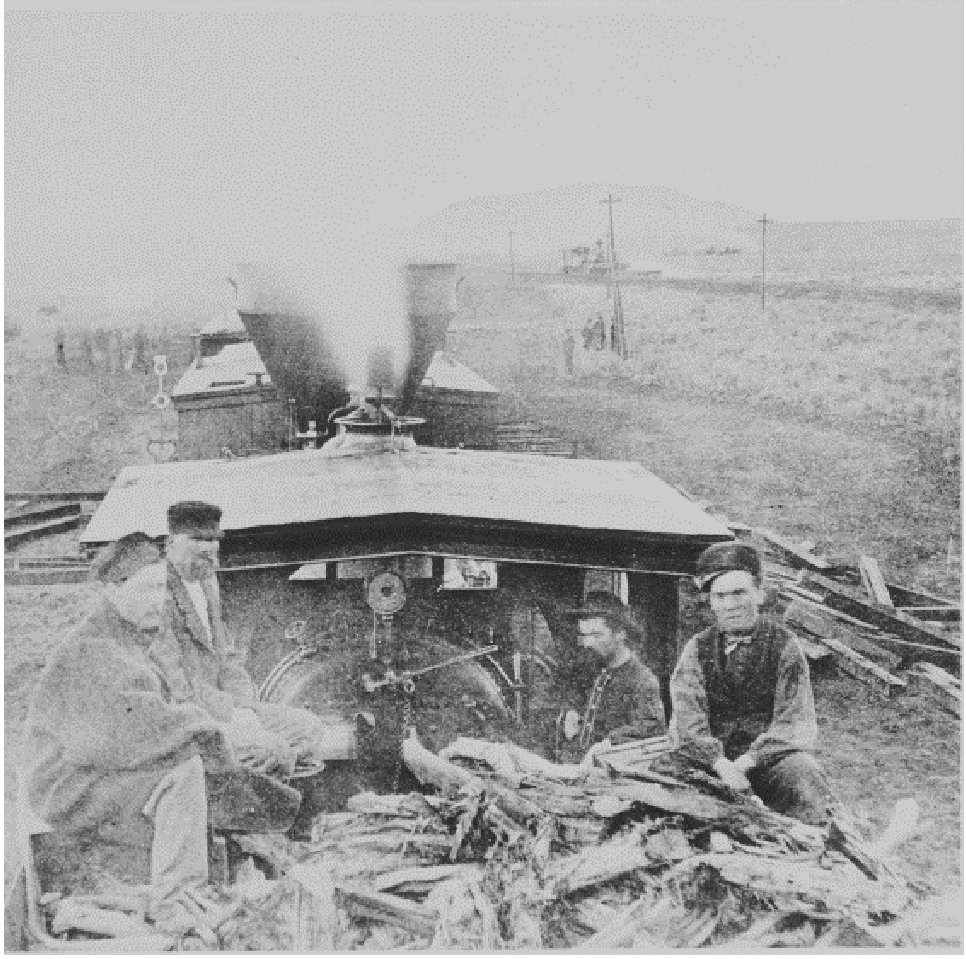

Figure 3: Men sitting on a wood pile used to fuel a Union Pacific locomotive. Credit: Nebraska State Historical Society.

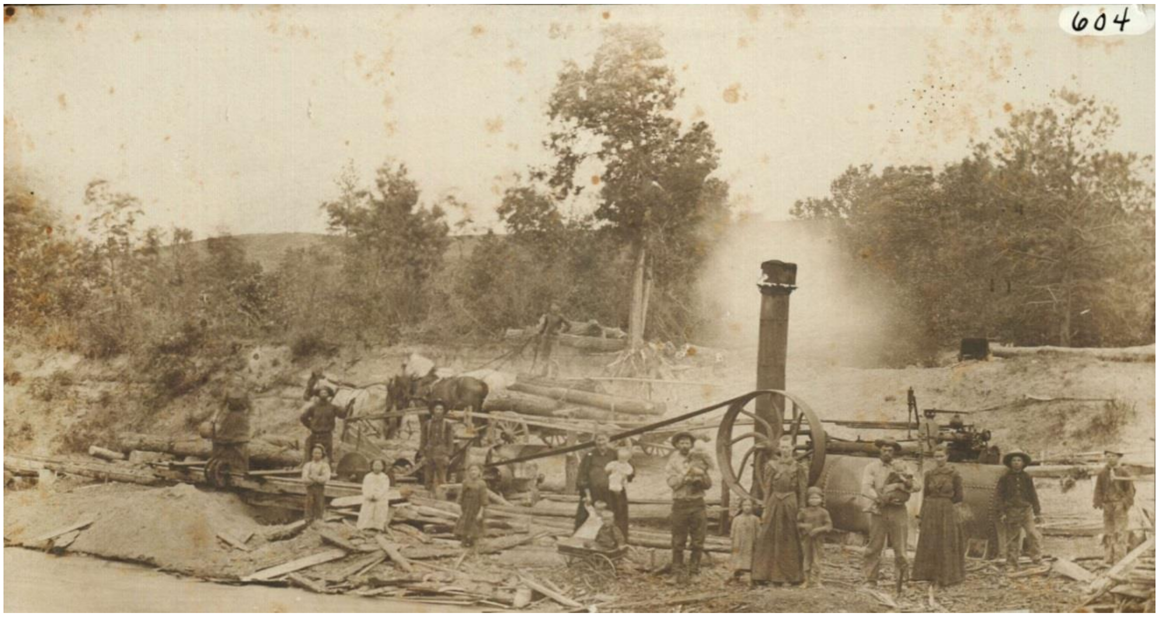

Figure 4: Andy Owens with his family and sawmill along Plum Creek, east of present-day Pine Canyon Dam, in Brown County, Nebraska. Credit: Brown County Museum in Ainsworth, Nebraska.

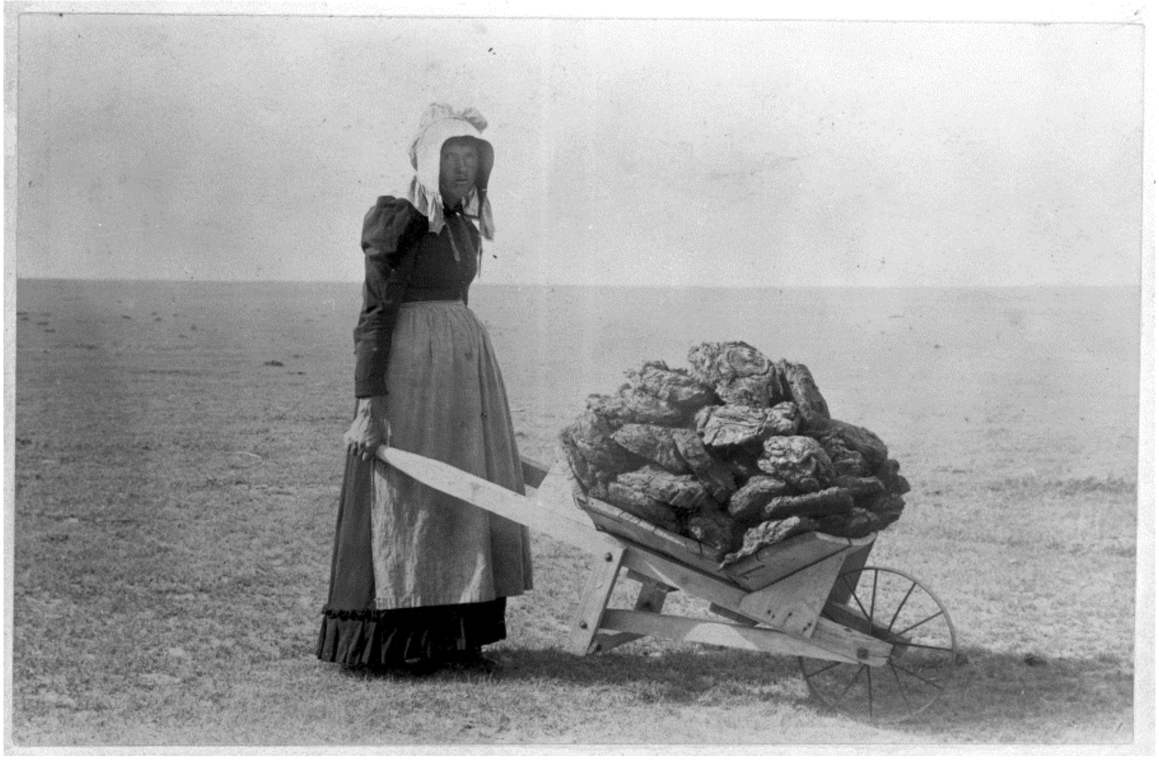

Figure 5: Polly Ann McColl collecting buffalo chips in 1893, in Kearny County, Kansas.

Credit: Kansas State Historical Society.

CHAPTER 3: COMPARISONS OF LONG-TERM AVIAN ABUNDANCES AND CROPLAND PROPORTIONS IN SEVEN NEBRASKA, U.S.A. COUNTIES

ABSTRACT

Land conversion is an economically important form of landcover change in human societies; however, it can also have negative ecological consequences. Over the past several centuries, large expanses of North American grassland have been converted to cropland, and over this same timeframe, North American grassland birds experienced widespread population declines. In the U.S.A., data on agricultural production and landuse has been collected annually at the county level since the mid-19th century through the U.S. Census of Agriculture, and data on avian abundances has been collected annually along 39.43 kilometer (24.50 mile) routes since the 1960s through the North American Breeding Bird Survey (BBS). Statistical exploration of the relationships between social and ecological variables in these datasets could be explored when BBS routes are situated within individual counties. In this chapter, I used generalized linear mixed model(s) (GLMM) to compare brown-headed cowbird (*Molothrus ater*), dickcissel (*Spiza americana*), eastern kingbird (*Tyrannus tyrannus*), and western meadowlark (*Sturnella neglecta*) abundances (i.e., counts) with proportions of land area enrolled in cropland in seven Nebraska, U.S.A. counties in seven years between 1969 and 2007. Statistically significant relationships were evidenced between avian counts and county cropland proportion in the final GLMM for all four avian species; however, GLMMs varied in their abilities to explain variability in avian counts along BBS routes, with the

best-performing model being for dickcissels and the worst-performing model being for brown-headed cowbirds. BBS data was not available for the late 19th and early 20th centuries, when the majority of conversion to cropland took place in Nebraska counties. Nevertheless, this chapter demonstrates one approach for assessing the long-term ecological consequences of conversion to cropland and related forms of landcover change in the context of social–ecological system(s) (SES) thinking, which emphasizes interconnections and interdependencies between human social systems and ecosystems. In this context, chapter results could also contribute to evaluations of the social–ecological tradeoffs associated with alternative trajectories in human-driven landcover change.

INTRODUCTION

Landcover change is an important global change process within social–ecological system(s) (SES) (Lambin et al. 2006), where it has diverse direct and indirect social and ecological causes and consequences (DeFries et al. 2004; Foley et al. 2005; Chhabra et al. 2006; Burgi et al. 2017). One socially, economically, and ecologically important form of landcover change that is directly driven by human activity is land conversion (Lambin & Meyfroidt 2011), and one important form of land conversion is conversion to cropland (Johnston 2014; Kuhn et al. 2016). A large proportion of global land area is presently devoted to growing crops (Ellis et al. 2010) and a large proportion of the world's human population relies on crop farming for their livelihoods (Zimmerer 2007). Although it yields food and energy for people, the ecological effects of crop production can be negative when it results in the transformations of species habitats. Globally, the intensification of agriculture has been associated with biodiversity and functional diversity losses at multiple scales, which can eventually impair the provisioning of essential ecosystem services to human populations (Benton et al. 2002; Tscharntke et al. 2005; Flynn et al. 2009).

In the State of Nebraska, U.S.A., displacement of Native Americans and subsequent resettlement by Euro-Americans in the 19th century initiated landscape transformations (Wishart 1994), which include the widespread conversion of grasslands and wetlands to cropland. An array of interacting social–ecological factors—including soil fertility, weather patterns, agricultural commodity prices, technological innovations, government farm policies and programs, and wars—continued to drive conversions to cropland in Nebraska landscapes throughout the 20th and early 21st centuries (Elder 1969; Parton et al. 2007; Hiller et al. 2009; Powell 2015). These conversions affected, and will continue to affect, food and energy production for people and habitat quality and quantity for grassland- and wetland-dependent species (Samson et al. 2004; Askins et al. 2007; Wright & Wimberly 2013); however, there are social–ecological tradeoffs in these effects that depend on various factors, such as landscape context and the landcover classes that conversions occur between (Uden et al. 2015).

The analysis of long-term social and ecological datasets can generate novel insights into the consequences of directly human-driven landcover change in SESs (Homewood et al. 2001). In Nebraska, the North American Breeding Bird Survey (BBS) has recorded bird abundances along established 39.43 kilometer (24.50 mile) routes since 1966, and the U.S. Census of Agriculture (i.e., Agricultural Census) has collected data on county-level agricultural production and landuse since the late-19th century (Gutmann 2005). In this chapter, I compare brown-headed cowbird (*Molothrus ater*), dickcissel (*Spiza americana*), eastern kingbird (*Tyrannus tyrannus*), and western meadowlark (*Sturnella neglecta*) abundances from the BBS with proportions of land area enrolled in cropland in seven Nebraska counties in seven years between 1969 and 2007 from the Agricultural Census. Examination of the long-term relationships between these variables in the context of SESs thinking could yield information that aids in the evaluation of future tradeoffs and decisions associated with alternative trajectories of human-driven landcover change and its relationships to resilience, adaptation, and transformation in Nebraska landscapes.

METHODS

Study areas

Comparisons between the BBS and U.S. Census of Agriculture datasets were undertaken in Boone, Brown, Buffalo, Dawson, Otoe, Seward, and Washington Counties in the eastern half of the State of Nebraska, U.S.A. (Figure 1). These counties were selected because of their relative similarity in size and because entire BBS routes were situated within, or nearly within, them. The BBS routes within these counties were Petersburg, Johnstown, Kearney, Sumner, Julian, Seward, and Irvington, respectively (Table 1). Grass is presently the dominant landcover class in Brown (87%), Buffalo (43%), and Dawson (46%) Counties—which are the westernmost of the seven focal counties—whereas cropland is the dominant landcover class in Boone (52%), Otoe (46%), Seward (58%), and Washington (54%) Counties, which are situated further to the east (Table 2; Figure 2).

Data

Agricultural census data was obtained from the website of the U.S. Census of Agriculture (https://www.agcensus.usda.gov/) and Gutmann (2005), who compiled U.S. Census of Agriculture data for the American Great Plains between 1870 and 1997. BBS data was downloaded from the North American Breeding Bird Survey website (https://www.pwrc.usgs.gov/bbs/). Thirty meter (m) resolution landcover data for the seven focal counties was provided by the Rainwater Basin Joint Venture (Bishop et al.

2011). Finally, shapefiles of Nebraska counties were downloaded from the website of the Nebraska Department of Natural Resources (dnr.ne.gov/data).

Although the BBS has been conducted annually since 1966, it is not available for all routes in all years. In addition, BBS datasets are prone to certain forms of error and bias (Sauer et al. 1994, 2003; Kendall et al. 1996; Link & Sauer 1998), which can necessitate the application of bias removal and normalization techniques. However, no such techniques were applied in this study. Instead, years in which data was not available for all seven BBS routes were simply eliminated from the dataset. Similarly, in order to match years between the BBS and Agricultural Census datasets, both datasets were truncated to the years in which full sets of observations for each were available: 1969, 1978, 1982, 1987, 1997, 2002, and 2007. Following truncation, the two datasets were merged into a single dataset.

Statistical models

Generalized linear mixed model(s) (GLMM) were used to statistically relate avian abundances from the BBS to proportions of counties enrolled in cropland from the Agricultural Census. GLMMs are subsets of mixed models that are comprised of fixed effects and random effects structures, which make them well-suited for hierarchical data analysis (Zuur et al. 2007, 2009; Bolker et al. 2008). Fixed effects structures are associated with predictor variables about which inferences are to be made, whereas random effects structures pertain to predictor variables about which inferences cannot be made, but by which the model intercept and/or parameter estimates contained in the fixed effects structure may vary. The utilization of random effects structures transforms generalized linear model(s) (GLM) into GLMMs, and in doing so, may explain additional variability in hierarchically organized datasets, conserve degrees of freedom, and account for autocorrelation (i.e., spatial and/or temporal dependencies) among observations.

Abundances (i.e., counts) of four regionally common grassland bird species—brown-headed cowbirds, dickcissels, eastern kingbirds, and western meadowlarks—served as GLMM response variables, while the proportion of county area in cropland served as the sole predictor variable in GLMM fixed effects structures, and model intercepts or intercepts and coefficient estimates (i.e., slopes) for the cropland proportion parameter that were allowed to vary among years served as the random effects structure. In other words, unique intercepts, or intercepts and cropland proportion slopes, were calculated for each of the seven study years in each of the models. The proportion of county area in cropland, which serves as a direct indicator of the spatial extent of landcover change, was calculated by dividing the area of cropland in a county by the total area of the county. Prior to model fitting, boxplots—constructed with the ggplot2 Package (Wickham 2009) for R (R Core Team 2016)—were used to represent the distributions of avian species abundances (i.e., counts) and cropland proportions within years and across BBS routes and Nebraska counties.

Given that all four response variables took the form of count data, a Poisson distribution with a log link function was assumed for all GLMMs. Within each GLMM, different random effects structures were tested and compared with Akaike's Information Criterion, corrected for small sample size (AICc). The fixed effects structure in all models consisted of county cropland proportion. All GLMMs were fit and compared with functions housed in the lme4 (Bates et al. 2015) and AICcmodavg (Mazerolle 2016) Packages for the program R. Following the identification of a final (i.e., best-supported) GLMM for each of the four bird species, coefficient estimates, significance values, and 95% confidence intervals were calculated for the models' fixed effects parameters (i.e., proportion county area in cropland).

The four final GLMMs were used to make predictions with the same data used for model training. These predictions were plotted as lines and overlaid onto scatterplots of observed avian abundances and cropland proportions. Because the random effects structure of the GLMMs allowed for the derivation of unique intercepts or intercepts and slopes for each of the seven study years, each of the plots contained seven predicted lines. Plots of bird–cropland relationships were constructed in the ggplot2 Package (Wickham 2009) for R.

Lastly, marginal and conditional pseudo-R^2 values were output for each GLMM with the r.squarredGLMM function in the MuMIn Package (Barton 2016) for R. In general, pseudo-R^2 values provide an indicator of the proportion of variation in the response variable that is explained by the predictor. However, in the case of GLMMs, it is possible to differentiate between the proportion of variation that is explained by the fixed effects structure of the GLMM alone (i.e., marginal pseudo-R^2) and that which is explained by the fixed and random effects structures together (i.e., conditional pseudo-R^2) (Nakagawa & Schielzeth 2013; Johnson 2014). Greater differences between conditional and marginal pseudo-R^2 values are indicative of greater proportions of variability being accounted for by the model's random effects structure.

RESULTS

Avian counts varied by species, within and among BBS routes, and within and among years (Figures 3–6). Over all seven BBS routes and all seven study years, the mean number of observed western meadowlarks was ~64, the mean number of brown-headed cowbirds was ~37, the mean number of dickcissels was ~33, and the mean number of eastern kingbirds was ~17 (Table 3). The proportion of county area in cropland also varied among the seven counties (Figure 7), although it was relatively constant among years (Figure 8). Over the seven study years, the mean proportion of land area enrolled in cropland was ~0.80 in Washington County, ~0.79 in Seward County, ~0.72 in Otoe County, ~0.69 in Boone County, ~0.61 in Buffalo County, ~ 0.55 in Dawson County, and ~ 0.19 in Brown County (Table 4).

GLMMs varied among avian species in their ability to explain variability in counts along BBS routes as a function of the proportion of county area in cropland. The marginal and conditional pseudo-R^2 values were ~0.33 and ~0.52 for the dickcissel GLMM, ~0.18 and ~0.18 for the western meadowlark GLMM, ~0.08 and ~0.10 for the eastern kingbird GLMM, and ~0.00 and ~0.00 for the brown-headed cowbird GLMM (Table 5). The random effects structures of the dickcissel (Table 6) and western meadowlark (Table 7) GLMMs consisted of random intercepts and slopes for each of the seven survey years, whereas the random effects structures for the eastern kingbird (Table

8) and brown-headed cowbird (Table 9) GLMMs only contained random intercepts for each of the seven study years. For eastern kingbirds, the GLMM with the random intercept and slope failed to converge; therefore, the GLMM with the random intercept alone was classified as the best-supported. The fixed effects structures of the four GLMMs—which contained only the cropland proportion predictor—indicate statistically significant relationships between cropland proportion and the abundances of all four species. The direction of the cropland proportion effect on bird counts was negative for brown-headed cowbirds (Table 10; Figure 9a) and western meadowlarks (Table 11; Figure 9d), and positive for dickcissels (Table 12; Figure 9b) and eastern kingbirds (Table 13; Figure 9c).

DISCUSSION

This chapter compared long-term (i.e., 1969–2007) trends in variables from ecological (i.e., BBS) and agricultural (i.e., Agricultural Census) datasets for the State of Nebraska, in order to increase understanding of the ecological effects of human-driven landcover change, specifically, conversion to cropland. Because BBS data is collected along 39.43 kilometer (24.50 mile) routes and the Agricultural Census data is collected for counties, comparisons were limited to instances (i.e., seven counties, seven routes, and seven years) in which entire, or nearly entire, BBS routes were contained within county boundaries. GLMMs—with the proportion of county area enrolled in cropland as the sole predictor in their fixed effects structures and intercepts or intercepts and slopes that varied among study years comprising the random effects structures—were used to statistically assess relationships between the abundances of brown-headed cowbirds, dickcissels, eastern kingbirds, and western meadowlarks and the proportion of counties enrolled in cropland.

Results showed avian counts to vary among species, within and among BBS routes, and within and among years, with the generally most abundant species being the western meadowlark and the least abundant species being the eastern kingbird. Statistically significant relationships between the proportion of county area in cropland and bird counts were evidenced for all four species, with negative relationships for brown-headed cowbirds and western meadowlarks, and positive relationships for dickcissels and eastern kingbirds. In regard to the proportion of the variability accounted for by the models, the GLMM for dickcissels was best, and was followed by the GLMMs for western meadowlarks, eastern kingbirds, and brown-headed cowbirds, with particularly low marginal and conditional pseudo-R^2 values for the brown-headed cowbird GLMM.

The conversion of grasslands and wetlands to cropland accompanied the cultural transformation associated with Native American dispossession and Euro-American resettlement. Since the initiation of the Agricultural Census in Nebraska in the late 19th century, large expanses of Nebraska were converted to cropland, and much of this conversion occurred in the late 19th and early 20th century (Hiller et al. 2009), as confirmed by the relative stability in the proportion of land area in cropland between 1969 and 2007 in the results of this chapter. Therefore, even in the long-term comparisons of this chapter, the unavailability of BBS data in the early 20th century limits exploration of the relationship between avian abundance and cropland conversion. Given that both BBS and Agricultural Census data are available throughout the U.S.A., this issue could be addressed by expanding or relocating the study area to counties—perhaps outside of Nebraska—where BBS data is available for time periods when active conversion to cropland occurred.

Despite the unavailability of early 20th century BBS data in Nebraska, the GLMMs for dickcissels and western meadowlarks explained substantial proportions of the variability in abundances as a function of proportion of county area enrolled in cropland. Curiously, the directions of the statistically significant relationships between dickcissel and western meadowlark abundances and cropland proportion are opposite. Examination of life history characteristics of dickcissels and western meadowlarks show that dickcissels are associated with grasslands, meadows, savannas, and cultivated and abandoned fields (Ehrlich et al. 1988), whereas western meadowlarks are also associated with grasslands, savannas, pastures, and cultivated fields but may also require larger grassland patches for breeding habitat (Helzer & Jelinski 1999). Additional analytical steps, such as assessments of temporal autocorrelation and cross-validation may also yield insights into the performances of the four GLMMs.

One aspect of landcover change not incorporated into this analysis is the intensity of agricultural landuse. Although changing baselines in farming practices and technology (e.g., irrigation and seed hybridization) could make comparisons in change over time challenging, certain variables contained in the Agricultural Census could serve as socially relevant indicators of changes in human behavior with important ecological effects. For example, decreases in the number of farms without corresponding decreased in cropland area—trends related to rural emigration in landscapes throughout the Great Plains (Drozd & Deichert 2007; Parton et al. 2007)—is interpreted as indicating increasing farm size and increasing mechanization (i.e., agricultural intensification) in Nebraska counties (Hiller et al. 2009). Other potentially important considerations for future studies are evaluations of relationships between avian counts and the proportions of different crops that collectively compose the cropland proportion predictor variable in this chapter.

This chapter demonstrates one approach for assessing the long-term ecological consequences of conversion to cropland and related forms of landcover change in the context of SESs thinking, which emphasizes interconnections and interdependencies between human social systems and ecosystems. In this context, chapter results could also contribute to evaluations of the social–ecological tradeoffs associated with alternative trajectories in human-driven landcover change, which could have important implications for future landuse- and landcover-based decision-making.

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TABLES AND FIGURES

Table 1: Selected Nebraska, U.S.A. county names with their corresponding areas (i.e., hectares) and Breeding Bird Survey (BBS) routes.

County	**Hectares**	**BBS route**
Boone	177,869	Petersburg
Brown	317,174	Johnstown
Buffalo	252,487	Kearney
Dawson	263,883	Sumner
Otoe	160,251	Julian
Seward	149,069	Seward
Washington	101,767	Irvington

Table 2: Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent in seven Nebraska, U.S.A. counties, based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011).

Class	**Boone**	**Brown**	**Buffalo**	**Dawson**	**Otoe**	**Seward**	**Washington**
Water	1,093 (1)	4,273 (1)	3,532 (1)	3,108 (1)	2,347 (1)	2,575 (2)	1,265 (1)
Trees	3,070 (2)	15,301 (5)	15,437 (6)	14,134 (5)	17,490 (11)	11,167 (7)	8,877 (9)
Grass	75,768 (43)	275,277 (87)	108,642 (43)	122,265 (46)	53,747 (34)	37,245 (25)	23,715 (23)
Crops	91,896 (52)	17,959 (6)	102,856 (41)	106,673 (40)	74,200 (46)	85,751 (58)	55,074 (54)
Developed	6,047 (3)	4,290 (1)	2,1960 (9)	17,680 (7)	12,565 (8)	12,385 (8)	12,892 (13)
Total	177,874	317,100	252,427	263,860	160,349	149,123	101,823

Table 3: Overall mean abundances (i.e., counts) for western meadowlarks (*Sturnella neglecta*), brown-headed cowbirds (*Molothrus ater*), dickcissels (*Spiza americana*), and eastern kingbirds (*Tyrannus tyrannus*) along the Petersburg, Johnstown, Kearney, Sumner, Julian, Seward, and Irvington Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

Species	**Mean abundance**
Western meadowlark	63.8367
Brown-headed cowbird	37.2653
Dickcissel	32.9796
Eastern kingbird	16.8776

Table 4: Overall mean proportions of area enrolled in cropland in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

County	Mean cropland proportion
Washington	0.7998
Seward	0.7948
Otoe	0.7223
Boone	0.6902
Buffalo	0.6122
Dawson	0.5463
Brown	0.1890

Table 5: Marginal and conditional pseudo-R^2 values for generalized linear mixed model(s) (GLMM) explaining variability in brown-headed cowbird (*Molothrus ater*), dickcissel (*Spiza americana*), eastern kingbird (*Tyrannus tyrannus*), and western meadowlark (*Sturnella neglecta*) abundances along seven Breeding Bird Survey routes in seven Nebraska, U.S.A. counties as a function of the proportion of county land area enrolled in cropland (i.e., fixed effect), with random effects in which the model intercept varies by survey year or in which both the model intercept and slope for the fixed effect variable (i.e., proportion cropland) vary by survey year.

Species	**Fixed effect**	**Random effect**	**Marg R^2**	**Cond R^2**
Dickcissel	Cropland	Intercept + Cropland	0.3297	0.5218
Western meadowlark	Cropland	Intercept + Cropland	0.1829	0.1838
Eastern kingbird	Cropland	Intercept	0.0761	0.1038
Brown-headed cowbird	Cropland	Intercept	0.0002	0.0002

Table 6: Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in dickcissel (*Spiza americana*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. In one random effects structure, the model intercept was allowed to vary among study years [i.e., (1 | Year)], and in the other random effects structure, both the model intercept and slope for cropland proportion were allowed to vary among study years [i.e., (Cropland | Year)]. Models were ranked with to Akaike's Information Criterion scores, adjusted for small sample size (AICc), relative AICc (ΔAICc), and AICc weight (w), with lower scores and higher weights indicating a greater degree of relative support for the model, given the data.

Model	**AICc**	**ΔAICc**	**w**
Abundance ~ Cropland + (Cropland | Year)	606.9058	0.0000	1.0000
Abundance ~ Cropland + (1 | Year)	727.0879	120.1821	0.0000

Table 7: Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in western meadowlark (*Sturnella neglecta*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. In one random effects structure, the model intercept was allowed to vary among study years [i.e., (1 | Year)], and in the other random effects structure, both the model intercept and slope for cropland proportion were allowed to vary among study years [i.e., (Cropland | Year)]. Models were ranked with Akaike's Information Criterion scores, adjusted for small sample size (AICc), relative AICc (ΔAICc), and AICc weight (w), with lower scores and higher weights indicating a greater degree of relative support for the model, given the data.

Model	**AICc**	**ΔAICc**	**w**
Abundance ~ Cropland + (Cropland | Year)	2,154.9690	0.0000	1.0000
Abundance ~ Cropland + (1 | Year)	2,182.0460	27.0765	0.0000

Table 8: Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in eastern kingbird (*Tyrannus tyrannus*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. In one random effects structure, the model intercept was allowed to vary among study years [i.e., (1 | Year)], and in the other random effects structure, both the model intercept and slope for cropland proportion were allowed to vary among study years [i.e., (Cropland | Year)]. Models were ranked with Akaike's Information Criterion scores, adjusted for small sample size (AICc), relative AICc (ΔAICc), and AICc weight (w), with lower scores and higher weights indicating a greater degree of relative support for the model, given the data. In cases where models failed to converge (NA), the alternative model was considered the best supported.

Model	**AICc**	**ΔAICc**	**w**
Abundance ~ Cropland + (1 | Year)	510.7800	0.0000	1.0000
Abundance ~ Cropland + (Cropland | Year)	NA	NA	NA

Table 9: Comparison of two generalized linear mixed model(s) (GLMM) with different random effects structures for explaining variability in brown-headed cowbird (*Molothrus ater*) counts (i.e., abundances) along seven Breeding Bird Survey (BBS) routes in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. In one random effects structure, the model intercept was allowed to vary among study years [i.e., (1 | Year)], and in the other random effects structure, both the model intercept and slope for cropland proportion were allowed to vary among study years [i.e., (Cropland | Year)]. Models were ranked with Akaike's Information Criterion scores, adjusted for small sample size (AICc), relative AICc (ΔAICc), and AICc weight (w), with lower scores and higher weights indicating a greater degree of relative support for the model, given the data.

Model	**AICc**	**ΔAICc**	**w**
Abundance ~ Cropland + (1 | Year)	1,360.1870	0.0000	0.6460
Abundance ~ Cropland + (Cropland | Year)	1,361.3907	1.2038	0.3539

Table 10: Generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between brown-headed cowbird (*Molothrus ater*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. Statistically significant coefficient estimates—assuming an alpha level of 0.05—are indicated by bolded font in p-values. The random effects structure of the GLMM allowed the model intercept to vary among years.

			95% CI		
Parameter	**Estimate**	**Std Error**	**Lower**	**Upper**	**p-value**
Intercept	3.7476	0.1147	3.5056	3.9859	< **0.0001**
Cropland proportion	-0.2521	0.1153	-0.4761	-0.0239	**0.0287**

Table 11: Table of generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between western meadowlark (*Sturnella neglecta*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. Statistically significant coefficient estimates—assuming an alpha level of 0.05—are indicated by bolded p-values. The random effects structure of the GLMM allowed the model intercept and coefficient for the cropland proportion parameter to vary among years.

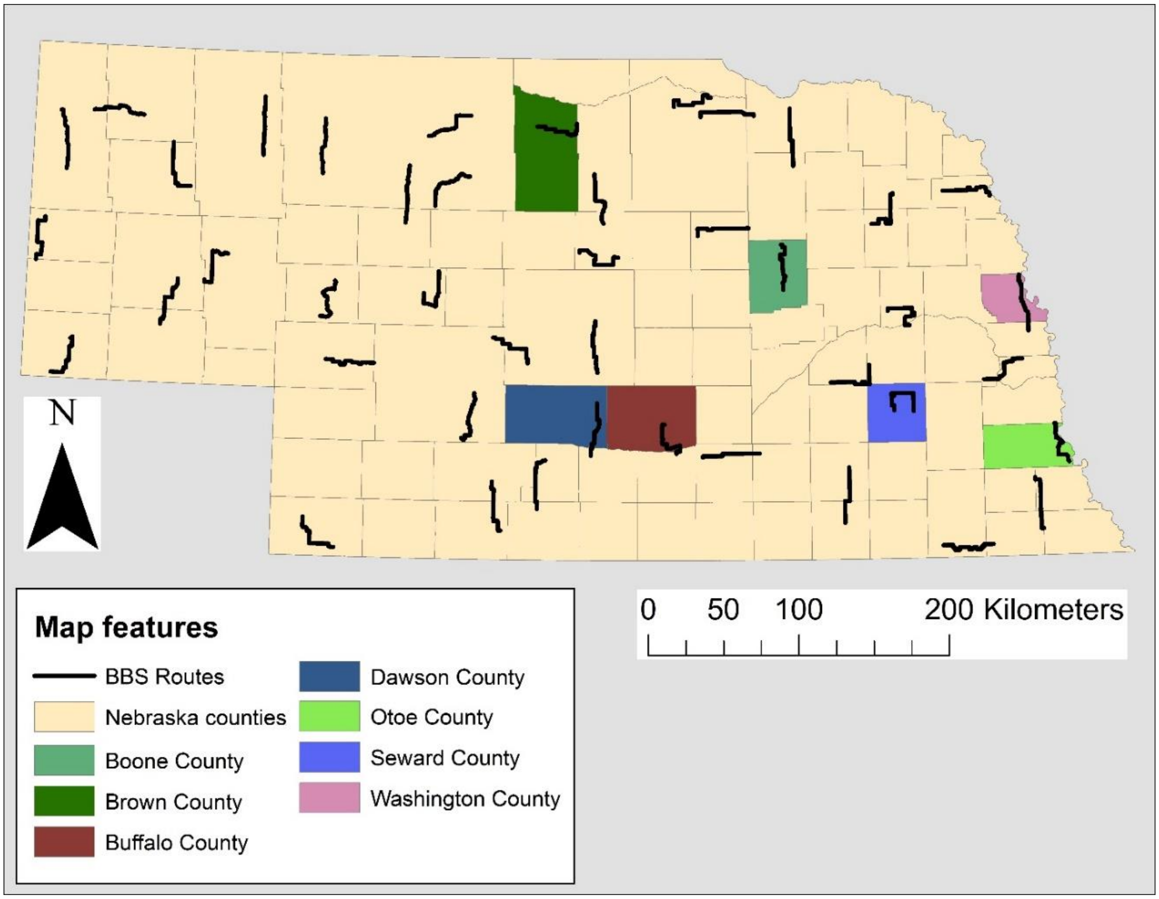
			95% CI		
Parameter	**Estimate**	**Std error**	**Lower**	**Upper**	**p-value**
Intercept	4.8887	0.1373	4.5717	5.1962	< **0.0001**
Cropland proportion	-1.2986	0.2018	-1.7508	-0.8438	< **0.0001**

Table 12: Table of generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between dickcissel (*Spiza americana*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. Statistically significant coefficient estimates—assuming an alpha level of 0.05—are indicated by bolded p-values. The random effects structure of the GLMM allowed the model intercept and coefficient for the cropland proportion parameter to vary among years.

			95% CI		
Parameter	**Estimate**	**Std error**	**Lower**	**Upper**	**p-value**
Intercept	1.5586	0.8538	-0.4316	3.4842	0.0679
Cropland proportion	2.7313	1.1850	0.0568	5.4776	**0.0212**

Table 13: Table of generalized linear mixed model (GLMM) fixed effect parameter coefficient estimates, standard errors, and 95% confidence intervals for explaining variability in the relationship between eastern kingbird (*Tyrannus tyrannus*) counts along seven Breeding Bird Survey (BBS) routes and the proportion of area enrolled in cropland in the seven Nebraska, U.S.A. counties in which the BBS routes are situated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007. Statistically significant coefficient estimates—assuming an alpha level of 0.05—are indicated by bolded p-values. The random effects structure of the GLMM allowed the model intercept to vary among years.

			95% CI		
Parameter	**Estimate**	**Std error**	**Lower**	**Upper**	**p-value**
Intercept	2.4095	0.1560	2.0897	2.7181	< **0.0001**
Cropland proportion	0.6171	0.1915	0.2476	0.9997	**0.0013**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50
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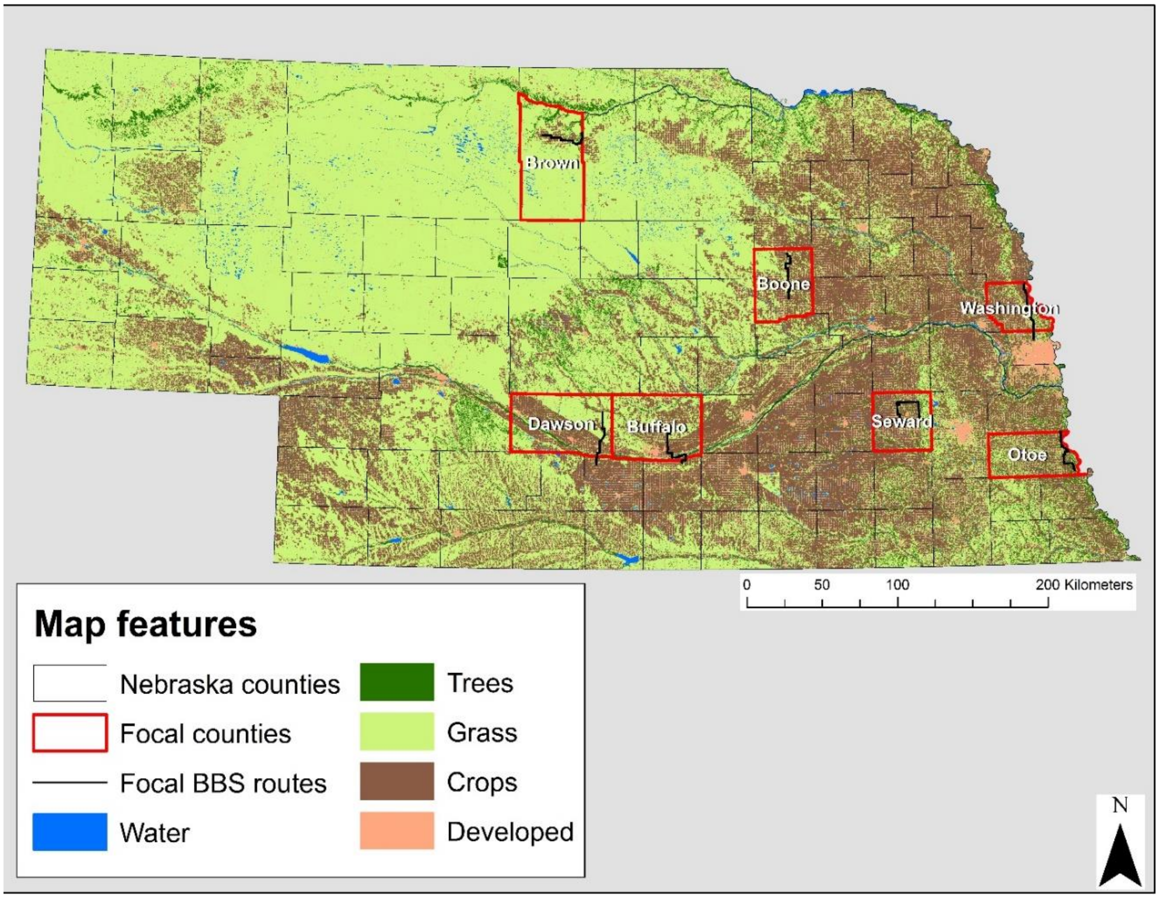
Dawson County
Otoe County
Seward County
Washington County

Figure 1: Locations of selected counties and Breeding Bird Survey (BBS) Routes within the State of Nebraska, U.S.A., where relationships between avian abundances and the proportion of county areas enrolled in cropland were evaluated in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.


Brown
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Focal BBS routes
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Trees
Grass
Crops
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Figure 2: Nebraska, U.S.A. reclassified 2010 landcover (Bishop et al. 2011), counties, and Breeding Bird Survey (BBS) routes in which avian abundances from the BBS were compared with metrics of cropland conversion from the U.S. Census of Agriculture in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

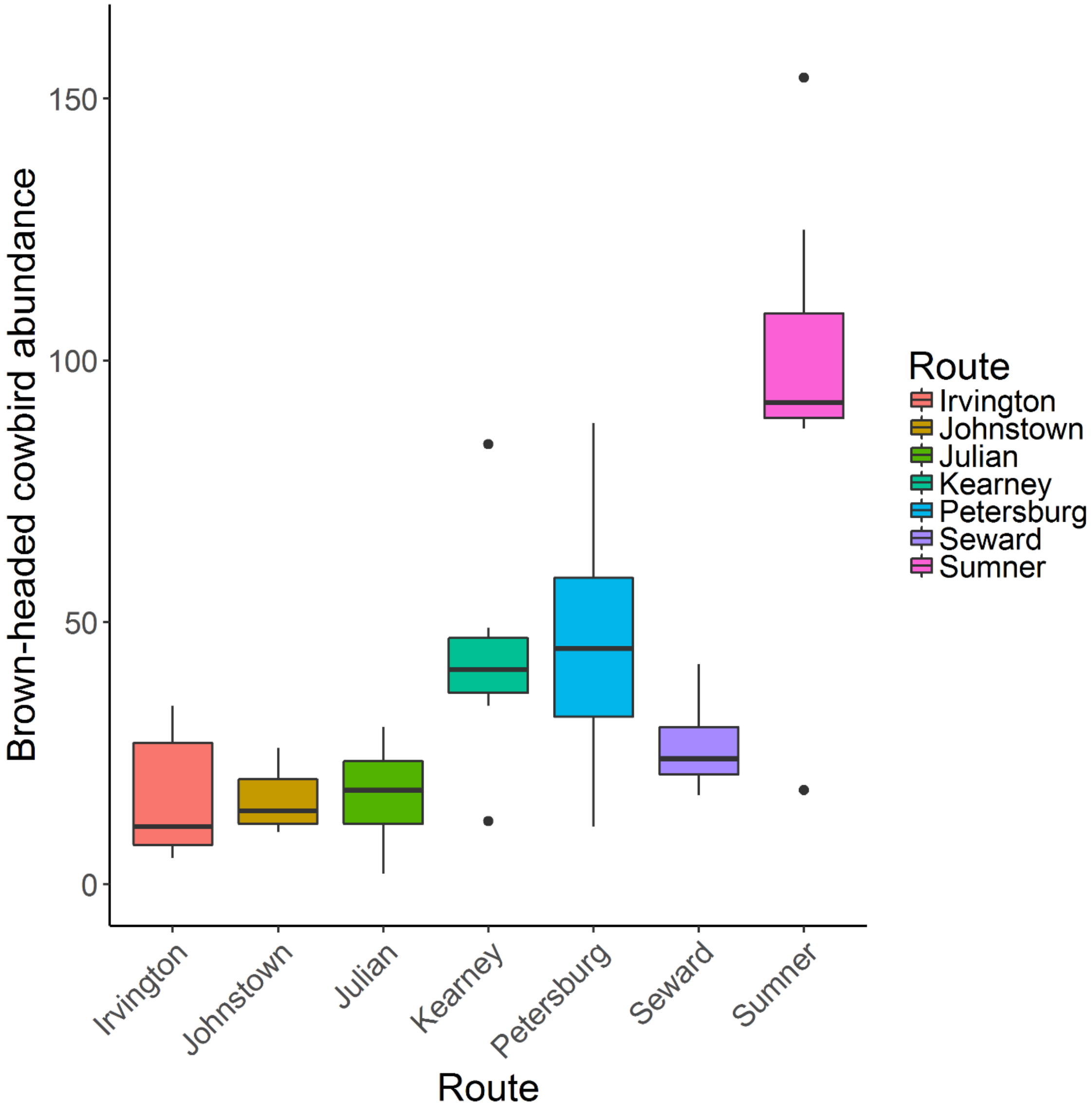

Figure 3: Distributions of brown-headed cowbird (*Molothrus ater*) abundances (i.e., counts) along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

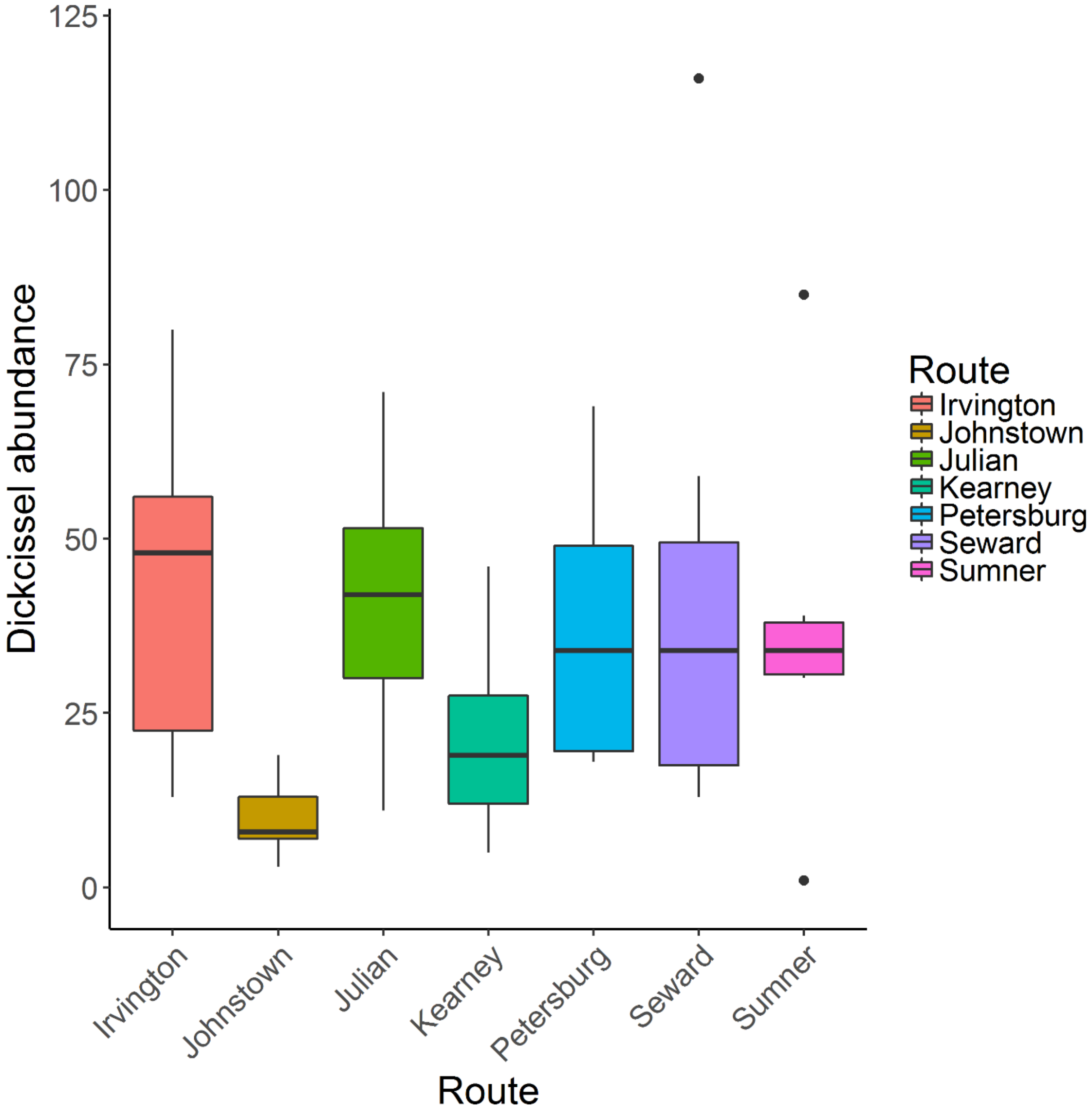

Figure 4: Distributions of dickcissel (*Spiza americana*) abundances (i.e., counts) along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

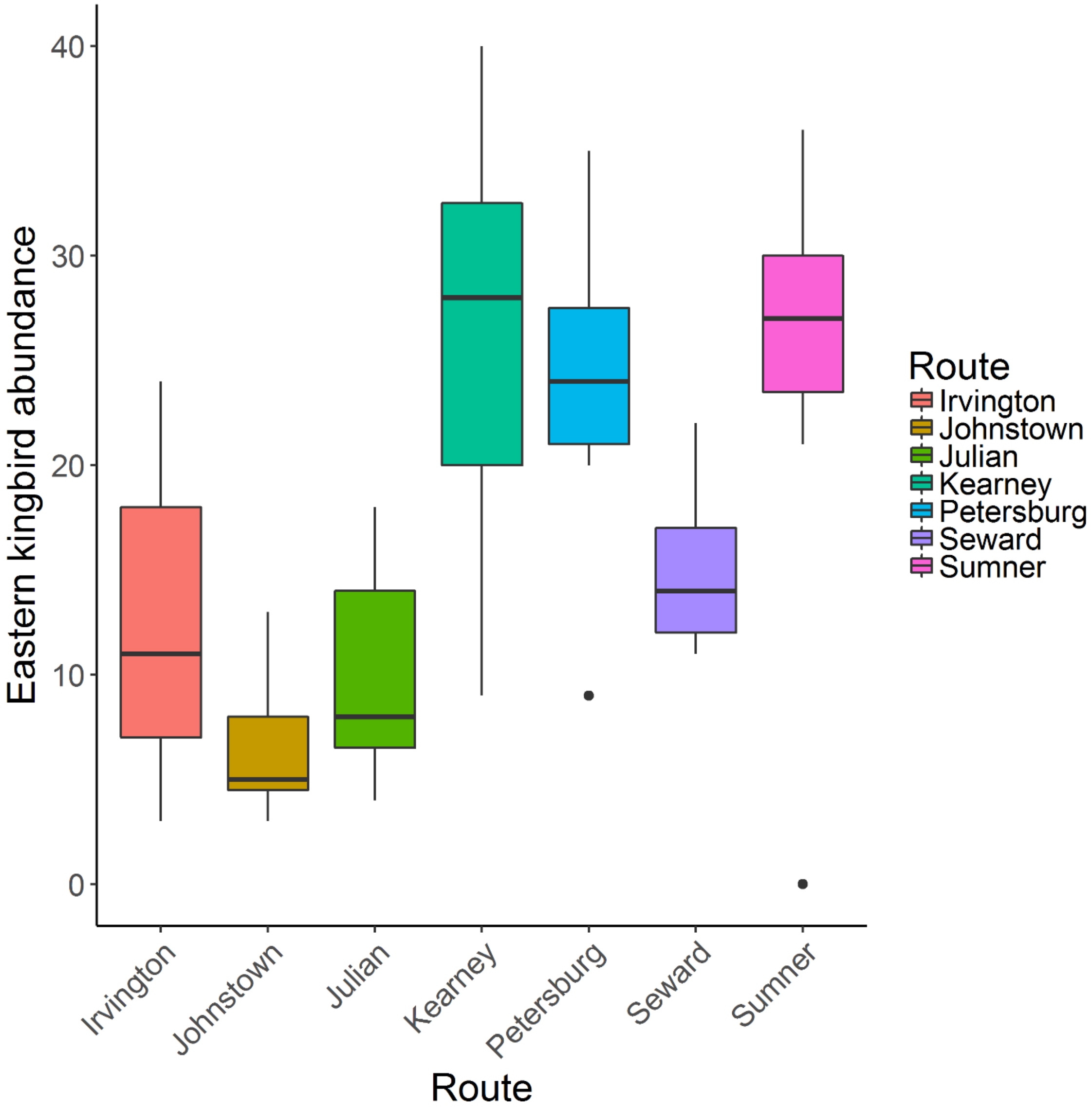

Figure 5: Distributions of eastern kingbird (*Tyrannus tyrannus*) abundances along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

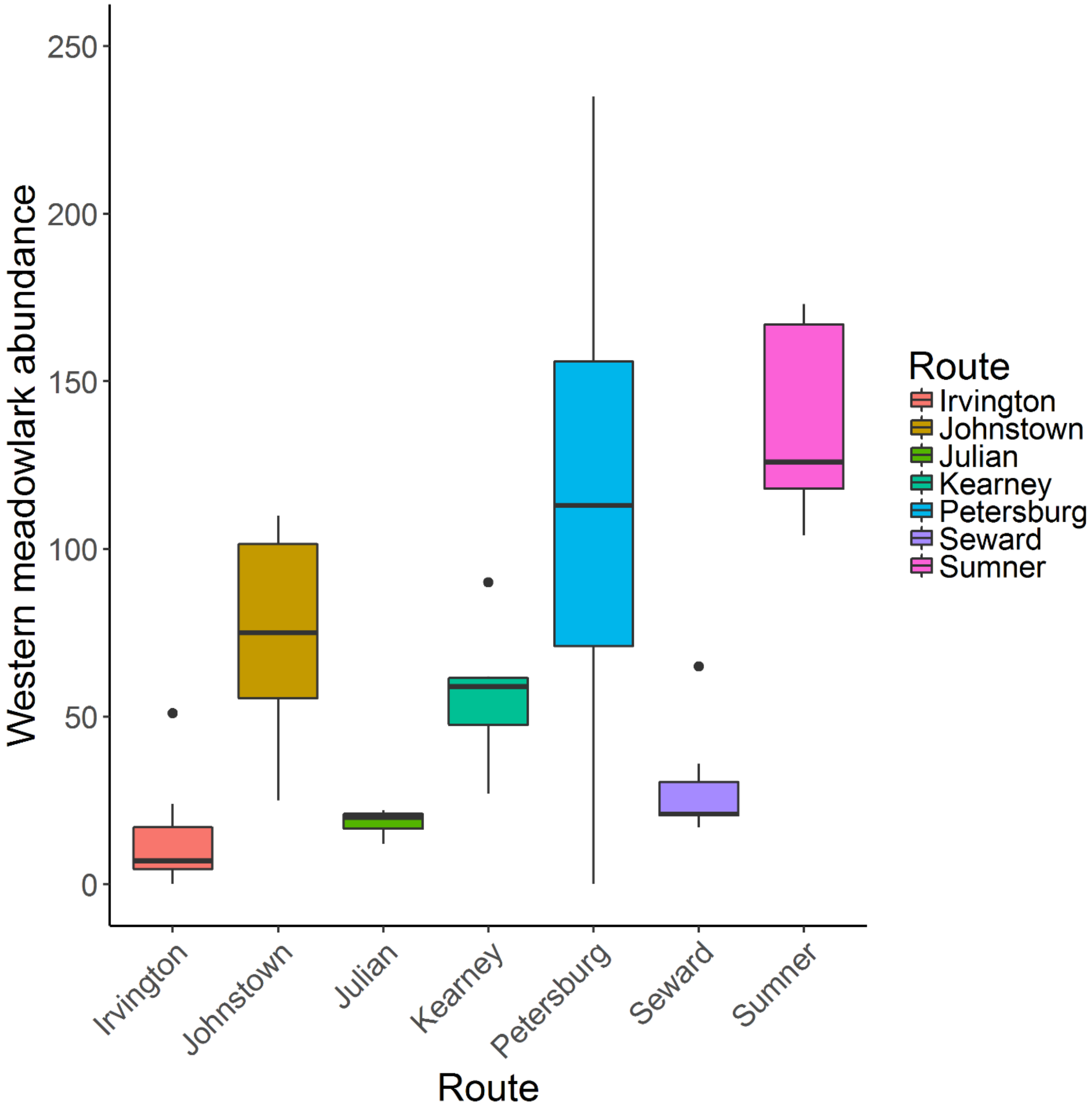

Figure 6: Distributions of western meadowlark (*Sturnella neglecta*) abundances along the Irvington (Washington County), Johnstown (Brown County), Julian (Otoe County), Kearney (Buffalo County), Petersburg (Boone County), Seward (Seward County), and Sumner (Dawson County) Breeding Bird Survey routes in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

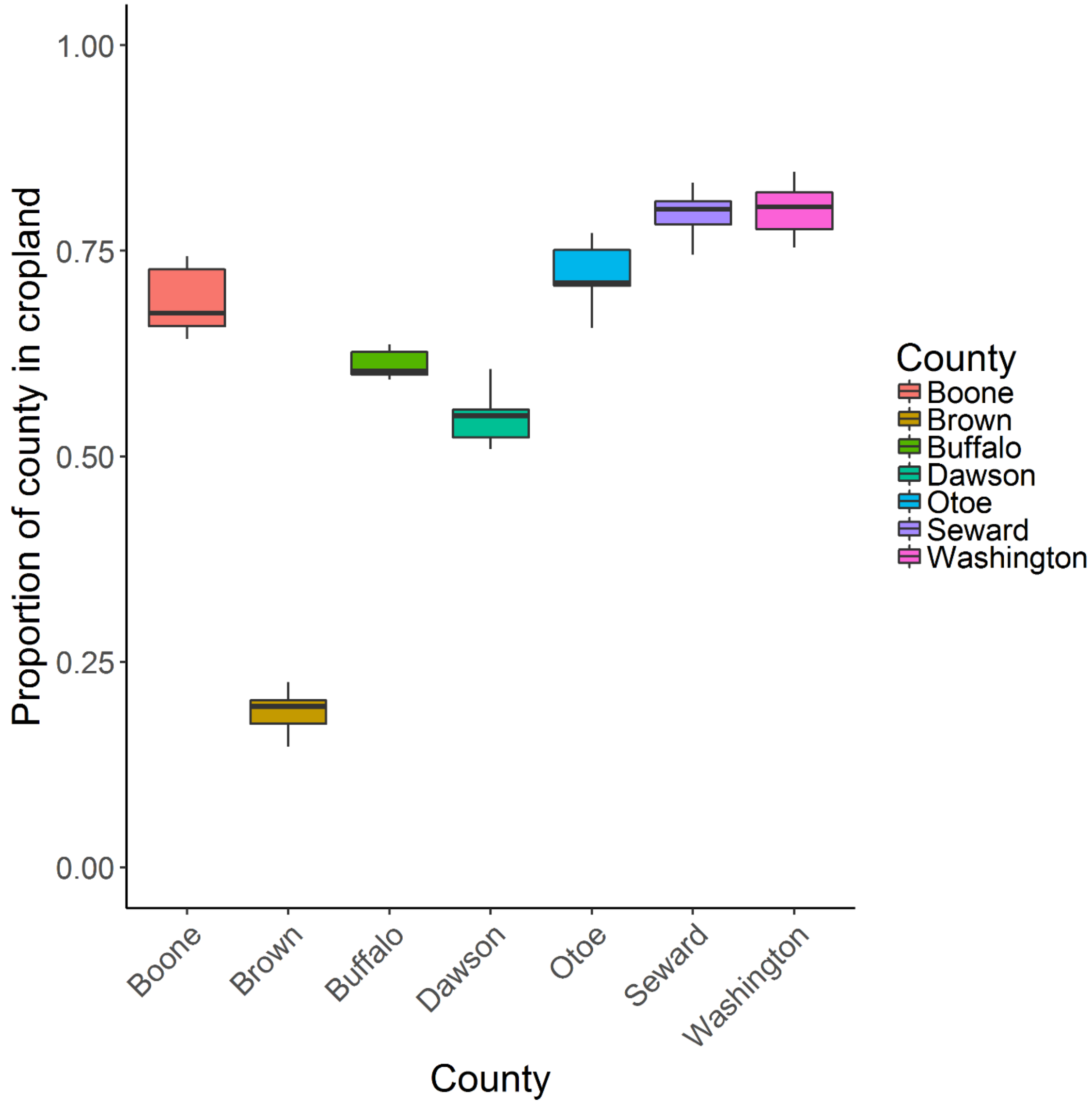

Figure 7: Distributions of proportions of area in cropland in Boone County, Brown County, Buffalo County, Dawson County, Otoe County, Seward County, and Washington County in Nebraska, U.S.A. in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

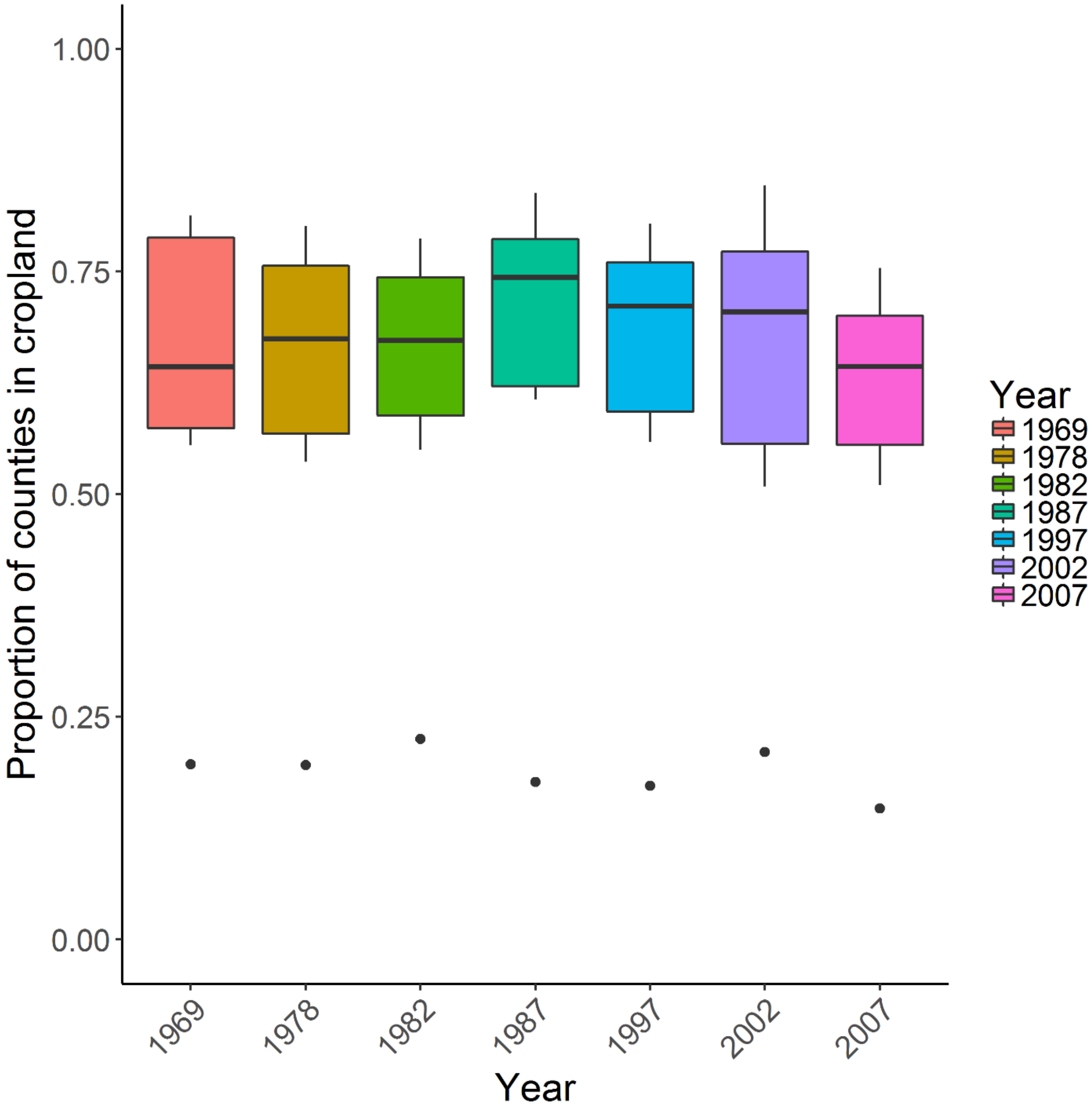

Figure 8: Distributions of proportions of area in cropland in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007 in Boone County, Brown County, Buffalo County, Dawson County, Otoe County, Seward County, and Washington County of Nebraska, U.S.A.

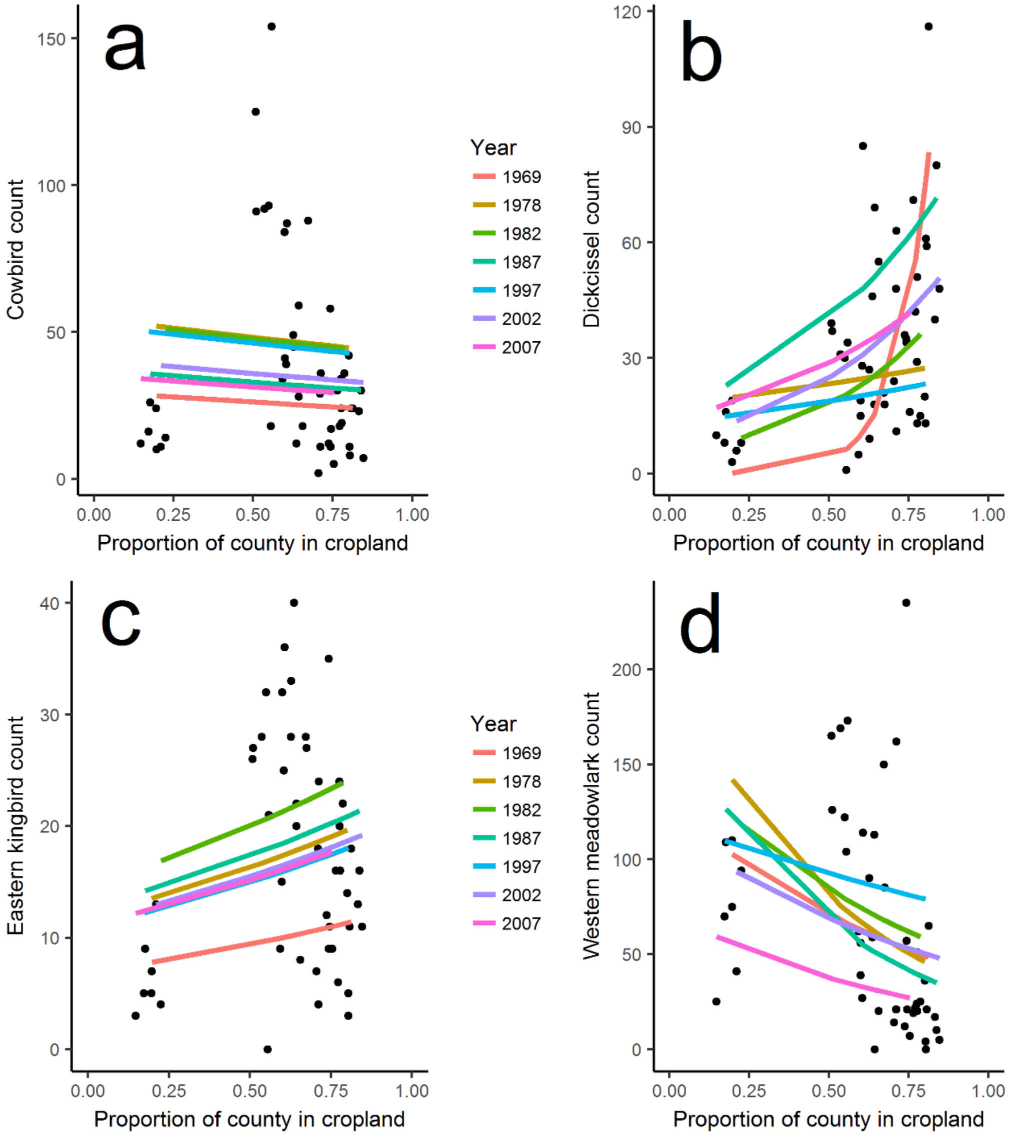

Figure 9: Generalized linear mixed model predictions of relationships between a) brown-headed cowbird (Molothrus ater), b) dickcissel (Spiza americana), c) eastern kingbird (Tyrannus tyrannus), and d) western meadowlark (Sturnella neglecta) abundances and the proportion of land area in cropland in seven Nebraska, U.S.A. counties in the years 1969, 1978, 1982, 1987, 1997, 2002, and 2007.

CHAPTER 4: DISTURBANCE REGIME ALTERATION, TREE SPECIES DISTRIBUTIONS, AND OAK CONSERVATION IN THE MISSOURI RIVER BLUFFS OF SOUTHEAST NEBRASKA, U.S.A.

ABSTRACT

Human disturbance regime alterations can indirectly drive landcover change in social–ecological system(s) (SES). Forested landscapes of eastern North America have experienced substantial changes in landcover over the past several centuries through human disturbance regime manipulation—perhaps most notably, fire suppression. The Missouri River bluffs of southeastern Nebraska, U.S.A. are one such landscape, where more than a century of fire suppression has transformed open-canopied oak (*Quercus* spp.) savannas and oak–hickory (*Carya* spp.) woodlands to closed-canopied forests dominated by more shade-tolerant tree species. To regain and maintain oak presence and dominance in these ecosystems, prescribed fire and manual understory and midstory tree thinning have been implemented, in order to increase light availability for oak seedlings and sprouts. In addition to light availability, the geographic distributions of mature tree species are factors of interest in oak conservation and restoration; however, information on landscape-scale tree species distributions is sparse. In this chapter, I model and map the geographic distributions of mature individuals of 14 tree species in Indian Cave State Park (ICSP) in southeastern Nebraska with an ensemble modeling approach. Results indicate that no modeling technique within the ensembles consistently outperformed any other; however, predictive performance was consistently better for certain species,

particularly American basswood (*Tilia americana*), red oak (*Quercus rubra*), chinkapin oak (*Quercus muehlenbergi*), black oak (*Quercus velutina*), and bur oak (*Quercus macrocarpa*), the predicted distributions of which largely correspond with prior descriptions in the scientific literature. When paired with predicted distributions of trees in smaller size classes, the results of this chapter could contribute useful information to ongoing oak restoration activities in ICSP. In a broader sense, results illustrate how social–ecological memory (SEM) can confer SESs with resilience amidst indirectly-driven landcover change and its drivers. Despite the trajectory of the SES toward a state dominated by shade-tolerant, non-oak woody species, the SEM of SESs-past that is retained in the geographic distributions of long-lived oaks preserves a window of opportunity for returning the forest to an open-canopied, oak-dominated state. Knowledge of such sources of SEM could provide much-needed avenues for responding to the challenges of landcover change in SESs.

INTRODUCTION

Forested landscapes of eastern North America have experienced substantial changes in landuse and landcover over the past several centuries, and these changes have a variety of direct and indirect social–ecological causes and consequences (Williams 1989; Whitney 1994; Foster 1998a, 1998b; Smith 2006). Gradual and rapid declines in oaks (*Quercus* spp.) and associated genera [e.g., hickories (*Carya* spp.), chestnuts (*Castanea* spp.), and beeches (*Fagus* spp.)] in forests of eastern North America have become subjects of economic and conservation concern (Lorimer 1989; Clark 1993; Frelich & Reich 2002; Smith 2006; Fei et al. 2011; Dey 2014; Cale et al. 2017). In the decades following the initiation of Native American dispossession and Euro-American resettlement, dense oak–hickory forest was so common that early ecologists considered it a climax stage in the successional development of regional ecosystems (Weaver & Clements 1938; Liming & Johnston 1944; Braun 1950; Whitney 1994). However, since approximately 1930, oak–hickory forests have steadily lost oaks and hickories, and gained individuals of more shade-tolerant, mesic tree species (Lorimer 1993; Soucy et al. 2002; Moser et al. 2006). In forest understories and midstories—often beneath oak-dominated overstories (i.e., canopies)—oak seedlings fail to germinate or advance beyond the seedling or sapling stages of growth (i.e., fail to recruit into the canopy) (Cottam 1949; Lorimer 1980, 1993; Abrams 1986; Dey 2014). Therefore, as mature oaks disappear from canopies, they are replaced by non-oaks, and landscapes transition away from oak dominance (McIntosh 1957; Crow 1988; Abrams 2005).

Interactions among oak regeneration, growth, and recruitment have been described as paradoxical, in that by achieving dominance in forest canopies and thereby increasing shade in forest understories, oaks discourage the recruitment and future dominance of their offspring (Curtis 1971; Crow 1988; Nowacki et al. 1990; McGee & Loftis 1993). In general, oak seedlings are shade-intolerant (Hodges & Gardiner 1993; Smith 1993; Guyette et al. 2002; Thomas & Packham 2007), and instead of investing heavily in early aboveground growth, develop extensive root systems, thick bark, and xeromorphic leaves (Abrams 1990; Dey 2002a; Van Lear & Brose 2002). These conservative growth characteristics allow oak seedlings to be outcompeted by faster-growing neighbors when light is limited (Bray 1958; Hodges & Gardiner 1993; Delcourt & Delcourt 2000); however, they also make them relatively drought-tolerant (Smith 1993) and fire resistant (Dey 2002b), which provides them with a competitive edge when moisture is limited and/or fire is frequent (Lorimer 1985).

Throughout much of the 20th century, human management interventions aimed at regaining and maintaining oak dominance [e.g., protection from disturbance, understory competitor suppression, logging, and supplemental oak planting (Carvell & Tyron 1961; Lorimer 1989)] were largely unsuccessful—or at least not consistently successful—in part because of knowledge gaps related to the historical drivers of North American oak dominance and decline (Johnson 1979; Brose 2014; Dey 2014). As noted by Lorimer (1985, 1989), the large-scale decline of oak–hickory forest must be associated with changes in similarly large-scale driver(s). Although a variety of factors are known to shape deciduous forest structure over time (Host et al. 1987; Bratton 1994; Abrams 2002;

Johnson et al. 2002), disturbance—especially fire—is important for oaks (Johnson 2002; Van Lear 2002). Although initially overlooked (Korstian 1927; Moore 1928; Liming & Johnston 1944; Johnson 1979), relationships between historical oak dominance and human fire regime manipulations were increasingly recognized in the closing decades of the 20th century (Dorney 1981; Abrams 1992; Van Lear & Watt 1993; Lorimer 1993; Sabo et al. 2002; Brose 2014). In other words, it was only in the context of social–ecological system(s) (SES) thinking—which emphasizes interconnections and interdependencies between people and their environments—that the historical dominance of oak trees in eastern North America began to be understood.

Native Americans and early Euro-American settlers frequently set fire to eastern North American forests (Lorimer 1985; Guyette & Dey 2002). Because oak seedlings exhibit lower fire mortality rates than their faster-growing competitors, frequent fire provides individual oaks with competitive advantages over their neighbors, which over time affects forest structure and species composition at larger spatial scales (Lorimer 1985; Brose et al. 2013). A similar phenomenon occurs in prairies, where frequent fire excludes shrubs and trees from grass-dominated uplands (Briggs et al. 2002; Ratajczak et al. 2014). Following centuries of human fire promotion in forests was a period of intense fire suppression (Pyne 1982; Nowacki & Carr 2013), which permitted shade-tolerant species to increase in forest understories at the expense of oaks, even while forest canopies remained dominated by long-lived oaks (Lorimer 1985; Van Lear & Watt 1993; Dey & Guyette 2000; Shang et al. 2007).

Although human fire regime manipulation provides a good general explanation for oak dominance and decline over the past several centuries, deeper evaluations of interactions among human actions, fire, and forest structure indicate that the effects of fire on long-term successional trajectories in forests likely depend on a variety of factors (e.g., mesic *versus* xeric site conditions, fuel characteristics, fire frequency and intensity, advance reproduction characteristics, light availability, and mammal browsing) (Brose et al. 2001; Johnson et al. 2002; Moser et al. 2006; Arthur et al. 2012). Among these, advance regeneration—the build-up (i.e., accumulation) of seedlings in forest understories—is especially important (Abrams 1992; Clatterbuck & Meadows 1993; Johnson et al. 2002; Dey & Hartman 2005; Shang et al. 2007; Fan et al. 2012; Dey 2014).

Advance regeneration of oaks in areas with frequent fire stems, quite literally, from their ability to continually resprout after experiencing aboveground fire mortality (Carvell 1979; Loftis 1993; Dey 2002a; Frelich & Reich 2002; Brose et al. 2013). These persistent populations of resprouting stumps and seedlings—grubs as they are known in grasslands and savannas—tend to have well-developed root systems from years of underground investment and growth (Hodges & Gardiner 1993; Johnson 1993; Loftis 1993; Bond & Midgely 2001; Johnson et al. 2002). When the forest understory experiences a pause or cessation in the constraining effects of fire, sprouts quickly advance to later growth stages (e.g., sapling, poletimber, and sawtimber), which substantially reduces their risk of experiencing aboveground mortality in future fire events (Van Lear & Watt 1993; Johnson et al. 2002; Brose et al. 2013). Therefore, oak advance regeneration and dominance is maintained by disturbance regimes characterized by frequent fire and infrequent fire-free periods, especially in areas where moisture is limited (Iverson et al. 2008).

Alternatively, under disturbance regimes characterized by infrequent fire, advance regeneration of shade-tolerant, mesic species [e.g., maples (*Acer* spp.) and hackberries (*Celtis occidentalis*)] gives them understory—and eventually overstory—advantages over oaks, especially in areas where light is limited (Lorimer 1980; Parker et al. 1985; Abrams 1986, 1998). In these instances, increases in light that follow overstory tree death or removal does not automatically tip the competition balance in favor of oaks, as the seedlings of shade-tolerant species will also rapidly advance to later life stages to fill canopy openings, and in doing so, continue to discourage oak regeneration (Lorimer 1980; Iverson et al. 2008). In addition, the accumulation of less flammable leaf litter from shade-tolerant tree species impedes the ability of fire to move through forest understories (Lorimer 1985; Washburn & Arthur 2003)—further promoting the dominance of shade-tolerant species.

Advance regeneration in forests is often influenced by initial floristic composition (Egler 1954). This means that the future state of a forest stand depends, at least in part, on past and present states (Hart 2015) and disturbance regimes (Johnson et al. 2002). For instance, a mature tree may produce both seeds and sprouts from its stump that have a chance of recruiting into the next generation of forest trees, depending in part on disturbances it and its neighbors do or do not experience. This emphasizes the role of history (i.e., ecological legacies; ecological memory) in influencing future forest states (Iverson 1988; Foster et al. 1998a, 1998b; Turner et al. 2003; Seidl et al. 2014).

The dense oak forests that covered much of eastern North America in the late 19th and early 20th centuries were the result of decades of advance oak regeneration amidst frequent fire and land clearing, followed by a sudden release from the constraints of fire (Nowacki & Carr 2013; Dey 2014). Years of frequent burning by Native Americans pushed SESs away from dense forested states and toward open grassland states (Nowacki & Abrams 2008). In addition to continuing—even intensifying—the burning practices of Native Americans, early Euro-American settlers cleared trees from savannas, woodlands, and forests for the provisioning of fuel (e.g., charcoal for the iron industry), lumber, and agricultural lands (Crow 1988; Williams 1989; Abrams 2002; Dey 2002a). However, oaks persisted through this period of frequent, intense disturbance via advance regeneration. Following initial land clearing, Euro-American settlers initiated a period of intense, widespread fire suppression, during which oak seedling and stump sprouts quickly advanced to later life stages, pushing SESs away from grassland states, through intermediate savanna and woodland states, and toward forested states (Bray 1955; Lorimer 1985, 1993; Abrams 1986; Van Lear & Watt 1993; Dey & Guyette 2000; Brose 2014). In other words, landuse change induced regime shifts (i.e., stable-state transitions) and landcover change in SESs of eastern North America (Schulte et al. 2007; Hanberry et al. 2012, 2014).

Presently, oak-focused conservation and restoration efforts recognize the importance of maintaining relatively open canopies for increased light availability, as well as promoting advance oak regeneration in forest understories via frequent fire (Abrams 2005; Arthur et al. 2012; Brose et al. 2013; Brose 2014; Dey 2014). In some instances, the manual thinning of shade-tolerant understory and midstory tree species is also used to increase light availability and oak recruitment into forest canopies (Iverson et al. 2002, 2008; Dey 2014). Monitoring and modeling of the long-term effects of management actions on forest structure and species composition are ongoing, with ultimate objectives of restoring and maintaining oak dominance (i.e., reversing or avoiding transitions to states dominated by shade-tolerant species) (Shang et al. 2007; Iverson et al. 2008; Arthur et al. 2012; Brose 2014; Dey 2014; Hart 2015). Therefore, a holistic perspective on oak conservation and restoration is necessarily long-term, and not only focuses on current tree species composition in forest understories, but also considers the species composing forest canopies.

Despite this knowledge of the history of oak dominance and decline, substantial uncertainty still exists regarding both the present and future states of eastern deciduous woodlands and forests, and this translates into difficult decisions for managers with limited resources (Johnson et al. 2002). However, uncertainties should not preclude the strategic implementation of management actions (Dey 2014). For example, in some locations, the full transition of forests to states dominated by shade-tolerant species—and the “mesophication” that accompanies that transition—may make restoration to an open-canopied oak-dominated state largely infeasible over the short term, even with intensive management, whereas other sites may be more easily restored or maintained in oak dominated states (Iverson et al. 2002, 2008; Abrams 2005; Nowacki & Abrams 2008). Given the influence of initial floristic conditions and legacy effects on future forest states (Johnson et al. 2002; Hart 2015), a useful first step in addressing the problem of oak decline may be to increase knowledge of current tree distributions. This could be accomplished through monitoring and modeling within adaptive management frameworks, where management actions are undertaken according to the best available knowledge, and then iteratively reassessed and adjusted according to newly acquired information (Allen et al. 2011). In this chapter, I develop ensemble models and maps of the geographic distributions of tree species in a southeast Nebraska, U.S.A. landscape at the western edge of eastern deciduous forest. In addition to filling knowledge gaps related to the present geographic extents of tree species of economic and conservation concern (Schneider et al. 2011), results may provide insights into how changes in landcover and SES states are indirectly driven by human activities over long periods of time. Finally, the use of multiple modeling techniques for multiple species allows for comparisons of modeling technique performance.

METHODS

Study area

Indian Cave State Park (ICSP) is an approximately 1,200 hectare (ha) landscape located along the bluffs of the Missouri River in extreme southeast Nebraska (Figure 1). Under the Nebraska Natural Legacy Plan (NNLP) (Schneider et al. 2011), ICSP is listed as a Natural Legacy demonstration site—an area for representing habitat conservation opportunities—within the larger Indian Cave Bluffs Biologically Unique Landscape (BUL). The position of ICSP in the Missouri River bluffs gives it a relatively rough topography, along with a microclimate that supports flora and fauna characteristic of more easterly North American regions.

In the late 19th and early 20th centuries, dominant landcover classes in the Indian Cave Bluffs BUL and neighboring landscapes included tallgrass prairie and oak savanna, with oak and American basswood (*Tilia americana*) woodlands and forests bordering the Missouri River (Bessey 1900; Pound & Clements 1900), although the advance of trees into tallgrass prairie uplands was also common at this time (Bessey 1899). Fires were observed in the Missouri River bluffs as late as 1868 (Snoddy et al. 2004), but since that time, human fire suppression and logging have reduced oak densities and permitted increases in densities of various shade-tolerant trees, with an overall increase in tree cover (Pool et al. 1918; Aikman 1929; Rolfsmeier & Steinauer 2010). Presently, woodland and forest dominate landcover in ICSP (Table 1), but still give way to tallgrass prairie and oak savanna on ridgetops (Rolfsmeier & Steinauer 2010; Schneider et al. 2011). Several oak species, along with a number of more shade-tolerant tree species, are important components of contemporary forests and woodlands.

Data collection

In June and July of 2014, tree community surveys were conducted at 360 locations within ICSP via stratified random sampling (Austin 1998), according to four aspect and three elevation classifications (i.e., 12 aspect–elevation combinations). Aspects were classified by the four cardinal directions: north (316–45°), east (46–135°), south (136–225°), and west (226–315°), and elevations were classified by the following natural breaks (i.e., groupings that combine similar values and maximize among-class differences) in the distribution of elevation within ICSP: low [263–301 meters (m)], middle (302–328 m), and high (329–380 m). Within each of the 12 aspect–elevation combinations, 30 survey points were randomly generated in ArcGIS (ESRI 2011), with the requirement that they be > 30 m from one another. The geographic coordinates of all survey points were uploaded to a Garmin eTrex handheld geographic positioning system (GPS) unit for the location of survey points during field surveys. At these same locations, values of a suite of topographic variables hypothesized to be important for understanding and predicting the geographic distributions of tree species and communities were extracted to each of the 360 survey points in a geographic information system (GIS).

Tree abundances

In tree community surveys, a releve (i.e., plot-based) approach (Thomas & Packam 2007) was used to document abundances of tree species/genera within a 10 m radius of each survey point. Trees identified only to the genus level were ashes (*Fraxinus* spp.), elms (*Ulmus* spp.), and mulberries (*Morus* spp.); all other trees were identified to the species level. Trees were classified as small [< 10 centimeters (cm) diameter at breast height (dbh)], medium (≥ 10 and < 30 cm dbh), or large (≥ 30 cm dbh)—size classes, based on Beightol and Bragg’s (1993) survey of bur oak (*Quercus macrocarpa*) forest in east-central Nebraska. In addition to size classifications, visual inspection of tree positions in relation to woodland and forest canopies were used to classify them as canopy-level or subcanopy-level.

Topographic variables

Thirty-m resolution digital elevation model(s) (DEM) for the Barada and Langdon Quadrangles (i.e., USGS Quadrangle IDs 40095B5 and 40096C5) encompassing ICSP were downloaded from the website of the Nebraska Department of Natural Resources (DNR) (http://dnr.nebraska.gov/elevation-data). The two DEMs were then mosaicked into a single DEM in ArcGIS and were cropped (i.e., clipped) to the boundaries of ICSP in the program R (R Core Team 2016). Although DEMs with higher resolutions (i.e., 10-m and 2-m) were available on the DNR website, the 30-m DEM was selected to ensure that each sampling unit (i.e., 10-m radius around survey points) could theoretically fit within one cell of the DEM and rasters used as predictor variables (Guisan & Thuiller 2005; Ferrier & Guisan 2006).

Topographic variables are commonly used to model tree species distributions, because they serve as proxies for soil moisture available (Collins & Carson 2004; Rathbun & Fei 2006; Iverson et al. 2008). Slope and aspect raster layers were derived from the mosaicked and cropped 30-m DEM, with slope and aspect measured in radians. The use of circular aspect measures (i.e., 1–360°) in statistical modeling can be problematic because of disparities imposed on similar directions by the circular mode of measurement. For example, 1° (0.023 radians) and 359° (6.27 radians) are both near north and one another, but they have disproportionately different values that frustrate linear regression. To address this issue, a raster layer of northness—which is bounded between -1 (south) and 1 (north)—was derived from the aspect raster with a cosine transformation. Rasters of cell latitude and longitude were also generated. Therefore, the final suite of predictors consisted of DEM (i.e., elevation), slope, northness (i.e., aspect), latitude, and longitude rasters (Figure 2), all of which were in 30-m resolution and were generated with the terrain or initialize functions in the raster Package (Hijmans 2016) for R. Although an array of factors (e.g., competition and disturbance) beyond soil moisture availability and its associated topographic variables have been hypothesized and observed to shape tree species distributions (Bazzaz 1996; Shipley 2010), data on such variables is sparse, especially at the temporal scale necessary to quantify effects on large—and presumably, old—trees.

Species distribution models

To model the distributions of presently dominant (i.e., canopy-level) trees within ICSP, I developed suites of statistical and machine learning models for large (i.e., ≥ 30 cm dbh) individuals of 16 tree species/genera (Table 2), validated models with 10-fold cross-validation, used the models to predict tree species occurrence likelihoods, converted occurrence likelihood predictions into presence/absence predictions, combined predictions in an ensemble approach, and assessed model-based uncertainty and predictive performance with numeric and map outputs.

The response variables in all models were species presence/absence values—derived from the original count data collected in 10-m radius circular plots and assigned to corresponding 30 m raster cells. Four modeling techniques were utilized to model the geographic distributions of the 16 tree species: generalized linear model(s) (GLM), a generalized additive model(s) (GAM), a boosted regression tree(s) (BRT), and a random forests (RF). Prior to model development, relationships among response and predictor variables were examined visually with pairplots (Zuur et al. 2007, 2009) and numerically with Pearson's correlation coefficient (PCC) (Pearson 1895) to avoid collinearity among predictors.

GLMs

GLMs are extensions of linear models that use link functions to quantify relationships between response and predictor variables when datasets and models fail to exhibit normal (i.e., Gaussian) error distributions, constant variance structures, and linear relationships (Guisan et al. 2002; Zuur et al. 2007, 2009). For example, response variables with Poisson (i.e., count data) and Bernoulli (i.e., binomial data) distributions may be modeled with GLMs, using the log and logit link functions, respectively. Because GLMs produce parameter estimates, standard errors, and significance values, they are generally useful for increasing understanding about the relationships between response and predictor variables (Guisan et al. 2002; Miller et al. 2004). GLMs are parametric models, in that they are founded on *a priori* assumptions about data distributions (Merow et al. 2014).

In the development of GLMs for tree species/genera in ICSP, a global model containing the additive effects—but no interactions—of the three topographic predictors was constructed and run with the glm function in the stats Package (R Core Team 2016) for R, with the logit link function (i.e., binary family) specified. Plots of global GLM residual values *versus* predictor variable values were used to check for major instances of heteroscedasticity (i.e., unequal variance) in model residuals.

In addition to ensuring that the assumptions of statistical models are met, it is important to consider the effects of spatial autocorrelation [i.e., spatial dependencies; Tobler (1970)] in spatial datasets (Dormann et al. 2007; Cliff & Ord 2009; Beale et al. 2010; Miller 2012; Merow et al. 2014). To determine if GLM residuals exhibited statistically significant levels of spatial autocorrelation (i.e., p-value < 0.05), the Moran's I (Moran 1950) autocorrelation coefficient was calculated with the ape Package (Gittleman & Kot 1990; Paradis et al. 2004) for R. Moran's I quantifies spatial dependence by comparing observed values and distances among observations with those that would be expected at random. In addition to the numerical outputs of Moran's I tests, correlograms—constructed with the spline.correlog function in the ncf Package (Bjornstad 2016) for R, which uses the Moran's I statistic (Moran 1950) to quantify spatial dependence—were constructed to visually assess how spatial autocorrelation in the global GLM residuals varied at different among-point distances.

In the context of this study, the existence of spatial autocorrelation means that the presence/absence of a tree species at one location is influenced by the presence/absence of that species at surrounding locations (Legendre 1993). Although understandable—even expected—in ecology (e.g., due to dispersal), spatial autocorrelation is statistically problematic, in that it violates the independence assumption of many statistical techniques and can distort model predictions by over- or under-emphasizing predictor effects (Diniz-Filho et al. 2003; McPherson & Jetz 2007). To reduce spatial autocorrelation in model residuals to acceptable levels, I first incorporated a spatial predictor (i.e., latitude or longitude) into the global GLM at hand. If spatial autocorrelation persisted following this incorporation, autologistic regression model(s) (ARM), which explicitly addresses spatial autocorrelation by incorporating a spatial neighborhood effects parameter (i.e., estimate of autocovariance at each point) (Ferrier et al. 2002; Lichstein et al. 2002; He et al. 2003; Miller et al. 2007; Crase et al. 2012), was applied to the data. ARMs were fit with the logistic.regression function in the spatialEco Package (Evans 2016) for R. Neither latitude nor longitude were used as predictors in ARMs. Although some have cautioned against the use of ARMs because of their potential to bias the parameter estimates of predictor variables (Dormann 2007; Kissling & Carl 2008), this may be most relevant when spatial autocorrelation is observed at broad scales in datasets (Miller et al. 2007). Because significant levels of spatial autocorrelation in the models of this chapter were consistently observed to only extend for distances of 0.50 to 1.00 km, ARMs were applied in instances where the incorporation of latitude or longitude did not sufficiently reduce spatial autocorrelation in the global GLM.

Once spatial autocorrelation in model residuals was sufficiently reduced, stepwise backwards selection (i.e., backwards selection) was used to sequentially eliminate predictor variables that did not produce a better model, with model performance assessed with Akaike’s Information Criterion (AIC) values. For GLMs, backward selection was carried out with the drop1 function in the stats package for R. The best-supported GLM for a tree species was determined to have been identified when the elimination of predictor variables no longer produced a model with a lower AIC score (Zuur et al. 2007, 2009). For ARMs, backward selection was carried out manually by comparing AIC values of different models, beginning with the global model and sequentially eliminating predictors.

The best-supported GLM for each tree species was subjected to 10-fold cross-validation with the CVbinary function in the DAAG package (Maindonald & Braun 2015) for R, in order to assess predictive performance with minimal bias. Ten-fold cross-validation evaluates quantifies predictive error in models by randomly subsetting data into training (i.e., 90% of data) and testing (i.e., 10% of data) sets, refitting the best-supported model with the training data, making predictions with the testing data, comparing predictions with known values, replacing observations, and repeating the process nine more times (Kohavi 1995, Fushiki 2011). Within the 10-fold cross validation process, the optimal.thresholds function in the PresenceAbsence package (Freeman & Moisen 2008) for R was used to compare all possible thresholds between 0.00 and 1.00 for transferring continuous occurrence likelihood predictions to binomial presence/absence predictions and identifying the threshold that was most successful in doing so. The success of different threshold values for converting continuous occurrence likelihoods to binomial presence/absence classes was quantified with the maximum Kappa statistic (Cohen 1960). Outputs, presence/absence classification thresholds, and 10-fold cross-validation results for the best-supported GLM of each tree species was saved as an R file (i.e., .RData file extensions) for later incorporation into the species' model ensemble. ARMs were not subjected to 10-fold cross-validation and were not incorporated into model ensembles; however, they were used to make predictions on the data that trained them to roughly assess predictive performance.

GAMs

GAMs are semi-parametric extensions of GLMs that assume no *a priori* data distribution and generally provide more detailed descriptions of response–predictor variable relationships than GLMs (Guisan et al. 2002; Zuur et al. 2007, 2009; Merow et al. 2014). This is accomplished by smoothing the effects of predictor variables on the response variable—in effect, stringing together multiple linear approximations along a gradient of predictor variable values—to better approximate non-linear relationships between that predictors and response. These smoothed relationships are based on the same link functions used to describe response–predictor relationships in GLMs. More smoothing splines (i.e., smoothers) correspond with more inflection points (i.e., smoothers minus one) along undulating non-linear relationships between predictor and response variables (Guisan et al. 2002; Zuur et al. 2007, 2009).

In the development of GAMs for tree species within ICSP, a global model containing the additive effects—but no interactions—of the three topographic predictors was fit with the gam function in the gam package (Hastie 2016) for R, with the logit link function (i.e., binary family) specified. Within the global model, the number of smoothers applied to each predictor was set at an arbitrarily determined high value of seven (i.e., six inflection points permitted), in order to allow for the approximation of complex non-linear relationships between the predictors and response. Plots of global GAM residual values *versus* predictor variable values were used to visually detect major instances of heteroscedasticity (i.e., unequal variance) in model residuals. Similarly, the Moran's I coefficient and correlograms were used to assess spatial autocorrelation levels in global GAM residuals. If significant spatial autocorrelation was detected, latitude or longitude—also with seven smoothers applied—was added to the global GAM. Because this sufficiently reduced spatial autocorrelation in all cases where it was evidenced, no additional steps for dealing with spatial autocorrelation were required. After spatial autocorrelation had been accounted for, backwards selection was used to sequentially eliminate smoothing terms and predictor variables that did not produce a GAM with a better fit (i.e., lower AIC value). Backwards selection was carried out with the step.gam function in the gam Package for R.

The best-supported GAM for each tree species was subjected to 10-fold cross-validation with the CVbinary function in the DAAG package for R. The optimal.thresholds function in the PresenceAbsence package for R was used to compare all possible thresholds between 0.00 and 1.00 for transferring continuous occurrence likelihood predictions to binomial presence/absence predictions and identifying the threshold that was most successful in doing so, according to the maximum Kappa statistic. Outputs, presence/absence classification thresholds, and 10-fold cross-validation results for the best-supported GAMs of each tree species were saved as R files and for later incorporation into model ensembles.

BRTs

BRTs are a machine learning modeling technique that combines two other modeling techniques, regression tree analysis and boosting, to produce optimal models for explaining variability in the dataset with a set of given predictors (De’ath 2007; Elith et al. 2008; Olden et al. 2008). Regression trees, and closely related classification trees, partition data into classes according to splitting rules derived from the data at hand (Iverson & Prasad 1998; De’ath & Fabricius 2000; Moisen & Frescino 2002). Through boosting, BRTs fit and combine the predictions of numerous—instead of individual—regression trees, which tends to improve predictive performance (De’ath 2007; Elith et al. 2008). BRTs are developed in discrete stages, with regression trees being used to explain unexplained variability in the residuals of the previously fit regression tree (Merow et al. 2014). This produces a final model (i.e., tree) composed of the additive effects of many regression trees, each of which explains variability in the data that the previous tree could not. Like GLMs and GAMs, BRTs use link functions for certain error distributions. Although generally better at explaining variation in datasets and making predictions than parametric (e.g., GLMs) or semi-parametric (i.e., GAMs) modeling techniques, BRTs, like other machine learning methods, are less interpretable—although not completely uninterpretable (Breiman 2001; De’ath 2007; Elith et al. 2008).

All boosted regression tree analyses were carried out using the gbm.step function in the dismo Package (Hastie et al. 2001; Hijmans et al. 2016) for R, with specifications based on the suggestions of De’ath (2007) and Elith et al. (2008) for managing tradeoffs among the learning rate, tree complexity, and the number of trees in the model, with the goal of minimizing predictive error. The learning rate determines the contribution of each regression tree to the overall tree, and the tree complexity specifies the level of interactions allowed among predictor variables (e.g., none, two-way, or three-way) within each regression tree (De'ath 2007; Elith et al. 2008). In addition, randomly drawing a given proportion of observations and using it to fit trees at each step of analysis (i.e., bagging) introduces a degree of stochasticity into the model that must be specified at the outset (Elith et al. 2008). In general, it is preferable to specify relatively small learning rates (e.g., 0.001) that result in the fitting of a relatively large numbers of trees (e.g., > 1,000) (De'ath 2007; Elith et al. 2008). In regard to tree complexity, it is often necessary to decrease the learning rate with higher levels of tree complexity, especially for small datasets (Elith et al. 2008). Based on these recommendations, a learning rate of 0.001, a tree complexity of 3, and a bagging proportion of 0.75 were initially set for the BRT of each tree species and then adjusted as necessary to produce BRTs composed of more than 1,000 individual regression trees.

BRT model residuals were inspected for significant levels of spatial autocorrelation with Moran's I statistics and correlograms. If significant spatial autocorrelation was detected, the BRT was refit with the addition of longitude and/or latitude as predictor variables. Because moderate correlation among predictor variables is not as great of a concern in BRTs as in statistical modeling techniques (Pittman et al. 2009), both latitude and longitude—which were negatively correlated (PCC = -0.79) among survey points—were used as predictors when the incorporation of one or the other did not satisfactorily reduce spatial autocorrelation.

Ten-fold validation of each BRT was conducted during its construction. BRT outputs for each species, which included the relative influences of predictor variables in the tree [i.e., indication of the number of times selected for splitting and effectiveness in splitting (Friedman & Meulman 2003; Elith et al. 2008)], presence/absence classification thresholds, and 10-fold cross-validation results, were saved as R files for subsequent incorporation into model ensembles. Saving the exact model run was particularly important for BRTs, as stochasticity introduced into the model by the drawing of a random subset of observations at each stage produces slightly different results with repeated model runs.

RFs

Like BRT, RF is a modeling technique based in machine learning and decision tree analysis (Breiman 2001). In a RF, numerous classification and regression trees—which individually partition data into subgroups of maximum homogeneity based on rules derived from the data at hand (Breimann et al. 1984)—are combined to increase predictive accuracy over that of individual classification trees (Cutler et al. 2007). Unlike BRT, which string multiple trees together, RF fits a group of individual trees (i.e., forest) and averages their predictions. Bootstrap sampling (i.e., random sampling and replacement) is used to fit each classification tree to a different random subset of the data, with the remaining observations being used to make and validate predictions (Merow et al. 2014). RFs are useful for modeling complex interactions among predictor variables and their outputs include predictor variable importance values (Cutler et al. 2007).

Although RF tend to be accurate predictors, they are not as useful as statistical techniques (e.g., GLMs and GAMs) for increasing understanding about relationships between predictor and response variables (Breiman 2001).

All RF analyses were carried out using the randomForest function in the randomForest Package (Liaw & Wiener 2002) for R. For each RF, 500 classification trees were fitted and combined. Because RF utilizes bootstrap sampling when fitting different trees, there is no need to conduct a 10-fold cross-validation of predictions, because a simple comparison of model predictions with observed values is roughly equivalent to 10-fold cross validation (Cutler et al. 2007). The optimal.thresholds function in the PresenceAbsence package for R was used to identify the best thresholds between 0.00 and 1.00 for transferring continuous occurrence likelihood predictions to binomial presence/absence predictions, according to the maximum Kappa statistic. The outputs, presence/absence classification thresholds, and accuracy results for RFs were saved as R files for subsequent incorporation into model ensembles.

Model ensembles

Averaged predictions from model ensembles (i.e., combinations) generally exhibit a lower mean error rate than any of the constituent models (Bates & Granger 1969; Araujo & New 2007). For this reason, ensemble approaches are promoted for increasing robustness and quantifying model-based uncertainty in predictions of species' geographic distributions (Elith et al. 2002; Hartley et al. 2006; Araujo & New 2007; Marmion et al. 2009; Thuiller et al. 2009). Indeed, tradeoffs in predictive ability and interpretability between statistical (e.g., GLMs) and machine learning (e.g., BRTs) modeling techniques make averaging their predictions in an ensemble model appealing. It is important to note the difference between ensemble approaches that select the best-supported model out of a group of competing models and those that explore the range in predictions across models, as I refer to the latter here. Methods of visually representing variability in model predictions include: mapping areas where a certain number of models predict a species to be; mapping the number of models that predict a species as present in an area; and mapping the averaged occurrence likelihood predictions in an area (Araujo & New 2007; Marmion et al. 2009). Even in ensemble predictions, it is important to remain aware of uncertainties that stem from a lack of understanding about component models and predictions (Elith et al. 2010).

For each tree species, continuous occurrence likelihood and binomial presence/absence predictions from a GLM, GAM, BRT, and RF—or any combination of these that were successfully fit—were combined within an ensemble approach, yielding the following map products: 1) mean occurrence likelihood; 2) standard deviation in occurrence likelihood; 3) number of models in the ensemble predicting presence; and 4) areas where all models in the ensemble predict presence.

RESULTS

Ten GLMs, three ALMs, 14 GAMs, 11 BRTs, and 16 RFs were successfully fit for large individuals of tree species/genera in ICSP. GLMs, GAMs, BRTs, and RFs were then combined in species/genera-specific ensembles (Table 2). Reasons for not fitting models were the failure to sufficiently reduce spatial autocorrelation in model residuals with latitudinal and/or longitudinal predictor variables—in which case ALMs were adopted—or failed model convergence. Although successfully fit, the RFs for American sycamore (*Platanus occidentalis*) and eastern cottonwood (*Populus deltoides*) were not incorporated into ensembles, as sparse data did not support the development of models for any of the remaining three techniques. In addition, the three ALMs for black oak (*Quercus velutina*), chinkapin oak (*Quercus muehlenbergi*), and shagbark hickory (*Carya ovata*) were not incorporated into ensembles because of the difficulties associated with deriving raster layers of autocovariance in model residuals within ICSP. However, 14 model ensembles were developed for 14 species, and out of these, eight ensembles included all four techniques (i.e., GLMs, GAMs, BRTs, and RFs), five ensembles included three techniques, and one ensemble included two techniques.

Statistically significant levels of spatial autocorrelation were evidenced in the residuals of four global GLMs (Table 3), five global GAMs (Table 4), and four initially fit BRTs (Table 5). With the exception of the global GAM for Kentucky coffeetree (*Gymnocladus dioicus*), the same species—American basswood, black oak, chinkapin oak, and shagbark hickory—displayed significant spatial autocorrelation in the three techniques. The incorporation of longitude only sufficiently reduced spatial autocorrelation in the GLM of American basswood; spatial autocorrelation was only effectively reduced for the other three species by transforming their GLMs to ARMs through the incorporation of an autoregressive model term (Table 2). The incorporation of longitude or latitude—with seven smoothers—effectively reduced spatial autocorrelation in the GAM residuals of all five species that evidenced elevated spatial autocorrelation (Table 3). The incorporation of latitude as a predictor in BRTs sufficiently reduced spatial autocorrelation for two of the four species that evidenced significant levels of it, and the incorporation of both latitude and longitude into BRTs reduced spatial autocorrelation for the remaining two species (Table 5).

In regard to the predictive ability of individual models in ten-fold cross-validation, performance ranged from poor [i.e., area under the curve (AUC) < 0.60] to good (i.e., AUC > 0.80), and varied among species and modeling techniques (Tables 6–9). Here, the AUC statistic represents the likelihood, that for any randomly-selected pair of observations of tree species presence and absence, the predictive model will assign a greater occurrence likelihood to the location where the species is truly present. Comparisons of model AUCs indicate that no modeling technique consistently outperformed other techniques; however, some general trends did emerge from comparisons of predictive performance across species.

The species with the consistently best-performing models (i.e., AUC ≥ 0.70) was American basswood (Tables 6–9). Black oak models also consistently performed well (i.e., AUCs ≥ 0.69), as did models for bur oak and red oak (*Quercus rubra*), with the exception of the RFs for bur oak and red oak, which exhibited poorer performance than the other three techniques for both species. Models for chinkapin oak and mulberry species consistently exhibited moderate levels of predictive ability (AUCs ranging from 0.61–0.69). Performance of bitternut hickory (*Carya cordiformis*) and shagbark hickory models tended to be poor, with the exception of the BRT for shagbark hickory (AUC =

0.67). Models for ash and elm species consistently exhibited the poorest predictive abilities of all species, with the majority of AUC scores indicating little-to-no improvement over random guesses in presence/absence predictions (i.e., AUC = 0.50). Models for other species exhibited more variability across techniques.

All four constituent models for American basswood indicate that northness and slope are related to its likelihood of occurrence in ICSP, with variable importance rankings within the BRT (Table 10) and RF (Table 11) showing northness to be the more influential of the two. As for the direction of these variable effects, the GLM (Table 12) and GAM (Table 13) for American basswood indicate that occurrence likelihood increases on steeper slopes and north-facing slopes. In addition to these effects, the GAM includes a negative elevation effect, which means that occurrence likelihood tends to be greater in lower-lying areas. In summary, north-facing slopes appear to be the predictor most closely associated with greater American basswood occurrence likelihood, and this likelihood may increase on lower and steeper slopes (Figure 3).

Like American basswood, the occurrence likelihood of red oak increases at lower elevations and on steeper slopes, although the rankings of these two factors between the BRT (Table 10) and RF (Table 11) outputs are reversed. In addition, the red oak GLM (Table 12) and GAM (Table 13) indicate an increasing likelihood of red oak occurrence on more north-facing slopes (Figure 4). All four chinkapin oak models indicate the importance of slope and northness for this species, with northness being most influential in BRT (Table 10) and RF (Table 11) outputs. The ARM (Table 14) and GAM (Table 13) show that the occurrence likelihood increases on steep and south-facing slopes (Figure 5).

For black oak and bur oak, the BRT (Table 10) and RF (Table 11) outputs of both species show northness and elevation to be the two most influential predictors, with northness being more important for black oak and elevation being more important for bur oak. The ARM (Table 14) and GAM (Table 13) for black oak and the GLM (Table 12) and GAM for bur oak all show occurrence likelihood of these species to decrease on more north-facing slopes and increase at greater elevations. Therefore, black oak and bur oak tend to be associated with greater elevations and more south-facing slopes (Figures 6–7), with slope direction being most important for black oak and elevation being most important for bur oak.

Predictions of tree species presence/absence largely correspond with occurrence likelihood predictions. Maps of areas where all ensemble models predict species presence represent portions of predicted species distributions where model-based uncertainty is lower, although not absent. Standard deviations in continuous occurrence likelihood predictions and degrees of overlap in binomial presence/absence predictions serve as indicators of model-based uncertainty at different locations in ICSP (Figures 3–16). As expected, levels of uncertainty in model predictions tend to be greater for models with poorer predictive ability, as indicated by AUC scores (Tables 6–9); however, maps of standard deviation and overlap in presence/absence predictions—or the lack thereof—provide more detailed indicators of how these overall levels of uncertainty are distributed in space.

DISCUSSION

In this chapter, I utilized four modeling techniques—two based in statistical inference (i.e., GLMs and GAMs) and two based in machine learning (i.e., BRTs and RFs)—to model the geographic distributions of large individuals of 16 tree species in ICSP of southeast Nebraska, along the bluffs of the Missouri River. In addition, ARMs were used to explicitly account for spatial autocorrelation (i.e., spatial dependencies) in the geographic distributions of three tree species that could not be sufficiently explained with predictors in the aforementioned modeling approaches. The best-supported or optimal GLM, GAM, BRT, and/or RF for each of the 14 tree species for which multiple models were fit were combined into 14 model ensembles (i.e., combinations) (Table 2), which are promoted for improving accuracies and addressing uncertainties in the development of species distribution models (Araujo & New 2007; Marmion et al. 2009; Thuiller et al. 2009). Map products derived from these model ensembles include: 1) mean species occurrence likelihoods; 2) standard deviations in averaged species occurrence likelihoods; 3) numbers of models in ensemble overlapping in predictions of species presence; and 4) areas where all models within ensemble predict species presence (Figures 3–18). In addition to relating topographic predictors to species distributions, these map products are useful for representing model-based uncertainty spatially and could be used to inform management actions and future studies in the landscape.

The predictive performance of models varied among species and modeling techniques. Although no technique appeared to consistently outperform other techniques, there were patterns in model predictive ability among tree species. Models for American basswood, black oak, bur oak, chinkapin oak, and red oak all performed well compared with other species (Tables 6–9). For these species, the outputs of different modeling techniques gave consistent indications of which variables were the most important predictors, as well as what the directions and strengths of their effects were (Tables 10–14). Correspondingly, levels of model-based uncertainty in predictions of these species distributions were low overall, although uncertainties did vary spatially within the landscape (Figures 3–7). Models for other species exhibited moderate and low levels of predictive ability, with the models for ash and elm species being consistently poor performers (Tables 6–9). As expected, model-based uncertainty for these species was greater (Figures 8 & 11). There are a number of potential explanations for differences in predictive ability among tree species models, including differential species responses to disturbance, differential treatment of species by people (e.g., selective logging), differential dispersal distances, differential seed dispersal mechanisms and distances, intraspecific and interspecific competition, and specialisms. Given that this chapter modeled distributions of large tree individuals, average tree species age could also account for among species differences in model predictive ability, as the distributions of older individuals may have been more tightly constrained by interactions between topographic variables and disturbance regimes (e.g., more intense fires at higher elevations). In other words, the distributions of long-lived oaks—which can reflect environments several centuries back—may be more closely associated with differences in topography than the distributions of younger oaks and elms that likely grew up in the 20th and 21st centuries.

Statistically significant levels of spatial autocorrelation were consistently evidenced in both the raw data and model residuals for American basswood, black oak, chinkapin oak, and shagbark hickory (Tables 3–5). Spatial dependencies in the presence/absence of these species extended for a maximum distance of ~1.00 km. The consistency of the distance in these spatial dependencies across several species and modeling techniques may be indicative of an ecological effect that introduces spatial dependencies in the landscape at this scale. One possibility—especially given that three out of the four species are mast producing—is dispersal by squirrels (*Sciurus* spp.), jays (*Cyanocitta* spp.), and woodpeckers (*Melanerpes* spp.). Indeed, the distance of spatial dependency in the presence/absence of these tree species corresponds with observed average bird and mammal acorn dispersal distances (Darley-Hill & Johnson 1981; Johnson & Adkisson 1985; Steele & Smallwood 2002). Given the presumably old age of large individuals of these species, it is more appropriate to note the possibility of birds and mammal populations of past decades and centuries introducing spatial autocorrelation into the dataset. Regardless, these spatial dependencies were reduced to acceptable levels by the introduction of spatial predictors (i.e., longitude and/or latitude) or the adoption of ARMs, which explicitly account for spatial dependencies in datasets with autocovariance terms (Miller et al. 2007; Miller 2012).

The results of this study support the results of a number of existing studies pertaining to oak ecology in general, and the distributions of tree species of the Missouri River bluffs in particular. Although this chapter represents—to the best of my knowledge—the first likelihood-based evaluation of mature tree distributions in the

Missouri River bluffs of southeast Nebraska, it is certainly not the first study that has considered the question of tree species and community distributions. In fact, steep environmental gradients between the Missouri River banks and the peaks of the bluffs have made the landscape an ideal for addressing questions related to the differentiation of species and communities for more than 100 years. For example, Pound and Clements (1900), Pool et al. (1918), Aikman (1929), Weaver (1960, 1965), Rolfsmeier and Steinauer (2010), and Schneider et al. (2011) all described the distributions of tree species and communities in southeast Nebraska. Although their descriptions have notable differences, they generally recognize that American basswood and red oak as dominant trees on lower slopes, just upslope from the floodplain. They also generally recognize bur oak to be the dominant species on the uppermost slopes and ridgetops, extending into tallgrass prairie as oak savanna. Between these two extremes are mixtures of chinkapin oak, black oak, and hickories. The results of this chapter largely support the general conclusions of previous studies undertaken in the Missouri River bluffs, which perhaps is not surprising, given the longevity of the trees surveyed. In fact, the trees surveyed in this study could easily have been present at the time of Lewis and Clark (Moulton 2003) and the German Prince Maximilian (Witte & Gallagher 2010, 2012) in the early 19th century.

Overlaying the maps where all ensemble models predict presence for the four oak species displays a general gradient in species dominance, with red oaks occupying lower slopes, chinkapin oaks dominating on steep, south-facing intermediate and upper slopes, and black oak and bur oak being present on upper slopes and ridgetops (Figure 19). Interestingly, the overlap that occurs between species in this map primarily involves the co-occurrence of black oak and bur oak on the upper slopes, with bur oak extending further out onto ridgetops. This echoes Aikman (1929), who describes the black oak–hickory community as a transition zone between the mesophytic red oak–American basswood community and the xerophytic bur oak community. Although soil moisture availability was not directly modeled in this chapter, each of the topographic variables is likely to be correlated with it, as observed by Iverson et al. (2002, 2008) and numerous others.

In addition to the role of soil moisture in shaping tree species distributions, the disturbance history in a given area is known to be an important determinant of tree species distributions (Iverson 1988; Foster et al. 1998a, 1998b; Turner et al. 2003; Seidl et al. 2014). Indeed, fire suppression from the late 19th century onward is hypothesized to have eroded oak dominance in landscapes throughout eastern North America (Dorney 1981; Abrams 1992; Van Lear & Watt 1993; Lorimer 1993; Sabo et al. 2002; Brose 2014). Prior to its establishment as a state park in the early 1960s, ICSP was privately owned and experienced logging, conversion to agriculture, and other disturbances following the initiation of Euro-American resettlement in the mid-to-late 19th century (Williams 1989). Since that time, fires have also greatly decreased in frequency through human fire suppression efforts. These disturbance regime manipulations have certainly affected tree species distributions, and continue to do so.

Management actions aimed at restoring and maintaining oak dominated woodlands and forests have recently been initiated in ICSP. These include prescribed fire and manual understory and midstory tree thinning (Schneider et al. 2011). The results of this chapter could help refine the spatial application and prioritization of fire and thinning to portions of ICSP in which the occurrence of oak likelihood is greatest. Although this chapter does not address acorn production specifically, its conservative estimates of widespread oak distributions indicate that the window for regaining and maintaining oak dominance in ICSP has not yet passed like it has in some landscapes of eastern North America (Abrams 2005). This assertion is further supported by the results of Hart (2015), who in exploring correlates of oak seedling abundance at the same 360 points surveyed in this chapter, found oak seedlings to be present at the majority of surveyed locations.

In a broader sense, the results of this chapter illustrate the role of long-lived organisms like oaks in carrying social–ecological memory (SEM) forward through time in SESs (Barthel et al. 2010; Andersson & Barthel 2016). Even after more than a century of fire suppression and its transformative effects on midstory and understory forest structure and species composition, the persistence of acorn-producing oaks in the forest canopy preserves a window of opportunity for returning the forest to an open-canopied, oak-dominated state. In the language of resilience theory and SESs thinking (Boyd et al. 2015), these memory carriers can be said to confer resilience on the oak-dominated system. However, a return to a disturbance regime that promotes the advance regeneration of oaks in the understory-level is necessary to prevent the further erosion of the resilience of the oak-dominated state and a more permanent shift to a shade-dominated state (Abrams 2005).

Empirical observation of management effects in ICSP indicates potential for future oak regeneration. For example, visual comparisons of fish-eye photographs from areas were burning and thinning have been conducted and areas where burning and thinning have not been conducted shows increased light availability in burned and thinned areas (Figure 20). If advance regeneration of oaks is increasing in the forest understory, then management actions are achieving important initial objectives. Eventually, a pause in burning will be necessary to allow oak seedlings and saplings to advance to life stages where they are better able to escape aboveground mortality during fire events.

The time scale of successful oak regeneration is mismatched with the time scales of research projects, management grants, and even careers of biologists. To regain oak dominance on a large-scale, similarly large scale human responses are needed—a fact noted by Lorimer (1985, 1989). A number of additional analyses could be conducted with the information in this dataset to gain insights into the successional trajectory of ICSP forests and to aid future management. Community-level analysis, such as ordination, could provide insights concerning relationships among species and predictor variables overlooked in the single-species models of this chapter. In addition, similar ensemble modeling analyses to those presented in this chapter—but for tree species in different size classes (i.e., small and medium) or canopy classifications (i.e., canopy or subcanopy)—could provide useful information. In particular, relationships between management variables (e.g., times burned) and the presence/absence and abundance of midstory and understory tree species could be evaluated in a similar ensemble modeling framework. Ultimately, predictions of tree community distributions (Ferrier & Guisan 2006; Baselga & Araujo 2009) could supplement the species distribution models presented in this chapter, in order to better understand successional trajectories of regional forests and how they might be effectively managed amid landcover and related global change processes.

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TABLES AND FIGURES

Table 1: Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent in Indian Cave State Park of southeast Nebraska, U.S.A., based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011).

Landcover class	Hectares	Percentage
Trees	1,055.61	87.67
Developed	103.23	8.57
Grass	35.64	2.96
Water	9.63	0.80
Total	1,204.11	100.00

Table 2: Constituent models of model ensembles for large [≥ 30 cm diameter at breast height (dbh)] individuals of 14 ICSP tree species. Modeling techniques included in ensembles were generalized linear model(s) (GLM), generalized additive model(s) (GAM), boosted regression trees (BRT), and random forests (RF).

Species	**GLM**	**GAM**	**BRT**	**RF**
American basswood	X	X	X	X
Ash species	X	X	X	X
Bitternut hickory		X		X
Black oak		X	X	X
Black walnut	X	X	X	X
Bur oak	X	X	X	X
Chinkapin oak		X	X	X
Elm species	X	X		X
Hackberry	X	X	X	X
Honeylocust	X	X	X	X
Kentucky coffeetree	X	X		X
Mulberry species	X	X	X	X
Red oak	X	X	X	X
Shagbark hickory		X	X	X

Table 3: Expected, observed and standard deviation in Moran's I values, which indicate levels of spatial autocorrelation in the global generalized linear model (GLM) and autologistic regression model (ARM) residuals for large [≥ 30 centimeters diameter-at-breast-height (dbh)] individuals of 14 tree species in Indian Cave State Park. P-values < 0.05 indicate significant levels of spatial autocorrelation in global GLM residuals and are bolded accordingly. Data on which residuals were evaluated included raw species presence/absence data (RAW), residuals of a GLM with topographic predictors (GLM T), residuals of a GLM with topographic and longitude predictors (GLM TX), and residuals of an ARM with topographic predictors (ARM T).

Species	Data	Observed	Expected	Std Dev	p-value
American basswood	RAW	0.027837	-0.00279	0.005563	**0.000000**
	GLM T	0.024688	-0.00279	0.005562	**0.000001**
	GLM TX	0.00742	-0.00279	0.005562	0.066510
Ash species	RAW	0.005151	-0.00279	0.005562	0.153573
	GLM T	0.003381	-0.00279	0.005561	0.26752
Bitternut hickory	RAW	0.006996	-0.00279	0.005527	0.076773
	GLM T	0.007375	-0.00279	0.005527	0.06602
Black oak	RAW	0.030299	-0.00279	0.005569	**0.000000**
	GLM T	0.02851	-0.00279	0.005567	**0.000000**
	GLM TX	0.028289	-0.00279	0.005567	**0.000000**
	ARM T	0.00232	-0.00279	0.005565	0.358864
Black walnut	RAW	0.006946	-0.00279	0.005557	0.079923
	GLM T	0.002706	-0.00279	0.005557	0.323044
Bur oak	RAW	0.005883	-0.00279	0.005566	0.119369
	GLM T	0.005494	-0.00279	0.005564	0.13676
Chinkapin oak	RAW	0.01758	-0.00279	0.005571	**0.000256**
	GLM T	0.012287	-0.00279	0.005569	**0.006798**
	GLM TX	0.010923	-0.00279	0.005569	**0.013833**
	ARM T	-0.00345	-0.00279	0.005567	0.904673
Elm species	RAW	0.000551	-0.00279	0.005554	0.548032
	GLM T	-0.00118	-0.00279	0.005554	0.771937
Hackberry	RAW	0.002159	-0.00279	0.005544	0.372473
	GLM T	-0.00056	-0.00279	0.005544	0.688357
Honeylocust	RAW	0.002013	-0.00279	0.005419	0.375935
	GLM T	-0.0012	-0.00279	0.005422	0.769789

Table 3: Continued.

Species	**Data**	**Observed**	**Expected**	**Std Dev**	**p-value**
Kentucky coffeetree	RAW	0.000975	-0.00279	0.005337	0.481112
	GLM T	0.002007	-0.00279	0.005358	0.37104
Mulberry species	RAW	0.008866	-0.00279	0.005526	**0.034983**
	GLM T	0.004315	-0.00279	0.005526	0.198829
Red oak	RAW	-0.00313	-0.00279	0.005571	0.950595
	GLM T	-0.0065	-0.00279	0.005569	0.50524
Shagbark hickory	RAW	0.026562	-0.00279	0.005553	**0.000000**
	GLM T	0.026047	-0.00279	0.005553	**0.000000**
	GLM TX	0.026227	-0.00279	0.005553	**0.000000**
	ARM T	-0.00533	-0.00279	0.005551	0.646820

Table 4: Expected, observed and standard deviation in Moran's I values, which indicate levels of spatial autocorrelation in the global generalized additive model (GAM) residuals for large (≥ 30 centimeters diameter-at-breast-height) individuals of 14 tree species in Indian Cave State Park. P-values < 0.05 indicate significant levels of spatial autocorrelation in global GAM residuals and are bolded accordingly. Data on which residuals were evaluated included raw species presence/absence data (RAW), residuals of a GAM with topographic predictors (GAM T), residuals of a GAM with topographic and longitude predictors (GAM TX), and residuals of a GAM with topographic and latitude predictors (GAM TY).

Species	**Data**	**Observed**	**Expected**	**Std Dev**	**p-value**
American basswood	RAW	0.027837	-0.00279	0.005563	**0.000000**
	GAM T	0.017969	-0.00279	0.005562	**0.000190**
	GAM TX	0.002893	-0.00279	0.00556	0.307181
Ash species	RAW	0.005151	-0.00279	0.005562	0.153573
	GAM T	-0.00085	-0.00279	0.00556	0.727159
Bitternut hickory	RAW	0.006996	-0.00279	0.005527	0.076773
	GAM T	0.006097	-0.00279	0.005528	0.108083
Black oak	RAW	0.030299	-0.00279	0.005569	**0.000000**
	GAM T	0.014079	-0.00279	0.005566	**0.002449**
	GAM TX	0.002172	-0.00279	0.005565	0.372978
Black walnut	RAW	0.006946	-0.00279	0.005557	0.079923
	GAM T	-0.00053	-0.00279	0.005555	0.68535
Bur oak	RAW	0.005883	-0.00279	0.005566	0.119369
	GAM T	0.003698	-0.00279	0.005564	0.243884
Chinkapin oak	RAW	0.01758	-0.00279	0.005571	**0.000256**
	GAM T	0.010336	-0.00279	0.005568	**0.018439**
	GAM TX	0.005957	-0.00279	0.005568	0.116348
Elm species	RAW	0.000551	-0.00279	0.005554	0.548032
	GAM T	-0.00507	-0.00279	0.005553	0.680152
Hackberry	RAW	0.002159	-0.00279	0.005544	0.372473
	GAM T	-0.00232	-0.00279	0.005544	0.932796
Honeylocust	RAW	0.002013	-0.00279	0.005419	0.375935
	GAM T	-0.00561	-0.00279	0.005452	0.604393

Table 4: Continued.

Species	**Data**	**Observed**	**Expected**	**Std Dev**	**p-value**
Kentucky coffeetree	RAW	0.000975	-0.00279	0.005337	0.481112
	GAM T	0.007834	-0.00279	0.005407	**0.049508**
	GAM TX	-0.00858	-0.00279	0.005384	0.281716
Mulberry species	RAW	0.008866	-0.00279	0.005526	**0.034983**
	GAM T	0.003758	-0.00279	0.005528	0.236524
Red oak	RAW	-0.00313	-0.00279	0.005571	0.950595
	GAM T	-0.009	-0.00279	0.005568	0.264594
Shagbark hickory	RAW	0.026562	-0.00279	0.005553	**0.000000**
	GAM T	0.015754	-0.00279	0.005553	**0.000842**
	GAM TY	0.007811	-0.00279	0.005552	0.056319

Table 5: Expected, observed and standard deviation in Moran's I values, which indicate levels of spatial autocorrelation in the boosted regression tree (BRT) residuals for large (≥ 30 centimeters diameter-at-breast-height) individuals of 11 tree species in Indian Cave State Park. P-values < 0.05 indicate significant levels of spatial autocorrelation in global BRT residuals and are bolded accordingly. Data on which residuals were evaluated included raw species presence/absence data (RAW), residuals of a BRT with topographic predictors (BRT T), residuals of a BRT with topographic and longitude predictors (BRT TX), residuals of a BRT with topographic and latitude predictors (BRT TY), and residuals of a BRT with topographic, longitude, and latitude predictors (BRT TXY).

Species	**Data**	**Observed**	**Expected**	**Std Dev**	**p-value**
American basswood	RAW	0.027837	-0.00279	0.005563	**0.000000**
	BRT T	0.021978	-0.00279	0.005563	**0.000009**
	BRT TX	0.010379	-0.00279	0.005562	**0.017946**
	BRT TY	0.006019	-0.00279	0.005562	0.113434
Ash species	RAW	0.005151	-0.00279	0.005562	0.153573
	BRT T	0.003742	-0.00279	0.005561	0.240487
Black oak	RAW	0.030299	-0.00279	0.005569	**0.000000**
	BRT T	0.020022	-0.00279	0.005567	**0.000042**
	BRT TX	0.008269	-0.00279	0.005566	**0.047009**
	BRT TY	0.013423	-0.00279	0.005566	**0.003593**
	BRT TXY	0.00532	-0.00279	0.005566	0.145324
Black walnut	RAW	0.006946	-0.00279	0.005557	0.079923
	BRT T	0.00316	-0.00279	0.005557	0.28467
Bur oak	RAW	0.005883	-0.00279	0.005566	0.119369
	BRT T	0.002322	-0.00279	0.005564	0.358709
Chinkapin oak	RAW	0.01758	-0.00279	0.005571	**0.000256**
	BRT T	0.011213	-0.00279	0.005569	**0.011949**
	BRT TX	0.00994	-0.00279	0.005569	**0.022316**
	BRT TY	0.006579	-0.00279	0.005569	0.092667
Hackberry	RAW	0.002159	-0.00279	0.005544	0.372473
	BRT T	0.001259	-0.00279	0.005544	0.465708
Honeylocust	RAW	0.002013	-0.00279	0.005419	0.375935
	BRT T	-0.00633	-0.00279	0.00542	0.512581
Mulberry species	RAW	0.008866	-0.00279	0.005526	**0.034983**
	BRT T	0.004177	-0.00279	0.005525	0.20765

Table 5: Continued.

Species	**Data**	**Observed**	**Expected**	**Std Dev**	**p-value**
Red oak	RAW	-0.00313	-0.00279	0.005571	0.950595
	BRT T	-0.00803	-0.00279	0.005569	0.345916
Shagbark hickory	RAW	0.026562	-0.00279	0.005553	**0.000000**
	BRT T	0.019734	-0.00279	0.005551	**0.000050**
	BRT TX	0.015629	-0.00279	0.005552	**0.000910**
	BRT TY	0.014343	-0.00279	0.005551	**0.002030**
	BRT TXY	0.008028	-0.00279	0.005551	0.051407

Table 6: Area under the curve (AUC) statistics for the best supported generalized linear model(s) (GLM) for 10 tree species and autologistic regression model(s) (ARM) for three tree species within Indian Cave State Park. AUC statistics for GLMs were obtained through 10-fold cross-validation, whereas AUC statistics for ARMs were obtained through comparison of model predictions with the same observed values that were used to train it. Models are ranked from best-to-worst predictive ability.

Species	**Model**	**Threshold**	**AUC**
Black oak	ARM	0.36	0.7472795
Kentucky coffeetree	GLM	0.03	0.7257098
Chinkapin oak	ARM	0.37	0.7088828
American basswood	GLM	0.21	0.7046091
Bur oak	GLM	0.29	0.6956154
Shagbark hickory	ARM	0.30	0.6843258
Red oak	GLM	0.41	0.6789467
Mulberry species	GLM	0.20	0.6566406
Black walnut	GLM	0.26	0.5975673
Hackberry	GLM	0.16	0.5805961
Honeylocust	GLM	0.05	0.5626817
Ash species	GLM	0.24	0.5160642
Elm species	GLM	0.24	0.5012591

Table 7: Area under the curve (AUC) statistics for the best supported generalized additive model(s) (GAM) for 14 tree species within Indian Cave State Park. AUC statistics were obtained through 10-fold cross-validation.

Species	**Model**	**Threshold**	**AUC**
Kentucky coffeetree	GAM	0.265	0.7452462
American basswood	GAM	0.32	0.7098354
Bur oak	GAM	0.31	0.6901154
Black oak	GAM	0.47	0.6886306
Chinkapin oak	GAM	0.38	0.6769019
Red oak	GAM	0.38	0.6704607
Mulberry species	GAM	0.14	0.6527344
Bitternut hickory	GAM	0.14	0.6145348
Black walnut	GAM	0.25	0.6063626
Hackberry	GAM	0.18	0.5905216
Honeylocust	GAM	0.11	0.5659520
Ash species	GAM	0.25	0.5418824
Shagbark hickory	GAM	0.28	0.5248332
Elm species	GAM	0.26	0.5022160

Table 8: Area under the curve (AUC) statistics for the optimal boosted regression tree (BRT) model for 11 tree species within Indian Cave State Park. AUC statistics were obtained through 10-fold cross-validation.

Species	**Model**	**Threshold**	**AUC**
Honeylocust	BRT	0.1469931	0.7658300
Black oak	BRT	0.4062001	0.7310000
American basswood	BRT	0.3536448	0.7226400
Bur oak	BRT	0.3295207	0.6950000
Mulberry species	BRT	0.195171	0.6945300
Chinkapin oak	BRT	0.3790124	0.6841400
Red oak	BRT	0.3963445	0.6795900
Shagbark hickory	BRT	0.2578163	0.6660900
Black walnut	BRT	0.2449991	0.6361700
Hackberry	BRT	0.177642	0.6179300
Ash species	BRT	0.2456863	0.5884800

Table 9: Area under the curve (AUC) statistics for the best supported random forests (RF) for 16 tree species within Indian Cave State Park.

Species	**Model**	**Threshold**	**AUC**
American sycamore	RF	0.20	0.8380414
Honeylocust	RF	0.14	0.7363735
Eastern cottonwood	RF	0.14	0.7261792
American basswood	RF	0.35	0.7120988
Black oak	RF	0.39	0.6994771
Mulberry species	RF	0.17	0.6339063
Kentucky coffeetree	RF	0.14	0.6221672
Chinkapin oak	RF	0.40	0.6149535
Bur oak	RF	0.42	0.6134038
Red oak	RF	0.41	0.6014615
Shagbark hickory	RF	0.26	0.5841781
Hackberry	RF	0.20	0.5748137
Elm species	RF	0.61	0.5729754
Black walnut	RF	0.545	0.5650292
Bitternut hickory	RF	0.19	0.5211408
Ash species	RF	0.58	0.5182888

Table 10: Relative influences of predictor variables within boosted regression tree (BRT) models for predicting the occurrence likelihoods of 11 tree species in Indian Cave State Park of southeast Nebraska, U.S.A. Relative influence indicates the number of times the variable was selected for splitting in the BRT and its effectiveness in doing so (Friedman & Meulman 2003; Elith et al. 2008).

Species	**Parameter**	**Relative influence**
American basswood	Northness	37.23609
	Latitude	29.63518
	Elevation	18.5816
	Slope	14.54713
Ash species	Elevation	56.06119
	Northness	25.23022
	Slope	18.70859
Black oak	Northness	33.35484
	Elevation	20.87859
	Coords.X	20.56029
	Slope	13.31842
	Latitude	11.88786
Black walnut	Slope	50.13965
	Elevation	28.01953
	Northness	21.84082
Bur oak	Elevation	69.88692
	Northness	19.12811
	Slope	10.98497
Chinkapin oak	Northness	38.43763
	Slope	31.73341
	Elevation	15.30427
	Latitude	14.52469
Hackberry	Elevation	58.80369
	Slope	24.809
	Northness	16.3873
Honeylocust	Slope	38.90676
	Northness	33.02824
	Elevation	28.065
Mulberry	Slope	35.59999
	Northness	33.43294
	Elevation	30.96707

Table 10: Continued.

Species	**Parameter**	**Relative influence**
Red oak	Elevation	41.79145
	Slope	30.36066
	Northness	27.84789
Shagbark hickory	Slope	29.66375
	Latitude	26.94346
	Coords.X	18.23744
	Northness	15.41643
	Elevation	9.738926

Table 11: Predictor variable importance values within random forests models for predicting the occurrence likelihoods of 16 tree species in Indian Cave State Park of southeast Nebraska, U.S.A., where importance is defined as the mean decrease in accuracy that accompanies the removal of the parameter across all classification trees composing the random forest.

Species	**Parameter**	**Importance**
American basswood	Northness	49.65977
	Slope	42.03008
	Elevation	41.94012
American sycamore	Northness	4.206151
	Elevation	3.845131
	Slope	3.384552
Ash species	Elevation	44.19355
	Northness	43.0081
	Slope	41.54558
Bitternut hickory	Slope	25.21269
	Northness	24.79223
	Elevation	22.55202
Black oak	Northness	59.02791
	Elevation	48.96642
	Slope	47.8922
Black walnut	Slope	41.49517
	Elevation	39.06216
	Northness	37.72246
Bur oak	Elevation	53.90307
	Northness	45.30438
	Slope	44.13293
Chinkapin oak	Northness	60.26374
	Slope	54.65091
	Elevation	49.75891
Eastern cottonwood	Slope	6.282688
	Elevation	6.12944
	Northness	4.663847
Elm species	Slope	36.86034
	Northness	36.82432
	Elevation	36.13776
Hackberry	Elevation	32.13834
	Slope	30.78781
	Northness	29.88081

Table 11: Continued.

Species	Parameter	Importance
Honeylocust	Slope	10.55417
	Northness	10.0199
	Elevation	9.531228
Kentucky coffeetree	Northness	7.527534
	Slope	7.283593
	Elevation	6.369203
Mulberry species	Northness	23.28118
	Elevation	23.02473
	Slope	22.85934
Red oak	Slope	55.70611
	Elevation	55.09204
	Northness	53.44743
Shagbark hickory	Slope	37.96602
	Northness	36.37695
	Elevation	34.05103

Table 12: Predictor variable coefficient estimates, standard errors, and 95% confidence interval estimates for the best-supported generalized linear models for predicting presence/absence of 10 tree species in Indian Cave State Park of southeast Nebraska, U.S.A.

				95% CI	
Species	**Parameter**	**Estimate**	**Std error**	**Lower**	**Upper**
American basswood	Intercept	259.5975	77.59639	110.4717	415.4437
	Longitude	-0.00033	9.80E-05	-0.00053	-0.00014
	Slope	1.617772	0.644874	0.380728	2.916357
	Northness	0.945916	0.214123	0.536372	1.378294
Ash species	Intercept	-1.19802	0.126397	-1.45203	-0.95575
	Northness	0.330884	0.190167	-0.03844	0.708909
Black walnut	Intercept	1.924991	1.677445	-1.35917	5.236887
	Elevation	-0.00238	0.001626	-0.00562	0.000777
	Slope	-1.49543	0.620008	-2.73012	-0.29334
Bur oak	Intercept	-10.6336	1.827475	-14.3424	-7.15919
	Elevation	0.00923	0.001721	0.005947	0.012714
	Northness	-0.31866	0.185726	-0.68556	0.044078
Elm species	Intercept	-0.89961	0.360378	-1.62252	-0.2053
	Slope	-1.03073	0.634298	-2.28579	0.207157
Hackberry	Intercept	2.497896	1.936441	-1.28434	6.330046
	Elevation	-0.0041	0.001896	-0.00788	-0.00042
Honeylocust	Intercept	2.224005	3.365195	-4.37205	8.924863
	Elevation	-0.00518	0.003332	-0.01193	0.001236
Kentucky coffeetree	Intercept	6.155281	4.016122	-1.38497	14.60163
	Elevation	-0.00849	0.004244	-0.01761	-0.00077
	Slope	-2.10915	1.427198	-5.00532	0.622475
Mulberry species	Intercept	3.007725	2.102072	-1.08415	7.196962
	Elevation	-0.00375	0.002088	-0.00796	0.00026
	Slope	-2.42462	0.81251	-4.05521	-0.85944
Red oak	Intercept	3.128388	1.568454	0.068228	6.231867
	Elevation	-0.00486	0.001543	-0.00794	-0.00188
	Slope	2.215544	0.575006	1.113306	3.373687
	Northness	0.399114	0.179066	0.050325	0.753703

Table 13: Predictor variable coefficient estimates, standard errors, number of smoothers for the best-supported generalized additive models for predicting presence/absence of 14 tree species in Indian Cave State Park of southeast Nebraska, U.S.A.

Species	**Parameter**	**Smoothers**	**Estimate**
American basswood	Intercept	1	223.0673
	Longitude	2	-0.00028
	Elevation	2	-0.00252
	Slope	2	1.28231
	Northness	4	0.848488
Ash species	Intercept	1	-3.33572
	Elevation	4	0.001421
	Slope	1	1.235076
Bitternut hickory	Intercept	1	-1.2046
	Elevation	7	-0.00078
Black oak	Intercept	1	56.43557
	Longitude	7	-8.72E-05
	Elevation	1	0.01128
	Slope	2	0.462271
	Northness	4	-0.88054
Black walnut	Intercept	1	2.797211
	Elevation	7	-0.00309
	Slope	6	-1.68236
	Northness	2	0.318944
Bur oak	Intercept	1	-10.5628
	Elevation	5	0.009169
	Northness	1	-0.31534
Chinkapin oak	Intercept	1	34.99539
	Longitude	3	0.0000416
	Elevation	2	-0.00368
	Slope	4	2.163436
	Northness	4	-0.88184
Elm species	Intercept	1	-0.7908
	Elevation	7	0.0000638
	Slope	1	-1.32917
Hackberry	Intercept	1	2.524156
	Elevation	4	-0.0036
	Slope	2	-0.89319
	Northness	2	0.143994

Table 13: Continued.

Species	**Parameter**	**Smoothers**	**Estimate**
Honeylocust	Intercept	1	4.37441
	Elevation	6	-0.00569
	Slope	7	-1.76894
	Northness	3	0.312672
Kentucky coffeetree	Intercept	1	240.0478
	Longitude	7	-0.00028
	Elevation	1	-0.02104
	Slope	1	-3.95863
	Northness	7	-0.2115
Mulberry species	Intercept	1	2.578168
	Elevation	3	-0.00363
	Slope	7	-1.25782
	Northness	3	0.021452
Red oak	Intercept	1	3.502262
	Elevation	4	-0.00489
	Slope	1	1.64622
	Northness	1	0.534496
Shagbark hickory	Intercept	1	548.4048
	Latitude	7	-0.00012
	Elevation	7	0.0000644
	Slope	7	1.395211

Table 14: Predictor variable coefficients, standard errors, and 95% confidence interval estimates for the best-supported autologistic regression models for predicting presence/absence of three tree species in Indian Cave State Park of southeast Nebraska, U.S.A.

Species	**Parameter**	**Estimate**	**Std error**	**Wald**	**Prob**
Black oak	Intercept	-8.53809	1.816216	-4.70103	0.000003
	Elevation	0.006849	0.001692	4.046976	0.000052
	Northness	-0.81722	0.191531	-4.26679	0.000020
	Autocov	33.16276	7.953455	4.169604	0.000031
Chinkapin oak	Intercept	-2.3024	0.391846	-5.87579	0.000000
	Slope	2.088644	0.587256	3.556618	0.000376
	Northness	-0.73927	0.184207	-4.01324	0.000060
	Autocovar	25.19152	6.751608	3.731189	0.000191
Shagbark hickory	Intercept	-2.86919	0.486665	-5.89561	0.000000
	Slope	1.425534	0.730481	1.9515	0.050998
	Northness	-0.38231	0.221053	-1.72949	0.083721
	Autocovar	47.56177	10.02122	4.746104	0.000002

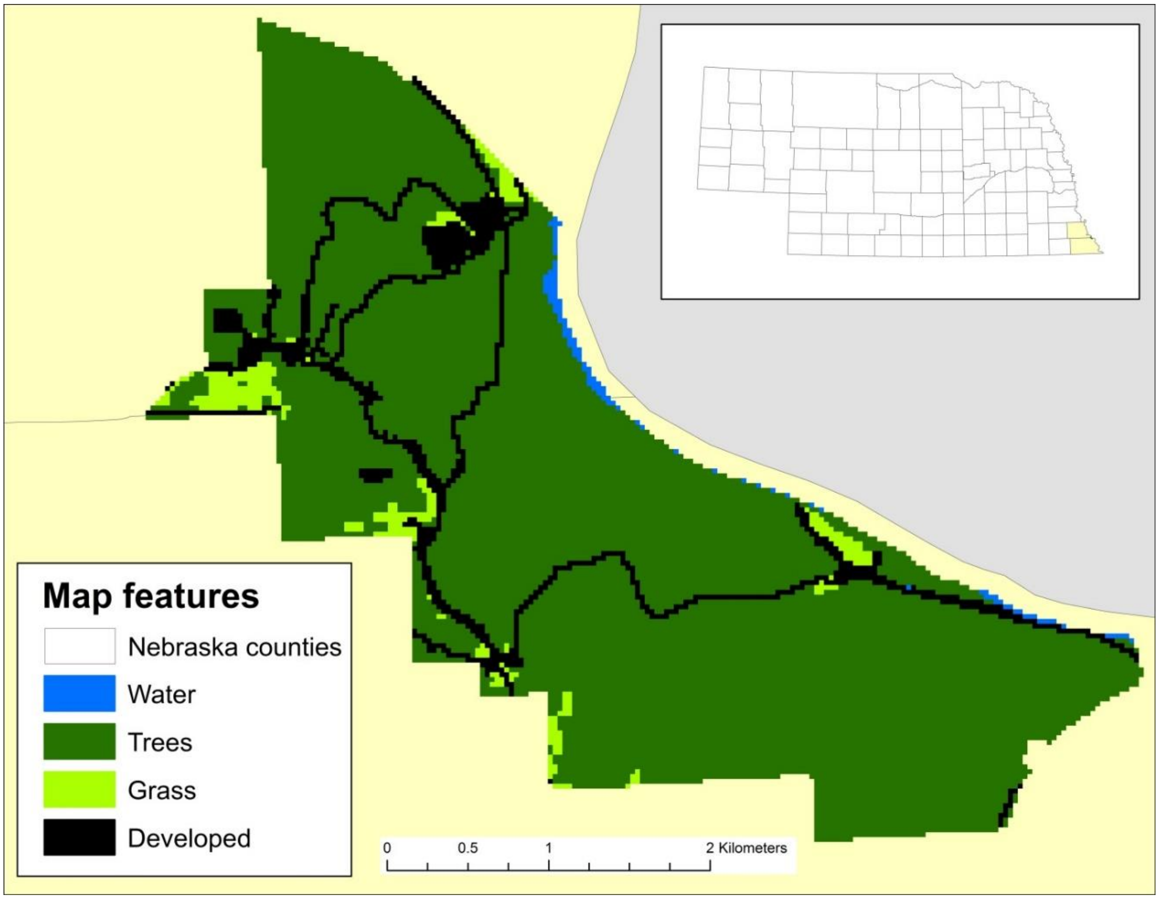
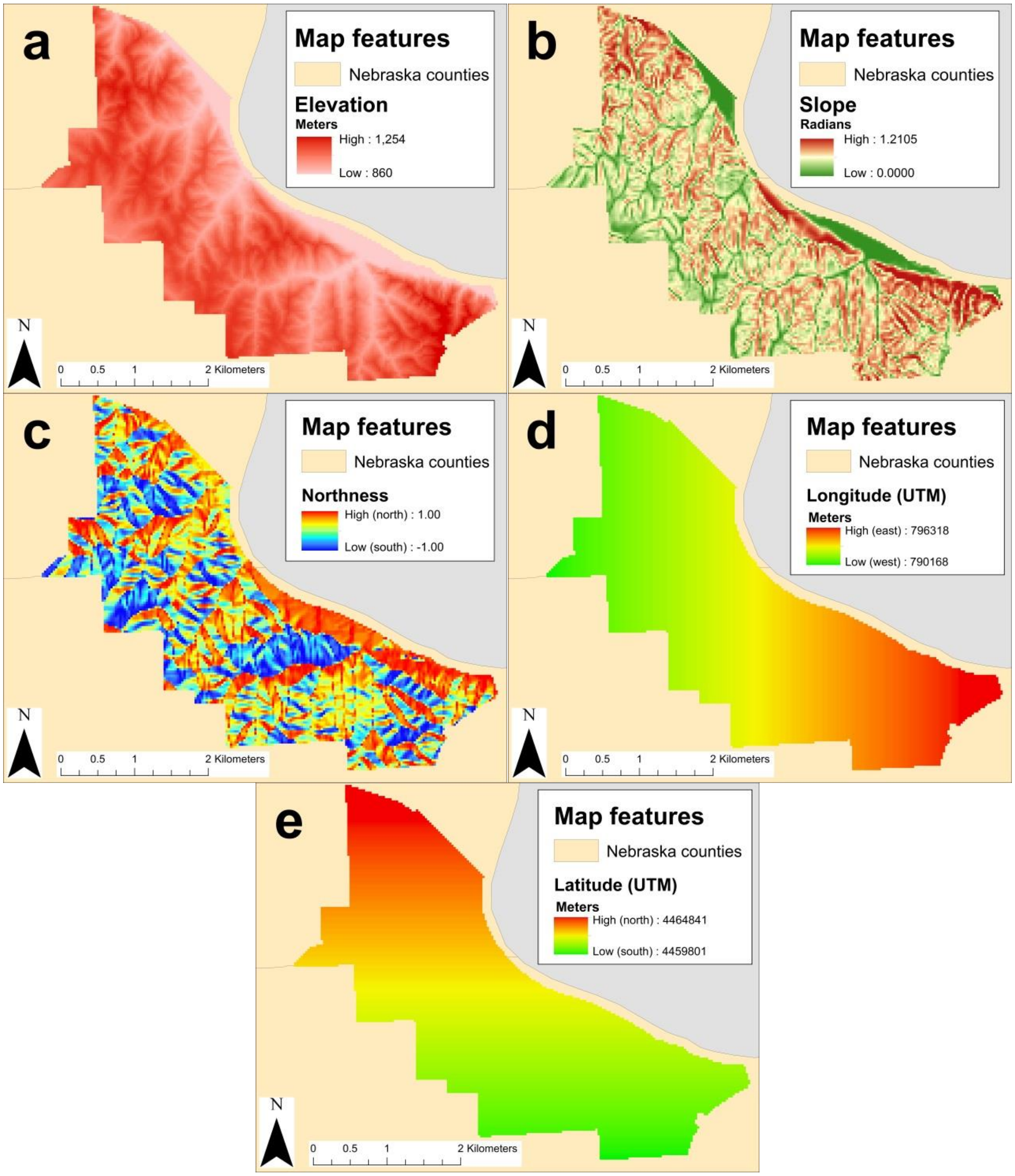

Map features
Nebraska counties
Water
Trees
Grass
Developed
0
0.5
1
2 Kilometers

Figure 1: Reclassified landcover of Indian Cave State Park in southeast Nebraska, U.S.A., from the 2010 landcover layer of the Rainwater Basin Joint Venture (Bishop et al. 2011).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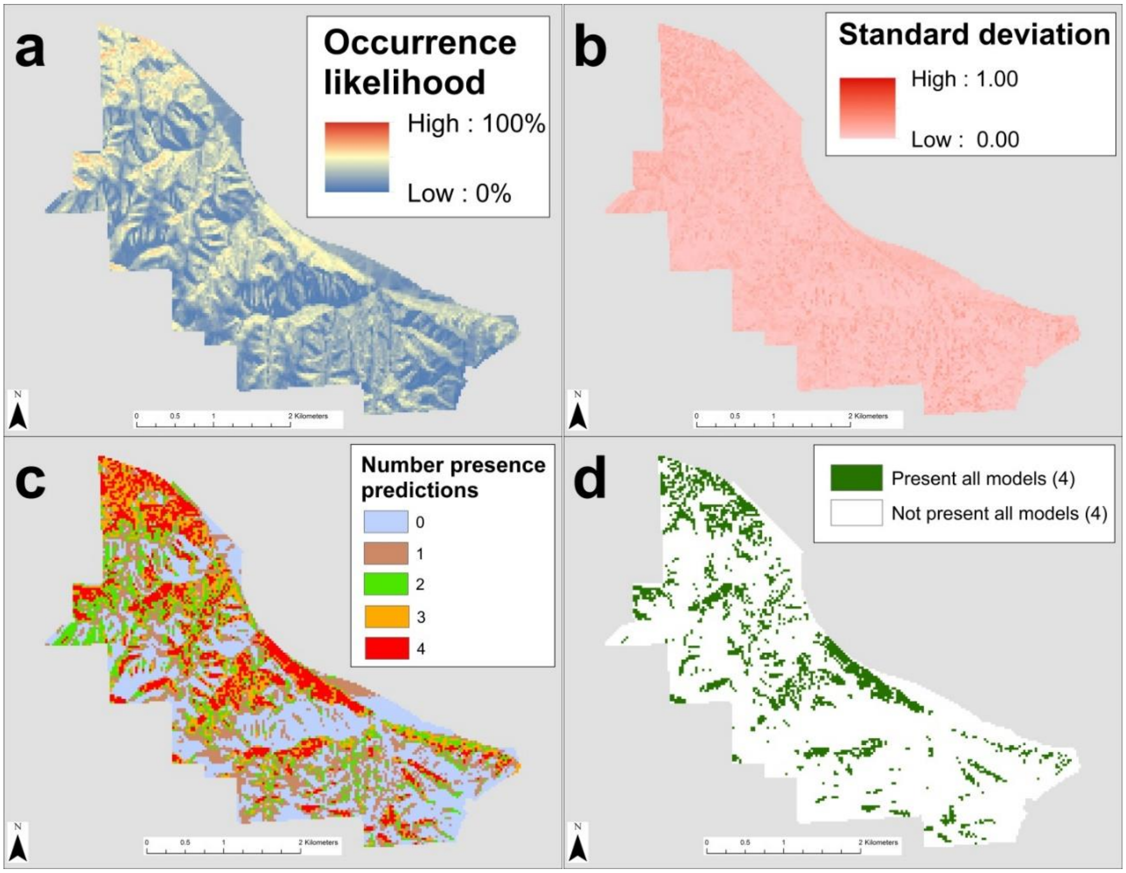
Nebraska counties
Elevation
Meters
High : 1,254
Low : 860
b
Map features
Nebraska counties
Slope
Radians
High : 1.2105
Low : 0.0000
c
Map features
Nebraska counties
Northness
High (north) : 1.00
Low (south) : -1.00
d
Map features
Nebraska counties
Longitude (UTM)
Meters
High (east) : 796318
Low (west) : 790168
e
Map features
Nebraska counties
Latitude (UTM)
Meters
High (north) : 4464841
Low (south) : 4459801
N
0 0.5 1 2 Kilometers

Figure 2: Predictor variables with which predictions of tree species occurrence likelihood and presence/absence were made with generalized linear models, generalized additive models, boosted regression tree models, and random forest models consisted of: a) elevation, b) slope, c) northness, d) longitude, and e) latitude.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Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0
0.5
1
2 Kilometers

Figure 3: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for American basswood (*Tilia americana*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

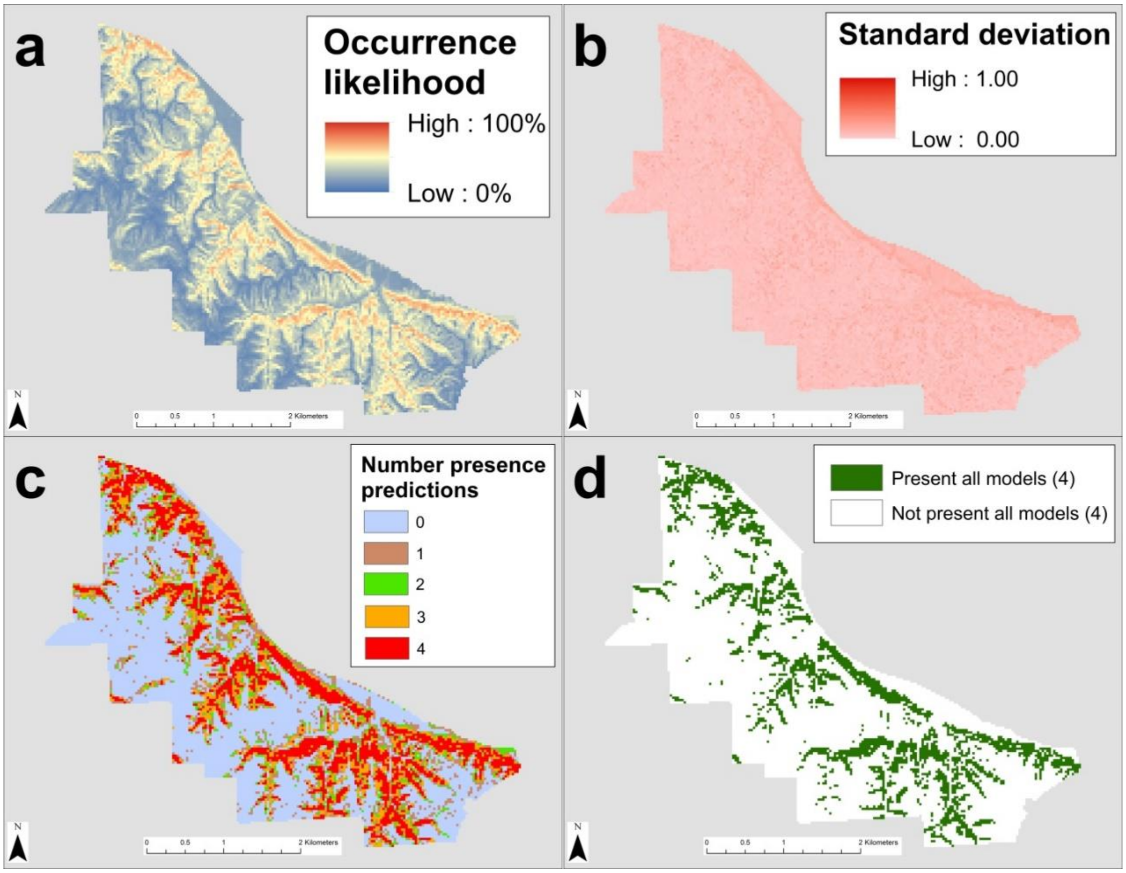
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0
0.5
1
2 Kilometers

Figure 4: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for red oak (*Quercus rubra*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

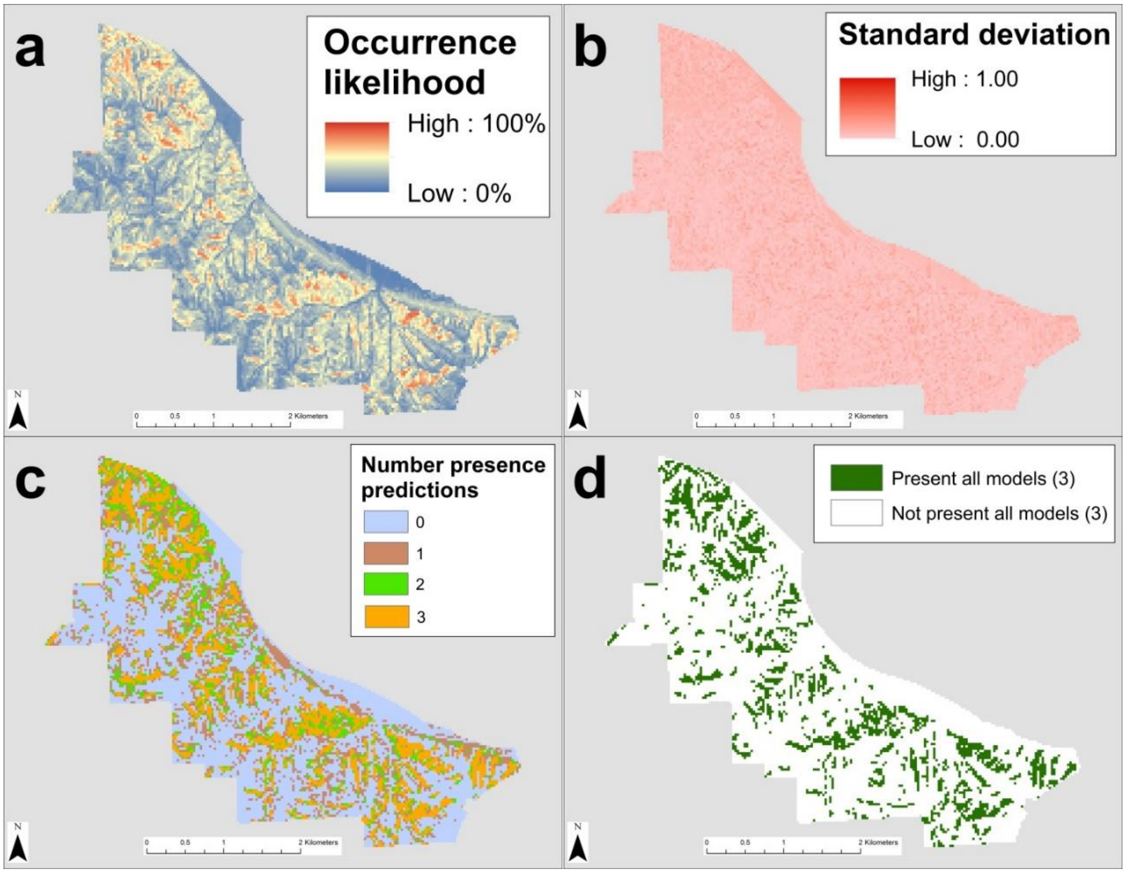
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
d
Present all models (3)
Not present all models (3)
N
0 0.5 1 2 Kilometers

Figure 5: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for chinkapin oak (*Quercus muehlenbergii*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

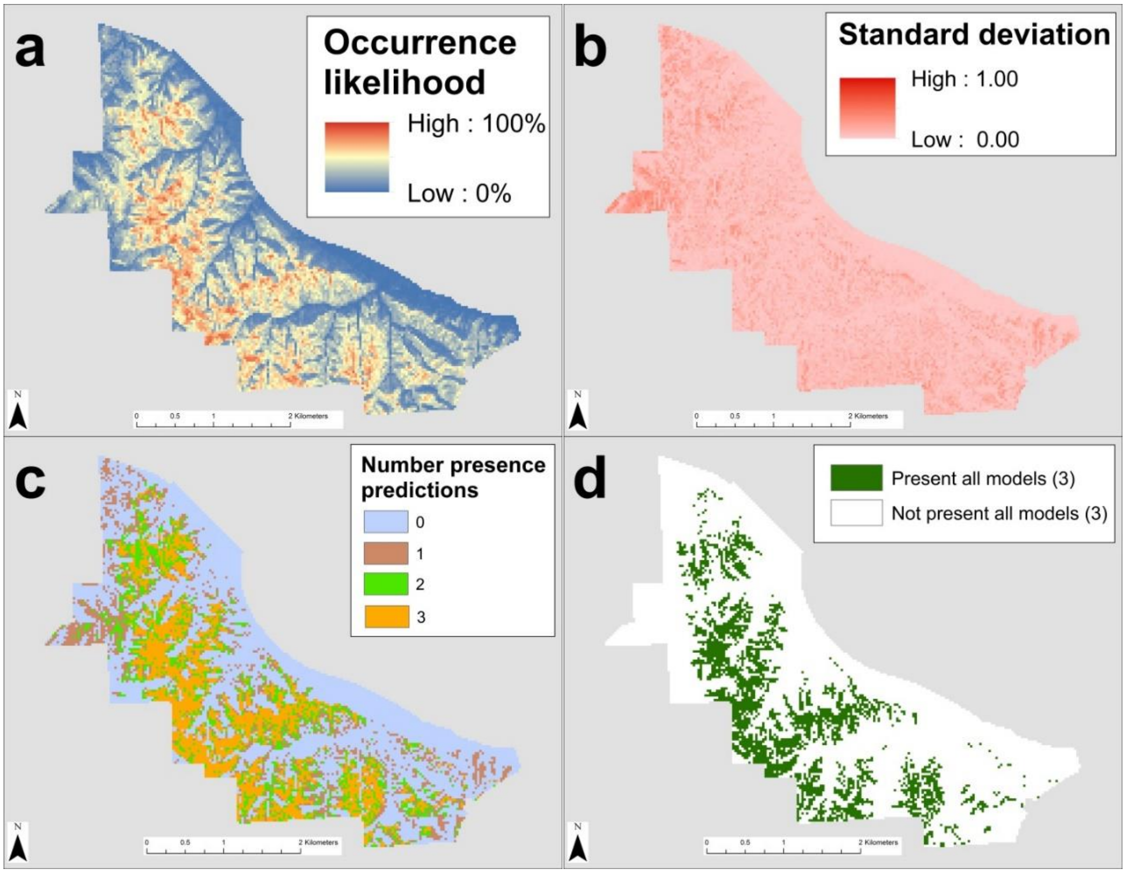
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
d
Present all models (3)
Not present all models (3)
N
0 0.5 1 2 Kilometers

Figure 6: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for black oak (*Quercus velutina*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

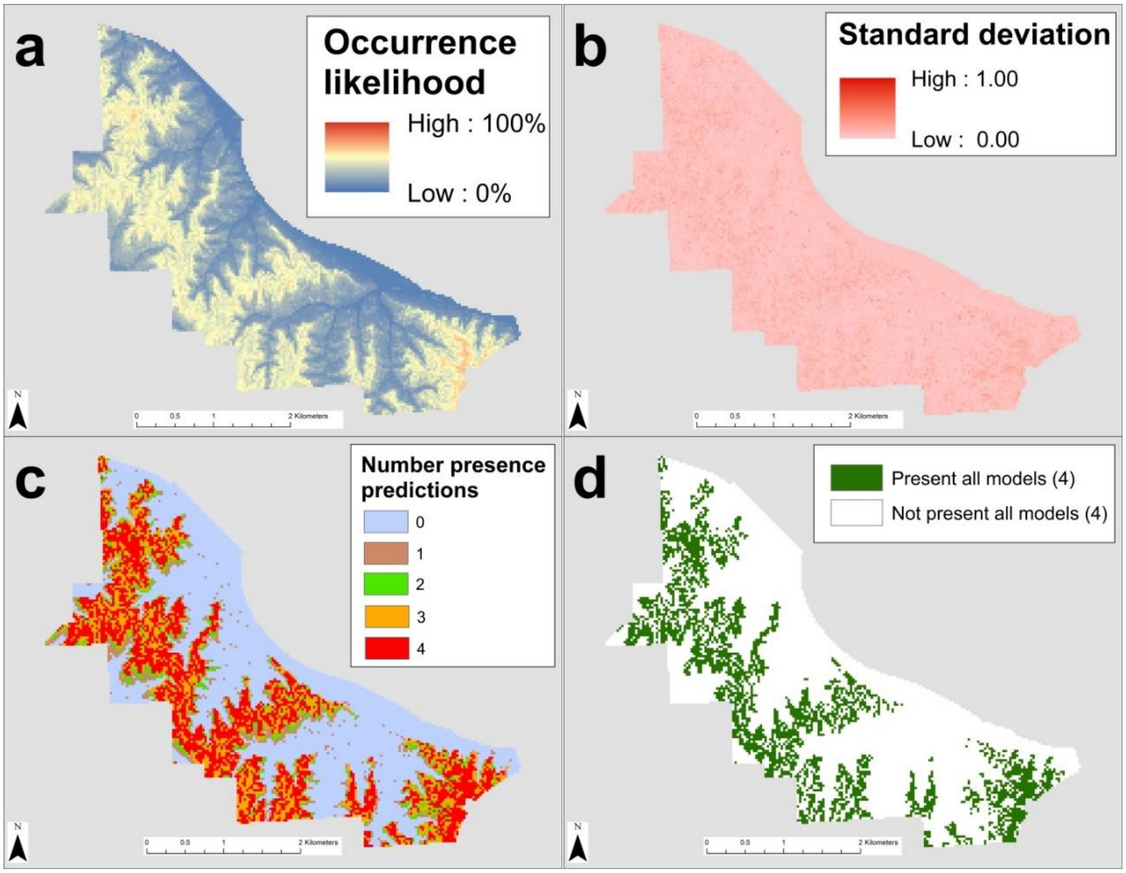
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0 0.5 1 2 Kilometers

Figure 7: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for bur oak (*Quercus macrocarpa*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

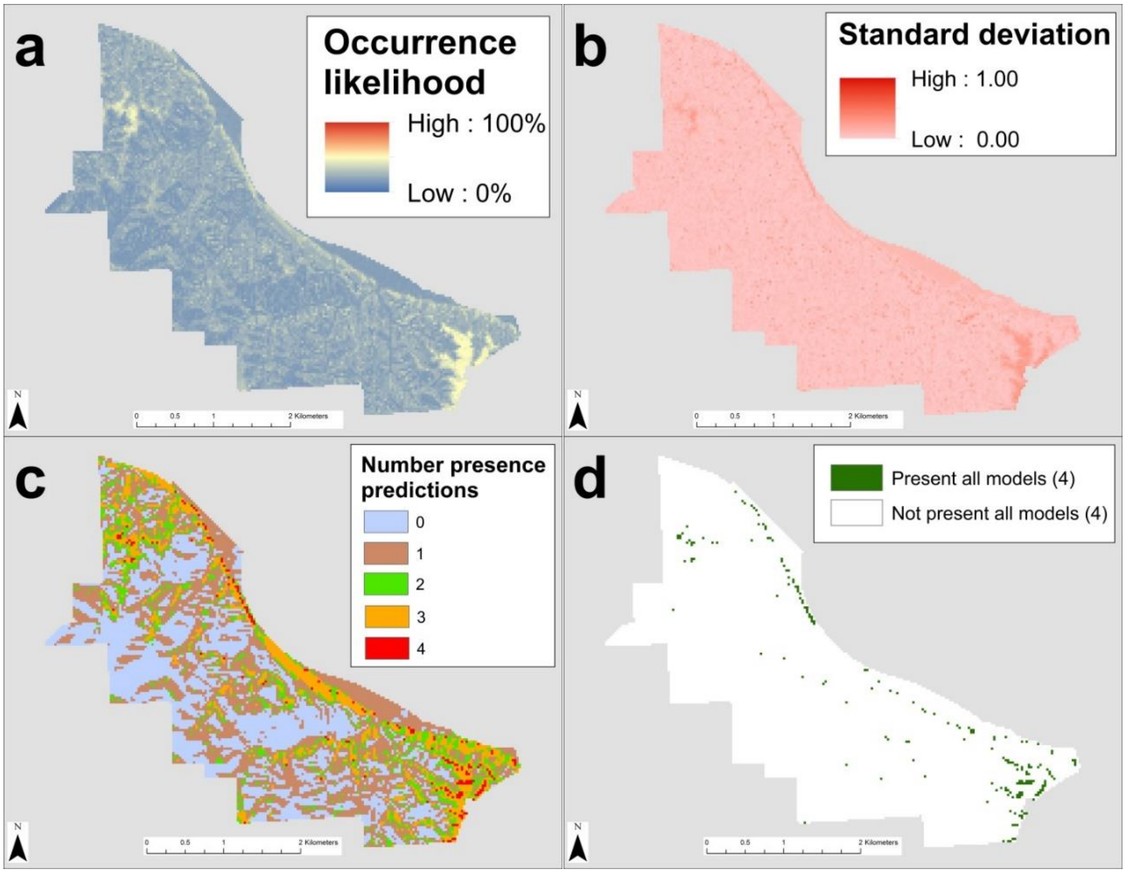
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0 0.5 1 2 Kilometers

Figure 8: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for ash (*Fraxinus* spp.) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

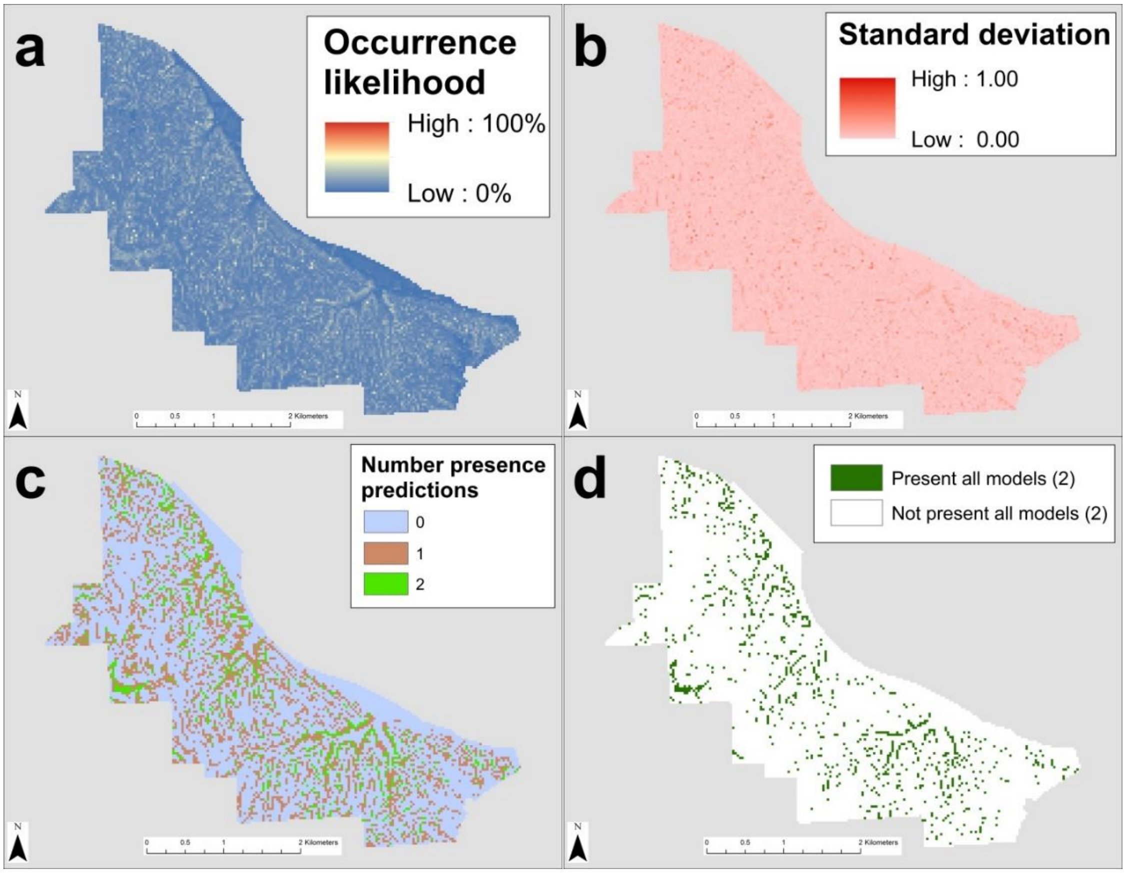
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
d
Present all models (2)
Not present all models (2)
N
0
0.5
1
2 Kilometers

Figure 9: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for bitternut hickory (*Carya cordiformis*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized additive model and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

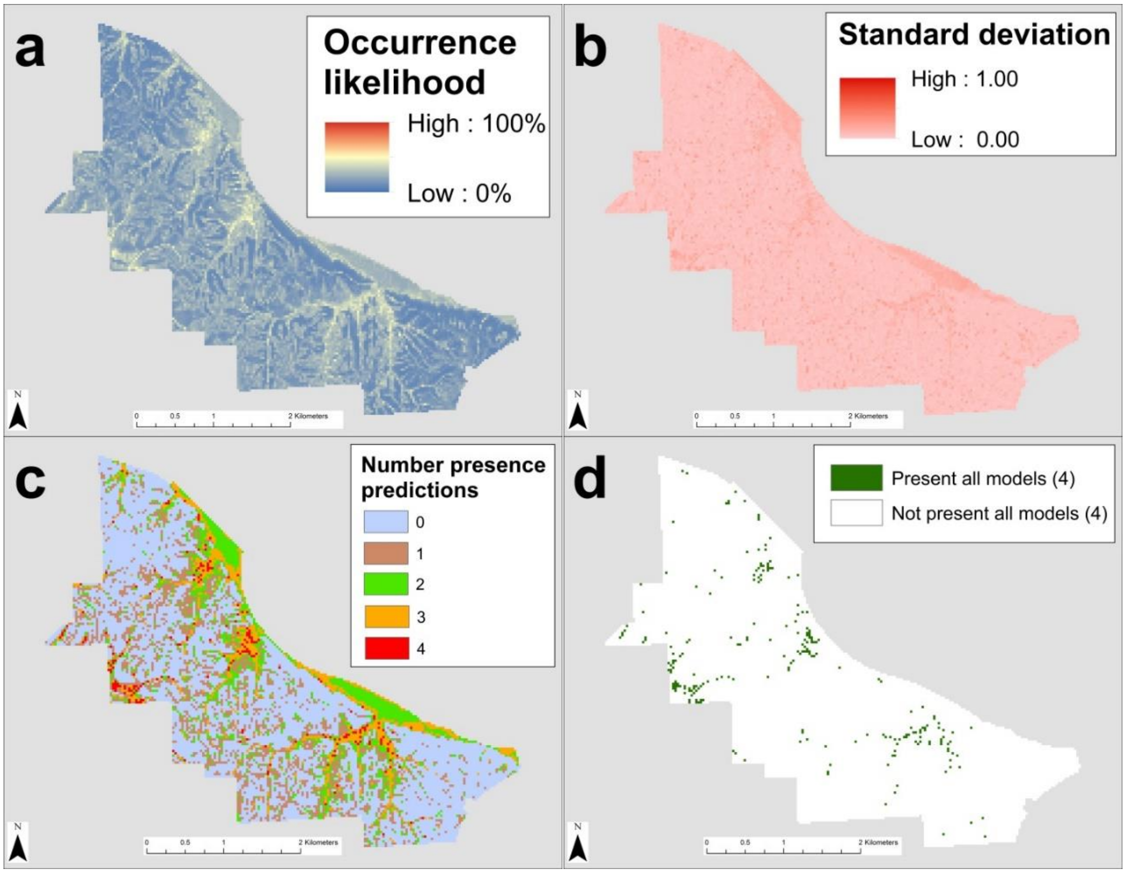
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0
0.5
1
2 Kilometers

Figure 10: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for black walnut (*Juglans nigra*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

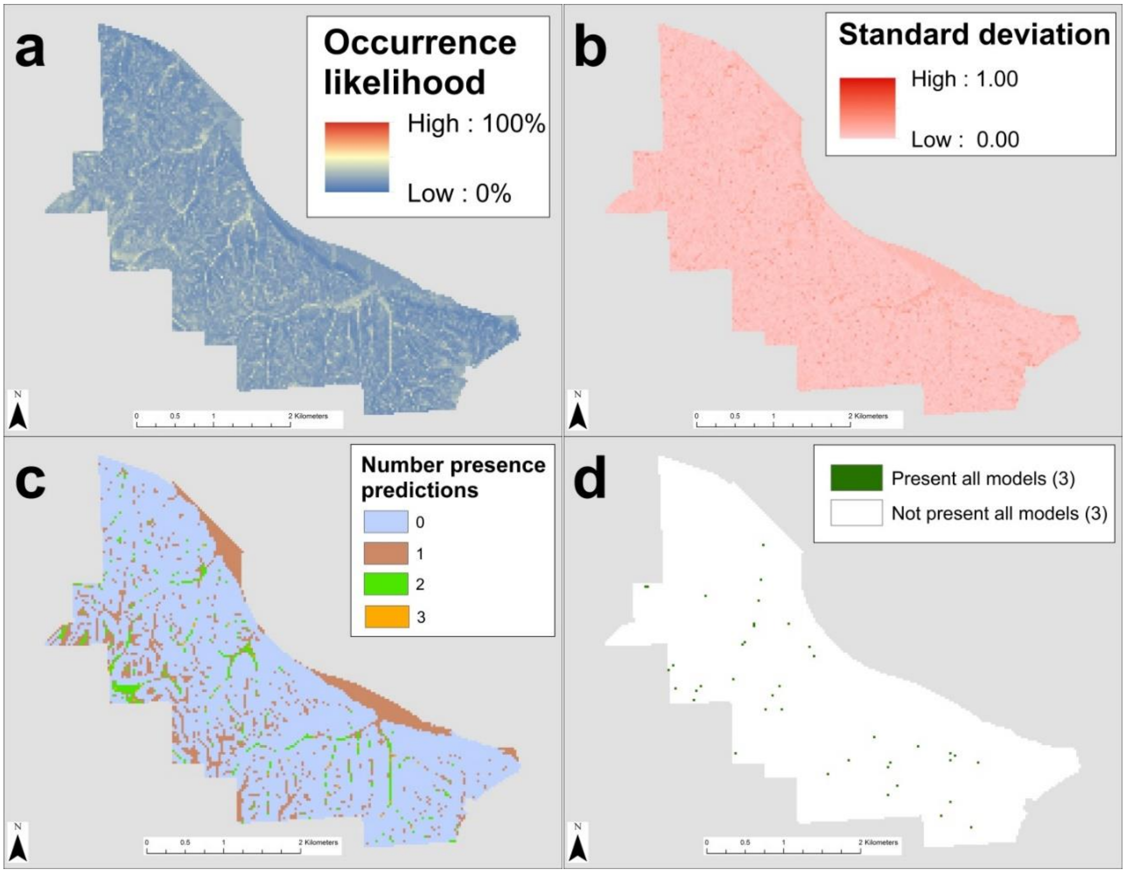
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
d
Present all models (3)
Not present all models (3)
N
0
0.5
1
2 Kilometers

Figure 11: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for elm (*Ulmus* spp.) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

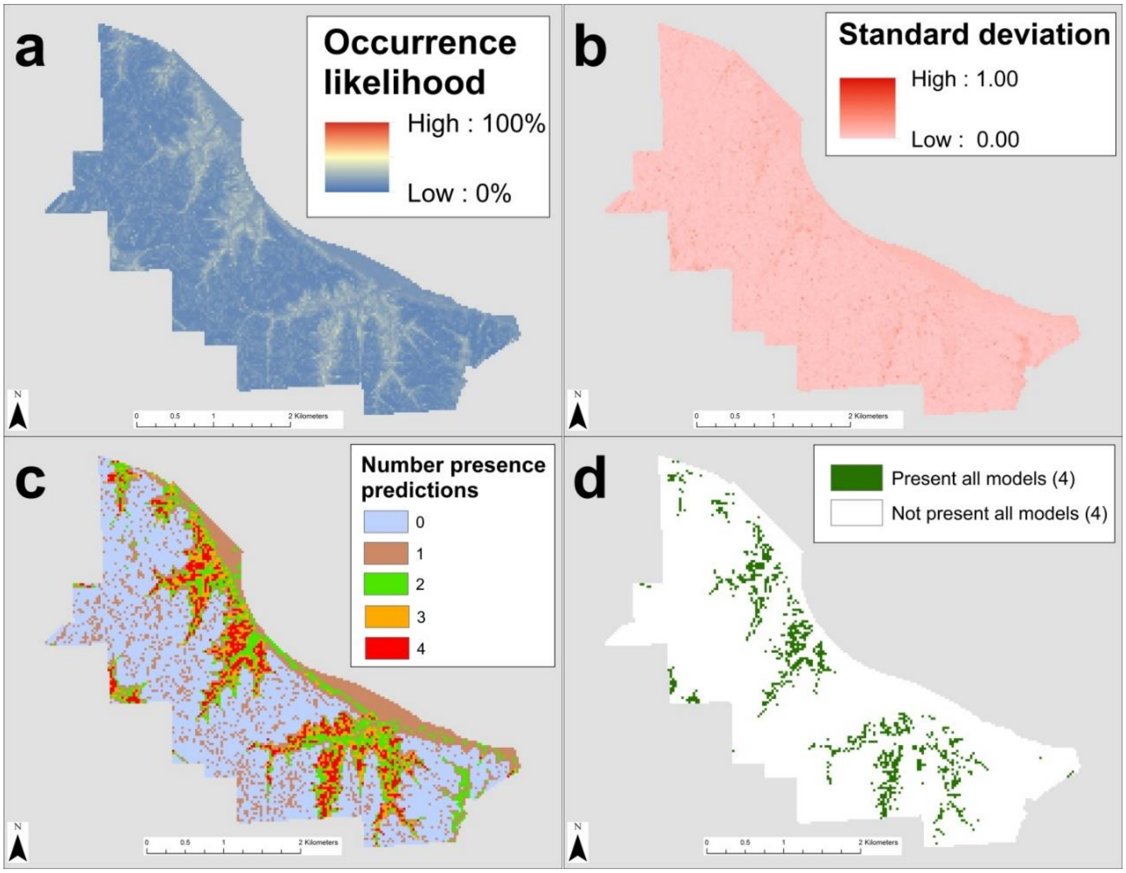
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0 0.5 1 2 Kilometers

Figure 12: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for hackberry (*Celtis occidentalis*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

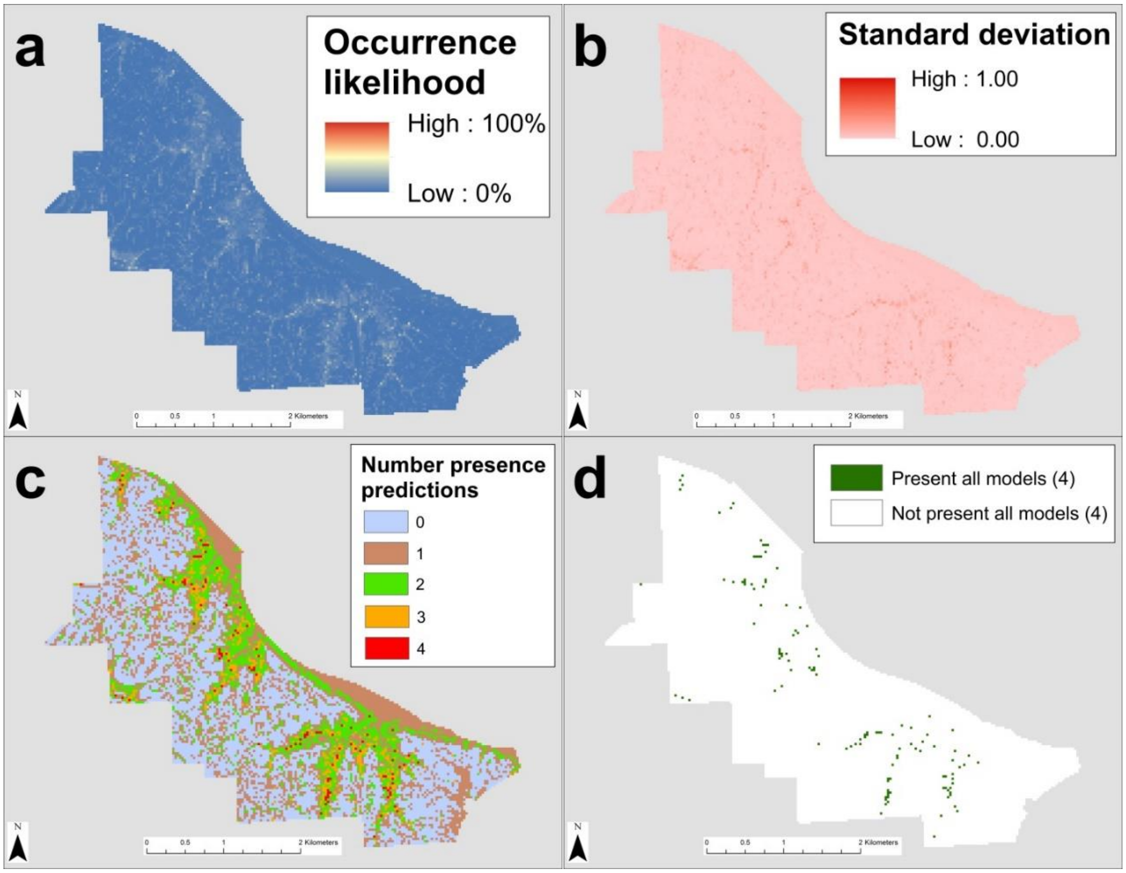
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0
0.5
1
2 Kilometers

Figure 13: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for honeylocust (*Gleditsia triacanthos*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

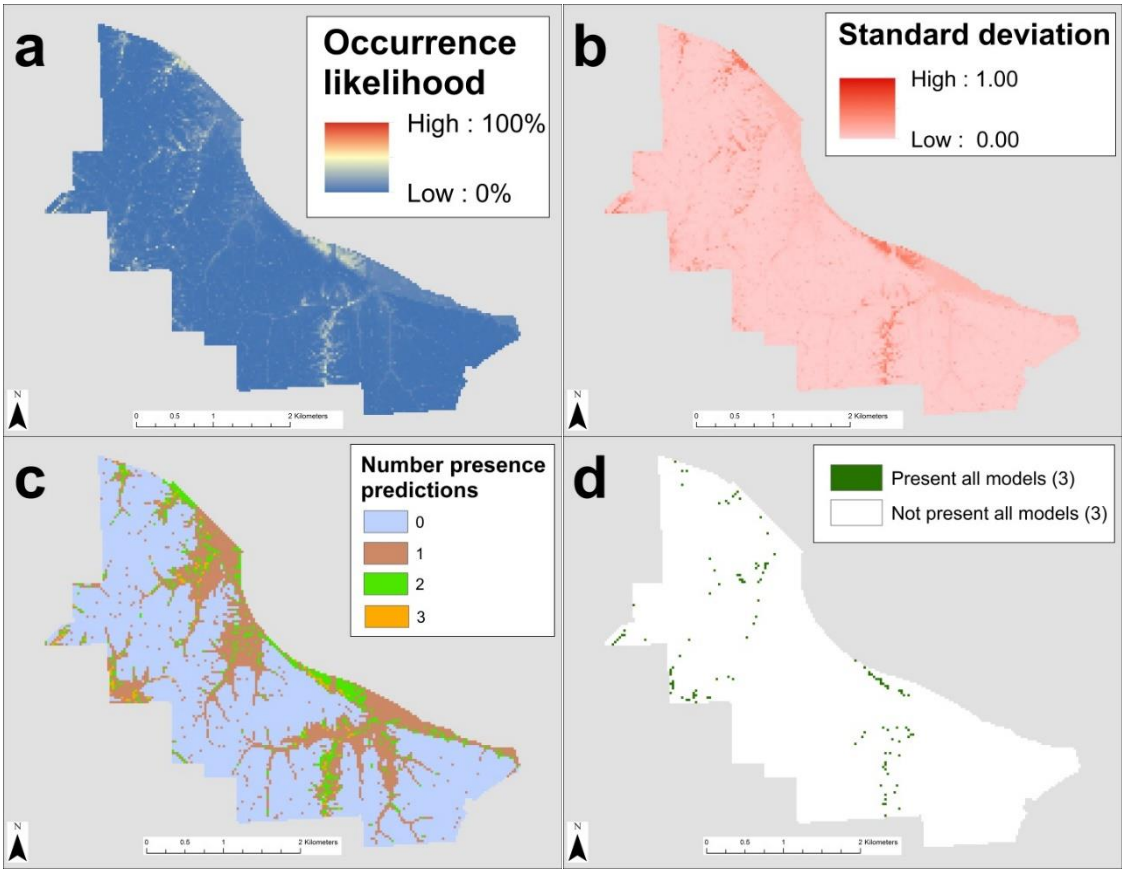
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
d
Present all models (3)
Not present all models (3)
N
0 0.5 1 2 Kilometers

Figure 14: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for Kentucky coffeetree (*Gymnocladus dioicus*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

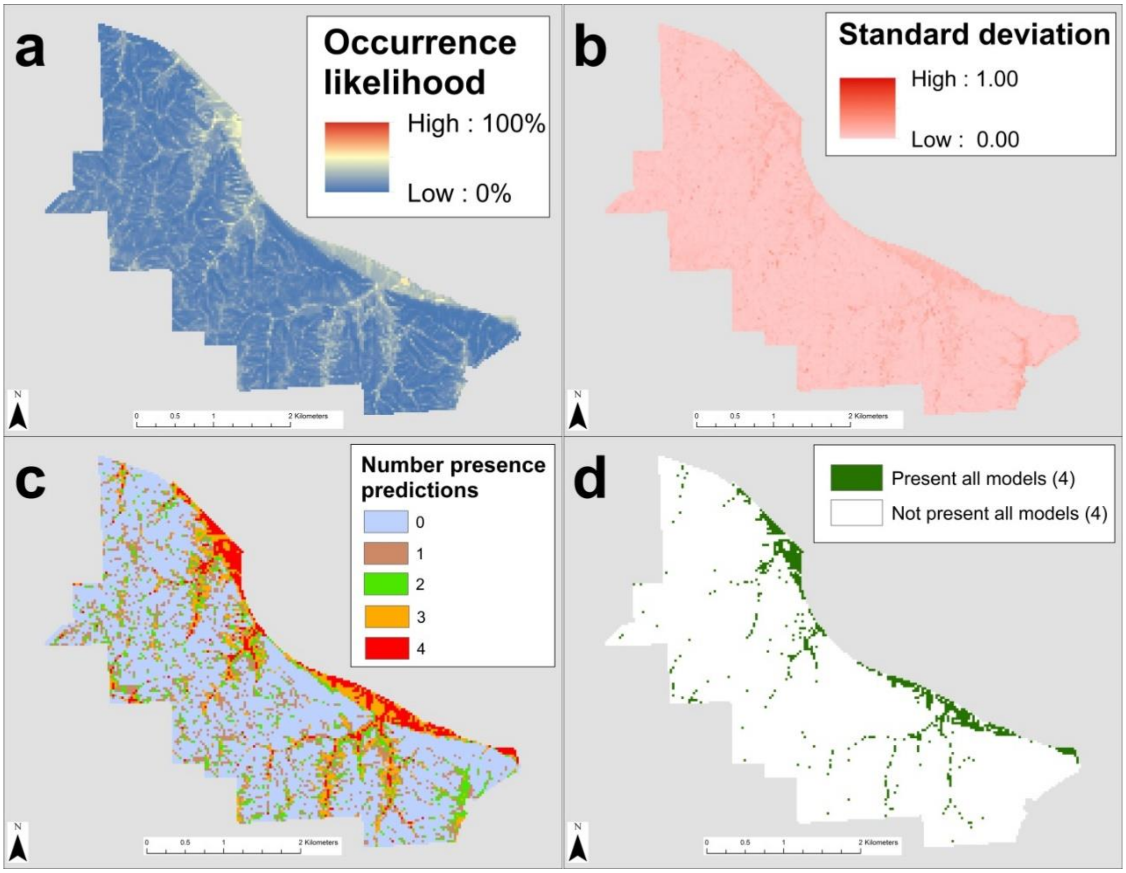
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
4
d
Present all models (4)
Not present all models (4)
N
0 0.5 1 2 Kilometers

Figure 15: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for mulberry (*Morus* spp.) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized linear model, a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

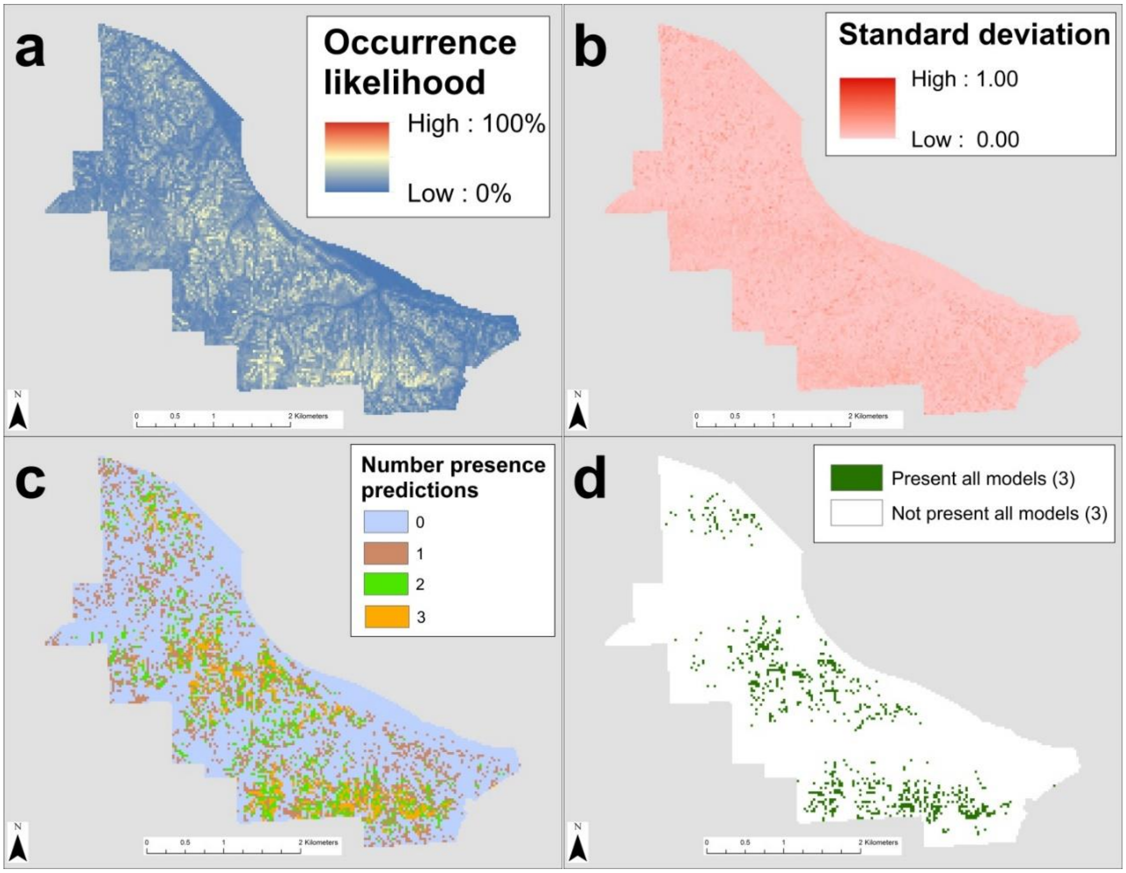
a
Occurrence likelihood
High : 100%
Low : 0%
b
Standard deviation
High : 1.00
Low : 0.00
c
Number presence predictions
0
1
2
3
d
Present all models (3)
Not present all models (3)
N
0 0.5 1 2 Kilometers

Figure 16: Maps of a) mean occurrence likelihood, b) standard deviation in occurrence likelihoods, c) number of models predicting presence, and d) areas for which all models predict presence for shagbark hickory (*Carya ovata*) within Indian Cave State Park. The modeling techniques with which predictions were made within this ensemble approach consisted of a generalized additive model, a boosted regression tree model, and a random forests model. Continuous occurrence likelihoods of individual models were averaged to produce a final occurrence likelihood estimate. Continuous occurrence likelihood predictions were also converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

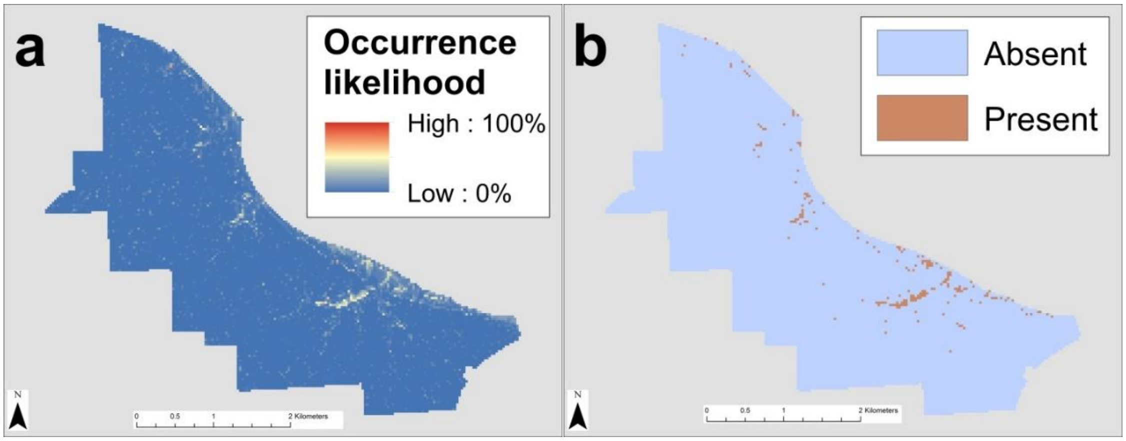
a
Occurrence likelihood
High : 100%
Low : 0%
b
Absent
Present
N
0
0.5
1
2 Kilometers

Figure 17: Maps of a) occurrence likelihood and b) presence/absence for American sycamore (*Platanus occidentalis*) within Indian Cave State Park, based a random forests model. Continuous occurrence likelihood predictions were converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

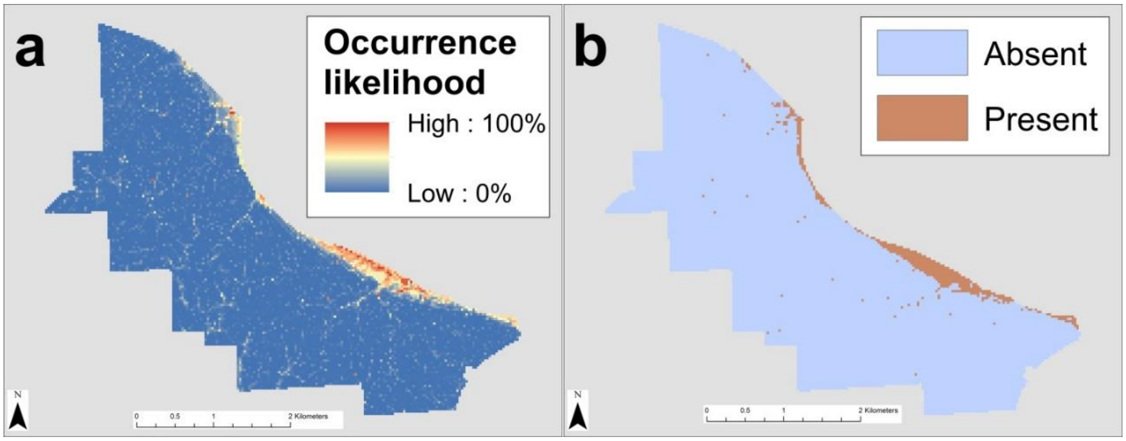
a
Occurrence likelihood
High : 100%
Low : 0%
N
0 0.5 1 2 Kilometers
b
Absent
Present
N
0 0.5 1 2 Kilometers

Figure 18: Maps of a) occurrence likelihood and b) presence/absence for eastern cottonwood (*Populus deltoides*) within Indian Cave State Park, based a random forests model. Continuous occurrence likelihood predictions were converted to presence/absence with the optimal threshold between 0.00 and 1.00 for doing so, as determined by the maximum Kappa statistic (Cohen 1960).

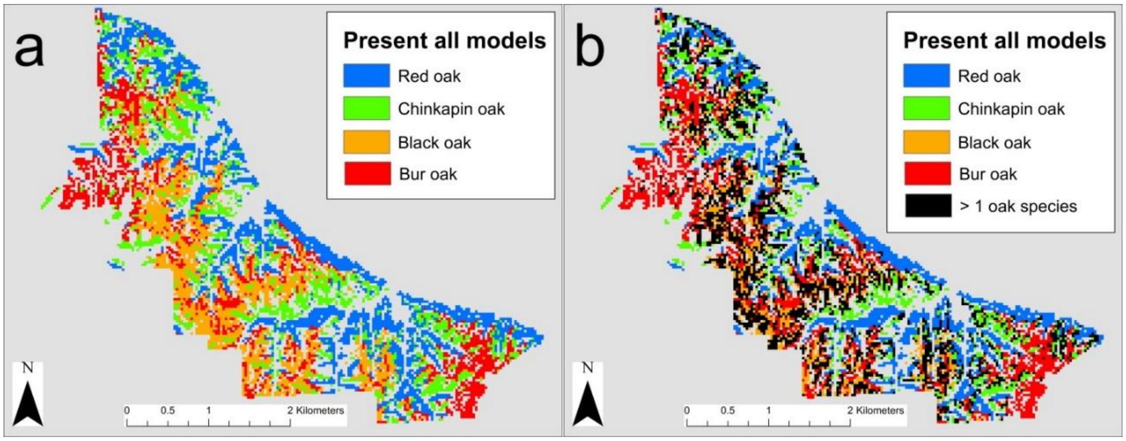
a
Present all models
Red oak
Chinkapin oak
Black oak
Bur oak
N
0 0.5 1 2 Kilometers
b
Present all models
Red oak
Chinkapin oak
Black oak
Bur oak
> 1 oak species
N
0 0.5 1 2 Kilometers

Figure 19: Areas for which all ensemble models predicted a) oak species presence, including b) areas where all models predict presence of more than one oak species.

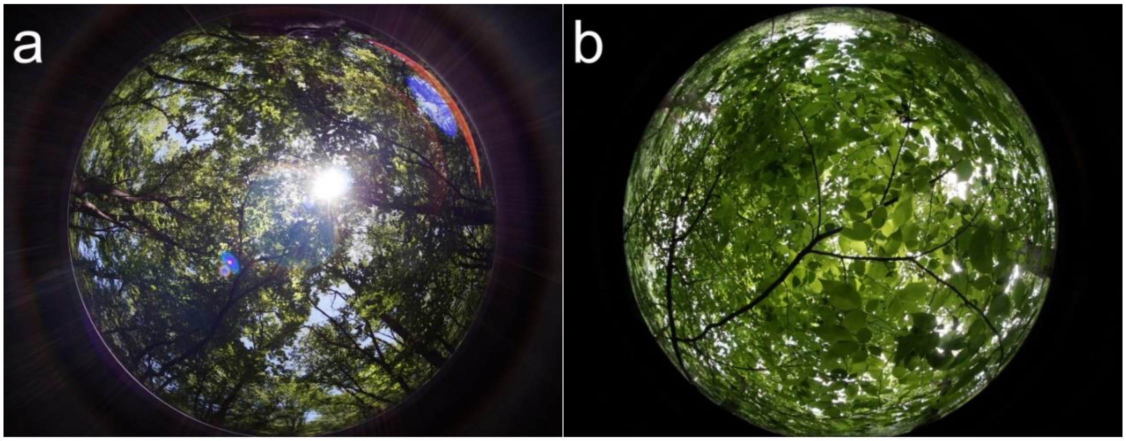

Figure 20: Examples of fish-eye lens photographs of the forest canopy in ICSP in locations where burning and/or thinning management actions a) have and b) have not been implemented. Although no formal analysis of differences in light availability were conducted across all images, empirical observation of differences in light availability between the images serve as an indicator of management effects.

CHAPTER 5: FUNCTIONAL CONNECTIVITY OF WETLANDS FOR HERPETOFAUNA IN THREE CENTRAL NEBRASKA, U.S.A. LANDSCAPES

ABSTRACT

The functional connectivity of isolated habitat patches is critical for metapopulations and other spatially structured populations. In addition to decreasing habitat quality, human-driven landcover change may erode functional connectivity in habitat networks by eliminating habitat patches that serve as stepping stones between other habitat patches, and by making the background matrix through which dispersing organisms travel less hospitable. In this chapter, I evaluated functional connectivity and modularity for herpetofauna in wetland networks of three Nebraska landscapes that have experienced different intensities of conversion to cropland over the past several centuries. I also assessed the level of clustering in wetland geographic distributions in each landscape. Among the three landscapes, wetland connectivity, modularity, and clustering were greatest in the Cherry County Wetlands, a landscape embedded in the large, relatively unbroken grasslands of the Nebraska Sandhills. Compared to the Cherry County Wetlands, connectivity and modularity are lower in the Central Loess Hills, a grass-dominated landscape that is presently experiencing landcover change via the conversion of grasslands and wetlands to rowcrop fields and woodland, and lowest in the Rainwater Basin, a landscape characterized by 20th century conversion to intensive rowcrop production. However, wetlands in the Rainwater Basin were more densely clustered than those in the Central Loess Hills. Thresholds in network-level connectivity

are evidenced in the Rainwater Basin and Central Loess Hills between certain assumed species dispersal distances; however, the majority of the Cherry County Wetlands are already functionally connected at the shortest assumed dispersal distance, making any connectivity thresholds unapparent, and therefore, likely more resilient to perturbations at multiple scales than the Central Loess Hills or Rainwater Basin. Evaluations of aerial imagery in the portion of each landscape with the densest wetland clusters reveal relatively unbroken grassland in the Cherry County Wetlands, rowcrop production in the Central Loess Hills, and industrial activity in the Rainwater Basin. Considering the combined influences of changes in habitat quality and functional connectivity for metapopulations of herpetofauna and other wetland-dependent species may assist with the representation of social–ecological tradeoffs associated with conversion to cropland and other forms of directly human-driven landcover change.

INTRODUCTION

The ability of species to emigrate and immigrate among habitat patches is critical for the persistence of metapopulations and other spatially structured populations (Wahlberg et al. 1996; Gonzalez et al. 1998; Fronhofer et al. 2012), especially as landscapes and social–ecological system(s) (SES) are increasingly affected by landcover change and related global change processes (Tscharntke et al. 2005; Keith et al. 2008; Lindenmayer & Fischer 2013). The movements of individuals among habitat patches can balance extinction and colonization within metapopulations (Pulliam 2000); however, at smaller scales, a diversity of factors (e.g., dispersal distance, topography, competition, mortality, and travel costs) affect dispersal and colonization success (Fahrig & Merriam 1994; D'Eon et al. 2002; Belisle 2005). When the characteristics and/or arrangement of habitat patches fail to meet the requirements for population persistence, an extinction debt is created, and without improvements in conditions, local extirpation is inevitable (Atmar & Patterson 1993; Kareiva & Wennergren 1995; Hanski & Ovaskainen 2002). Therefore, maintaining sufficient levels of connectivity among habitat patches is important for conserving scattered and isolated populations (Wahlbert et al. 1996; Gibbs 2000; Wiens 2002).

In the academic subdiscipline of landscape ecology, functional connectivity refers to relationships among habitat patches that result from their spatial distributions and the movement of organisms among them (Fahrig & Merriam 1994; With et al. 1997; Haig et al. 1998). Among-patch movements of species may be promoted or impeded by landscape characteristics at different spatial scales (Taylor et al. 1993; Tischendorf &

Fahrig 2000; D’Eon et al. 2002). Apart from how well they are functionally connected for species, the quality of habitat patches is important for breeding, foraging, and refuge. The availability of suitable and functionally connected habitat patches may be limited in landscapes that have undergone significant changes in landuse and/or landcover as a result of human activity (e.g., conversion to cropland) (Fischer et al. 2006; Janin et al. 2009). Setting aside lands for conservation (i.e., establishing reserves) can help ameliorate the negative ecological effects of landcover change; however, conservation can be costly and reserves themselves will be subject to various stressors as global change continues to unfold (Bengtsson et al. 2003; De Vos et al. 2016). In addition, the efficiency of protected areas for maintaining imperiled populations may depend on suboptimal habitat patches that are critical for facilitating dispersal among higher-quality patches (Urban & Keitt 2001), as well as the characteristics of the matrix (i.e., dominant landcover class) that the patches are embedded in (Ricketts 2001).

Network analysis has emerged as an important tool for the study of SESs and their resilience in the face of perturbations (Sole & Montoya 2001; Janssen et al. 2006; Cumming et al. 2010; Bodin & Tengo 2012; Moore et al. 2016; Yletyinen et al. 2016). In addition to asymmetries and information processing, network characteristics are spatially relevant aspects of complexity (Norberg & Cumming 2008). Studies in network connectivity and resilience—the ability of a system to withstand component losses while maintaining connectivity—can increase understanding of how the arrangement of system components in relation to one another, information exchange among components, and other network properties affect system function under varying internal and external conditions (Cumming 2011). Intermediate levels of connectivity and modularity [i.e., a network-level metric that measures the separation of networks into smaller, connected clusters (Newman 2006)] are hypothesized to confer SESs with resilience—more specifically, with spatial resilience (Nystrom & Folke 2001; Cumming 2011; Allen et al. 2016)—by facilitating the spread of beneficial elements (e.g., genetic information in species) within patches clusters, while at the same time restricting the spread of detrimental elements (e.g., disease outbreaks) to a relatively small number of patches and/or clusters (Holling 2001; Gunderson & Holling 2002; Walker & Salt 2006; Ash & Newth 2007; Webb & Bodin 2008).

In this chapter, I evaluate patterns in the geographic distribution and functional connectivity of wetlands for anuran (i.e., frog and toad) and reptile (i.e., aquatic turtle) species in three landscapes of central Nebraska, U.S.A. that are identified as locations for targeted conservation action under the Nebraska Natural Legacy Plan (NNLP) (Schneider et al. 2011). In addition to being characterized by different landcover classes, the three landscapes have experienced different forms and degrees of human landscape modification over the past several centuries, with the Rainwater Basin being most and the Cherry County Wetlands least characterized by the conversion of the landscape to cropland. Yet, despite these differences in conversion to cropland, all three landscapes possess high densities of wetlands, which provide important habitat for amphibians, reptiles, and other wetland-dependent taxa. Therefore, results of this study may be useful for informing wetland conservation and restoration activities (Pullinger & Johnson 2010; Mitsch & Hernandez 2013), for contributing to evaluations of social–ecological tradeoffs associated with alternative landcover-based decisions, and for providing insights into how different degrees of landcover change—specifically regarding the destruction and construction of natural and anthropogenic wetlands—affects the functional connectivity and resilience of landscapes for at-risk herpetofauna metapopulations (Cushman 2006; Gardner et al. 2007; Adams et al. 2013; Bohm et al. 2013).

METHODS

Study areas

Cherry County Wetlands

The Cherry County Wetlands Biologically Unique Landscape (BUL) is located in the northern portion of the Sandhills ecoregion, in Cherry County, Nebraska (Figure 1; Schneider et al. 2011). Numerous lakes, wet meadows, marshes and fens are situated in valleys between sand dunes covered in Sandhills mixedgrass prairie. These wetland areas provide habitat for waterbirds, reptiles, and amphibians. Agricultural landuse consists primarily of haying and cattle grazing, although some rowcrop production is supported by center-pivot irrigation in river valleys. Seven anuran and five aquatic turtle species are known to occur in the Cherry County Wetlands (Tables 1–2).

Central Loess Hills

The Central Loess Hills BUL is located in central Nebraska and consists of rolling to steep hills, dissected by the Middle Loup and North Loup River Valleys (Figure 1; Schneider et al. 2011). Hilly upland areas were traditionally reserved for grazing, but rowcrop production is now moving beyond the flat river valleys and into farmable upland areas. Playa wetlands can be found in the flatter tablelands portion of the landscape. Nine anuran and four aquatic turtle species are known to occur in the Central Loess Hills (Tables 1–2).

Rainwater Basin

The Rainwater Basin BUL is an intensively farmed landscape in south-central Nebraska (Figure 1; LaGrange 2005; Schneider et al. 2011). Soil surveys from the early 20th Century document the existence of as many as 1,000 major and 10,000 minor shallow, precipitation-fed playa wetlands at the time of Euro-American resettlement, less than 10% of which remain today (Gersib 1991; Bishop & Vrtiska 2008). Technological advances and agricultural intensification during the 20th Century resulted in wetland loss and degradation via draining, development, culturally-accelerated sediment accumulation, and conversion to agriculture (Gersib et al. 1989; LaGrange et al. 2011). In addition, thousands of anthropogenic wetlands (i.e., irrigation reuse pits) have been constructed for temporary water storage in rowcrop fields—often replacing natural wetlands. Although these changes in landcover have increased food production for humans, they have decreased habitat availability and connectivity for migratory waterbirds (Uden et al. 2015) and anurans (Uden et al. 2014). Ten anuran and six aquatic turtle species are known to occur in the Rainwater Basin (Tables 1–2).

Data sources

Wetland locations

Geographic information system (GIS) shapefiles of wetland polygons for the State of Nebraska were obtained from the 2014 National Wetlands Inventory (NWI) (https://www.fws.gov/wetlands/). The reliability of the NWI has been questioned by a number of authors (Stolt & Baker 1995; Kudray & Gale 2000), with several evaluations focusing on the Rainwater Basin (Kuzila et al. 1991; Tang et al. 2012, 2015). It is true that the reliability of the NWI may be compromised by errors, as well as changes in landcover that have taken place since its development in the 1980s and/or updates in subsequent decades. Tang et al. (2015) compared actual observations of wetland inundation from the Annual Habitat Survey—an aerial imagery survey of migratory waterbird habitat conducted by the Rainwater Basin Joint Venture—to wetlands documented in the NWI and other wetland databases. Over nine years, 30.7% of NWI wetlands were inundated and 60.5% of NWI wetlands supported the growth of hydric vegetation (Tang et al. 2015). At the same time, only 67.9% of areas observed to be inundated in the Annual Habitat Survey over the same time period were included in the NWI. This means that the use of NWI data for functional connectivity assessments could introduce bias from either direction—by over- or under-representing the number of wetland nodes. However, the uncertainties introduced into functional connectivity assessments by NWI error rates may be encompassed by the uncertainties associated with understanding and reliably predicting wetland ponding (Uden et al. 2015).

Regardless, wetlands within the geographic extents of each of the three BULs were selected and exported as individual shapefiles in ArcGIS (ESRI 2011). Within each of these shapefiles, the following wetland types were selected and retained: freshwater emergent wetlands, freshwater forested/shrub wetlands, and freshwater ponds. This is similar to the approach adopted by Tang et al. (2015) in their assessment of inundation in NWI wetlands of the Rainwater Basin BUL. From these wetland sets, all wetlands with areas ≥ 0.10 hectares (ha) [1,000 square meters (m)] were retained, with the goal of eliminating wetlands that were infrequently inundated. To facilitate network construction, all retained wetland polygons were converted to point features, with the wetland centroid set at location nearest the center of the polygon that still fell within its boundaries. This resulted in totals of 13,050, 5,786, and 18,270 wetland centroid points for the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin BULs, respectively (Figure 2).

Surrounding landcover

In addition to the characteristics and spatial arrangement of habitat patches, the characteristics of the landcover matrix surrounding wetlands has important effects on functional connectivity for species that must traverse it (Ricketts 2001; Compton et al. 2007; Zeller et al. 2012). For example, a meadow or forest matrix may place less resistance on amphibian movement between wetlands than a rowcrop matrix (Janin et al. 2009). The dominant landcover classes in the Cherry Count Wetlands, Central Loess Hills, and Rainwater Basin BULs were tallgrass and mixedgrass prairie, historically

(Schneider et al. 2011). Beginning in the late 19th century, Euro-American landuse practices produced large-scale landcover changes that continue to the present—notably the conversion of wetlands and grasslands to rowcrop production (Cunfer 2005; Wright & Wimberly 2013; Johnston 2014) and the encroachment of woody plants into grasslands (Meneguzzo & Liknes 2015; Ratajczak et al. 2016). Other areas, despite experiencing landuse change [e.g., conversion to cattle (*Bos taurus*) pasture] have remained in grassland and wetland states.

Although all three BULs considered in this study have all experienced human-driven landcover change over the past several centuries, the degree of human influence and modification via conversion to cropland has been greatest in the Rainwater Basin, followed by the Central Loess Hills and Cherry County Wetlands, respectively. Indeed, landcover data from the Rainwater Basin Joint Venture (Bishop et al. 2011) shows that the proportions of total landcover enrolled in cropland in the Rainwater Basin, Central Loess Hills, and Cherry County Wetlands in 2010 was 68.70%, 17.49%, and 0.08%, whereas the proportions of the same landscapes in grassland was 19.23%, 69.54%, and 95.82%, respectively (Table 3; Figure 3).

Functional connectivity evaluations

To assess the functional connectivity of wetland habitats for herpetofauna in the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin BULs, I applied a customized version of the graph theoretic approach of Uden et al. (2014). In graph theory, individual habitat patches are represented as nodes and the connections between them as edges—in this case, Euclidian distances (Figure 4; Bunn et al. 2000; Urban & Keitt 2001; Calabrese & Fagan 2004; Estrada & Bodin 2008). The network is constituted by the combination of all nodes and edges, including isolated nodes, and the term cluster refers to groups of functionally connected nodes (i.e., within a given distance of one another), with ≥ 1 cluster(s) forming the larger network. Paths are defined as ≥ 1 edge between any unique set of network nodes that does not cross any one node more than once (Bunn et al. 2000; Pascual-Hortal & Saura 2006). In addition, I evaluated the relative density of wetland points in each of the three BULs with the average nearest neighbor distance tool in ArcGIS, which uses a z-test to compare the observed mean distance between points with the expected mean distance between the points, assuming a random distribution of the points in the same area (ESRI 2011).

When information regarding the dispersal abilities of target species is lacking, comparisons of the level of connectivity among several nested spatial scales is recommended for gaining information about the effects of scale on connectivity (Calabrese & Fagan 2004). Ten anuran and six aquatic turtle species are known to occur throughout the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin (Tables 1–2). Because limited information was available concerning the dispersal capabilities of these particular species, I assumed four dispersal distances that represent a range of herpetofauna dispersal potentials in grasslands, woodlands/forests, and rowcrop fields: 0.50, 1.00, 1.50, and 2.00 kilometers (km) (Uden et al. 2014). The maximum value of this range is nearly identical to the reported mean maximum dispersal distance of anurans (i.e., 2.02 km) in a variety of landscapes (Smith & Green 2005); therefore, the dispersal potentials of anurans and aquatic turtles of the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin BULs were assumed to lie within it.

Wetland networks for the three BULs were built and analyzed using ArcGIS (ESRI 2011) and the program R (R Core Team 2016), with functions housed in the sp (Pebesma & Bivand 2005; Bivand et al. 2013), rgdal (Bivand et al. 2016), SDMTools (VanDerWal et al. 2014), and igraph (Csardi and Nepusz 2006) packages. For each of the three wetland networks, Euclidian distances between each wetland point and every other wetland point in the network were calculated, and connections with distances ≤ each of the four dispersal distances were retained and used to create lists of edges representing connections between wetland nodes at each dispersal distance. Wetland nodes and edges were then combined to produce a network for each of the three BULs at each of the four dispersal distances, which resulted in a total of 12 networks. Because of high random access memory (RAM) requirements in constructing and analyzing networks in R, these analyses were run on the Crane Supercomputer in the Holland Computing Center at the University of Nebraska-Lincoln (http://hcc.unl.edu/).

Herpetofauna, like many other species, are unlikely to traverse landscapes in straight lines; therefore, true dispersal distances between wetlands may be underrepresented. However, given the lack of information regarding species-specific dispersal capabilities in the three BULs—as well as in other landscapes worldwide (Jacobson & Peres-Neto 2010)—Euclidian (i.e., straight-line) distance was utilized as a measure of travel cost between wetlands. Furthermore, because information was lacking regarding the directional movement of anuran and aquatic turtle species in the BULs, I assumed between-node travel to be random (i.e., undirected).

Diverse methods and metrics have been applied to examinations of node- and network-level connectivity, and to the determination of individual node contributions to network-level connectivity (Calabrese & Fagan 2004; Pascual-Hortal & Saura 2006; Saura & Rubio 2010; Cumming 2016). I quantified node-level connectivity with node degree (i.e., the number of direct connections a node maintains with adjacent nodes) (Estrada 2007; Estrada & Bodin 2008). To visually represent the spatial distribution of node-level connectivity, I produced continuous inverse distance weighted (IDW) raster surfaces for interpolating degree values among nodes. Ecologically, this represents the ability of an anuran or aquatic turtle occupying a wetland to emigrate to a number of neighboring wetland patches in the event that the wetland they are occupying becomes unsuitable. Similarly, if a local extinction occurs in a wetland with a high degree centrality, anurans and aquatic turtles from neighboring wetlands may eventually immigrate to recolonize it.

Network-level connectivity was evaluated according to mean degree centrality, the total number of clusters in the network, the mean number of nodes among network clusters, the percentage of total nodes contained in the largest cluster, and a network modularity score. The more distinct clusters of connected habitat patches that exist in a network, the more disconnected the patches and the species inhabiting them become, with the maximum possible number of clusters being equal to the total number of patches (i.e., individual nodes). Alternatively, the greater the percentage of total patches that are contained in the single largest cluster, the more patches in the network a species can reach from any given patch within that cluster, until connectivity increases to the point that the entire network consists of a single cluster and any given patch can be directly or indirectly reached from any other patch. Therefore, habitat networks with fewer, but larger, clusters provide species with the greatest opportunities for across-network movement. Although high levels of connectivity maximize the potential for among-patch movement and the resulting exchange of genetic information within herpetofauna metapopulations (Stevens et al. 2006), it may also facilitate biological invasions and the spread of disease and other detrimental elements through habitat networks and spatially-structured populations. Modularity is a network-level metric that measures the separation of networks into smaller connected clusters and is greatest in networks where connections are dense within clusters and sparse between them (Newman 2006). Habitat networks with intermediate levels of connectivity and modularity are hypothesized to permit the movement of species among patches and clusters, while still restricting detrimental events to individual clusters, thereby minimizing the potential for their spread through, and negative effect on, the larger network (Ash & Newth 2007; Webb & Bodin 2008).

RESULTS

Wetland functional connectivity

Of the three BULs, the Rainwater Basin has more wetland nodes than the Cherry County Wetlands and Central Loess Hills, respectively (Table 4). At all four dispersal distances, mean wetland degree (i.e., number of direct connections with neighboring wetlands) was greatest in the Cherry County Wetlands BUL, with the Central Loess Hills following and the Rainwater Basin having the least mean degree (Figure 5). The Rainwater Basin had the greatest number of clusters—with fewer clusters in the Central Loess Hills and Cherry County Wetlands—at the 0.5 and 1.0 km dispersal distances (Figure 6). At the 1.50 and 2.00 km dispersal distances, results were mixed, with the Rainwater Basin and Cherry County Wetlands having the most clusters, respectively. There were also mixed results in the mean number of wetlands per cluster at the four dispersal distances, with the mean for the Cherry County Wetlands being greatest at the 0.50 and 1.00 km dispersal distances and the Rainwater Basin being greatest at the 1.50 and 2.00 km distances (Figure 7). The Cherry County Wetlands had the highest—and the Rainwater Basin the lowest—modularity score at all four dispersal distances (Figure 8).

Wetland spatial distributions

The geographic distributions of wetland centroids in the three BULs were all significantly clustered (i.e., the observed mean distance between wetlands was significantly greater than the expected mean distance between them, assuming their random distribution in the same area); however, those in the Cherry County Wetlands were more densely distributed than those in the Rainwater Basin and Central Loess Hills, respectively (Table 4). Differences in wetland distributions and densities among the BULs and dispersal distances were also evident from comparisons of wetland degree centrality IDW maps (Figures 9–12). The most and largest connectivity hotspots were associated with the 2.00 km (i.e., greatest) dispersal distance in all three BULs, with the

Cherry County Wetlands displaying more and larger hotspots than the Central Loess Hills or Rainwater Basin.

Dispersal distance connectivity thresholds

Functional connectivity was affected by dispersal distance, and dramatic shifts in network-wide connectivity in different BULs were detected between certain dispersal distances. In the Rainwater Basin, the percentage of total wetlands in the largest cluster increased from 2.27% to 91.18% between the 0.50 and 1.00 km dispersal distances, and then more gradually increased to 98.72% and 99.80% total inclusion at the 1.50 and 2.00 km dispersal distance (Figure 13), indicating a dispersal threshold between 0.50 and 1.00 km dispersal distances where the majority of wetlands were all directly or indirectly connected with one another. A similar, yet more gradual increase in connectivity was evident in the Central Loess Hills, where the percentage of wetlands in the largest cluster increased from 19.62% to 79.04% between the 0.50 and 1.00 km dispersal distances, and then to 97.60% and 99.52% at the 1.50 and 2.00 km dispersal distances, respectively. Alternatively, 86.02% of wetlands were connected in a single cluster at the 0.50 km dispersal distance in the Cherry County Wetlands, which only left room for a gradual increase to 99.48% inclusion over the 1.00, 1.50, and 2.00 km distances.

Node contributions to connectivity

Specific wetland nodes that contributed most to connectivity in each of the three BULs varied with the dispersal distance considered; however, some general trends in their geographic locations were evident. The top 10% of nodes with the greatest degrees (i.e., direct connections with neighboring nodes) were more widely dispersed through each of the BULs at shorter dispersal distances (e.g., 0.50 km) than they were at longer dispersal distances (e.g., 2.00 km) (Figures 14–17). Dense clusters of the most highly connected wetland nodes are apparent in the east-central portion of the Cherry County Wetlands, in the northwestern portion of the Central Loess Hills, and in the central portion of the Rainwater Basin. However, evaluation of 2012 aerial imagery of these areas reveals that the densest wetland cluster in the Cherry County Wetlands is embedded in a grassland matrix (Figure 18), the densest wetland cluster in the Central Loess Hills is embedded in rowcrop fields (Figure 19), and the densest wetland cluster in the Rainwater Basin to consist of what are likely human-constructed water bodies—possibly manure ponds near cattle or hog barns—in a landscape with a high degree of human modification (Figure 20).

DISCUSSION

This chapter considers functional connectivity for herpetofauna in three central Nebraska landscapes that have experienced differing degrees of directly human-driven landcover change—specifically, conversion to cropland—over the past several centuries. The least altered of the three BULs is the Cherry County Wetlands, where the dominant landcover class is grassland (Table 3). In contrast, the Rainwater Basin is the most altered of the BULs, as it experienced a high degree of landcover change in the 20th century that stemmed primarily from the conversion of grasslands and wetlands to rowcrop fields

(Gersib 1991; Bishop & Vrtiska 2008; Uden et al. 2014). Lastly, the Central Loess Hills BUL has experienced a moderate level of conversion to cropland compared to the Cherry County Wetlands and Rainwater Basin BULs. Although the Central Loess Hills remains a grass-dominated landscape, remaining grassland is actively transitioning to eastern redcedar woodland and rowcrop fields (Schneider et al. 2011). It is likely that these different intensities of landcover change have affected herpetofauna metapopulations, which rely heavily on wetland habitats that are structurally—but not necessarily functionally—isolated from one another.

Overall, the Cherry County Wetlands displays the greatest level of wetland connectivity and modularity among the three BULs (Figures 5 & 8). Wetlands in the Cherry County Wetlands are also the most clustered of the three BULs, although wetlands in all three BULs are significantly clustered (Table 4). Visual inspection of satellite imagery in the portion of the Cherry County Wetlands BUL with the largest and densest wetland cluster at all four assumed dispersal distances (Figures 14–17) reveals a landscape characterized by dense wetlands amidst virtually unbroken grassland (Figure 18). Here, the majority of human landuse involves cattle production. The majority of wetlands in the Cherry County Wetlands BUL are joined in a single large wetland cluster at all four assumed dispersal distances, whereas this only occurs in the Central Loess Hills and Rainwater Basin at the three greatest dispersal distances (Figure 13).

Following the Cherry County Wetlands, there are mixed indicators between the Central Loess Hills and Rainwater Basin as far as which BUL maintains the greatest level of wetland connectivity. Comparisons between the two BULs are complicated by several factors, including the Rainwater Basin being nearly three times larger (Table 3) and containing more than three times as many wetland nodes (Table 4) as the Central Loess Hills. Although wetlands in the Rainwater Basin are more clustered than those in the Central Loess Hills, other metrics (e.g., mean node degree) indicate connectivity to be greater in the Central Loess Hills (Figure 5). In addition, modularity in the Central Loess Hills is greater than that in the Rainwater Basin (Figure 8). Finally, satellite imagery of the portions of both BULs with the largest and densest wetland clusters at all four assumed dispersal distances show intensive human-driven landcover change (Figures 19–20), with more extreme modifications in the Rainwater Basin, where the wetlands themselves may in actuality be pits constructed for the storage of irrigation water or livestock manure.

Thresholds in functional connectivity between the 0.50 and 1.00 km dispersal distances were apparent in the Central Loess Hills and Rainwater Basin BULs, with the change between these dispersal distances being starker in the Rainwater Basin (Figure 13). No such thresholds were observed in the Cherry County Wetlands BUL, because the majority of wetlands were already contained in the single largest cluster at the 0.50 km dispersal distance. These potential thresholds in connectivity lend additional support to Uden et al.’s (2014) speculation that larger, longer-dispersing anurans (e.g., bullfrogs and leopard frogs) may be favored by human landscape modifications in the Rainwater Basin, whereas smaller, shorter-dispersing species may be disadvantaged. While this could be occurring in the Rainwater Basin and Central Loess Hills BULs, it appears less likely in the Cherry County Wetlands BUL. Alternatively, it is possible that the Rainwater Basin and Central Loess Hills would too fail to show such thresholds if wetlands with areas < 0.10 hectares were included in their respective networks. Indeed, the inclusion of these small wetlands would add 29,357, 4,101, and 3,975 wetlands to the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin networks, respectively. However, these extremely small bodies of water are also not likely to consistently provide habitat for anuran and aquatic turtle species (Tang et al. 2015), which could bias connectivity estimates. Regardless, the lack of apparent thresholds in connectivity in the Cherry County Wetlands BUL is likely to make the wetland network and populations of wetland-dependent species within it more resilient to perturbations at multiple scales than the Central Loess Hills and Rainwater Basin BULs.

In addition to affecting functional connectivity, differing intensities of landcover change may be driving disparities in herpetofauna habitat quality among Nebraska landscapes. For instance, dense clusters of wetlands in all three BULs likely facilitate the movement of anuran and aquatic turtle species among wetland patches—thereby increasing the resilience of metapopulations to disturbances (e.g., desiccation) occurring in single or multiple wetlands. However, an individual's ability to immigrate/emigrate is not, in and of itself, enough to ensure persistence; habitat quality—among other factors—is also critical. As an example, the largest and densest wetland cluster in the Cherry County Wetlands BUL (Figure 18) likely provides higher quality habitat for anurans and aquatic turtles—including the State-threatened Blanding's turtle—than the largest and densest wetland cluster in the Rainwater Basin (Figure 20).

The results of this chapter may be compared to the results of Uden et al. (2014), who considered the importance of reserves and human-constructed wetlands for functional connectivity of wetlands for anurans in the Rainwater Basin. Although that study and this chapter used different data sources, they applied the same general approach to network construction and analysis. One of the primary conclusions of Uden et al. (2014) was that the construction of irrigation reuse pits for water storage may help maintain functional connectivity for anurans within the Rainwater Basin, assuming they do not act as population sinks. Furthermore, Uden et al. (2014) posited that the scale of human landscape modification (i.e., natural wetland destruction and irrigation reuse pit construction) may be biasing connectivity to benefit large, longer-dispersing, non-native species like bullfrogs over smaller, shorter-dispersing, native species like cricket frogs. This assertion is supported by the results of this chapter, which identified thresholds in network-wide connectivity between 0.50 and 1.00 km dispersal distances in the Rainwater Basin and Central Loess Hills BULs, but not the less modified Cherry County Wetlands BUL. On the other hand, Uden et al. (2014) detected a similar connectivity in the historical Rainwater Basin landscape—as indicated by soil survey data and other information from the early 20th century—which means that such connectivity thresholds are not necessarily a hallmark of human landscape modification.

Additional information could be used to improve and expand upon the approaches adopted in this chapter and Uden et al. (2014). Because of information gaps related to travel costs and directions associated with species movements in the three BULs, Euclidian distance was used to represent travel paths within the network. Future studies—informed by species-specific movement data in different landcover classes—could expand upon this approach by applying resistance weights to movements across specific landcover classes and specifying movement direction, in order to identify population sources and sinks. Future studies could also explore the use of alternative wetland datasets, such as county-level SSURGO data or the Annual Habitat Survey in the Rainwater Basin, for functional connectivity assessments. Then, comparisons of results from different studies could be aggregated to address uncertainties related to dataset-specific effects of functional connectivity evaluations. Still another area for future improvement involves studying the use of small, ephemeral wetlands by herpetofauna. By only considering wetlands with areas ≥ 0.1 ha, this study eliminated thousands of potential wetland nodes that could be used by anuran and aquatic turtle species as habitat or stepping stones to more suitable habitats. However, the duration for which these wetlands are inundated, as well as their use by herpetofauna, are unclear. Finally, future studies could explore the role of dispersal barriers and conduits in facilitating the movement of herpetofauna among wetland habitat patches. Indeed, the construction of fences and culverts under highways in the Nebraska Sandhills has reduced vehicle mortality for Blanding's turtles and other herpetofauna in the Cherry County Wetlands BUL. In a broader sense, the results of this chapter could aid decision-makers in the evaluation of social–ecological tradeoffs amidst cropland conversion and other forms of human-driven landcover change.

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TABLES AND FIGURES

Table 1: Anuran species with the potential to rely on wetland habitats in the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) biologically unique landscapes, according to Fogell (2010). Species presence in each landscape is signified with an "X".

Species	**CCW**	**CLH**	**RWB**
Great Plains toad (*Anaxyrus cognatus*)	X	X	X
Woodhouse's toad (*Anaxyrus woodhousii*)	X	X	X
Blanchard's cricket frog (*Acris blanchardi*)	X	X	X
Cope's gray treefrog (*Hyla chrysoscelis*)		X	X
Boreal chorus frog (*Pseudacris maculata*)	X	X	X
Great Plains narrowmouth toad (*Gastrophryne olivacea*)			X
Plains leopard frog (*Lithobates blairi*)		X	X
Bullfrog (*Lithobates catesbeianus*)	X	X	X
Northern leopard frog (*Lithobates pipiens*)	X	X	X
Plains spadefoot (*Spea bombifrons*)	X	X	X

Table 2: Aquatic turtle species with the potential to rely on wetland habitats in the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) biologically unique landscapes, according to Fogell (2010).

Species	**CCW**	**CLH**	**RWB**
Common snapping turtle (*Chelydra serpentina*)	X	X	X
Northern painted turtle (*Chrysemys picta*)	X	X	X
Blanding's turtle (*Emydoidea blandiningii*)	X	X	X
Yellow mud turtle (*Kinosternon flavescens*)	X		X
Smooth softshell (*Apalone mutica*)			X
Spiny softshell (*Apalone spinifera*)	X	X	X

Table 3: Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent in the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) Biologically Unique Landscapes, based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011).

Class	**CCW**	**CLH**	**RWB**
Grass	679,553 (96)	394,747 (70)	305,901 (19)
Water	21,520 (3)	5,594 (1)	29,414 (2)
Developed	5,623 (< 1)	17,832 (3)	112,334 (7)
Trees	1,946 (< 1)	50,170 (9)	50,237 (3)
Crops	562 (< 1)	99,271 (17)	1,092,844 (69)
Total	709,204	567,614	159,0731

Table 4: Results of nearest neighbor analysis for the Cherry County Wetlands (CCW), Central Loess Hills (CLH), and Rainwater Basin (RWB) biologically unique landscapes. In each landscape, the number of wetlands (No. wets) in the associated area was used to calculate a mean expected distance (Exp dist) between points, assuming their random distribution. This expected mean distance among points was then compared to the observed mean distance (Obs dist) among points via a chi-squared test. Lower z-scores represent more clustered wetland distributions, and p-values < 0.05, which are listed in bold font, indicate significantly clustered points.

BUL	**No. wets**	**Exp dist**	**Obs dist**	**z-score**	**p-value**
CCW	13,050	458.71	227.44	-110.18	**< 0.01**
CLH	5,786	586.69	452.19	-33.36	**< 0.01**
RWB	18,270	655.32	411.43	-96.24	**< 0.01**

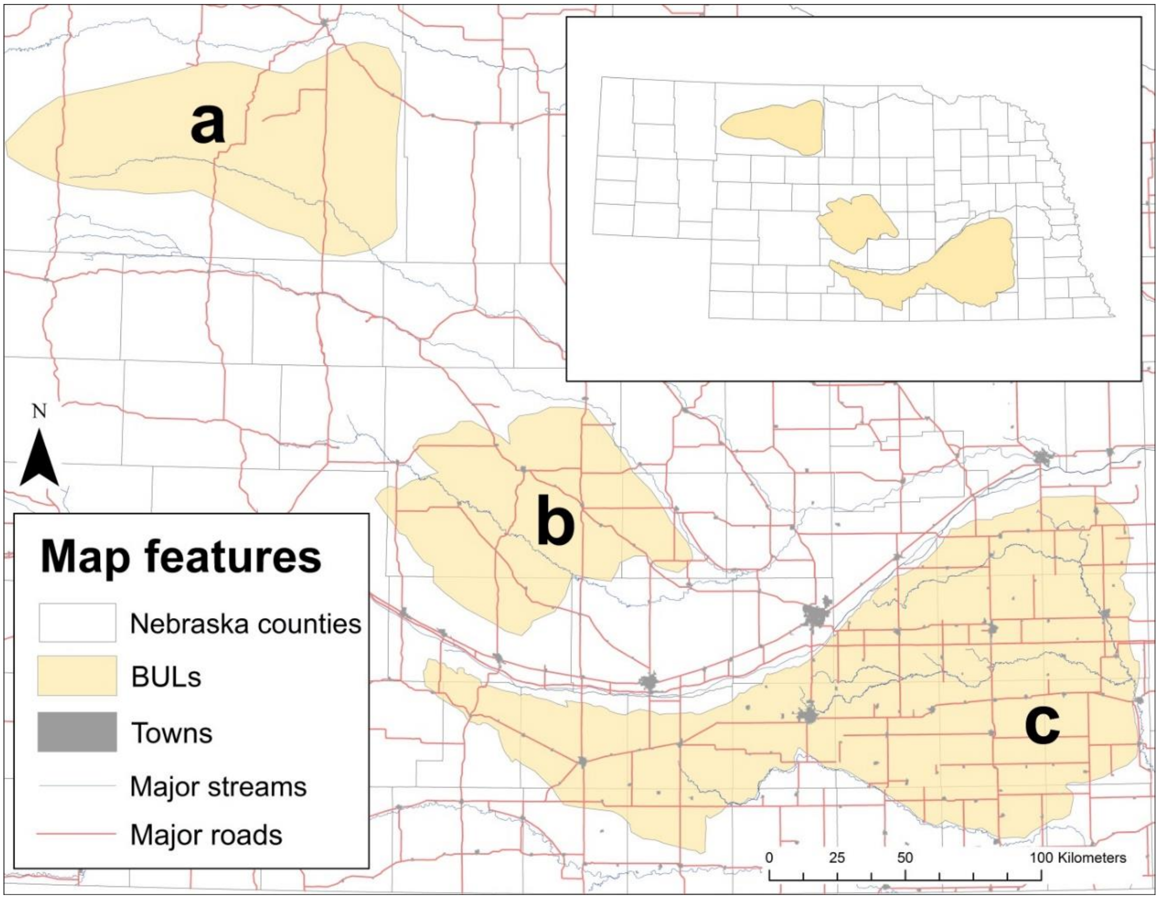
a
b
c
N
Map features
Nebraska counties
BULs
Towns
Major streams
Major roads
0
25
50
100 Kilometers

Figure 1: Locations of the a) Cherry County Wetlands, b) Central Loess Hills and c) Rainwater Basin biologically unique landscape(s) (BUL) in north-central, central, and south-central Nebraska, U.S.A., respectively.

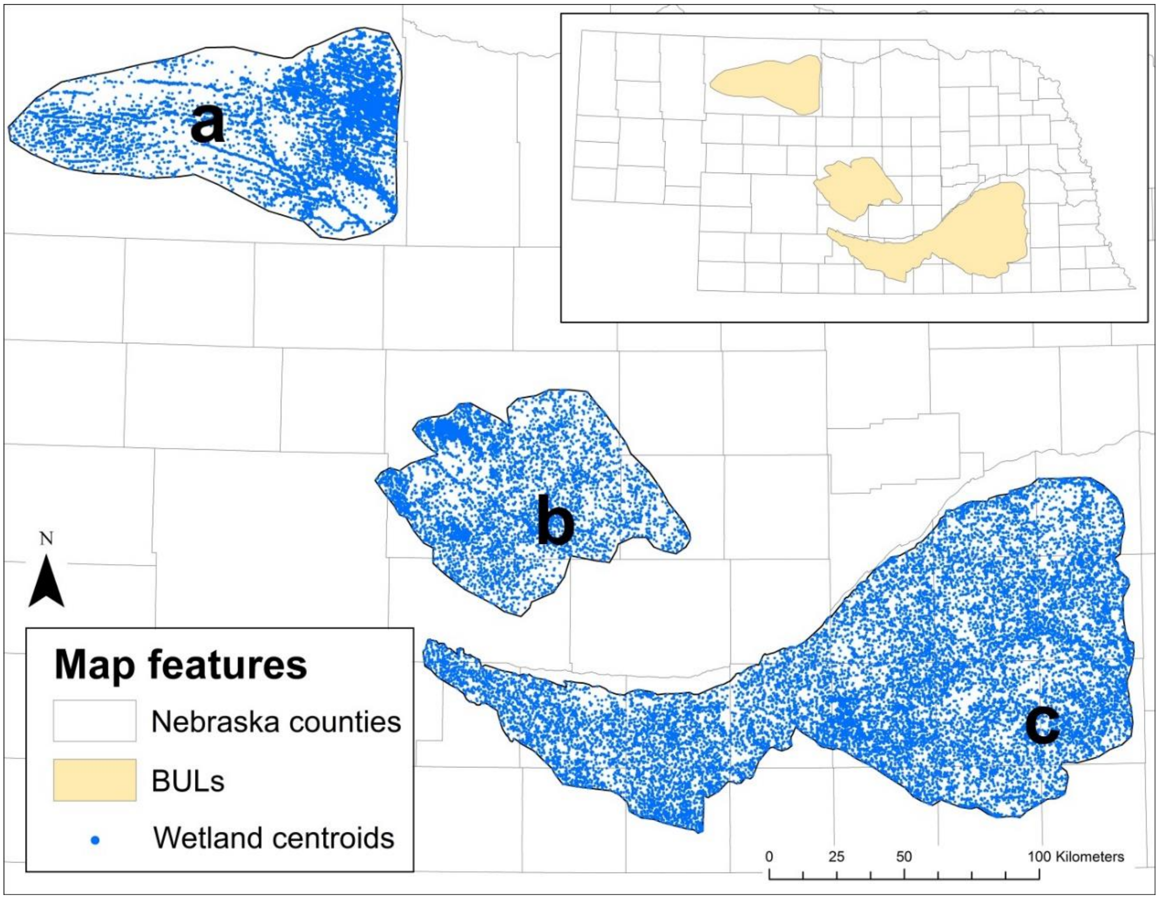
a
b
c
N
Map features
Nebraska counties
BULs
Wetland centroids
0
25
50
100 Kilometers

Figure 2: Wetland centroids in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL) of Nebraska, U.S.A.

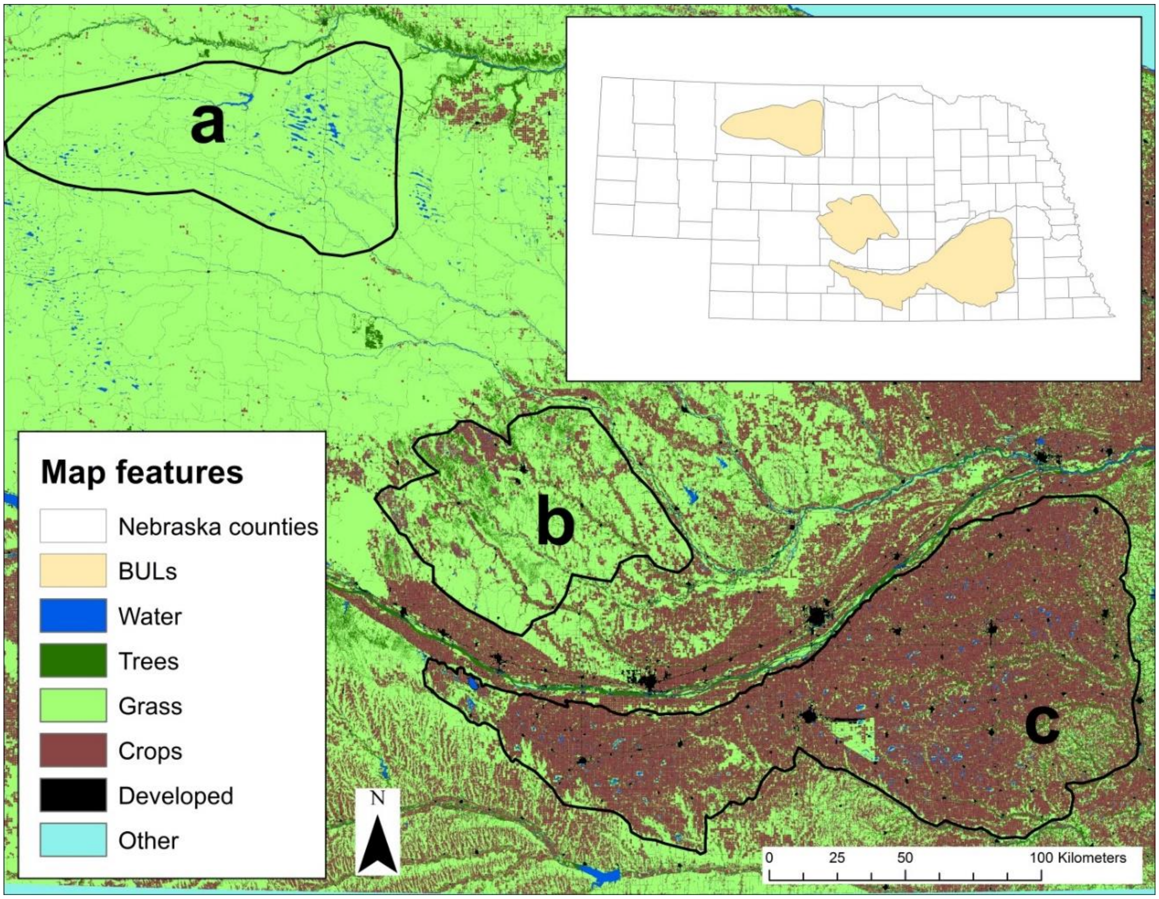
a
b
c
Map features
Nebraska counties
BULs
Water
Trees
Grass
Crops
Developed
Other
N
0
25
50
100 Kilometers

Figure 3: Reclassified Nebraska, U.S.A. landcover within the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011).

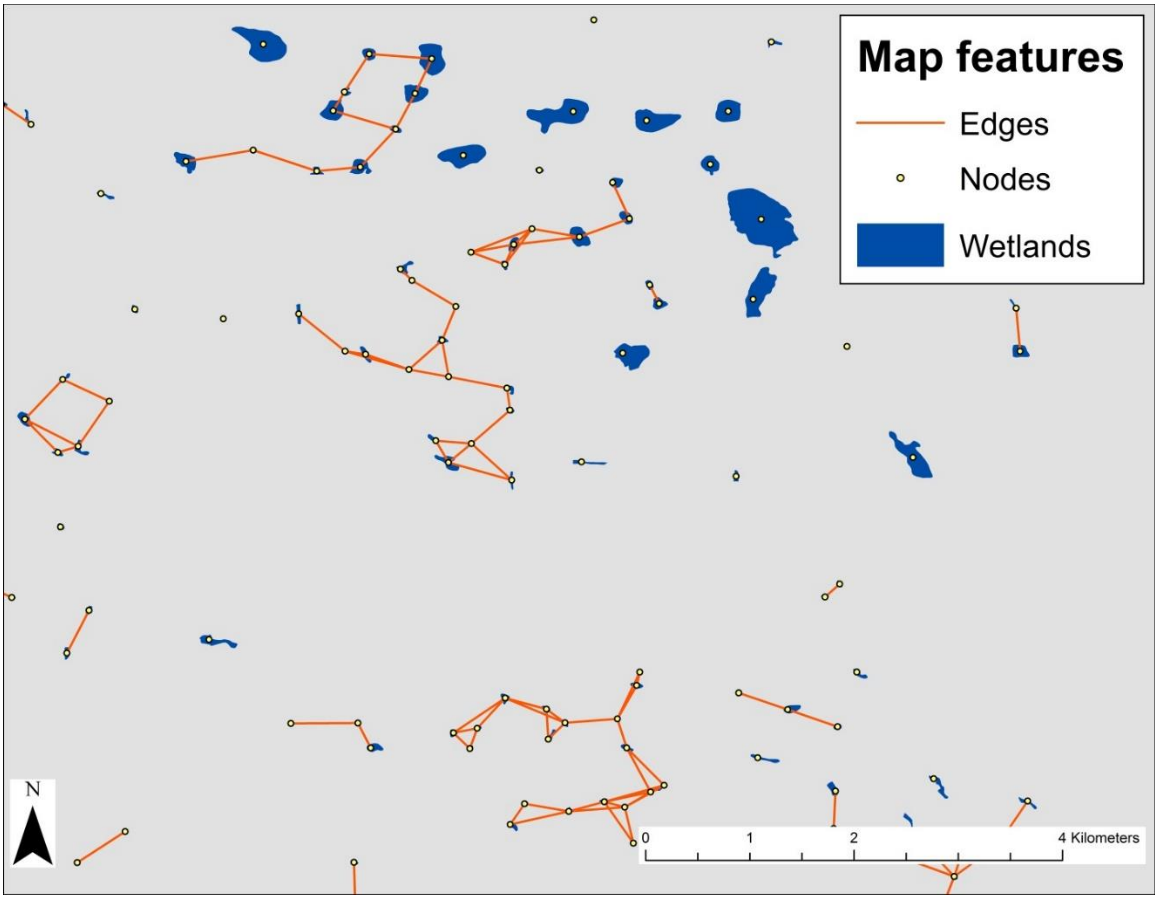
Map features
Edges
Nodes
Wetlands
N
0
1
2
4 Kilometers

Figure 4: Example of wetland connectivity network, where wetland centroids constitute nodes and Euclidian (i.e., straight-line) distances between centroids constitute edges.

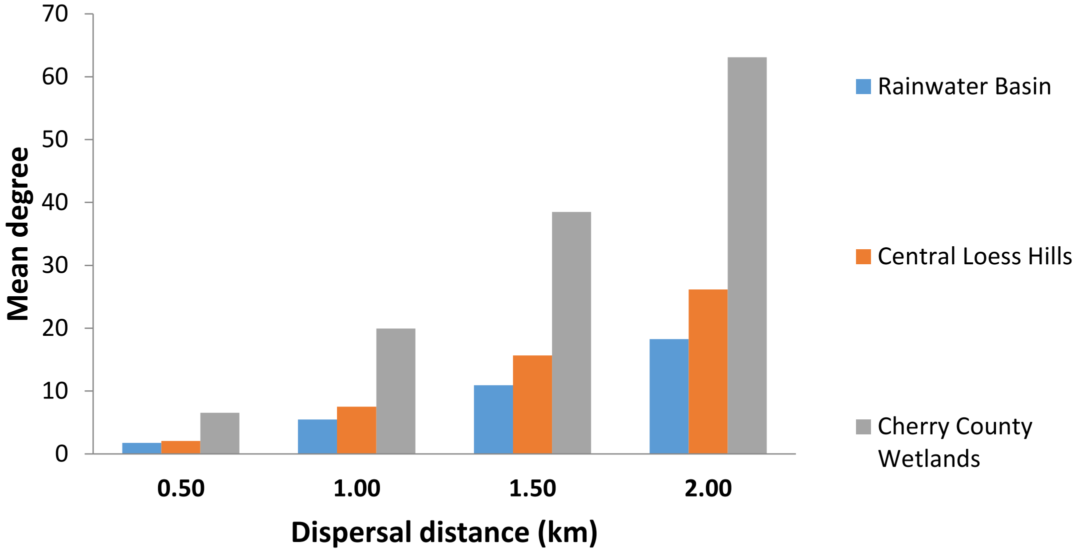

Figure 5: Mean wetland degree within the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. Here, wetland degree represents the number of direct connections a wetland maintains with neighboring wetlands at a given dispersal distance.

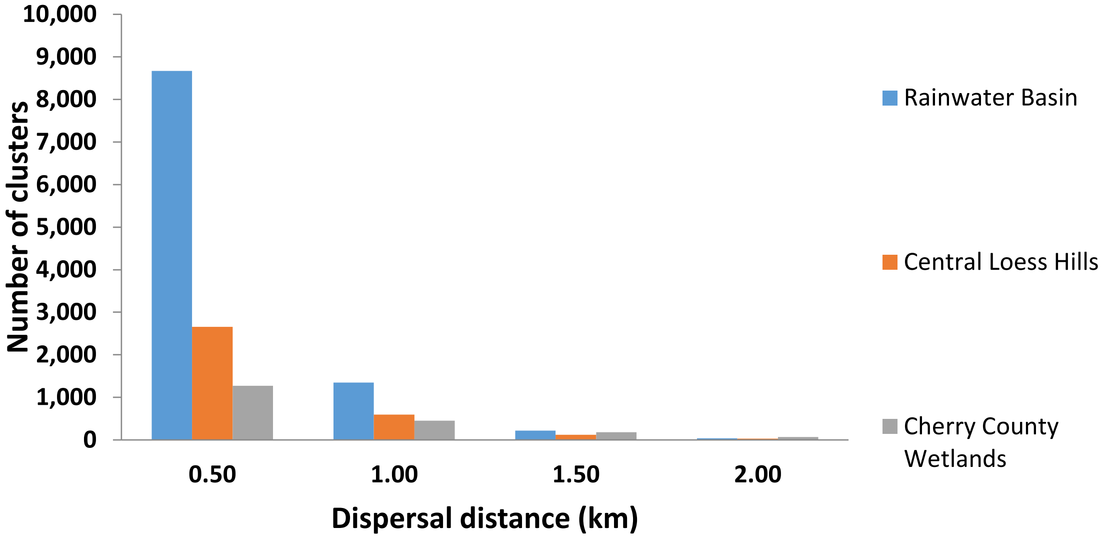

Figure 6: Total number of wetland clusters within the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. Here, wetland clusters represent groups of functionally connected wetlands at a given dispersal distance.

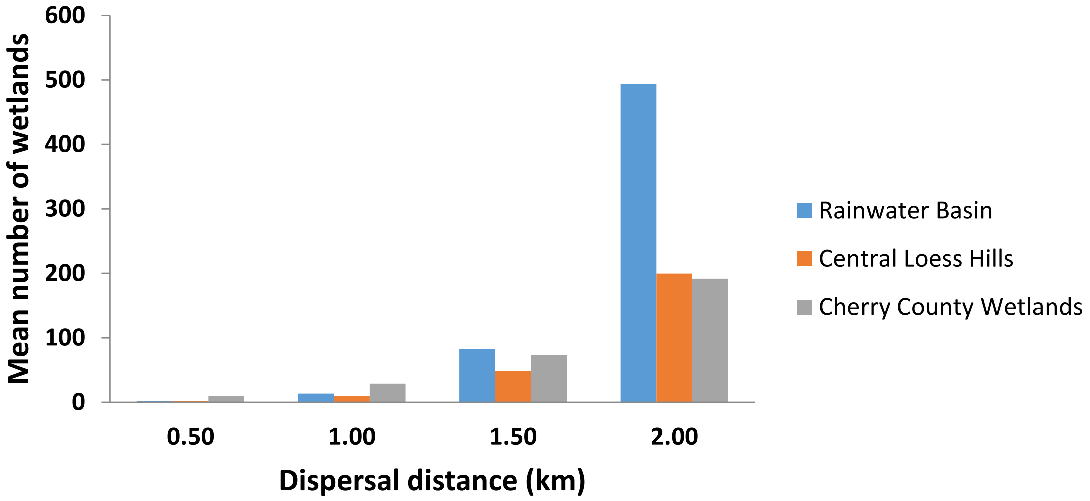

Figure 7: Mean number of wetlands per wetland cluster in the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. Here, wetland clusters represent groups of functionally connected wetlands at a given dispersal distance.

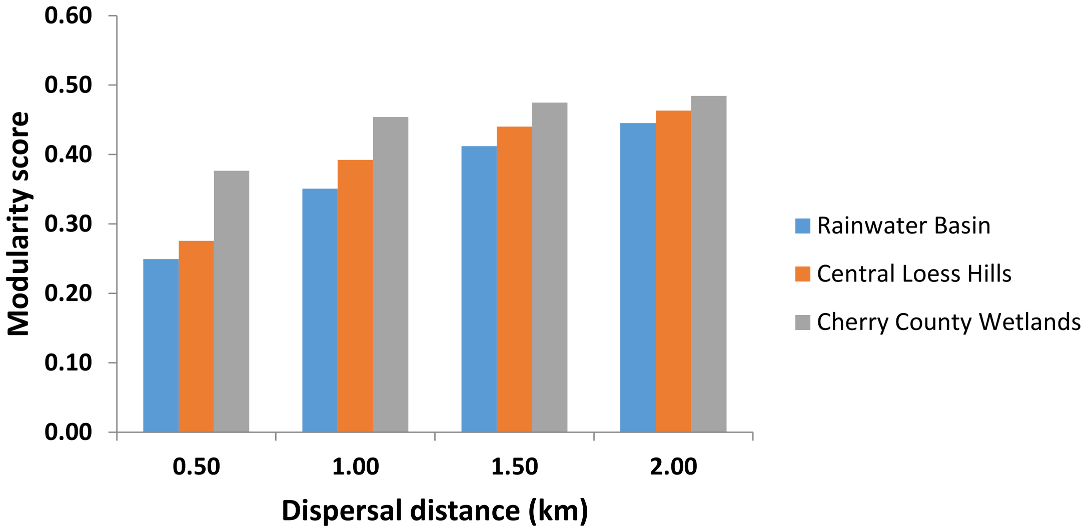

Figure 8: Network-level modularity for the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. Here, modularity describes the separation of network nodes into highly connected clusters that are sparsely connected with one another.

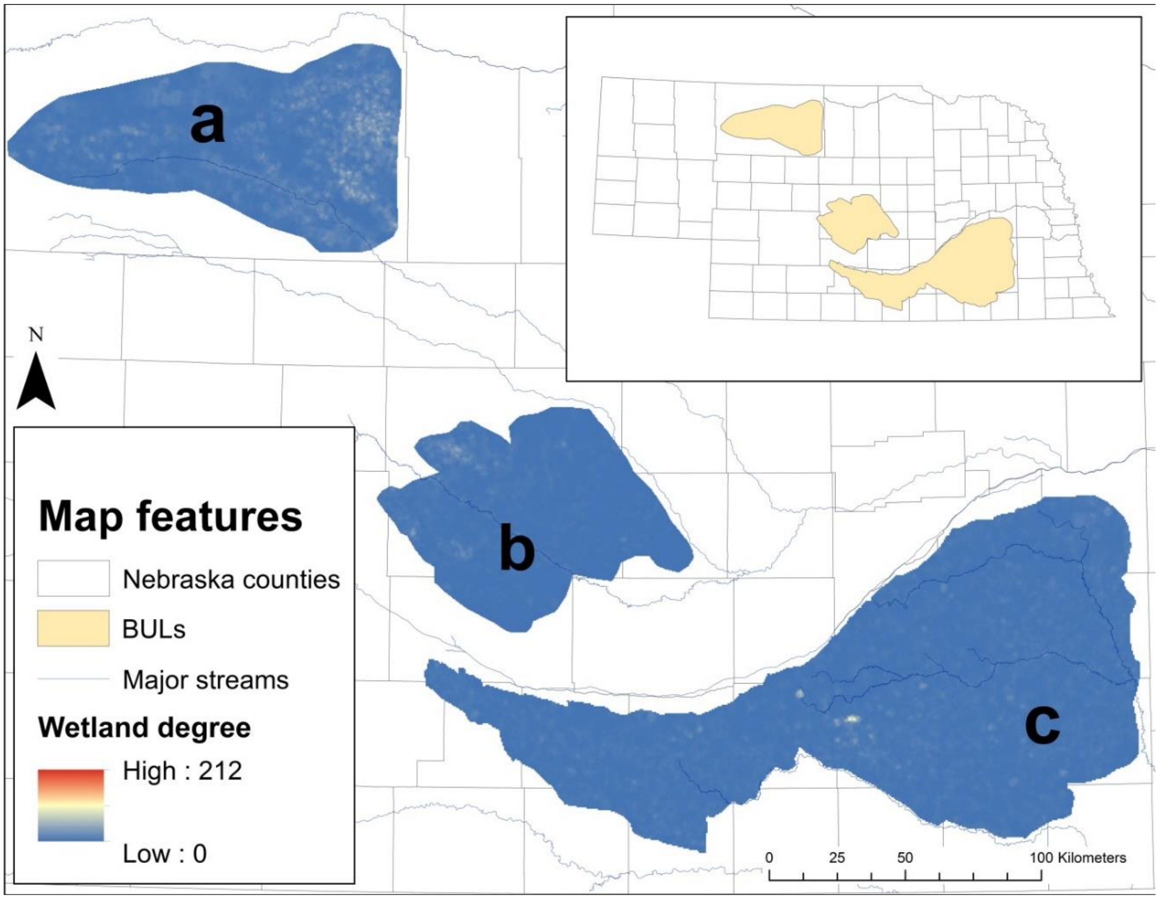
a
b
c
N
Map features
Nebraska counties
BULs
Major streams
Wetland degree
High : 212
Low : 0
0
25
50
100 Kilometers

Figure 9: Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 0.50 kilometers.

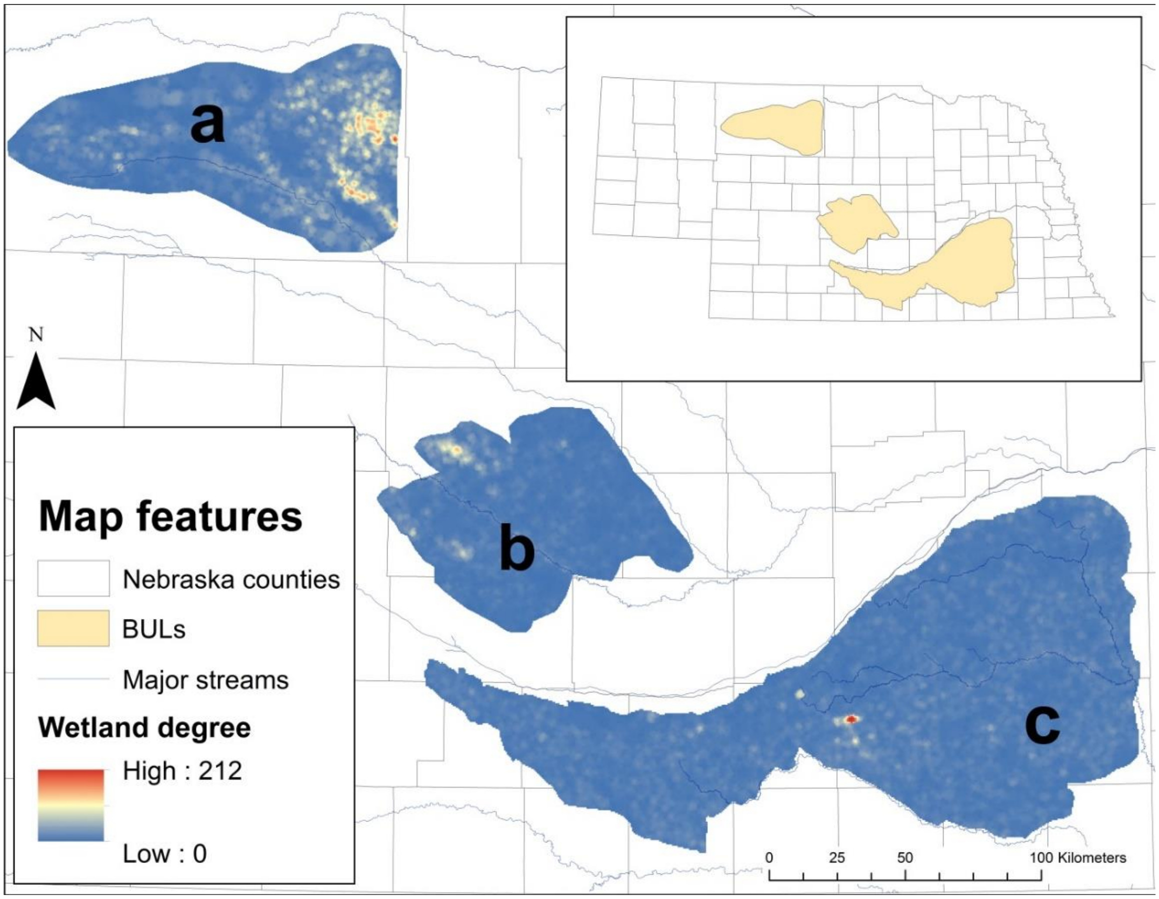
a
b
c
N
Map features
Nebraska counties
BULs
Major streams
Wetland degree
High : 212
Low : 0
0
25
50
100 Kilometers

Figure 10: Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.00 kilometers.

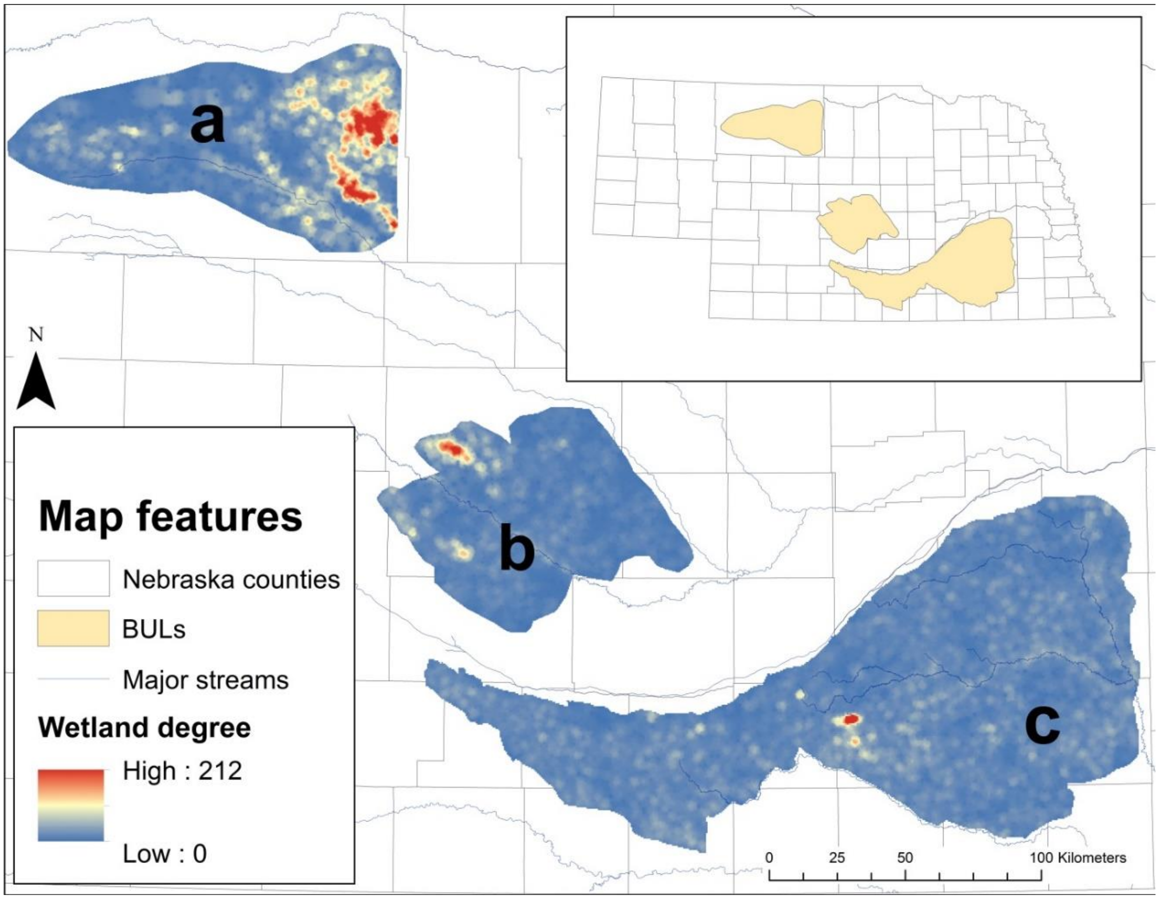
a
b
c
N
Map features
Nebraska counties
BULs
Major streams
Wetland degree
High : 212
Low : 0
0
25
50
100 Kilometers

Figure 11: Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.50 kilometers.

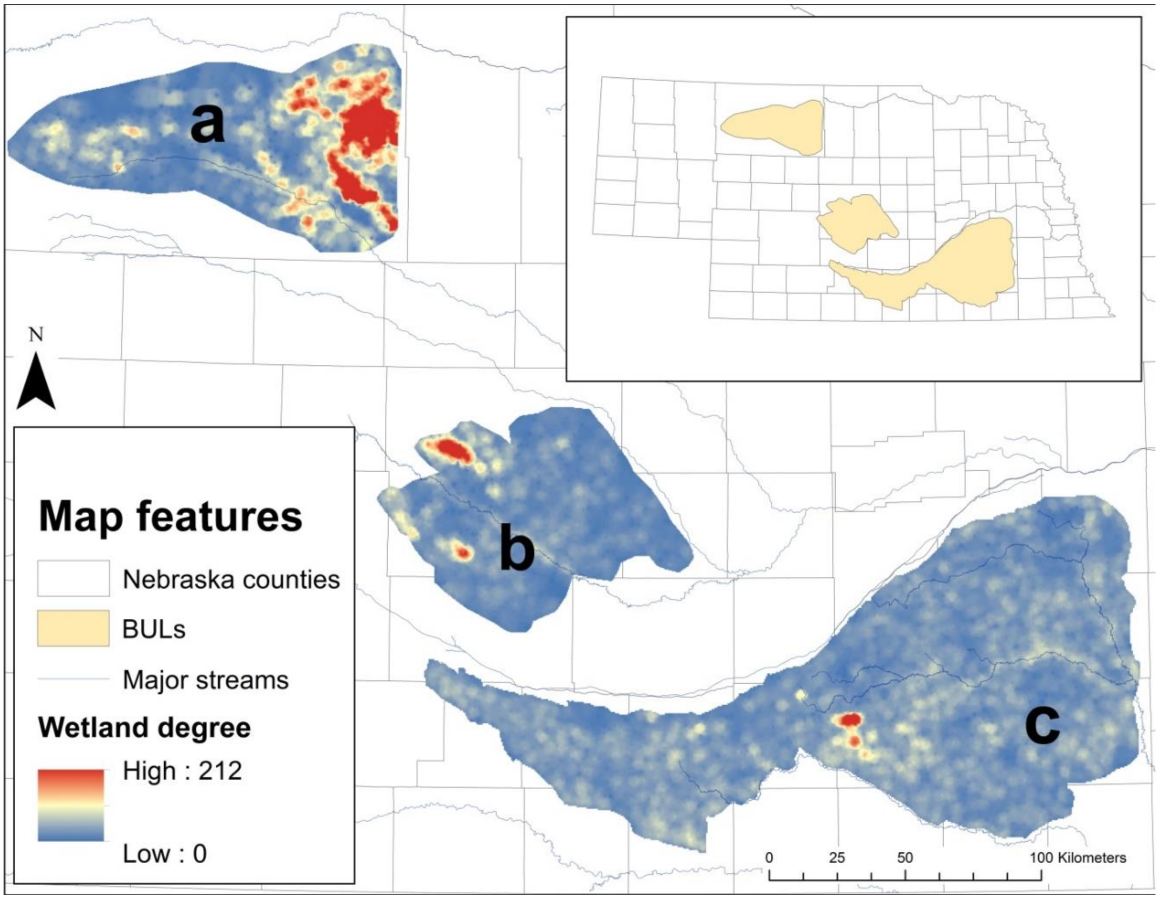
a
b
c
N
Map features
Nebraska counties
BULs
Major streams
Wetland degree
High : 212
Low : 0
0
25
50
100 Kilometers

Figure 12: Inverse distance weighted (i.e., interpolated) surface of wetland degree in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 2.00 kilometers.

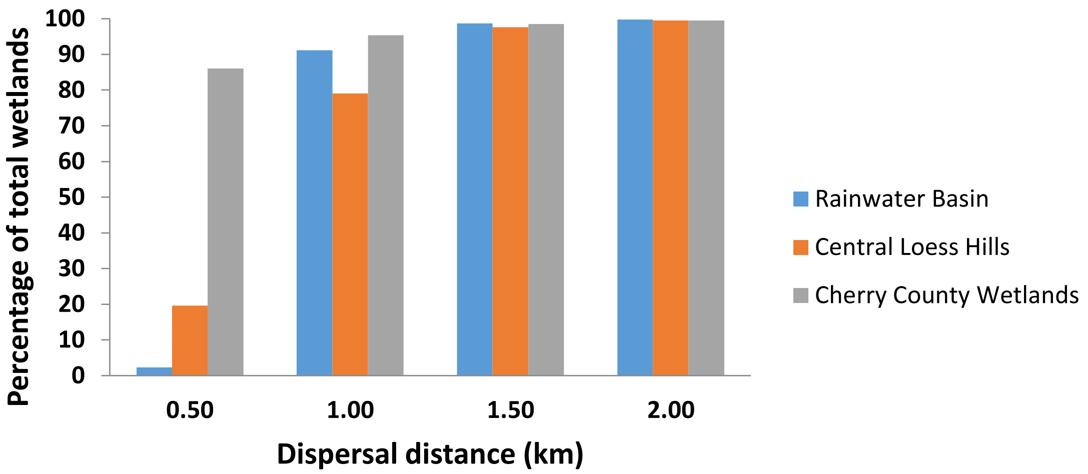

Figure 13: Percentages of total network wetlands within the single largest wetland cluster in the Cherry County Wetlands, Central Loess Hills, and Rainwater Basin biologically unique landscape(s) (BUL) at assumed maximum dispersal distances of 0.50, 1.00, 1.50, and 2.00 kilometers. Here, wetland clusters represent groups of functionally connected wetlands at a given dispersal distance.

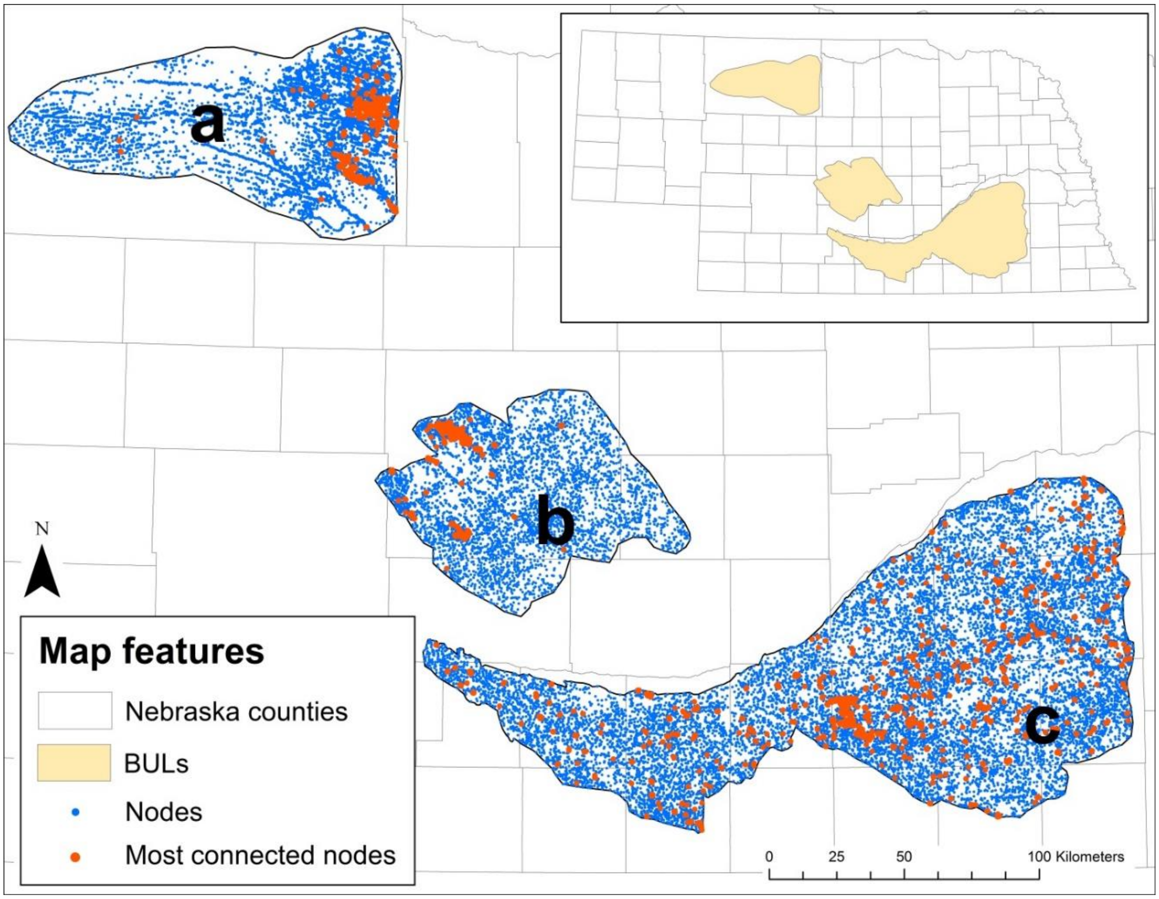
a
b
c
N
Map features
Nebraska counties
BULs
Nodes
Most connected nodes
0
25
50
100 Kilometers

Figure 14: Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 0.50 kilometers. Connectivity rankings are based on the number of direct connections each node maintains with adjacent nodes (i.e., degree).

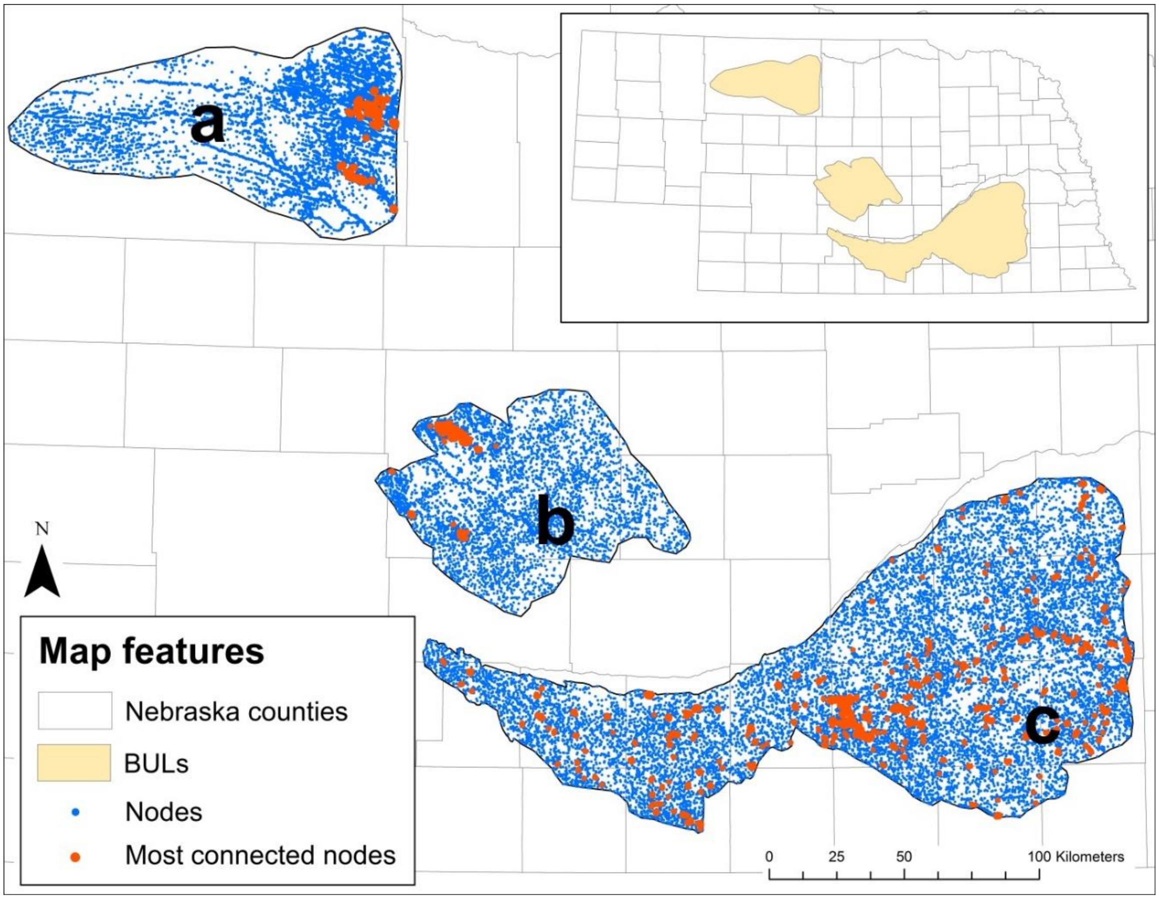
a
b
c
N
Map features
Nebraska counties
BULs
Nodes
Most connected nodes
0
25
50
100 Kilometers

Figure 15: Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.00 kilometers. Connectivity rankings are based on the number of direct connections each node maintains with adjacent nodes (i.e., degree).

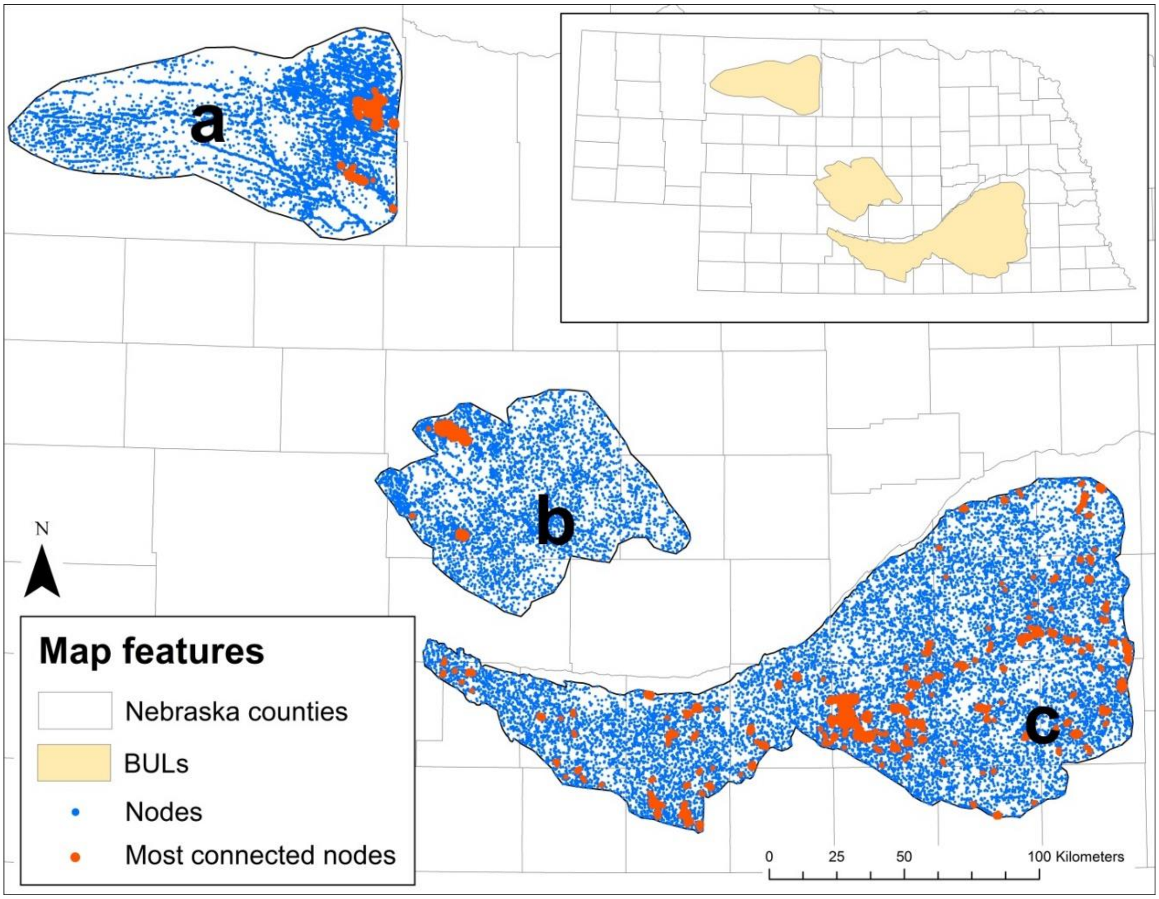
a
b
c
N
Map features
Nebraska counties
BULs
Nodes
Most connected nodes
0
25
50
100 Kilometers

Figure 16: Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 1.50 kilometers. Connectivity rankings are based on the number of direct connections each node maintains with adjacent nodes (i.e., degree).

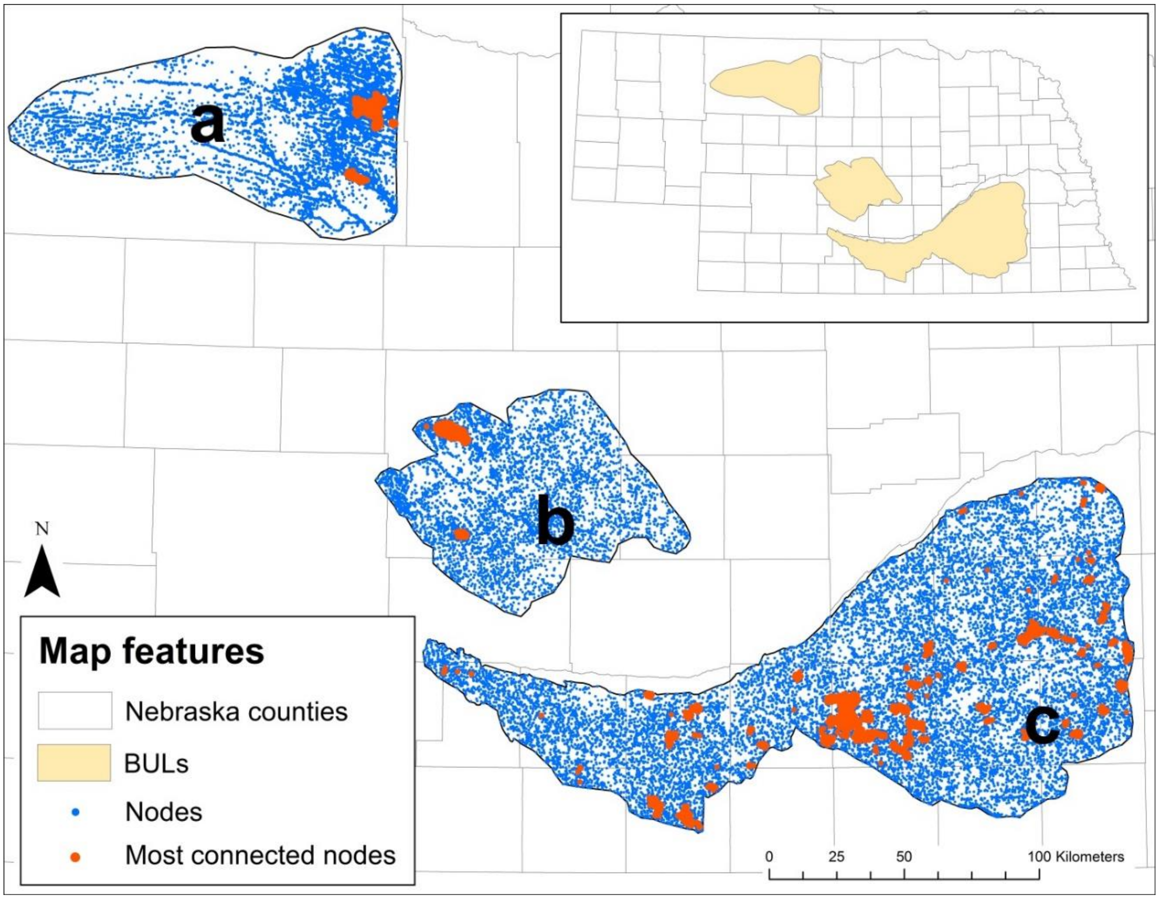
a
b
c
N
Map features
Nebraska counties
BULs
Nodes
Most connected nodes
0
25
50
100 Kilometers

Figure 17: Most connected wetland nodes overlaid on all wetland nodes in the a) Cherry County Wetlands, b) Central Loess Hills, and c) Rainwater Basin biologically unique landscape(s) (BUL), assuming a maximum dispersal distance of 2.00 kilometers. Connectivity rankings are based on the number of direct connections each node maintains with adjacent nodes (i.e., degree).

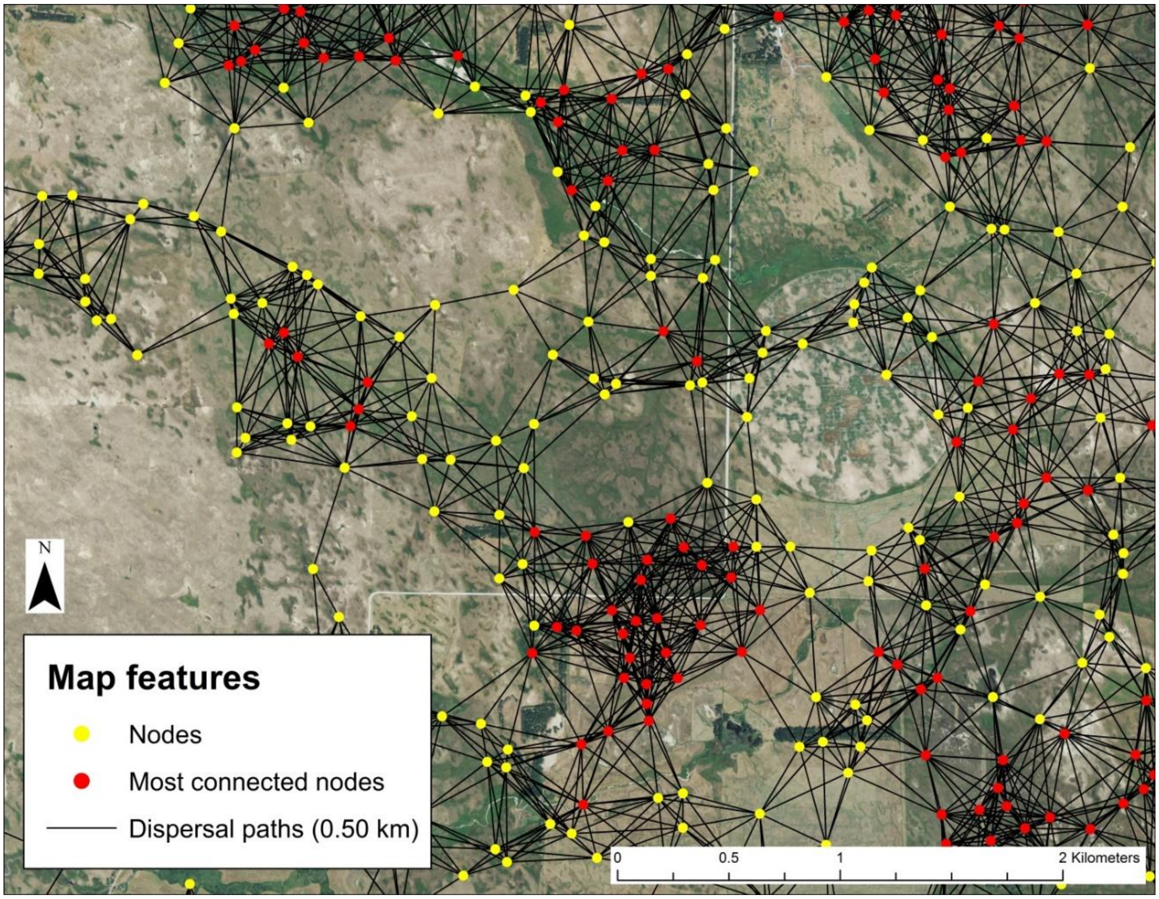
N
Map features
Nodes
Most connected nodes
Dispersal paths (0.50 km)
0
0.5
1
2 Kilometers

Figure 18: 2012 aerial imagery of the portion of the Cherry County Wetlands BUL with particularly high levels of functional wetland connectivity for herpetofauna, assuming a maximum dispersal distance of 0.50 kilometers. Connectivity rankings are based on the number of direct connections each node maintains with adjacent nodes (i.e., degree). The most connected nodes are those with degree scores in the top 10%. The dominant landcover class in which wetlands are embedded is Sandhills mixedgrass prairie.

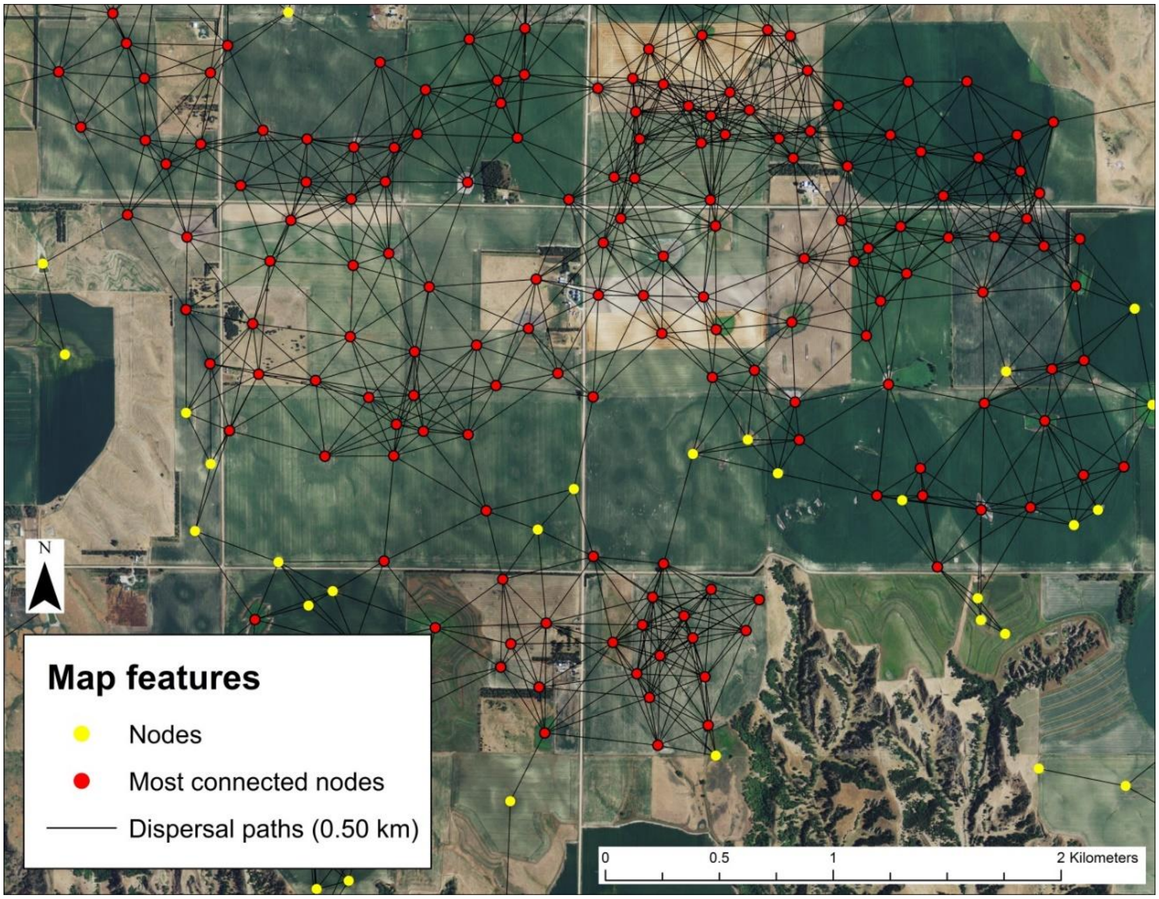
N
Map features
Nodes
Most connected nodes
Dispersal paths (0.50 km)
0
0.5
1
2 Kilometers

Figure 19: 2012 aerial imagery of the portion of the Central Loess Hills BUL with particularly high levels of functional wetland connectivity for herpetofauna, assuming a maximum dispersal distance of 0.50 kilometers. Connectivity rankings are based on the number of direct connections each node maintains with adjacent nodes (i.e., degree). The most connected nodes are those with degree scores in the top 10%. The dominant landcover class in which wetlands are embedded is rowcrop agriculture.

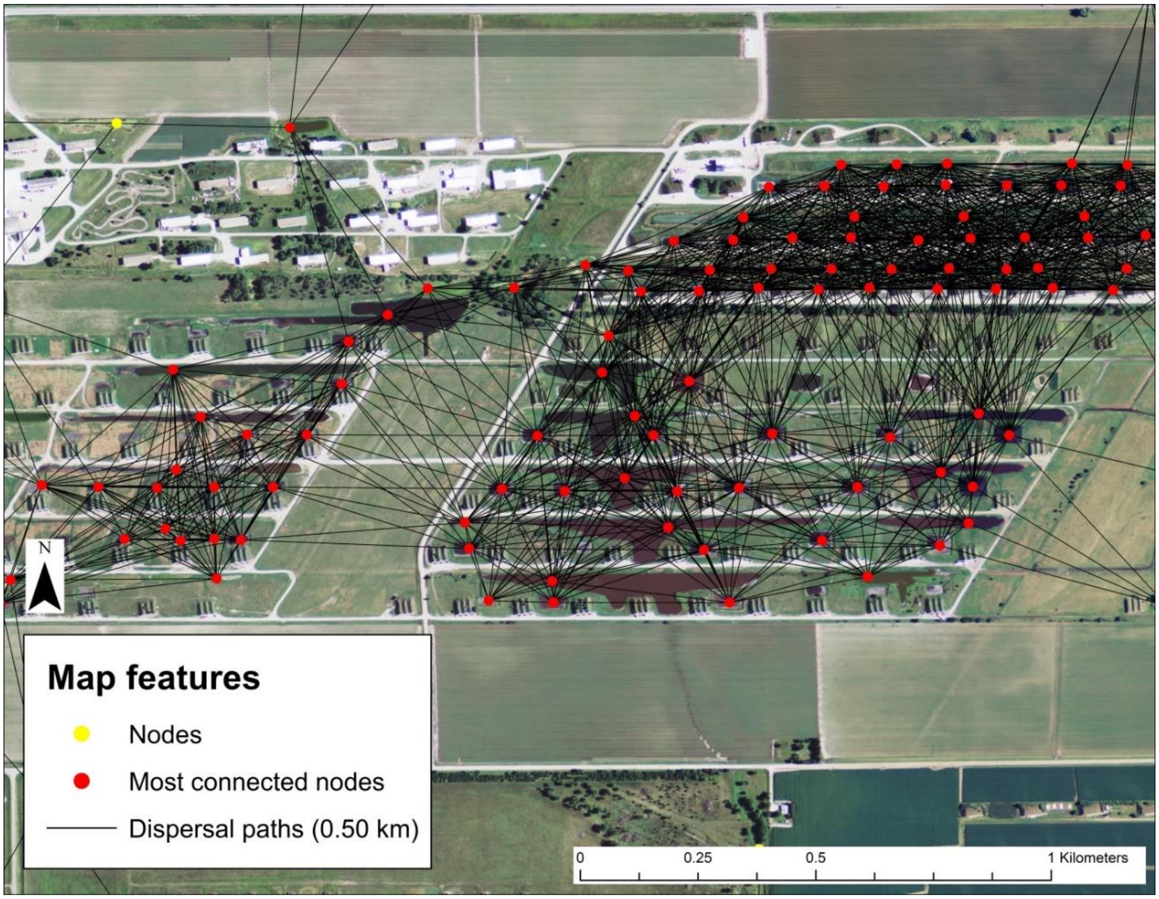
N
Map features
Nodes
Most connected nodes
Dispersal paths (0.50 km)
0
0.25
0.5
1 Kilometers

Figure 20: 2012 aerial imagery of the portion of the Rainwater Basin BUL with particularly high levels of functional wetland connectivity for herpetofauna, assuming a maximum dispersal distance of 0.50 kilometers. Connectivity rankings are based on the number of direct connections each node maintains with adjacent nodes (i.e., degree). The most connected nodes are those with degree scores in the top 10%. The landcover class in which wetlands are embedded is highly modified by human activity, as are the wetlands themselves.

CHAPTER 6: A LANDCOVER CHANGE-BASED ADPATIVE INVASIVE SPECIES DISTRIBUTION MODEL FOR AN AQUATIC SNAIL IN SOUTHEAST NEBRASKA, U.S.A.

ABSTRACT

Changes in landcover and associated human activities may facilitate the spread of introduced species in social–ecological system(s) (SES). The Chinese mystery snail (*Bellamya chinensis*) is a large aquatic snail that has recently been observed in water bodies of southeast Nebraska, U.S.A. Recent local studies have tested methodologies for mark retention in mark–recapture studies, estimated population sizes in individual water bodies, estimated fecundity, documented tolerances to desiccation and extreme temperatures, documented population die-offs, and modeled pathways of spread in human recreation. However, assessments of landscape-scale habitat suitability and the relationship between habitat suitability and human-driven landcover change have not yet been undertaken. In this chapter, I apply Uden et al.’s (2015) 10-step framework for adaptive invasive species distribution model(ing) (iSDM) to develop an iSDM for the Chinese mystery snail in Lancaster County, Nebraska. Within the framework, a random forests model was trained with presence/absence data from 13 surveyed water bodies, validated with a comparison of predicted *versus* observed Chinese mystery snail presence/absence, and then extrapolated to predict Chinese mystery snail presence/absence in 1,791 additional water bodies in Lancaster County. Predictor variables used to explain variability in Chinese mystery snail presence/absence were

water body area, road density, and the Euclidian distance to the City of Lincoln, with the last two landcover-based predictors serving as proxies for human activity and movement. Road density was the most important variable for describing variability in snail presence/absence, and was followed by water body area and distance from Lincoln, respectively. Model predictive ability was relatively poor, based on the area under the curve statistic of 0.58 from the comparison of predicted and observed presence/absence values. Nevertheless, this exercise represents an important first step for informing Chinese mystery snail management and for improving iSDM predictive ability. Comparative iSDM exercises in eastern Nebraska and elsewhere in the Chinese mystery snail's invaded and native ranges could increase understanding of the landcover change-based factors driving its distribution and help inform management decisions and actions.

INTRODUCTION

Urbanization and transportation network development are two forms of human-driven landcover change that may directly and indirectly facilitate the spread of introduced species in social–ecological system(s) (SES) (Hulme 2009). For instance, activities associated with the spread of aquatic invasive species include recreation (Vander Zanden & Olden 2008) and commerce (Keller & Lodge 2007). Proactively modeling and managing the spread of aquatic invasive species greatly reduces the likelihood of negative consequences to human populations within social–ecological system(s) (SES) (Mehta et al. 2007).

Species distribution models(s) (SDM) and related invasive species distribution model(s) (iSDM)—are promoted for increasing knowledge about species' geographic distributions, improving understanding about the factors that drive them, and aiding management decisions and actions (Elith and Leathwick 2009; Vaclavik and Meentemeyer 2009). However, distributional models for invasive species often suffer from the failure to meet important ecological model assumptions—perhaps most notably the assumption of equilibrium between a species and its environment (Elith et al. 2010). Meanwhile, the most effective point for management to intervene in the invasion process is early, before environmental equilibrium has been achieved (Leung et al. 2002). Despite violations and limitations, iSDMs continue to be promoted for their utility for addressing biological invasions and related social–ecological challenges (Cote & Reynolds 2002).

Uden et al. (2015) proposed a 10-step framework for iSDM development (Figures 1 and 2) that promotes consistency and transparency in iSDM development, allows for changes in invasive drivers and filters, integrates mechanistic and correlative modeling techniques, balances the avoidance of type 1 (i.e., false positives/presences) and type 2 (i.e., false negatives/absences) errors in predictions, encourages the linking of monitoring and management actions, and facilitates incremental improvements in models and management across space, time, and institutional boundaries. Developing and iteratively improving iSDMs may increase their utility for addressing social–ecological challenges associated with invasive species establishment.

In this chapter, I apply the framework of Uden et al. (2015) to the development of a landcover change-based iSDM for the Chinese mystery snail (*Bellamya chinensis*), a large aquatic gastropod—native to Asia—that has recently been introduced and established in a number of eastern Nebraska, U.S.A. water bodies (Chaine et al. 2012; Haak et al. 2017). This chapter represents an initial iSDM for the Chinese mystery snail in southeast Nebraska that could be iteratively improved within an adaptive iSDM framework (Uden et al. 2015), in order to inform management decisions, actions, and tradeoffs associated with landcover change and invasive species spread in the context of SESs thinking.

METHODS

Framework implementation

The 10-step adaptive iSDM framework of Uden et al. (2015) (Figure 2) was used as a guide in the production of an iSDM for the Chinese mystery snail in water bodies of Lancaster County in southeast Nebraska. Uden et al.'s (2015) framework consists of the following 10 steps: 1) invasion characterization; 2) objectives statement; 3) assumption and uncertainty articulation; 4) scale recognition and assignment; 5) predictor variable selection; 6) modeling technique adoption; 7) autocorrelation supervision; 8) prediction, validation and mapping; 9) management and monitoring; and 10) refinement. Although all 10 steps of the framework pertain broadly to adaptive invasive species modeling, monitoring, and management, steps 9 and 10 deal specifically with management, monitoring, and model improvement. Because this chapter represents the initiation of the first iteration of the development of an iSDM for the Chinese mystery snail in Lancaster County, it has not yet been applied to management, additional monitoring based on its predictions has not yet been undertaken, and it has not yet entered subsequent iterations of development, in which it could be improved. Therefore, implementation of the framework in this chapter was limited to steps 1–8, which are detailed below.

Step 1: Invasion characterization

The Chinese mystery snail is a large aquatic gastropod that is native to Asia and which has recently been introduced and established in a number of eastern Nebraska water bodies (Chaine et al. 2012; Haak et al. 2017). A number of recent studies have tested methodologies for mark retention in mark–recapture studies (Wong et al. 2013), estimated population sizes in individual water bodies (Chaine et al. 2012), estimated fecundity (Stephen et al. 2013), documented tolerances to desiccation (Unstad et al. 2013) and extreme temperatures, documented large-scale die-offs (Haak et al. 2013), and modeled pathways of spread via anthropogenic recreational activities (Haak et al. 2017).

At the scale of Lancaster County, Nebraska, the Chinese mystery snail is likely in the transport, establishment, and/or spread stages of the transport–establishment–spread–impact process of Williamson (1996) and Lockwood et al. (2007). The ecosystems being invaded and at risk of being invaded are water bodies in Lancaster County, Nebraska, which include natural wetlands and human-constructed ponds and flood control reservoirs. In addition to containing the state's second largest city, Lincoln, Lancaster County is situated within the Salt Valley Region of southeast Nebraska (Figure 3; Martin 2013; Haak et al. 2017). Geographic data on Nebraska water bodies was obtained from the U.S. Geological Survey National Hydrography Dataset (NHD) website (https://nhd.usgs.gov/), clipped to the boundaries of Lancaster County in ArcGIS (ESRI 2011), and then truncated to only include only those water bodies with areas > 1,000 square meters (m^2).

Field surveys of Chinese mystery snail occupancy were conducted from 2011–2013 by members of the Nebraska Cooperative Fish and Wildlife Research Unit. Surveys were conducted in a number of southeast Nebraska water bodies, including 13 in Lancaster County. During surveys, researchers searched for snails by hand and with nets from shore, by wading, and from kayaks and canoes. If any Chinese mystery snails were detected, they were classified as present; otherwise they were classified as absent. Snails were also considered present in the water body if empty shells were observed, collected, and verified as Chinese mystery snails.

Step 2: Objectives statement

Despite recent advances in increasing information about populations of Chinese mystery snails in water bodies of Lancaster County, there remains a basic lack of information regarding the biology species, its modes of spread, its habitats, and its current geographic distribution. For example, no assessments of landscape-scale habitat suitability and the relationship between habitat suitability and human-driven landcover change have been conducted because of the availability of only sparse data on local species' occurrences. In addition, although Haak et al. (2017) modeled potential pathways of Chinese mystery snail spread, the mechanisms by which it spread are uncertain.

Given these general uncertainties about Chinese mystery snail habitats and distributions, the established relationships between invasive species spread and human activity and movement, and the availability of geographic data for quantifying human activity and movement, the overarching objective of this study is to explore relationships between observed Chinese mystery snail presence and variables associated with human activity and movement (e.g., urban and road network development). Results could yield additional insights into the likelihood of future spread and associated social–ecological tradeoffs in Lancaster County and surrounding areas.

Step 3: Assumption and uncertainty articulation

There are a number of assumptions and uncertainties concerning the presence and spread of Chinese mystery snails that could affect the construction of an iSDM for them in Lancaster County, Nebraska. First, the presence/absence data with which the model was trained could contain errors. Although false positives (i.e., type 1 error) can be assumed not to have occurred, false negatives (i.e., type 2 error) are likely, given the fact that entire water bodies were not searched and the difficulties in searching for aquatic snails in general. Secondly, the temporal lag between the collection of data in 2011–2013 and the initiation of the adaptive iSDM framework in 2016–2017 means that snails could have established or vanished from Lancaster County water bodies since the data collection period. In other words, model predictions may be outdated. Finally, the small sample size of water bodies surveyed could make predicting the geographic distribution of Chinese mystery snails difficult.

Step 4: Scale recognition and assignment

In the academic subdiscipline of Landscape Ecology, spatial scale encompasses both extent (i.e., total area) and grain (i.e., resolution) (Wiens 1989). Although Chinese mystery snails are capable of withstanding weeks—even months—of desiccation (Unstad et al. 2013), they have not been observed moving overland between water bodies, and can therefore be assumed to be remain in the water bodies to which they are introduced. The geographic extent of this chapter is Lancaster County, and the finest grain of analysis is 30-m^2.

Step 5: Predictor variable selection

Three variables—water body area, road density (Figure 4), and Euclidian distance to Lincoln (Figure 5)—served as predictor variables for explaining variability in the presence/absence of the Chinese mystery snail in Lancaster County water bodies. For water body area, surface area (m^2) was determined in ArcGIS and added to the attribute table. Road density and Euclidian distance to Lincoln served as landcover-based indicators of human movement and activity, which are hypothesized to facilitate to spread of invasive species (Hulme 2009). A continuous raster of road densities in Lancaster County was generated at 2-km resolution with TIGER road shapefiles downloaded from the website of the Nebraska Department of Natural Resources (http://dnr.nebraska.gov/data). In addition, a continuous raster of Euclidian distance from the City of Lincoln was generated at 30-m^2 resolution for Lancaster County with a TIGER shapefile of the City of Lincoln downloaded from the website of the Nebraska Department of Natural Resources.

Step 6: Modeling technique adoption

Random forests (RF)—a machine learning technique based in decision tree analysis (Breiman 2001)—was used to model Chinese mystery snail distributions, primarily because of its flexibility and ability to generate accurate predictions with sparse data (Cutler et al. 2007). In a RF, numerous classification and regression trees—which individually partition data into subgroups of maximum homogeneity based on rules derived from the data at hand (Breimann et al. 1984)—are combined to increase predictive accuracy over that of individual classification trees (Cutler et al. 2007). Bootstrap sampling (i.e., random sampling and replacement) is used to fit each classification tree in the forest to a different random subset of the data, with the remaining observations being used to make and validate predictions (Merow et al. 2014). RFs are useful for modeling complex interactions among predictor variables and their outputs include predictor variable importance values (Cutler et al. 2007). Although RF tend to be accurate predictors, they are not as useful as statistical techniques [e.g., generalized linear model(s) (GLM) and generalized additive model(s) (GAM)] for increasing understanding about relationships between predictor and response variables (Breiman 2001). All RF analyses were carried out using the randomForest function in the randomForest Package (Liaw & Wiener 2002) for the program R (R Core Team 2016). For each RF, 500 classification trees were fitted and combined.

Step 7: Autocorrelation supervision

Spatial autocorrelation is used to quantify spatial dependencies among observations in datasets (Tobler 1970; Legendre 1993; Dormann et al. 2007; Cliff & Ord 2009). In the context of this study, the existence of spatial autocorrelation means that the presence/absence of Chinese mystery snails is influenced by the presence/absence of Chinese mystery snails at surrounding locations. Although understandable—even expected—as a result of dispersal, spatial autocorrelation can be statistically problematic, in that it violates the independence assumption of many statistical techniques and can distort model predictions by over- or under-emphasizing predictor effects (Diniz-Filho et al. 2003; McPherson & Jetz 2007). However, because of the adoption of random forests as a non-parametric machine learning technique, it was not necessary to control for the effects of spatial autocorrelation in this analysis.

Step 8: Prediction, validation, and mapping

The random forests model for Chinese mystery snail occurrence trained in 13 Lancaster County water bodies was used to make predictions for the remaining 1,804 water bodies in the county with areas > 1,000 m^2. Predictions were carried out with the predict function from the stats Package in R (R Core Team 2016). Because RF utilizes bootstrap sampling when fitting different trees, there is no need to conduct a formal cross-validation (Kohavi 1995, Fushiki 2011) of predictions, because a simple comparison of model predictions with observed values is roughly equivalent to 10-fold cross validation (Cutler et al. 2007). The optimal.thresholds function in the PresenceAbsence package (Freeman & Moisen 2008) for R was used to identify the best thresholds between 0.00 and 1.00 for transferring continuous occurrence likelihood predictions from the Chinese mystery snail RF model to binomial presence/absence predictions, according to the maximum Kappa statistic (Cohen 1960).

RESULTS

For Lancaster County water bodies, the mean water body area was 117.22 hectares, the mean road density was ~2.69 kilometers (km) per km^2, and the mean Euclidian distance from the City of Lincoln was ~10.00 km (Table 1). The RF model for explaining and predicting the presence/absence of Chinese mystery snails in Lancaster County, Nebraska returned an area under the curve (AUC) statistic of 0.58, which indicates relatively poor predictive performance. The AUC statistic represents the likelihood that for any randomly-selected pair of observations of tree species presence and absence, the predictive model will assign a greater occurrence likelihood to the location where the species is truly present.

Among the three predictors, road density was the most important variable for describing variability in Chinese mystery snail presence/absence, and was followed by water body area and distance from Lincoln, respectively (Table 2). The optimal threshold value identified for transferring continuous occurrence likelihood predictions to binomial presence/absence predictions was 0.29. When the RF model was used to predict Chinese mystery snail occurrence likelihood in the 1,804 Lancaster County water bodies—which included the 13 water bodies used to train the model—the mean occurrence likelihood was 0.58. The conversion of continuous occurrence likelihoods to binomial presence/absence values via the optimal threshold resulted in predictions of Chinese mystery snail presence in 1,705 of the total 1,804 (94.51%) Lancaster County water bodies (Figure 6).

DISCUSSION

This chapter represents an initial iteration of Uden et al.'s (2015) 10-step framework for the development of an adaptive iSDM for explaining variability in and predicting the geographic distribution of the Chinese mystery snail in water bodies of

Lancaster County, Nebraska, U.S.A., where it has recently been introduced and in some cases established. This chapter dealt with development of the iSDM in steps 1–8 of the framework. In the future, results may be used to inform management and improve the iSDM in steps 9 and 10 of the framework.

Although there was only limited data available for model development (13 presence/absence observations) and model predictive performance was relatively poor (AUC = 0.58), the initiation of the process of iterative model prediction and improvement within Uden et al.'s (2015) framework could contribute to future invasive species and conservation management efforts that address Chinese mystery snail introduction, establishment, and spread. Furthermore, because it is both economically and ecologically effective to address invasions at earlier (e.g., introduction and establishment) rather than later (e.g., spread and impact) stages of invasion processes (Leung et al. 2002; Lockwood et al. 2007), having modeling frameworks in place before an invasive species is already widespread is advisable.

Recent assessments of the geographic distributions of Chinese mystery snails by Solomon et al. (2010) and Haak et al. (2017) note the role of humans in transporting propagules between water bodies. In this sense, landcover changes—specifically transportation network development—may facilitate the dispersal of invasive species like the Chinese mystery snail from human population centers into water bodies of the surrounding countryside. Future iSDM iterations for the Chinese mystery snail in southeast Nebraska may be able to increase predictive ability by more effectively incorporating anthropogenic dispersal effects and other modes of spread (Keller & Lodge

2007; Vander Zanden & Olden 2008; van Leeuwen et al. 2013). In addition, predictive performance may increase with more data from additional surveys in water bodies where the present RF model predicted Chinese mystery snail presence and absence. The accumulation of more data will also support the use of statistical modeling techniques (e.g., GLMs and GAMs) for describing the geographic distributions of Chinese mystery snails, which although often less successful at making predictions than RF and related machine learning techniques, are generally more interpretable (Breiman 2001; Guisan et al. 2002; Miller et al. 2004). Ultimately, the results of this chapter constitute an initial adaptive iSDM iteration for the Chinese mystery snail and potential landcover change-based facilitators of its spread that could be iteratively improved in the context of SESs thinking.

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TABLES AND FIGURES

Table 1: Mean area, road density, and Euclidian distance to the City of Lincoln for 13 water bodies in Lancaster County, Nebraska, U.S.A. surveyed for Chinese mystery snails (*Bellamya chinensis*) in 2011–2013. Water body area (hectares), surrounding road density [kilometers (km) per km^2], and Euclidian distance to Lincoln (km) were used as predictor variables in a random forests model of Chinese mystery snail occurrence likelihood.

Variable	**Mean value**
Area	117.2173
Euclidian distance to Lincoln	9.9576
Road density	2.6945

Table 2: Predictor variable importance values in the random forests model explaining variability in Chinese mystery snail (*Bellamya chinensis*) presence/absence in Lancaster County of Nebraska, U.S.A., where importance is defined as the mean decrease in accuracy that accompanies the removal of the parameter across all classification trees composing the random forest.

Variable	**Importance**
Road density	0.11257381
Water body area	-0.01271905
Euclidian distance to Lincoln	-0.04825476

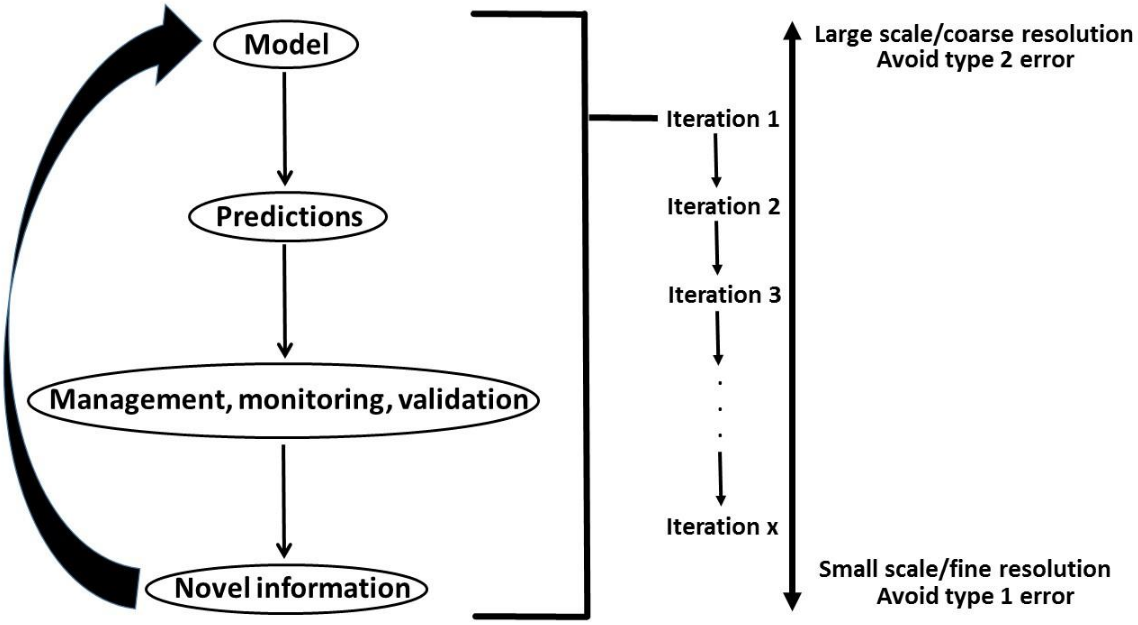
Model
Predictions
Management, monitoring, validation
Novel information
Iteration 1
Iteration 2
Iteration 3
Iteration x
Large scale/coarse resolution
Avoid type 2 error
Small scale/fine resolution
Avoid type 1 error

Figure 1: Generalized example of the adaptive invasive species distribution model (iSDM) framework, with an emphasis on the practice of adaptive inference within it. During initial modeling iterations, when information related to the distribution of the invasive species is limited, predictions are made at larger spatial scales and coarse resolutions, with a primary focus on avoiding type 2 error (i.e., false negatives/absences). In subsequent iterations, as knowledge increases through management, monitoring and model validation at alternative scales and finer resolutions, the focus shifts to increasing predictive accuracy through avoidance of type 1 error (i.e., false positives/presences). Ideally, decreases in uncertainty and increases in precision accompany each iteration.

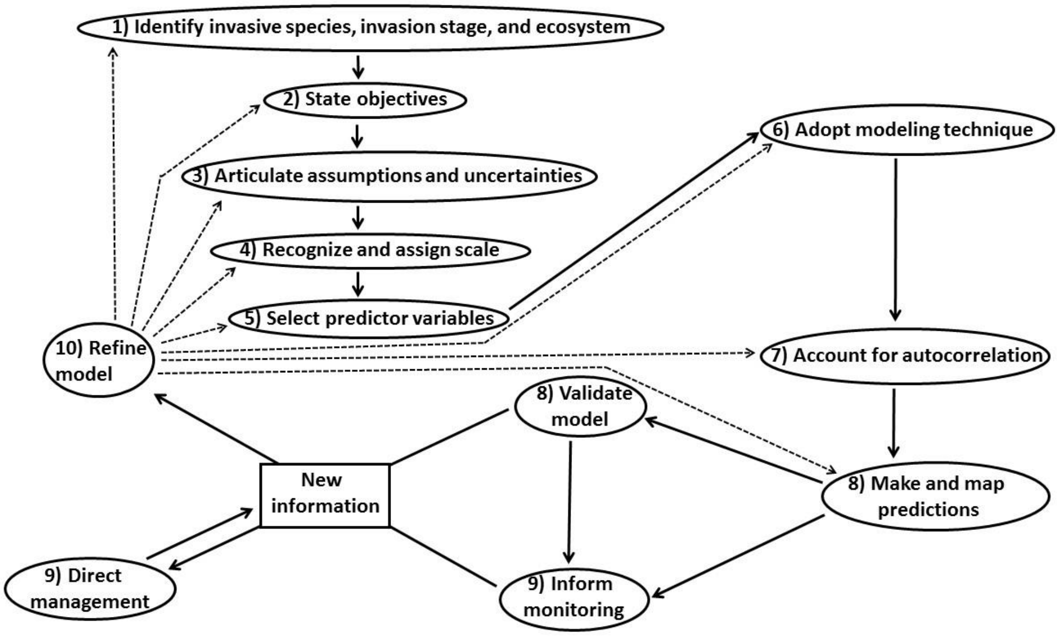
1) Identify invasive species, invasion stage, and ecosystem
2) State objectives
3) Articulate assumptions and uncertainties
4) Recognize and assign scale
5) Select predictor variables
6) Adopt modeling technique
7) Account for autocorrelation
8) Validate model
8) Make and map predictions
9) Inform monitoring
9) Direct management
New information
10) Refine model

Figure 2: A detailed explanation of the framework for development of adaptive invasive species distribution models (iSDM), where newly-acquired information related to invasive species distributions is used for subsequent model improvements. Solid arrows show the sequential progression through the first nine steps of the iSDM construction process, whereas dashed arrows show alternative options for the application of novel information to model improvement in the 10th and final step. The "articulate assumptions and uncertainties" step of the framework (i.e., step 3) may also be applied to the "adopt modeling technique" (i.e., step 6) and "make and map predictions" (i.e., step 8) steps. Although presented here individually, some model stages (e.g., monitoring and management) are likely to be accomplished simultaneously in practice, and are therefore assigned identical step numbers.

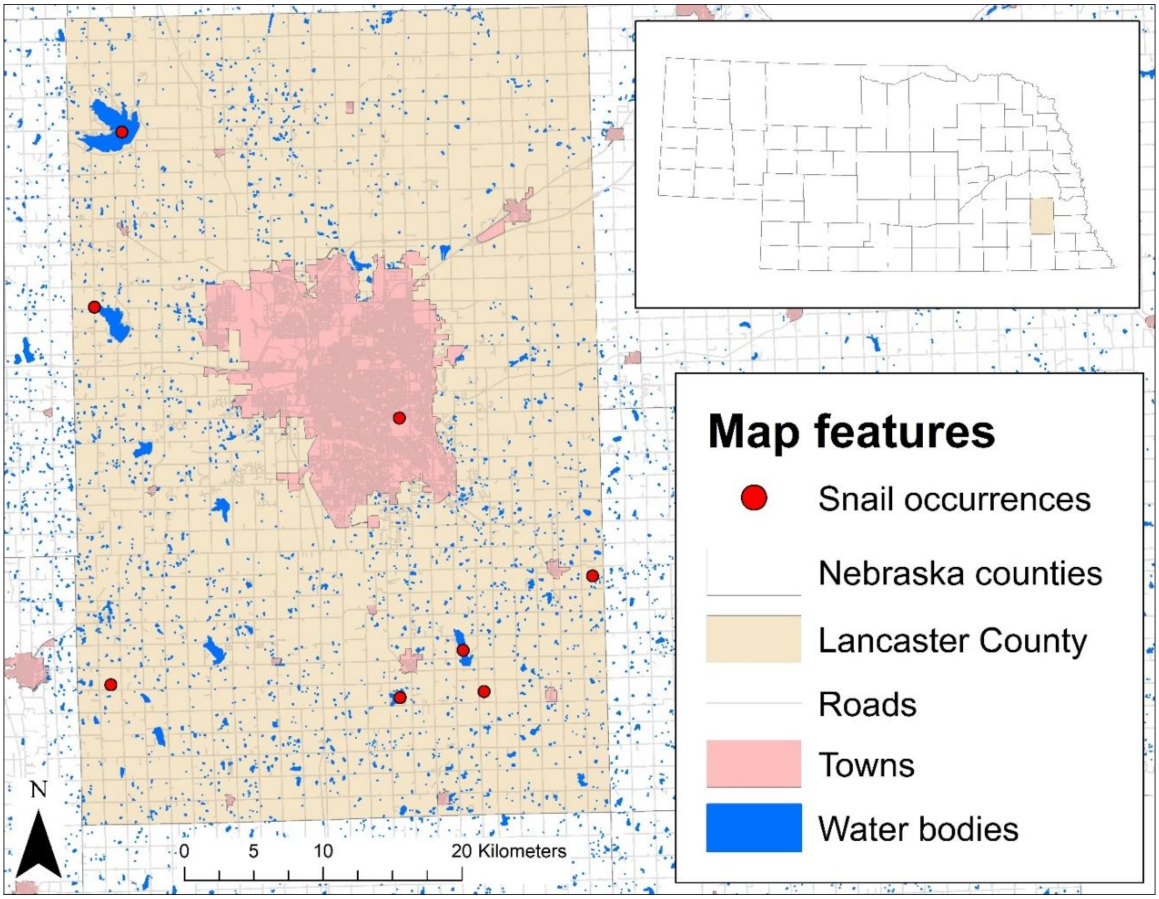
Map features
Snail occurrences
Nebraska counties
Lancaster County
Roads
Towns
Water bodies
N
0
5
10
20 Kilometers

Figure 3: Chinese mystery snail (*Bellamya chinensis*) occurrence records in water bodies of Lancaster County, Nebraska, U.S.A.

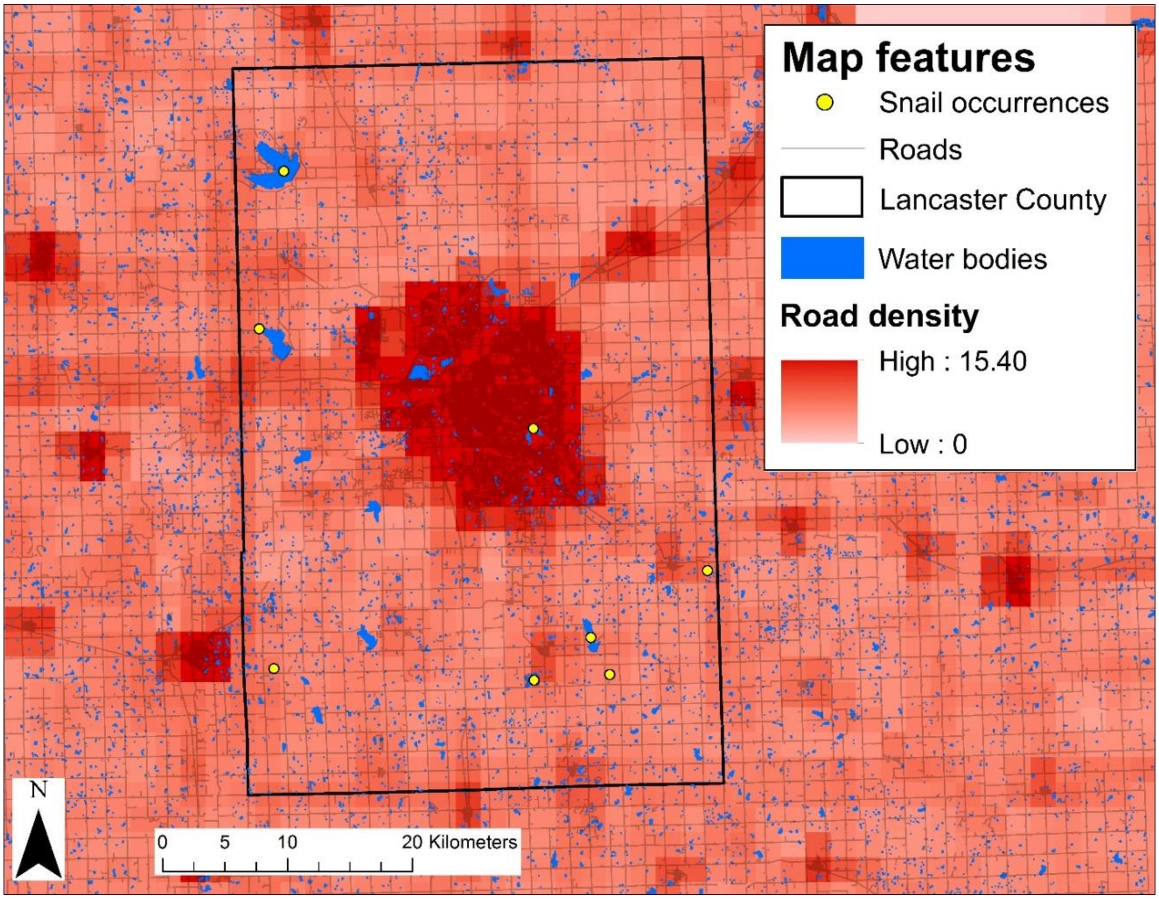
Map features
Snail occurrences
Roads
Lancaster County
Water bodies
Road density
High : 15.40
Low : 0
N
0
5
10
20 Kilometers

Figure 4: Road density in Lancaster County, Nebraska, U.S.A., measured in kilometers (km) per km^2.

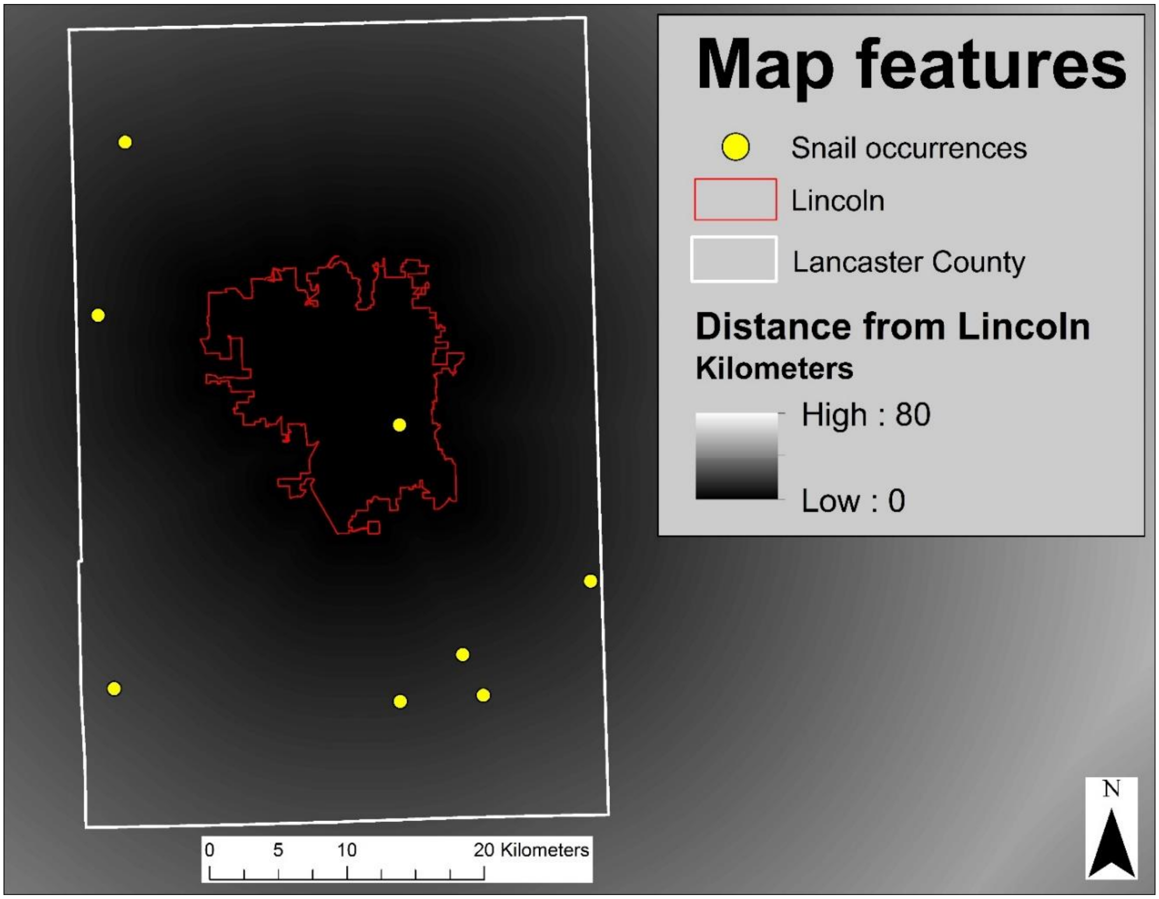
Map features
Snail occurrences
Lincoln
Lancaster County
Distance from Lincoln
Kilometers
High : 80
Low : 0
0
5
10
20 Kilometers
N

Figure 5: Euclidian (i.e., straight-line) distance to the City of Lincoln, Nebraska, U.S.A.

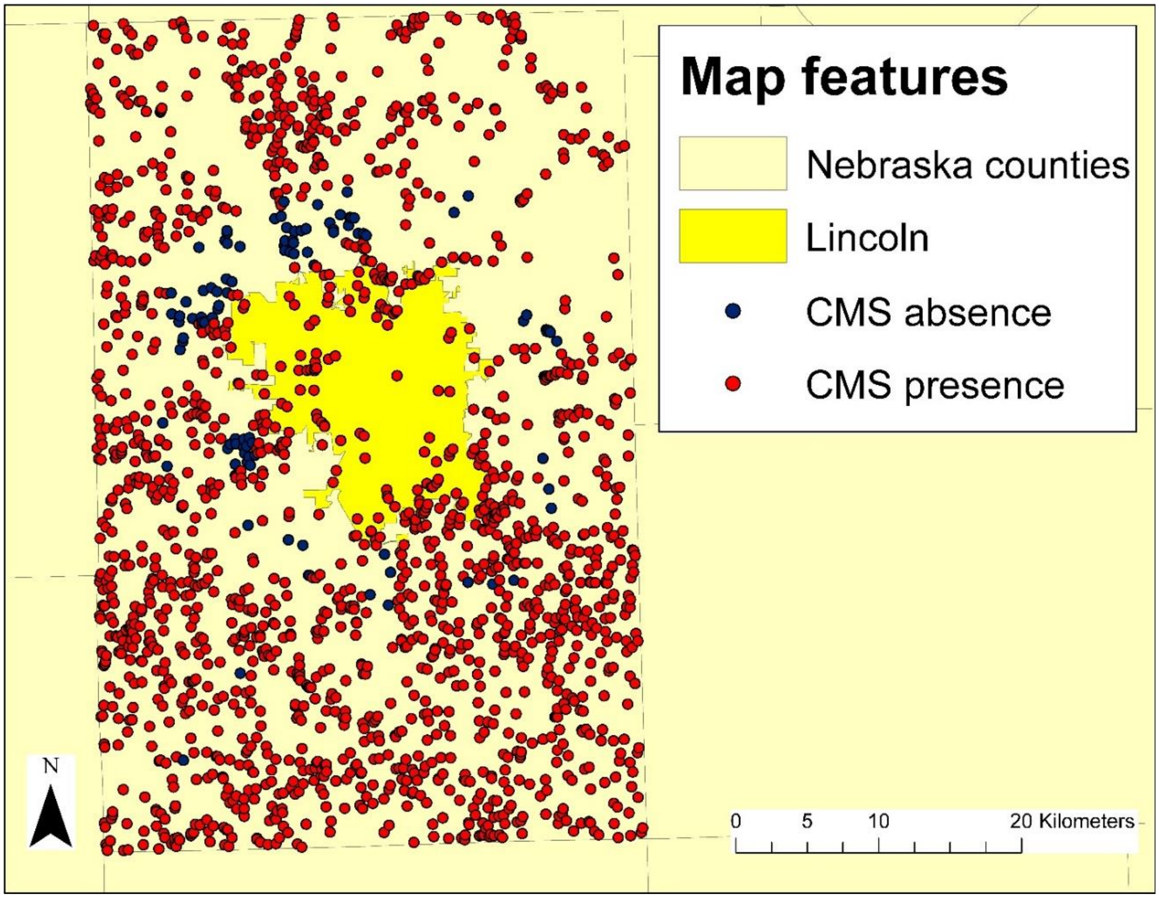
Map features
Nebraska counties
Lincoln
CMS absence
CMS presence
N
0
5
10
20 Kilometers

Figure 6: Predicted Chinese mystery snail presence/absence in water bodies of Lancaster County, Nebraska, U.S.A.

CHAPTER 7: LANDUSE AND LANDCOVER CHANGE SCENARIOS AND SIMULATIONS FOR A NORTHWEST NEBRASKA, U.S.A. LANDSCAPE

ABSTRACT

Landcover change is an important global change process within social–ecological system(s) (SES), yet future changes in landcover are often highly uncertain and difficult to predict. Although uncertainties about the future cannot be entirely eliminated, they can be strategically addressed, reduced, and used to increase preparedness for the future. Scenario planning is a commonly utilized approach for addressing future uncertainties, and when coupled with landcover change simulations, can be used to evaluate alternative possible changes in—and social–ecological effects of—landcover change. In this chapter, I report on a scenario planning exercise for the Pine Ridge Biologically Unique Landscape (BUL) of northwest Nebraska, U.S.A. In a participatory scenario planning approach, local stakeholders identified and ranked factors they perceived as being important drivers of future change in the Pine Ridge BUL. This list of drivers (e.g., tourism, climate change, and landowner decisions) was refined to retain those about which uncertainty was high and perceived control was low. Remaining drivers were aggregated to produce alternative, plausible scenario storylines of landcover change in the Pine Ridge from 2015–2045. Storylines informed the parameterization of cellular automata landcover change simulations, which along with scenario storylines, were iteratively refined, according to stakeholder feedback. In addition to tangible products of uncertainty ranks and simulated future landcover maps, the scenario planning exercise

may have produced intangible benefits, such as broadened perspectives and stronger partnerships between individuals and agencies. Furthermore, participatory scenario planning exercises could be used in coordination with adaptive management to assign potential drivers of landcover change to further consideration in scenario planning or adaptive management processes. Finally, in the context of SESs thinking, participatory scenario planning could not only be used to consider future trajectories of landcover change, but also to increase the resilience of SESs to landcover change and related global change processes and to facilitate SES adaptation and transformation under their influences.

INTRODUCTION

Land managers within the social component of social–ecological system(s) (SES) face uncertainties about the future of landcover change, especially under the influences of other global change processes and their interactions [e.g., climate change (Chhabra et al. 2006; Jantz et al. 2015; Mantyka-Pringle et al. 2015)]. Landuse and landcover history are important determinants of present and future landcover (Foster 1998; Kettle et al. 2000; Klein Goldewijk 2001, 2004); however, the potential for rapid transformations in SESs make predicting future landuse and landcover change difficult, especially over the long term (Muller et al. 2014). Although uncertainties about the future cannot be eliminated entirely, they can be strategically addressed and used for preparation and learning (Regan et al. 2002; Walker et al. 2002; Folke et al. 2005; Armitage et al. 2009; Thrush et al. 2009; Allen et al. 2011; Tyre & Michaels 2011; Williams 2012). One method for strategically encountering future uncertainties in land management is scenario planning.

Scenario planning is an approach used to identify future opportunities and avoid future traps under conditions of high uncertainty and low control (Peterson et al. 2003a; Chermack 2004, 2007; Alcamo 2008a; Williams et al. 2009; Bowman et al. 2013; Oteros-Rozas et al. 2015; Bai et al. 2016; Bennett et al. 2016; Maier et al. 2016). The utility of scenario planning is rooted in the consideration of arrays of alternative plausible futures (Peterson et al. 2003b). Because the consideration of uncertainties in just a few key variables can give rise to several scenarios (Durance & Godet 2010; Amer et al. 2013), no single scenario is expected to constitute the most likely version of the future—a facet of scenario planning that differentiates it from prediction, forecasting, and speculation

(Peterson et al. 2003b; Carpenter et al. 2005; Zurek & Henrichs 2007). Scenario planning objectives regarding a given question(s) may include increasing awareness of uncertainties, promoting the consideration of alternative mitigation or adaptation strategies, integrating different types of relevant data, identifying potential actions and reactions, stretching mental models, challenging preconceived notions, accelerating learning, and increasing understanding of driving factors (Wack 1985; Bood & Potsma 1997; Dortmans & Eiffe 2004; O'Brien 2004; Chermack 2007; Alcamo 2008a). As a bottom-up approach to scenario development, participatory scenario planning is particularly useful for integrating diverse stakeholder views and tracing realistic paths to positive outcomes (Walker et al. 2002; Alcamo & Henrichs 2008; Alcamo et al. 2008; Pahl-Wostl 2008; Oteros-Rozas et al. 2015). Recent notable examples of the application of scenario planning to environmental and ecological research include the Special Report Emission Scenarios produced by the Intergovernmental Panel on Climate Change (Nakicenovic et al. 2000), the Millennium Ecosystem Assessment (Carpenter et al. 2005), and the Global Environmental Outlook (2012).

Successful scenario planning efforts have been observed to exhibit high levels of trust between scenario planners and managers (Burt & van der Heijden 2003), establish consensus across a large number of informed opinions, and take place over a period of 12–18 months (Durance & Godet 2010). In addition, useful and credible scenario planning exercises tend to synthesize diverse perspectives and uncertainties, challenge assumptions about the future, exhibit transparency, and be communicated coherently and engagingly (O'Brien 2004; Durance & Godet 2010). Although scenarios may be rooted in multiple hypotheses, incorporating large numbers of hypotheses and their uncertainties rapidly increases the number of scenarios required to consider each of their possible combinations, which in turn makes tracking different alternative futures difficult. Although the appropriate number of scenarios required to address a question may vary, between three and five scenarios that arise from four to six fundamental hypotheses is generally recommended (Walker et al. 2002; Durance & Godet 2010; Amer et al. 2013).

There are qualitative and quantitative approaches to scenario planning, each with strengths and weaknesses. In general, qualitative scenarios—useful for giving stakeholders ownership in the scenario planning process—are generally produced through collective brainstorming activities, whereas quantitative scenarios—useful for clearly documenting scenario assumptions and providing numerical outputs—are typically produced through modeling (Alcamo 2008c; Alcamo & Henrichs 2008; Sleeter et al. 2012). Qualitative and quantitative approaches may be combined in an iterative passing of scenarios between planners and modelers—a process hypothesized to improve the overall utility and legitimacy of scenario planning exercises.

Scenario planning and landuse and landcover change modeling can be integrated to consider and visualize alternative, plausible changes in landuse and landcover, as well as their social–ecological causes and consequences (Etter & McAlpine 2008; Hill & Aspinall 2008; Swetnam et al. 2011; Sleeter et al. 2012). In this union, knowledge of past, present, and potential future changes may help expand perspectives, inform management, and encourage and facilitate desirable adaptations and transformations in SESs amidst rapidly unfolding global change. In this chapter, I combine participatory scenario planning with cellular automata simulations of landcover change to imagine, quantify, and visualize alternative, plausible landcover change futures in the Pine Ridge Biologically Unique Landscape (BUL) of northwest Nebraska, U.S.A., where a number of factors (e.g., wildfires, insect pests, and tourism) make the future uncertain (Schneider et al. 2011). In addition to gaining insights into potential trajectories of future landcover change, the value of this exercise lies in its potential to address questions of resilience, adaptation, and transformation in the context of SESs thinking.

METHODS

Study area

The Pine Ridge BUL consists of an elevated, rugged escarpment in portions of Sioux, Dawes and Sheridan Counties in extreme northwest Nebraska (Tolstead 1947; Weaver & Albertson 1956; Nixon 1967; Schneider et al. 2011). Mixedgrass prairie and ponderosa pine (*Pinus ponderosa*) forests and woodlands dominate much of the area (Table 1; Figure 1). A number of extreme fire events since the mid-20th century have altered landcover and species composition (Schneider et al. 2011; Roberts et al. 2016). The ~20,575 ha Pine Ridge Division of the Nebraska National Forest, ~8,500 ha Fort Robinson State Park, and ~1,475 hectare (ha) Ponderosa Pine Wildlife Management Area are the most notable ecological reserves in the landscape (Schneider et al. 2011; Nebraska Game and Parks Commission 2016).

Storyline development

On September 17, 2014, foresters and other land managers from various organizations with a presence in the Pine Ridge BUL were assembled at Chadron State College in Chadron, Nebraska for a planning meeting (Figure 2). A portion of the meeting was set aside for the initiation of a scenario planning exercise, with the objectives of broadening perspectives, addressing key uncertainties, and informing future management decisions in the Pine Ridge BUL. At the start of the scenario planning exercise, I provided a short introduction to scenario planning and its use.

In a group brainstorming session, participants were given ~10 minutes to list on a sheet of paper factors they felt were important determinants of the future in the Pine Ridge, classifying factors according to if they were internal or external to the BUL. Participants then took turns copying these internal and external factors onto 63.5 x 76.2 centimeter (25 x 30 inch) self-stick sheets of paper that were mounted at the front of the room. When a factor was listed by more than one participant, checkmarks next to the factor name were used to indicate the number of additional participants who perceived the factor as important. Once all factors had been listed, the group further condensed related factor descriptions into single factors.

With all condensed internal and external factors listed on sheets of paper at the front of the room, the group was asked to collectively provide each driver with a low, medium, or high rank for each of the following criteria: 1) potential impact on conservation targets in the Pine Ridge; 2) level of uncertainty about that impact; and 3) level of control managers have over the driver (Figure 2). Before each ranking was assigned, discussion among group participants ensued and continued until a consensus on the ranking was reached.

Once all factors had been assigned rankings, factors with relatively high impact, high uncertainty, and low control rankings were identified as those most useful for constructing scenario storylines (Tables 2–3). These factors were then grouped into four broad classifications: travel and tourism (i.e., Roadside Development Scenario), climate change (i.e., High and Dry Scenario), wood commodities development (i.e., Wood Commodities Scenario), and biological invasions (i.e., Biological Invasions Scenario). This concluded the scenario planning portion of the September 17th meeting.

Over the next three weeks, I contacted forest and land managers by phone and email for additional input on the identified driving factors and their combinations in the four scenarios. The information obtained through these conversations was used to develop and refine scenario storylines, and to inform the collection of data for conducting simulations of landuse and landcover change under each scenario (Figure 2). This work continued until the 2014 Nebraska Natural Legacy Conference, which was held October 8th and 9th in Gering, Nebraska.

At the 2014 Natural Legacy Conference, I co-led a scenario planning workshop with Kristal Stoner, the Wildlife Diversity Program Manager at the Nebraska Game and Parks Commission. During the workshop, foresters, land managers, and other conference participants—a number of who were involved with the September 14th scenario planning exercises in Chadron—were presented with rough drafts and maps of scenario storylines and landcover change simulations, and then asked for additional feedback. The discussions and feedback from the session were applied to the continued refinement of scenario storylines and the initiation of landcover change simulations over the next several months.

Landcover change simulations

A variety of modeling approaches have been proposed for explaining and predicting changes in landcover and landuse in SESs worldwide. Trends in landuse and landcover change are realized to vary according to unique drivers, contexts, and locations (Rounsevell et al. 2005; Geist et al. 2006). Prior to simulation development, I performed an extensive literature review of landuse and landcover change modeling techniques and determined that cellular automata—which can be used to model transitions between landuse and landcover classes at discrete time-steps, according to pre-determined transition rules—was a valid approach for simulating landcover change under the Pine Ridge landcover change scenarios.

For cellular automata simulations of landcover change in the Pine Ridge BUL, I used customized versions of the SIMLANDER model (Hewitt et al. 2013) within the program R (R Core Team 2016). The SIMLANDER model—which was originally developed for modeling urban expansion (Hewitt et al. 2013)—was updated with various rules and probabilities for transitions among landcover classes in the Pine Ridge BUL. Within each scenario, a landcover raster was loaded, experienced probability-based changes in selected cells, and was fed back into the model for subsequent iterations. This produced an updated landcover raster for each scenario in each year from 2015 to 2045.

Functions used to carry out simulations were housed in the lattice (Sarkar 2008), aod (Lesnoff & Lancelot 2012), sp (Pebesma & Bivand 2005; Bivand et al. 2013), rgdal (Bivand et al. 2016), raster (Hijmans 2016), and SDMTools (VanDerWal et al. 2014) packages for R. Data preparation and map-making were carried out in R and ArcGIS (ESRI 2011). Because of high random access memory (RAM) requirements for conducting landcover change simulations in R, these analyses were run on the Crane Supercomputer in the Holland Computing Center at the University of Nebraska-Lincoln (http://hcc.unl.edu/).

Geographic data

A 30-meter (m) resolution 2010 landcover raster for the State of Nebraska was provided by the Rainwater Basin Joint Venture (Figure 1; Bishop et al. 2011). A 30-m resolution digital elevation model (DEM), a Soil Survey Geographic Database (SSURGO) shapefile, and 2010 TIGER shapefiles of Nebraska roads, streams, cities, and quadrangles were downloaded from the website of the Nebraska Department of Natural Resources (http://dnr.nebraska.gov/data). TIGER shapefiles of roads for the States of South Dakota and Wyoming were downloaded from the website of the U.S. Census Bureau (https://www.census.gov/geo/maps-data/data/tiger.html). Each of these rasters was cropped to a bounding box surrounding the Pine Ridge BUL, with the western boundary of the box set at the westernmost point of the Pine Ridge BUL at the Nebraska–Wyoming border, the northern boundary of the box set at the northernmost point of the Pine Ridge BUL at the Nebraska–South Dakota border, and the eastern and southern boundaries extending for 10 kilometers (km) beyond the easternmost and southernmost points of the Pine Ridge BUL, respectively. Finally, shapefiles of conservation properties and recorded wildfires within the Pine Ridge BUL were provided by the Nebraska Game and Parks Commission (Figure 3).

ArcGIS and the raster Package (Hijmans 2016) for R were used to derive additional shapefiles and rasters from the cropped shapefiles and rasters prior to the initiation of landcover change simulations. The landcover raster was reclassified to generate individual rasters for major landcover classes, such as ponderosa pine (*Pinus ponderosa*) woodland and forest, cropland, and developed areas (e.g., roads and buildings). Slope, aspect, and related topographic rasters were derived from the original DEM raster, with slope measured in percentages and aspect measured in degrees (Figure 4). Rasters of Euclidian distance from features of interest (e.g., roads, towns, and pine trees) were generated in with shapefiles of the features (Figure 5). The Network Analyst Extension in ArcGIS was used to calculate buffers of travel distance along roads (i.e., service areas) from the City of Chadron to surrounding portions of the landscape.

Transition rules

Within the customized SIMLANDER cellular automata, rules governing transitions among landuse/landcover classes were assigned according to guiding scenario assumptions and information related to the phenomena generating the transition of interest. For example, under the assumption of a warmer and drier climate in the High and Dry Scenario, the likelihood of pine mortality and transition to grassland was greater on ridgetops than lowlands. In this case, elevation values of a DEM raster were reclassified from their original values (i.e., 900–1,600 m) to selected transition likelihood values between 0.00 and 1.00. Each scenario considered different driving factors, and therefore, different probability based raster reclassifications. Neighborhood weights were also established at varying distances to represent the spatial spread of certain processes (e.g., construction along roadways and pine regeneration in close proximity to existing pines) (Figure 6). Finally, varying degrees of stochasticity were introduced into landcover change likelihoods by generating a raster of random transition probabilities (Figure 6). Transition likelihoods of all transition likelihood rasters were multiplied together to produce a final transition likelihood raster that determined which cells transitioned at each iteration of the model run.

The number of 30-m cells to be converted to alternative landcover classes at each iteration (i.e., time step; year) within each scenario was set *a priori* using either linear or exponential growth rate functions. Within each iteration, the cells to be converted were identified as those with the greatest transition likelihoods in the final transition likelihood raster. Changes in these cells produced an updated landcover raster, which was then fed back into the model as the basis for transition likelihood calculations the next iteration. Therefore, each iteration of each scenario produced new rasters of transition likelihoods, which were combined as a final transition likelihood raster, which was used to generate a new landcover raster.

Simulations of landcover change under three out of the four scenarios (i.e., Roadside Development, High and Dry, and Wood Commodities) were run and refined in

2015 with the customized R script for the SIMLANDER model. For each of these three scenarios, the landcover raster produced at each of the 30 iterations for the years 2015–2045 was exported as an .asc file, loaded into ArcGIS, mapped, and exported as a .jpeg file.

Further refinement

On December 3, 2015, an update meeting for the Pine Ridge BUL was held in Chadron, Nebraska. A number of meeting participants were participants in the September 2014 scenario planning exercise and/or the October 2014 scenario planning workshop. A review and update of the scenario planning project, including scenario storylines and output landcover maps, was presented to managers, after which managers provided input related to future refinement. Following the December 2015 update meeting, the four original scenarios were condensed into three scenarios by integrating aspects of invasive species spread from the Biological Invasions Scenario—particularly [i.e., ips beetle (*Ips* spp.), cheatgrass (*Bromus tectorum*), and smooth brome (*Bromus inermis*) spread]—into the other three scenarios.

RESULTS

Scenario 1: Roadside Development

Drivers of landcover change

Under the Roadside Development Scenario, probabilities of roadside and ranchette construction were driven by combinations of the following factors: proximity to a primary road (i.e., highway), proximity to a secondary road (i.e., non-highway), proximity to the Heartland Expressway (i.e., Highway 385), proximity to existing developed areas, road distance to Chadron, percent slope, existing landcover, and a random (i.e., stochastic) effect. The combination of these factors produced the transition likelihood raster at each of the 30 model iterations, which in turn produced an updated landcover raster at each iteration.

Storyline and simulation

In the Roadside Development Scenario, an increased focus on North American travel and trade spurred infrastructural, housing, and energy development, human population increases, and associated landuse and landcover changes in the Pine Ridge BUL (Figure 7). Change was initiated by the beginning of construction on the Heartland Expressway, the regional stretch of the longer, Port-to-Plains Alliance Corridor highway connecting Canada, the United States, and Mexico. In the Pine Ridge, this stretch was once the two-lane U.S. Highway 385/Gold Rush Byway, but it became a “Super-2” highway facility with 12-ft lanes, 10-ft shoulders, and auxiliary turn and passing lanes (Figure 8). From 2015–2045, the average number of total vehicles and trucks (i.e., semis) passing through the Pine Ridge on the roadway daily increased by ~1,000 and ~150, respectively, to 4,400 and 380 [Nebraska Department of Roads (NDOR) 2012]. A sizeable portion of this traffic increase resulted from the eastward shifting of Interstate 25 traffic.

The greater degree of connectivity that lane expansion and increased traffic on the highway provided between the Pine Ridge and other cities and towns had a variety of direct and indirect economic, demographic, and ecological effects. Road-side billboards as far away as Rapid City, Denver, and Kearney now promote Nebraska's Pine Ridge as the ideal weekend getaway and vacation destination for activities like big game hunting, wildlife-viewing, camping, hiking, dining, wine-tasting, and shopping. These developments led to landuse and landcover changes, which were most noticeable in the immediate vicinity of the Heartland Expressway, where privately-owned properties were subdivided, and ranchette and cabin construction skyrocketed (Figure 8). Although publicly-owned properties adjacent to the highway were not sub-divided or developed, privately-owned lands around them were. The regional increase in recreational activity had less extreme effects on landuse; however, it did further increase overall human activity on the landscape.

The swift influx of both temporary and permanent residents into the once sparsely-populated landscape spurred additional developments and local economic growth, especially in Chadron. Businesses like restaurants, hotels, sporting goods stores, and home heating/cooling installation and maintenance, which were previously only moderate contributors to the local economy, now employ a substantial proportion of local residents. Road, business and housing construction has also boomed and brought with it a host of short-term workers. In addition to vacationing, the Pine Ridge has increased in popularity as a regional education destination. Chadron State College reported record enrollment in five of the last 10 years, and as a result of greater amenities and employment opportunities, a growing percentage of students began opting to remain in the area after graduation.

The greater overall human presence in the landscape increased the wildlife urban interface, especially in the vicinity of the Heartland Expressway. Chadron State Park and several other publicly-owned properties south of Chadron, along the Heartland Expressway, experienced increased development and disturbance along their edges, although the properties themselves were not developed. Conversely, the majority of privately-owned properties bordering the park were sold and sub-divided so that ranchettes and cabins could be constructed on them. Although road construction and expansion in these areas increased connectivity of the landscape for humans, it had mostly detrimental effects on wildlife populations. Deer-vehicle collisions rose sharply, and a number of collisions with bighorn sheep also occurred. In several instances, sheep grazing and browsing along roadway edges caused traffic backups and minor accidents. Bighorn sheep movements between the eastern and western sides of the Heartland Expressway were increasingly restricted. Increased traffic and construction-based soil disturbance also facilitated the establishment and spread of opportunistic invasive species like cheatgrass [i.e., downy brome (*Bromus tectorum*) and Japanese brome (*Bromus japonicus*)], smooth brome (*Bromus inermis*), Russian knapweed (*Rhaponticum repens*), Dalmatian toadflax (*Linaria dalmatica*), scotch thistle (*Onopordum acanthium*), houndstongue (*Cynoglossum officinale*), and other state- and county-listed noxious weeds in the highway corridor.

The role of fire, both prescribed and wild, became the subject of intense discussion and debate in the landscape. During previous large-scale fire events, there were fewer houses in the landscape; therefore, evacuations could be conducted quickly and firefighters could concentrate their efforts on preventing or minimizing damage to existing structures. This changed with the increasing human presence in the landscape, as the proposal of even small-scale prescribed fires on publicly-owned lands incited worry and discontent among local residents, most of whom were ranchette and cabin owners concerned more about potential property losses than the future ecological condition of the landscape. As a result of this resistance, prescribed fire was not actively adopted as a management tool in the central portion of the landscape, and managers focused on reducing fuel loads and preventing future wildfires through tree thinning, road construction, and grazing.

Although the central portion of the Pine Ridge BUL experienced a substantial transformation in terms of human population density and activity, landscape connectivity, biological invasions, and landuse changes, transitions in the eastern and western portions of the landscape were less noticeable. In these areas, sparser human populations—mostly longtime farmers and ranchers—were still situated in relatively unbroken matrices of pine forest, pine woodland, and mixedgrass prairie, although the overall level of human activity associated with recreational activities and energy development increased. In these areas, managers had more freedom to use prescribed fire as a management tool on public lands, the successful demonstration of which piqued the interest of several private landowners in conducting prescribed burns on portions of their properties that had been previously thinned or burned.

The sharp east–west divide that the completion of the Heartland Expressway imposed on the Pine Ridge BUL s led some, especially those involved in conservation, to begin referring to the region as “The Pine Ridges”, “The Eastern Ridge”, or “The Western Ridge.” Although the Pine Ridge BUL’s economy—which continued to transition from an agricultural to service base—was vibrant in 2040, its ecosystems were stressed.

Landcover changes

Over the 30 simulation iterations (i.e., years) of the Roadside Development Scenario, landcover classes that increased in area were ranchette development and roadside development; landcover classes that experienced no change in area were crops and water; and landcover classes that decreased in area were deciduous trees, grass, and coniferous trees (Table 4; Figure 9). The majority of landcover change that occurred was from coniferous trees to ranchette development, and the majority of this change occurred on the peripheries of pine woodland and forest patches (Figure 8).

Scenario 2: High and Dry

Drivers of landcover change

Under the High and Dry Scenario, probabilities of conversions between pine forest and grassland, between irrigated and dryland rowcrop production, and between rowcrop production and grassland, were driven by combinations of the following factors: elevation, aspect, percent slope, wildfire history, soil productivity, proximity to existing pine trees, and a random effect. The combination of these factors produced the transition likelihood raster at each of the 30 model iterations, which in turn produced an updated landcover raster at each iteration.

Storyline and simulation

In the High and Dry Scenario, regional climatic changes occurred and were evidenced in the Pine Ridge BUL through a gradual shift towards higher mean annual minimum daily temperatures, more intense but less frequent precipitation events, and an increase in drought frequency and severity (Figure 10). Warmer and drier conditions kept the likelihood of wildfire occurrence high throughout summer months, and despite active mitigation actions, two additional landscape-scale wildfire events occurred between 2015 and 2040 in areas that had and had not already been burned since 1965. The cumulative effects of 70 years of wildfire markedly decreased wooded area and increased grassland area in the landscape, with burned areas being in various stages of recovery (Figure 11). In many re-burned areas, “green islands” of trees that had survived previous fires were killed or severely stressed as extremely hot fires consumed downed logs and other materials that had not been consumed in previous fires.

In addition to wildfires, pine forests and woodlands experienced stress from heat and drought, which increased their vulnerability to insect infestations. Under the warmer and drier conditions, mountain pine beetle densities remained low and continued to be restricted to portions of the landscape west of Fort Robinson, especially on wetter north- and east-facing slopes. Ips beetles, which were historically more abundant in the landscape than mountain pine beetles, had much greater effects on forest health. The already widespread distribution of ips beetles in the Pine Ridge allowed them to infect an ever-increasing number of old, sick, and otherwise stressed trees. Eventually, ips beetles became so dense that they even began infecting healthy trees. In addition to widespread pine mortality, ips beetle proliferation reduced the overall quality and quantity of pine timber in the landscape, which precluded the development of any substantial lumber markets.

Given the bleak prospects for widespread natural or assisted pine regeneration and survival under now warmer and drier climatic conditions, management began focusing pine conservation efforts primarily on the remnant populations occupying wetter, north- and east-facing slopes, while facilitating transitions from pine forest and woodland to pine savannah and mixed-grass prairie on the drier, south- and west-facing slopes, especially those with histories of wildfire and beetle infestation. Although local residents lament the decrease in landscape-level pine densities, which are certainly low by 20th century standards, these densities are likely similar to those of the early-to-middle 19th century.

Lower tree densities increased opportunities for utilizing prescribed fire as a management tool. Initially, burns were small in spatial extent and occurred only on public properties. In time, private landowners noticed burns being conducted safely and at minimal cost, and became less skeptical regarding the logistics of using fire as a management tool. They also observed various economic and environmental benefits of using fire, including increased vigor in springtime forage for grazing and reductions in invasive species densities. In wetter years where sufficient over-winter vegetation was retained, a number of landowners cooperated with public agencies to burn portions of or entire properties where tree densities and fuel loads were relatively low.

Warmer and drier conditions, and most importantly the increased drought frequency and intensity, decreased long-term agricultural productivity in the Pine Ridge, much to the detriment of the local economy. During multi-year droughts, wheat failed to sprout in many areas, so farmers resorted to sowing cover crops and allowing the land to lay fallow until the following year. A number of cattlemen similarly sold off large portions of their herds when forage availability in woodland and prairie pastures and the hay produced in alfalfa fields decreased. The availability of surface and groundwater for irrigation was gradually restricted, and Natural Resource Districts began to monitor well pumping on private lands. Farmers increasingly experimented with alternative, drought tolerant crops as annual irrigation allotments fell below crop requirements in many years. Decreased agricultural productivity also reduced the number of jobs available to local residents. Given the bleak opportunities for local employment, many younger individuals left to seek work in Denver or other metropolitan areas. Although the population of Chadron decreased, it remained a shopping and employment destination for residents who stayed. Smaller neighboring towns did not fare as well and lost many of their residents as businesses disappeared with their client bases.

Local agricultural and economic declines drove changes in local land ownership and landuse practices, which had both positive and negative ecological consequences. The ever-decreasing availability of forage on the landscape resulted in the intensive annual haying and grazing of woodland and prairie pastures with insufficient recovery time between uses. As a result, plant species diversity in most ecological communities decreased, opportunistic invasive species (e.g., cheatgrass) established and spread. Extremely low fuel loads and drier conditions also often precluded the use of prescribed fire as a management tool. As private landowners were faced with shrinking profit margins and prospects of continued drought, some put the least productive portions of their properties up for sale, which given their condition and the circumstances, were not highly desired by neighboring landowners. Public entities, conservation organizations, and the Oglala Sioux Tribe, purchased several properties at low prices and began implementing restoration and conservation practices on them. Private landowners also increased their enrollment in a number of conservation easement programs put forth in a succession of Farm Bills that were aimed largely at providing relief to farmers and ranchers in drought stricken landscapes like the Pine Ridge. Although most publicly-acquired and privately-enrolled conservation lands were in poor ecological condition, the overall area of conservation properties in the landscape increased.

Landcover changes

Over the 30 simulation years in the High and Dry Scenario, the only landcover class that increased in area was grass; landcover classes that experienced no change in area were deciduous trees, developed areas, and water; and landcover classes that decreased in area were irrigated cropland, dryland cropland, and coniferous trees (Table 5; Figure 12). The majority of landcover change that took place occurred through the conversion of coniferous trees to grass, and then through the conversion of dryland cropland to grass. Spatially, the conversion from coniferous trees to grass increased from west-to-east (Figure 11) along the high-to-low elevation gradient (Figure 4a).

Scenario 3: Wood commodities

Drivers of landcover change

Under the Wood Commodities Scenario, probabilities of conversions between young pine forest (i.e., previously burned) and old pine forest (i.e., not previously burned), and between pine forest and grassland were driven by combinations of the following factors: road distance to Chadron, proximity to any road, proximity to existing pine trees, and a random effect. The combination of these factors produced the transition likelihood raster at each of the 30 model iterations, which in turn produced an updated landcover raster at each iteration.

Storyline and simulation

In the Commodities Scenario, the development of regional and local markets for ponderosa pine products (e.g., lumber and woodchips) had substantial effects on economies, forest health, fire intensity and frequency, and conservation management practices in the Pine Ridge BUL and surrounding areas (Figure 13). As markets for wood commodities emerged and gained additional support in the public and political spheres, the construction of logging roads, sawmills, and other tree-processing infrastructure was embraced as an opportunity for growing the local economy, providing supplemental income to landowners, and decreasing the likelihood of major wildfires in the future (Figure 14). Woodland pastures were also moderately-grazed to decrease forest fuel loads and decrease the risk of wildfire occurrence. When coupled with increasing local and regional demands for wood products, substantial investment from private and government entities provided a sufficient jump-start for the timber industry in the Pine Ridge. Several local logging companies initially dominated the local market, but upon observing their success, others from surrounding areas arrived in mass and began competitively biding for contracts on public and private properties. In the beginning, tree thinning projects on public lands produced most of the harvested timber in the landscape. However, private landowners, who had at first been cautious about entering into contracts with loggers, observed the economic benefits associated with timber harvest and gradually increased their participation.

A few logging companies focused on the selective harvest of old, large, high-quality trees for the production of high-grade products like lumber and plywood; however, the majority of loggers harvested smaller, younger, and often dead or diseased trees for the production of lower-grade products like woodchips for burning in boilers or landscaping. The continued and expanding use of boilers for heating in Chadron State College, the Chadron hospital, and other local community buildings greatly increased local demand for woodchips, in addition to public awareness of the utility of pine products for energy production. The radius at which woodchips were collected via tree thinning activities around the town of Chadron doubled, now extending to 25 miles and encompassing a substantial proportion of the Pine Ridge BUL. Tree harvesting focused heavily on publicly- and privately-owned lands southeast of Chadron, which represented some of the last vestiges of forest and woodland that had not experienced wildfire at some point since 1965, and as such, the densest pine stands in the landscape. Forested areas southeast of Chadron were also more accessible through the existing road network than areas to the southwest, which allowed for reduced transportation costs between harvest sites and boilers.

Both public and private landowners had an interest in retaining at least some pine trees when thinning forest and woodland stands; however, the condition of retained trees differed between organizations and individuals. Thinning operations on most public lands focused on harvesting mid-sized and middle-aged trees and retaining large, old trees in low to moderately-dense stands with a diversity of tree ages. Meanwhile, the majority of private landowners, whose primary concern was economic, allowed loggers to preferentially harvest the most valuable old and large trees, while retaining smaller and younger trees in low to moderately-dense and more uniformly-aged stands. These differential harvest practices, when combined with the heterogeneity imposed by wildfire mortality and recovery, and landowner-specific grazing practices, promoted a diversity of conditions of pine forest, woodland, and mixedgrass prairie at the landscape-scale in the Pine Ridge.

The development of a wood commodities market made the accomplishment of certain conservation objectives in the Pine Ridge—such as the reduction of pine tree densities and stemming the expansion of eastern red-cedar—a reality. Furthermore, the construction of logging roads slowed the spread of wildfires and increased the effectiveness of firefighters in extinguishing them. The development of markets and infrastructure also had positive effects on the local economy. However, not all of the changes induced by market development were positive. Soil disturbances from logging road construction and tree harvest allowed several invasive species—most notably cheatgrass, smooth brome and houndstongue—to spread through pine forests, woodlands, and grasslands, although disturbance did increase species diversity in less-invaded areas, due to the setting back of ecological succession. Cheatgrass and houndstongue invasions severely reduced the quality and quantity of forage available for grazing livestock—and in turn reducing fuel loads—in woodlands, although cattle still actively fed in smooth brome-dominated areas. Therefore, differences in palatability among the dominant flora of woodland pastures resulted in different levels of wildfire risk among and within properties. Concern over the direct and indirect effects of increasing logging activities and logging road densities on edge-intolerant wildlife species also increased.

After a decade of selective tree harvest, many private landowners—who by this time had become accustomed to the supplementary income associated with active forest management on their properties—began to run out of trees to harvest. Although the annual production of tree biomass at the landscape scale still dwarfed landscape-scale harvest, this was not the case on every individual property, where harvest rates could outpace biomass production rates. Several landowners entered into secondary contracts with loggers to harvest additional pines from previously-thinned areas. These new contracts were welcomed by the logging companies, who were now willing to place lower bids on projects, due at least in part to a decrease in the number of new contracts on public lands, where live tree densities approached desirable levels and there were an ever-decreasing number of wildfire- and insect-killed trees available for harvest. By 2040, there were only a handful of easily accessible, highly-dense stands of pine remaining on private lands in the Pine Ridge BUL. Publicly-owned forests tended to be more age-diverse than privately-owned forests, and tree densities varied among landowners. The risk of large-scale wildfire events was the lowest it had been at any point in the last century, which coupled with the diversification of income that tree harvest offered, satisfied the strong majority of landowners. There were a number of properties, however, with relatively low tree densities and understories dominated by cheatgrass, where the potential for wildfire occurrence was higher. The degraded state of these properties illustrated the consequences of overharvesting trees in locations which also favored invasive species establishment and spread. Finally, the future of the timber industry in the Pine Ridge became uncertain, as was the future condition of pine stands on privately-owned lands where biomass harvest was exceeding natural production.

Landcover changes

Over the 30-year simulation in the Wood Commodities Scenario, the only landcover class that increased in area was grass; landcover classes that experienced no change in area were deciduous trees, developed areas, cropland, and water; and landcover classes that decreased in area were thick coniferous trees and thin coniferous trees (Table 6; Figure 15). The majority of landcover change that occurred took the form of coniferous trees to grass conversions, with more thin than thick coniferous tree stands transitioning. These changes decreased with increasing distance from the City of Chadron (Figure 14).

DISCUSSION

This chapter used scenario planning to address uncertainties pertaining to the future of the Pine Ridge BUL in northwest Nebraska. As a participatory approach to scenario planning, scenario storylines are based in stakeholder perspectives (Figure 2) concerning factors that may not only be particularly impactful drivers of future change, but also about which there are high levels of uncertainty and low levels of control. The exercise produced the tangible products of ranked drivers of change (Tables 2–3), qualitative storylines of future change, flowcharts of interactions among processes, events, and changes in landcover (Figures 7, 10, & 13), estimates of changes in landcover class area (Tables 4–6; Figures 9, 12, & 15), and maps of spatially explicit landcover change simulations (Figures 8, 11, & 14). In addition, intangible products such as expanded perspectives and stronger partnerships between individuals and agencies may have developed. Both the tangible and intangible products of the exercise are likely to increase readiness for avoiding traps and seizing opportunities in the future of the Pine Ridge BUL. Although the most benefit may be in the intangible products, the tangible products provide vehicles for producing intangible products, as well as devices for organizing, recalling, and building upon them.

A variety of factors contributed to landcover change in the three scenarios and simulations; however, by far the greatest amount of change in land area occurred under the High and Dry (i.e., climate change) Scenario. Under this scenario, grass increased by 22,000 hectares at the expense of coniferous trees, dryland cropland, and irrigated cropland, respectively (Table 5). Indeed, interactions between landcover change and climate change could synergistically affect landcover and climate in the future in landscapes worldwide (Chhabra et al. 2006; Jantz et al. 2015; Mantyka-Pringle et al. 2015). The Wood Commodities Scenario had the next greatest change in area among landcover classes, which again involved the conversion of coniferous trees to grass (Table 6). Coniferous trees also exhibited the greatest decrease among the landcover classes in the Roadside Development Scenario, although these conversions were primarily to ranchettes (Table 4).

Collectively, the three scenarios trace different trajectories by which future decreases in pine woodland and forest could occur in the Pine Ridge BUL. There are indeed a number of uncertainties related to current and future pine regeneration, or the lack thereof. The dense pine forests that have characterized the region for nearly a century are threatened by an array of stressors, which include climate change, wildfire, and insects (Schneider et al. 2011). It is worth noting that trees were likely less common under historical fire regimes than they are presently, after more than a century of active fire suppression. Intense wildfire events, such as those that occurred in the summer of

2012, may increase in frequency when presently high fuel loads in many locations experience projected warmer and drier climatic conditions. Management activities, such as tree thinning activities and prescribed fire, may help stave off wildfire and conserve pine forest in some areas, but in other locations, transitions from pine forest and woodland to pine savanna or mixedgrass prairie may be inevitable. In such instances, where and when the resilience of the pine system to perturbations (e.g., fire and insect outbreaks) is exceeded, management efforts should focus on learning, addressing uncertainties, and facilitating adaptations and assisting transformations in the SESs of the landscape for the greatest possible benefit (Folke 2005, 2007; Folke et al. 2010).

Despite the active incorporation of expert knowledge into storylines and simulations, even these relatively simple exercises required a number of arbitrary decisions to be made during development, and this certainly introduces bias into the analysis. Uncertainty is often high in these instances; however, storylines and simulations necessitate the specification of events and parameters. The iterative nature of the participatory scenario planning approach (Figure 2) allows for repeated feedback between stakeholders and modelers, so that over time, the views of the larger group are more accurately represented in storylines and simulations. It is also important to remember that even if consensus pertaining to series of events, landcover transition likelihoods, areas of change, and related aspects of a scenario planning exercise is reached, the envisioned futures are still likely to be a poor representation of the actual future. For this reason, the primary focus of scenario planning exercises should be on capturing, evaluating, and addressing uncertainties about the future, not accurately predicting it. Nevertheless, it is appropriate to focus on events with reasonable likelihoods of occurring, unless events with low likelihoods of occurrence (i.e., surprises) are of special interest (Goodwin 2009; Goodwin & Wright 2010). Indeed, a common request among Pine Ridge BUL scenario exercise participants is a combination of aspects of the three developed scenarios, with a focus on simulating events with perceived greater likelihoods of occurrence. When compared with its constituent scenarios, such a scenario ensemble could be useful for more carefully evaluating future uncertainties. This addition to the scenario planning exercise has yet to be initiated.

Scenario planning exercises may be useful components of larger conservation and planning exercises. The scenario planning exercise for the Pine Ridge BUL is nested within the larger Nebraska Natural Legacy Plan (Schneider et al. 2011). Because the Nebraska Natural Legacy Plan utilizes adaptive management (Holling 1978; Walters 1986; Allen et al. 2011) for conservation planning with BULs, this scenario planning exercise can be said to have occurred within a larger adaptive management framework. Although adaptive management and scenario planning are commonly described as alternative approaches suitable under different combinations of uncertainty and controllability (Williams et al. 2009), the results of this chapter demonstrate how they might be combined within conservation and planning efforts.

The incorporation of scenario planning into adaptive management frameworks has the potential to facilitate adaptive management and increase its effectiveness. This may especially be true when participatory approaches to scenario planning (i.e., participatory scenario planning) and adaptive management (i.e., collaborative adaptive management)—which emphasize stakeholder participation in planning and management—are adopted. Once stakeholders are assembled under an adaptive management plan, they may identify drivers they believe are important for the future of the SES, and then rank them according to the same three criteria utilized in the Pine Ridge scenario planning exercise: 1) impact; 2) uncertainty; and 3) control. In a first step of evaluating and trimming the list of drivers, those with "low" impact rankings can be set aside. In a second step, drivers with "medium" or "high" impact rankings, but "low" uncertainty rakings, could be set aside and relegated to "hedging" or "optimal control" management strategies within larger adaptive management plans (Williams et al. 2009). Next, remaining drivers could be separated according to their control rankings, with "high" and "medium" ranks assigned to consideration in collaborative adaptive management (Armitage et al. 2009), and "low" ranks assigned to scenario planning exercises, as applied in this chapter.

With the identified variables, collaborative adaptive management proceeds as normal, according to the steps outline by Allen et al. (2011), Beratan (2014), and others. Participatory scenario planning similarly ensues with its identified variables, in which qualitative storylines are developed and matched with quantitative models aimed at improving preparation for the future. At each loop of the collaborative adaptive management process, the driver brainstorming and ranking system is repeated, according to the same three criteria. At each step, drivers may be assigned, reassigned, switched between, or eliminated from collaborative adaptive management or scenario planning exercises, according to the discretion of the group. Therefore, this process would utilize participatory scenario planning as a decision support tool within collaborative adaptive management frameworks, as alluded to by Kofinas (2009). More specifically, it would allow for the differential treatment of potentially important drivers, about which uncertainty is high, according to the level of control stakeholders perceive themselves as having over the drivers and larger system. Potential benefits of this approach could include increased learning, greater stakeholder participation, and more focused recommendations for management within larger adaptive management frameworks.

Although uncertainty about the future of the Pine Ridge BUL is high and many impactful future events and processes are outside the control of land managers, the future can still be encountered strategically. Participatory scenario planning is one approach that can inform strategic thinking and planning. The scenario planning process itself and its qualitative and quantitative outcomes will ideally continue to be used to increase awareness of current and potential future stressors and trajectories of change in the Pine Ridge BUL. When applied in the context of SESs thinking, participatory scenario planning could not only be used to consider future trajectories of change, but also to increase the resilience of SESs to landcover change and related global change processes, and to facilitate SES adaptation and transformation under their influences.

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TABLES AND FIGURES

Table 1: Areas (i.e., hectares) of major landcover classes and the percentages of total landcover they represent the Pine Ridge Biologically Unique Landscape of southeast Nebraska, U.S.A., based on reclassified 2010 landcover from the Rainwater Basin Joint Venture (Bishop et al. 2011).

Landcover class	**Hectares**	**Percentage**
Grass	158,040.36	74.15
Trees	47,439.18	22.26
Developed	3,898.26	1.83
Crops	3,525.84	1.65
Water	243.54	0.11
Total	213,147.20	100.00

Table 2: Internal factors listed by participants in the Pine Ridge scenario planning exercise to be potentially important drivers of change in the Pine Ridge Biologically Unique Landscape in the coming 30 years. Participants assigned each factor low, medium, or high rankings according to three criteria: 1) potential impact; 2) level of uncertainty concerning effects; and 3) level of control over it.

Internal driver	**Impact**	**Uncertainty**	**Controllability**
Fire regime	High	Low	Medium
Management actions	High	Medium	High
Biological invasions	High	Low	Medium
Forest health	High	Low	Medium
Landscape connectivity	Medium	High	Medium
Landowner desire and ability	High	Low	Medium
Endangered species listings	Medium	High	Low
Hunting and recreation	Medium	Medium	High

Table 3: External factors listed by participants in the Pine Ridge scenario planning exercise to be potentially important drivers of change in the Pine Ridge Biologically Unique Landscape in the coming 30 years. Participants assigned each factor low, medium, or high rankings according to three criteria: 1) potential impact; 2) level of uncertainty concerning effects; and 3) level of control over it.

External driver	**Impact**	**Uncertainty**	**Controllability**
Climate change	Medium	Medium	Low
Drought and timing	High	Low	Low
Livestock market	Medium	Medium	Low
Human development/landuse	High	Low	Medium
Energy development	High	Medium	Medium
Wood commodities	High	High	Medium
Heartland Express	Medium	Medium	Low
Farm and ranch policy	High	High	Low
Diseases	High	High	Medium

Table 4: Changes in landcover class area (hectares) from 2015–2045 under the Roadside Development Scenario.

Landcover class	**Area change**
Developed (ranchette)	3,241.35
Developed (roadside)	20.34
Crops	0.00
Water	0.00
Deciduous trees	-5.58
Grass	-20.61
Coniferous trees	-3,235.50

Table 5: Changes in landcover class area (hectares) from 2015–2045 under the High and Dry Scenario.

Landcover class	**Area change**
Grass	22,605.21
Deciduous trees	0.00
Developed	0.00
Water	0.00
Crops (irrigated)	-1,869.21
Crops (dryland)	-7,929.27
Coniferous trees	-12,806.70

Table 6: Changes in landcover class area (hectares) from 2015–2045 under the Wood Commodities Scenario.

Landcover class	**Area change**
Grass	4,362.57
Deciduous trees	0.00
Developed	0.00
Crops	0.00
Water	0.00
Coniferous trees (thick)	-1,093.68
Coniferous trees (thin)	-3,268.89

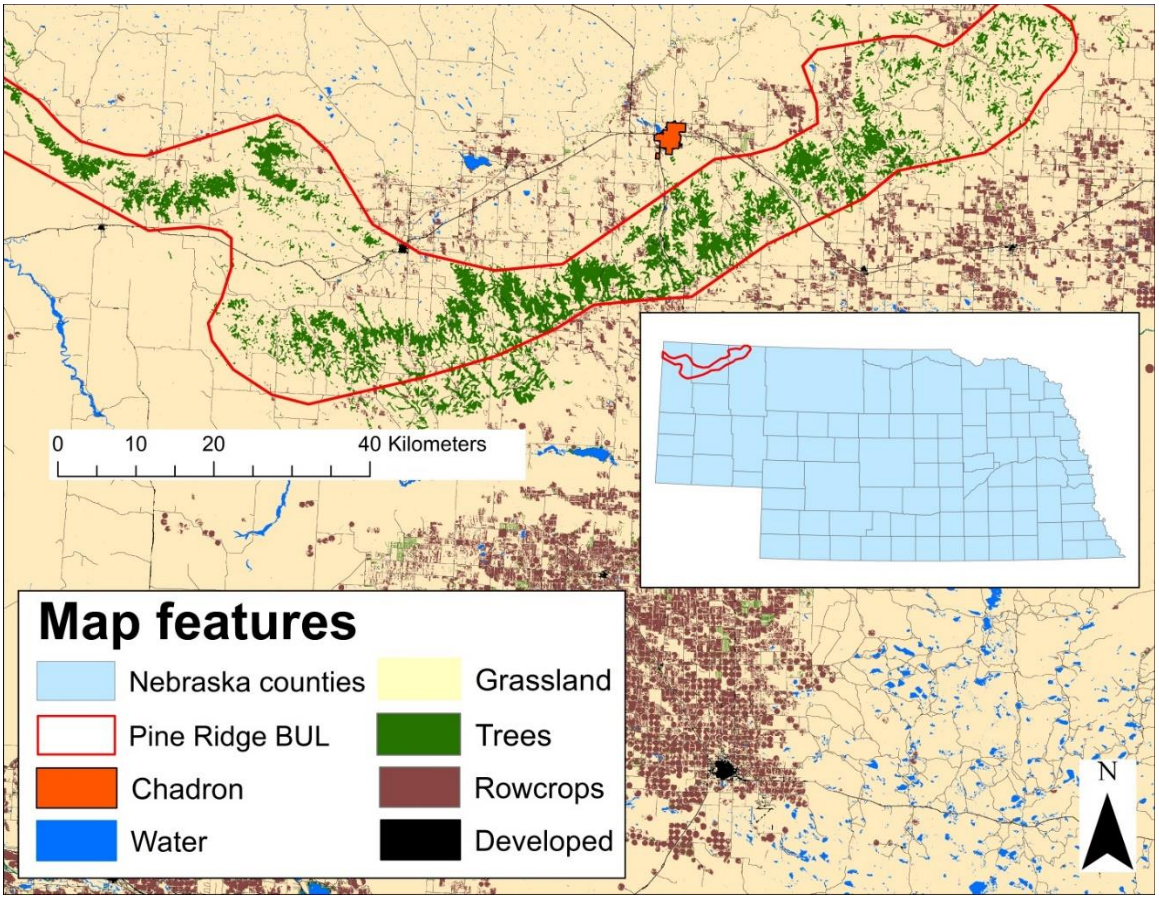
0
10
20
40 Kilometers
Map features
Nebraska counties
Pine Ridge BUL
Chadron
Water
Grassland
Trees
Rowcrops
Developed
N

Figure 1: Reclassified landcover (Bishop et al. 2011) in and around the Pine Ridge Biologically Unique Landscape (BUL) of northwest Nebraska, U.S.A.

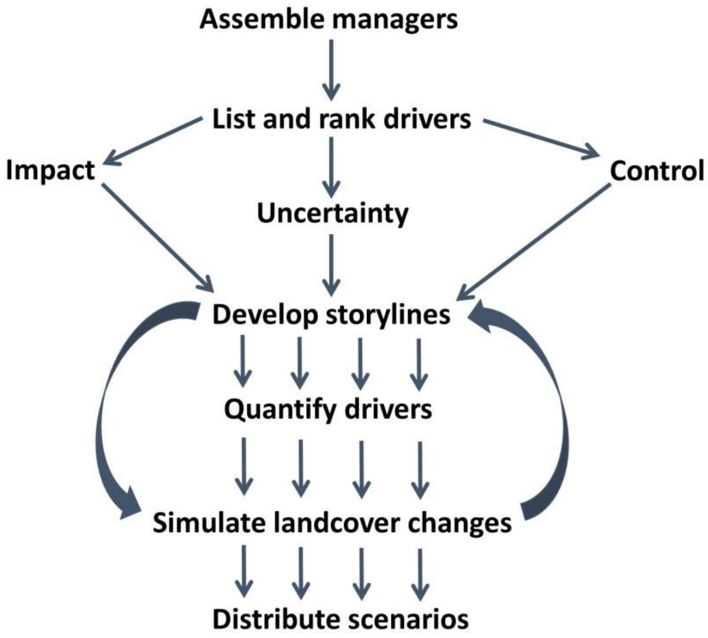
Assemble managers
List and rank drivers
Impact
Control
Uncertainty
Develop storylines
Quantify drivers
Simulate landcover changes
Distribute scenarios

Figure 2: Iterative process used to conduct the scenario planning exercise in the Pine Ridge Biologically Unique Landscape.

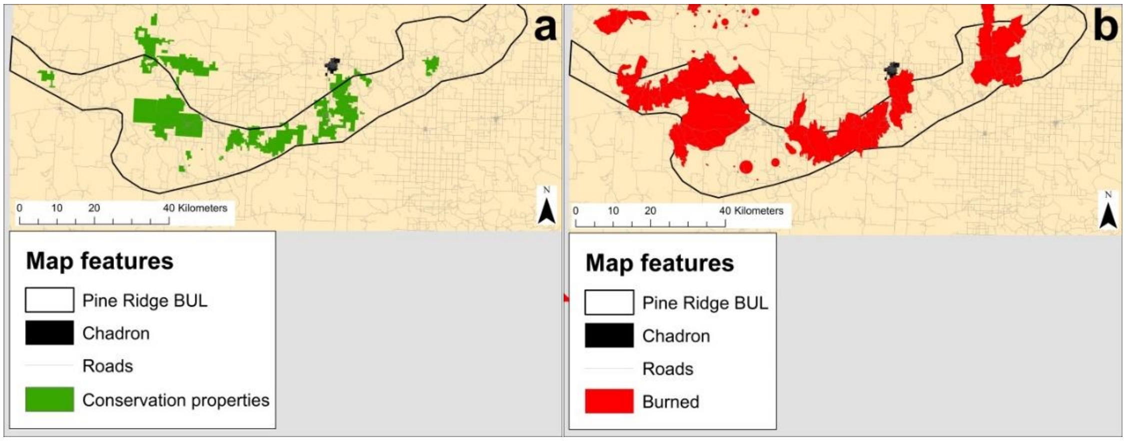
a
0 10 20 40 Kilometers
N
Map features
Pine Ridge BUL
Chadron
Roads
Conservation properties
b
0 10 20 40 Kilometers
N
Map features
Pine Ridge BUL
Chadron
Roads
Burned

Figure 3: Maps of a) conservation properties and b) areas that have experienced wildfire since the mid-20th century in the Pine Ridge Biologically Unique Landscape (BUL).

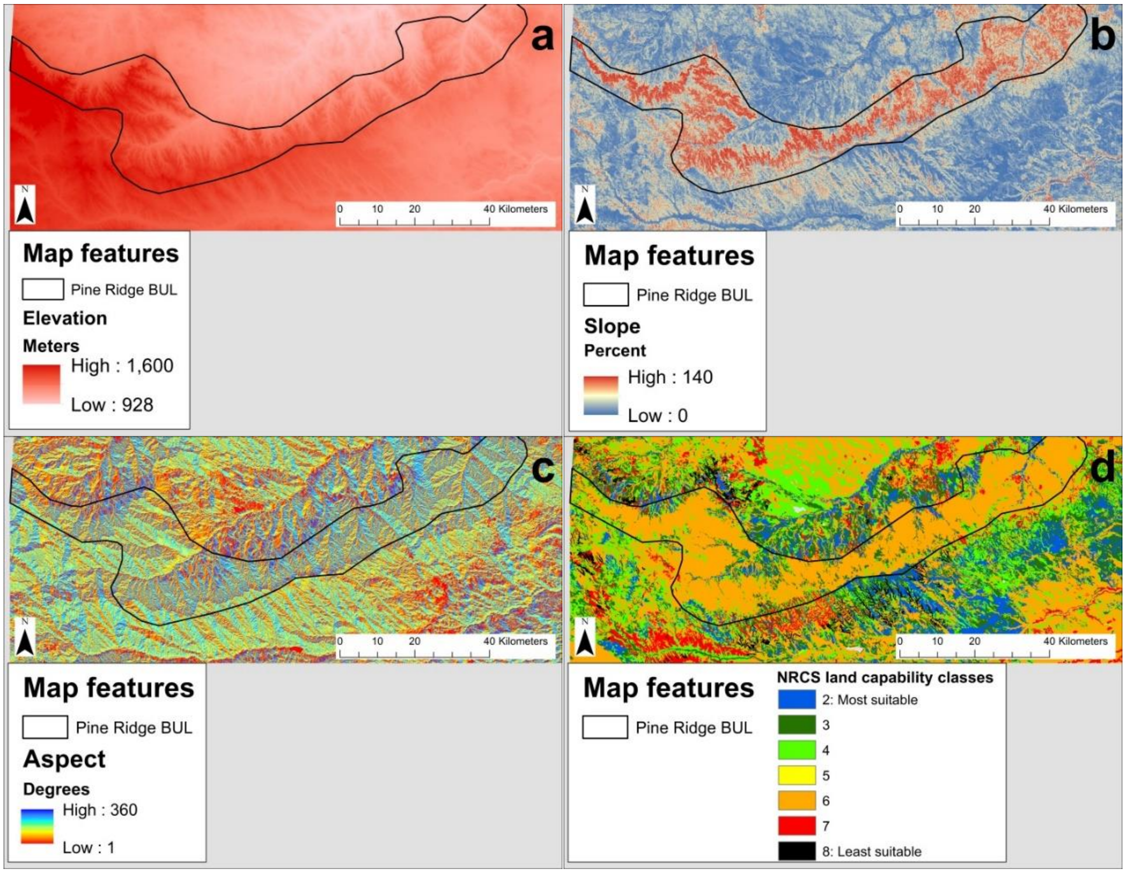
a
b
c
d
N
0 10 20 40 Kilometers
Map features
Pine Ridge BUL
Elevation
Meters
High : 1,600
Low : 928
Slope
Percent
High : 140
Low : 0
Aspect
Degrees
High : 360
Low : 1
NRCS land capability classes
2: Most suitable
3
4
5
6
7
8: Least suitable

Figure 4: Maps of a) elevation, b) percent slope, c) aspect, and d) National Resource Conservation Service Land Capability Classes in the Pine Ridge Biologically Unique Landscape (BUL).

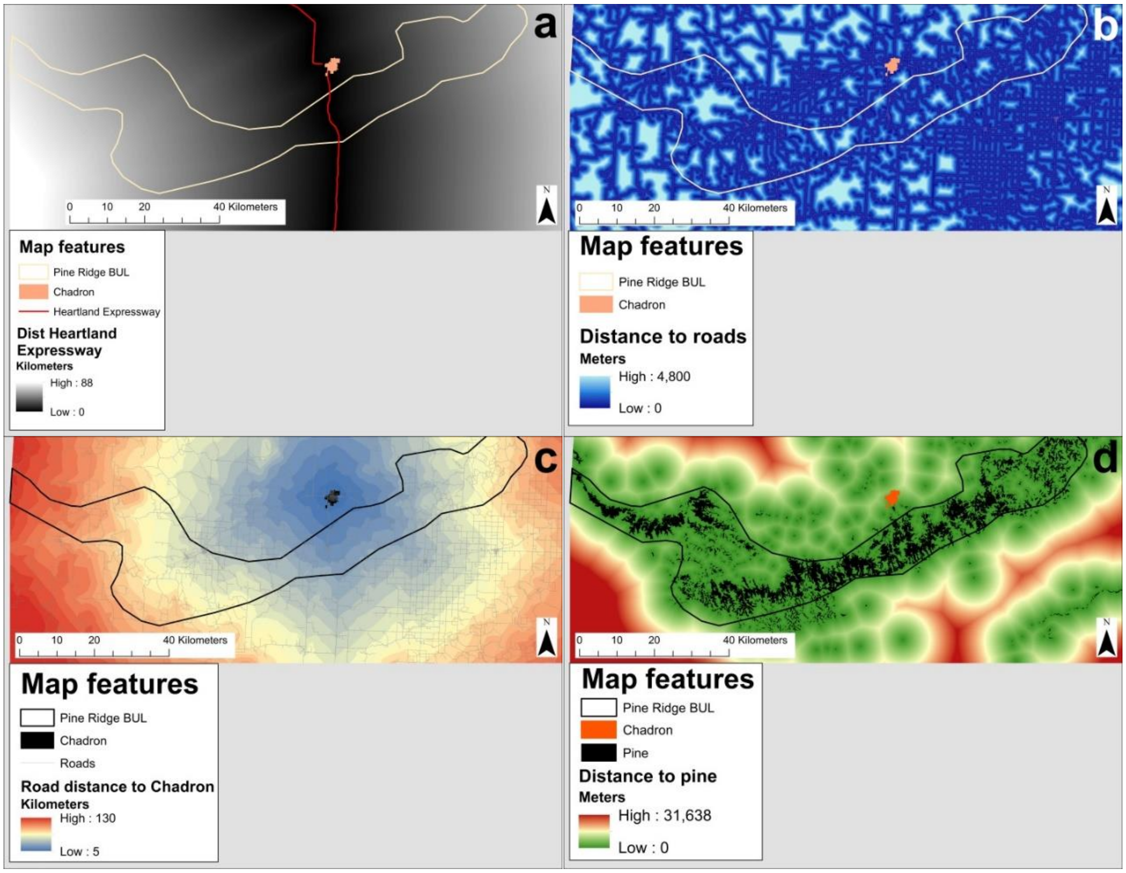
a
0 10 20 40 Kilometers
N
Map features
Pine Ridge BUL
Chadron
Heartland Expressway
Dist Heartland Expressway
Kilometers
High : 88
Low : 0
b
0 10 20 40 Kilometers
N
Map features
Pine Ridge BUL
Chadron
Distance to roads
Meters
High : 4,800
Low : 0
c
0 10 20 40 Kilometers
N
Map features
Pine Ridge BUL
Chadron
Roads
Road distance to Chadron
Kilometers
High : 130
Low : 5
d
0 10 20 40 Kilometers
N
Map features
Pine Ridge BUL
Chadron
Pine
Distance to pine
Meters
High : 31,638
Low : 0

Figure 5: Euclidian (i.e., straight-line) distance from a) Highway 385, b) all roads, c) City of Chadron, and d) pine trees in the Pine Ridge Biologically Unique Landscape (BUL).

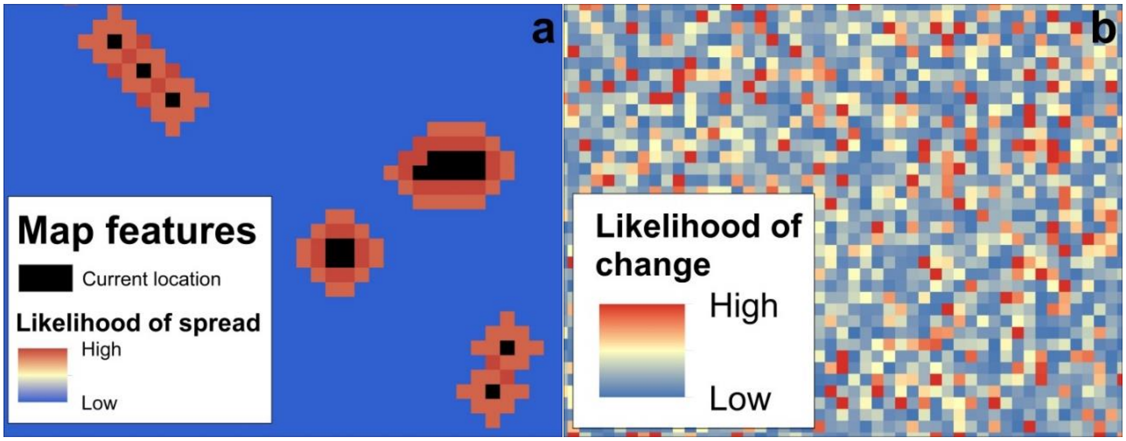
a
Map features
Current location
Likelihood of spread
High
Low
b
Likelihood of change
High
Low

Figure 6: Representations of a) neighborhood and b) random (i.e., stochastic) effects introduced into cellular automata models of landcover change.

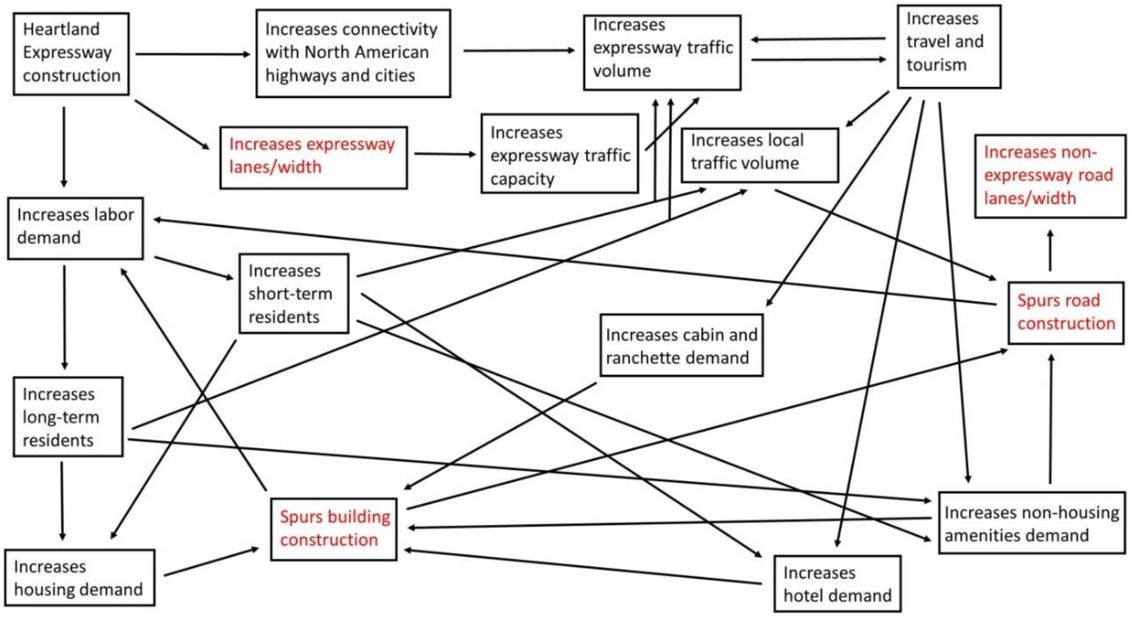
Heartland Expressway construction
Increases connectivity with North American highways and cities
Increases expressway traffic volume
Increases travel and tourism
Increases expressway lanes/width
Increases expressway traffic capacity
Increases local traffic volume
Increases non-expressway road lanes/width
Increases labor demand
Increases short-term residents
Spurs road construction
Increases cabin and ranchette demand
Increases long-term residents
Spurs building construction
Increases non-housing amenities demand
Increases housing demand
Increases hotel demand

Figure 7: Drivers of landcover change in the Pine Ridge Biologically Unique Landscape under the Roadside Development Scenario. Landcover changes are listed in red-colored font.

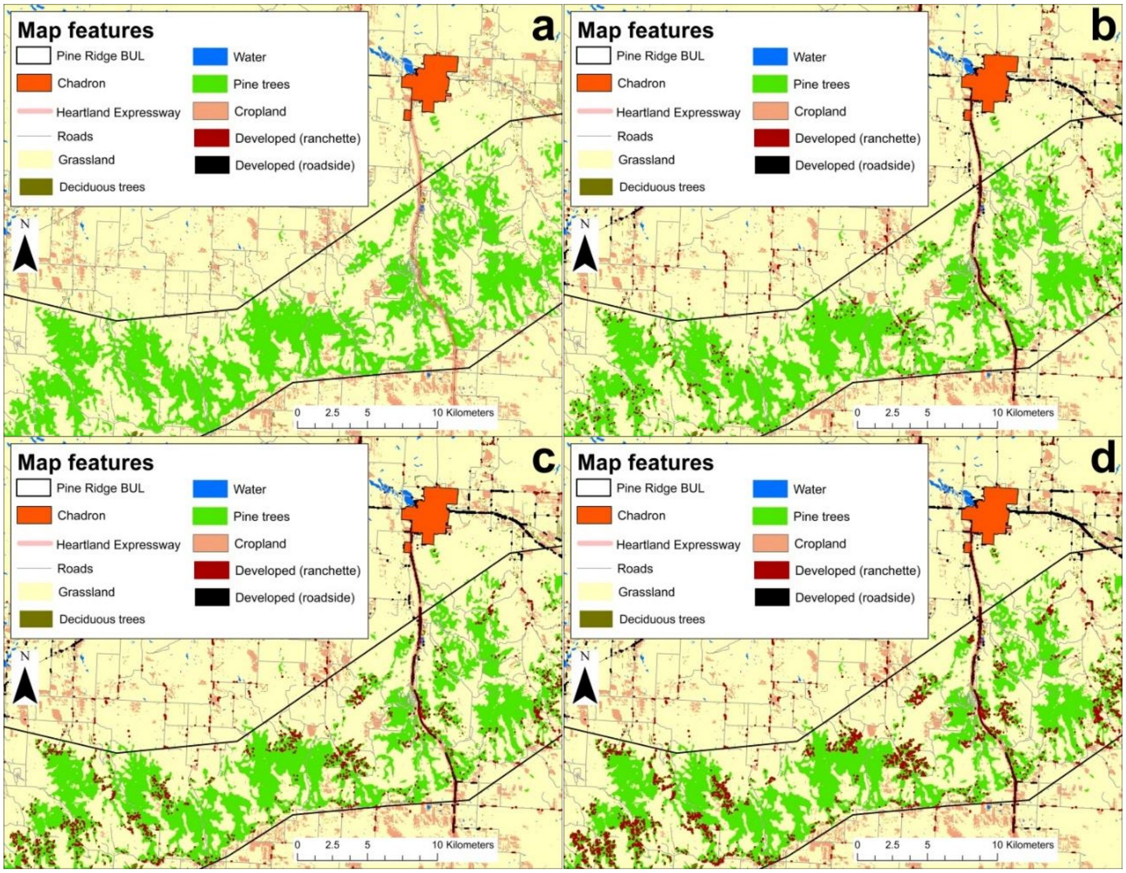
a
b
c
d
Map features
Pine Ridge BUL
Chadron
Heartland Expressway
Roads
Grassland
Deciduous trees
Water
Pine trees
Cropland
Developed (ranchette)
Developed (roadside)
N
0
2.5
5
10 Kilometers

Figure 8: Landcover in the Pine Ridge Biologically Unique Landscape (BUL) under the Roadside Development Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. Two forms of development are assumed to occur: 1) roadside development, along the Heartland Expressway; and 2) ranchette and cabin development at other locations throughout the BUL.

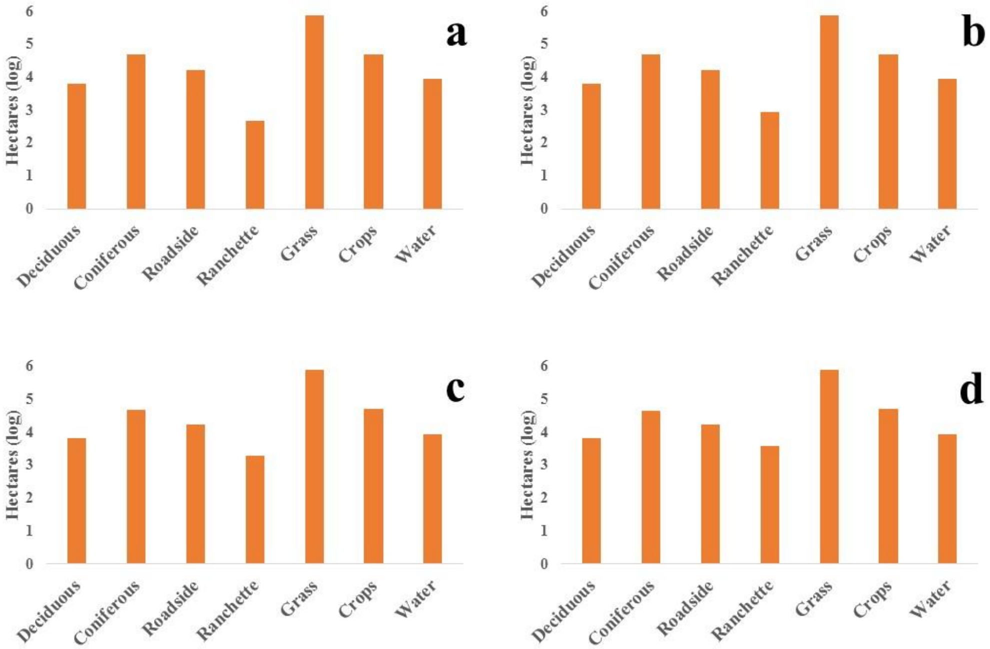

Figure 9: Major landcover class areas (log-transformed hectares) under the Roadside Development Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. Landcover class areas were log-transformed to reduce the influence of the dominant landcover class (i.e., grass) and facilitate visual comparisons among classes.

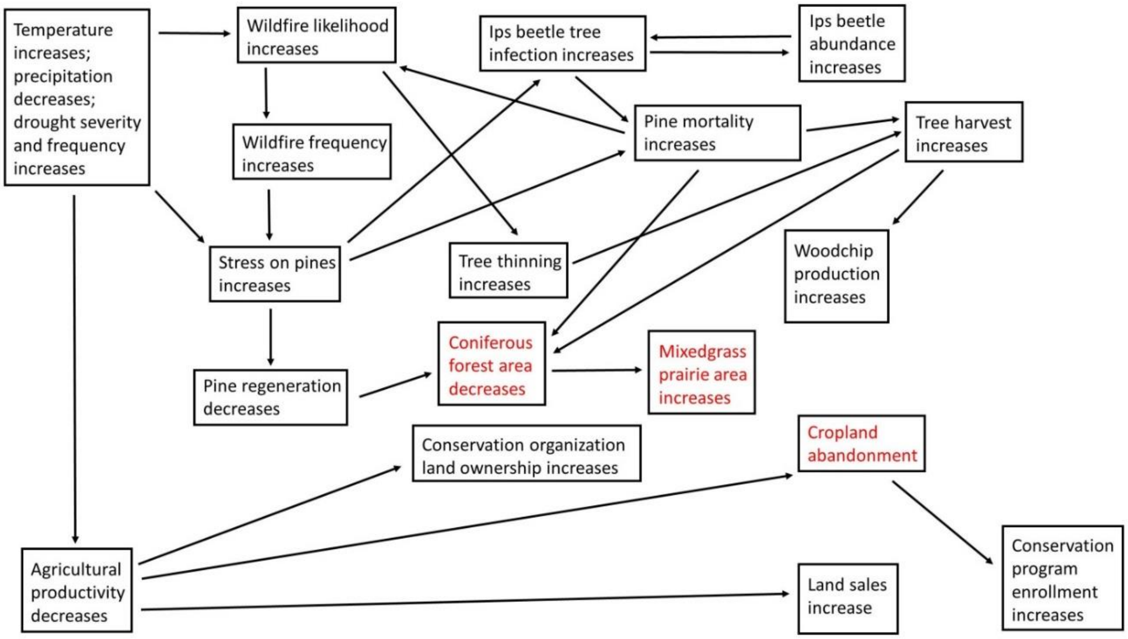
Temperature increases; precipitation decreases; drought severity and frequency increases
Wildfire likelihood increases
Ips beetle tree infection increases
Ips beetle abundance increases
Wildfire frequency increases
Pine mortality increases
Tree harvest increases
Stress on pines increases
Tree thinning increases
Woodchip production increases
Coniferous forest area decreases
Mixedgrass prairie area increases
Pine regeneration decreases
Conservation organization land ownership increases
Cropland abandonment
Agricultural productivity decreases
Land sales increase
Conservation program enrollment increases

Figure 10: Drivers of landcover change in the Pine Ridge Biologically Unique Landscape under the High and Dry Scenario. Landcover changes are listed in red-colored font.

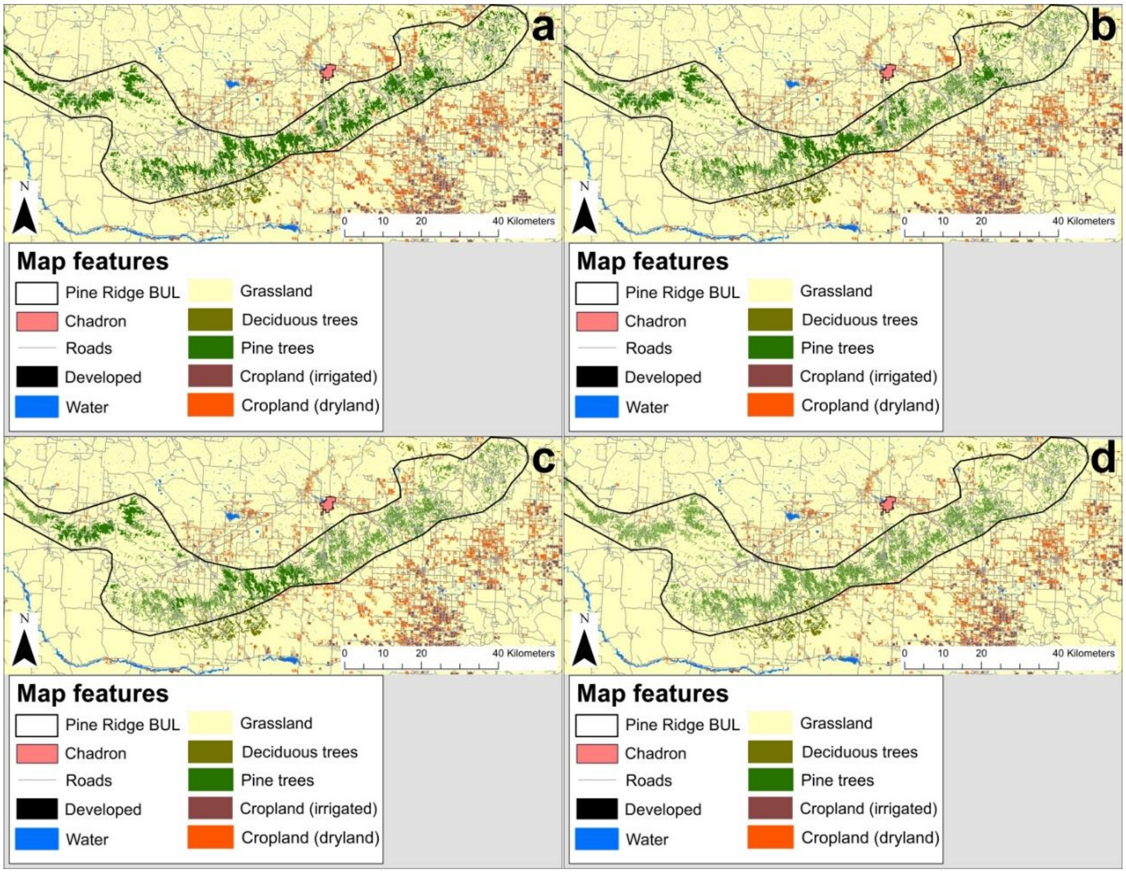
a
N
0 10 20 40 Kilometers
Map features
Pine Ridge BUL
Chadron
Roads
Developed
Water
Grassland
Deciduous trees
Pine trees
Cropland (irrigated)
Cropland (dryland)
b
N
0 10 20 40 Kilometers
Map features
Pine Ridge BUL
Chadron
Roads
Developed
Water
Grassland
Deciduous trees
Pine trees
Cropland (irrigated)
Cropland (dryland)
c
N
0 10 20 40 Kilometers
Map features
Pine Ridge BUL
Chadron
Roads
Developed
Water
Grassland
Deciduous trees
Pine trees
Cropland (irrigated)
Cropland (dryland)
d
N
0 10 20 40 Kilometers
Map features
Pine Ridge BUL
Chadron
Roads
Developed
Water
Grassland
Deciduous trees
Pine trees
Cropland (irrigated)
Cropland (dryland)

Figure 11: Landcover in the Pine Ridge Biologically Unique Landscape (BUL) under the High and Dry Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045.

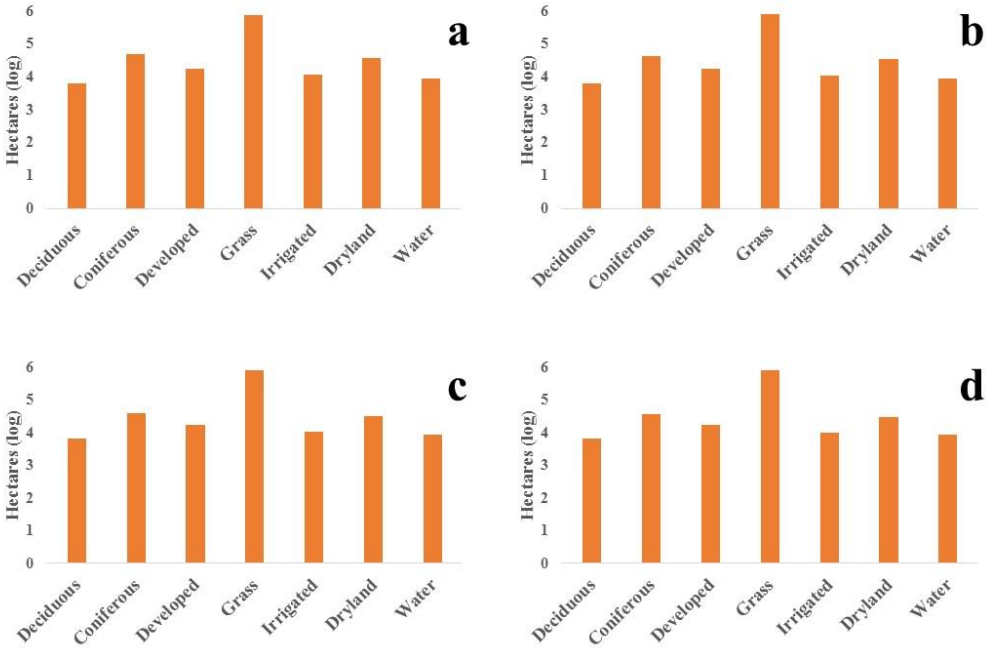

Figure 12: Major landcover class areas (log-transformed hectares) under the High and Dry Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. Landcover class areas were log-transformed to reduce the influence of the dominant landcover class (i.e., grass) and facilitate visual comparisons among classes.

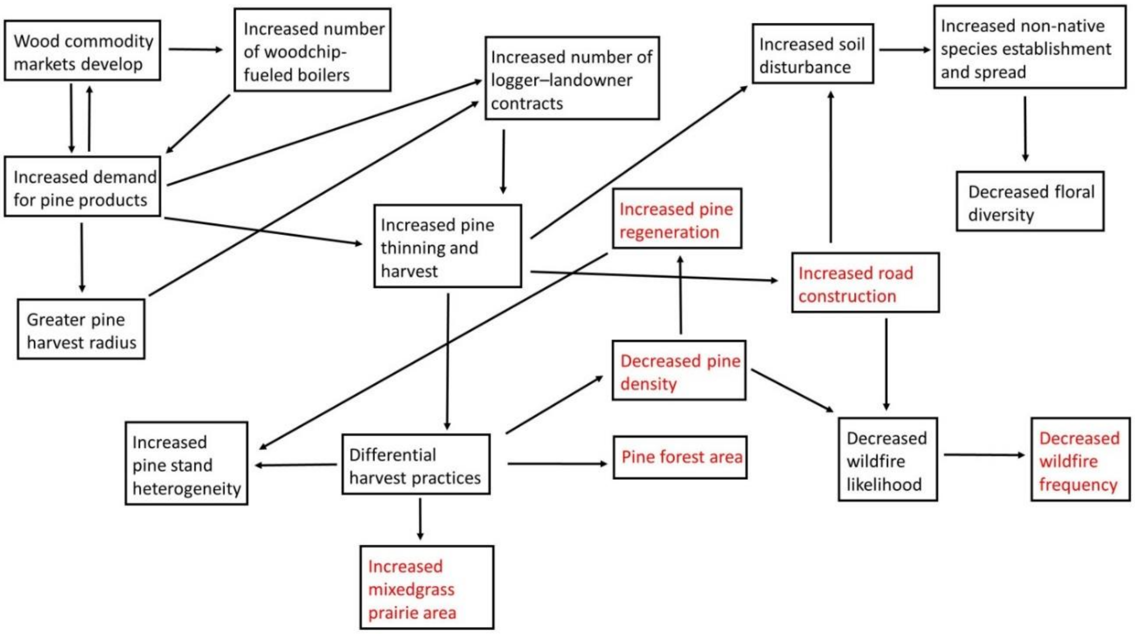
Wood commodity markets develop
Increased number of woodchip-fueled boilers
Increased number of logger–landowner contracts
Increased soil disturbance
Increased non-native species establishment and spread
Increased demand for pine products
Decreased floral diversity
Increased pine regeneration
Increased pine thinning and harvest
Increased road construction
Greater pine harvest radius
Decreased pine density
Increased pine stand heterogeneity
Differential harvest practices
Pine forest area
Decreased wildfire likelihood
Decreased wildfire frequency
Increased mixedgrass prairie area

Figure 13: Drivers of landcover change in the Pine Ridge Biologically Unique Landscape under the Wood Commodities Scenario. Landcover changes are listed in red-colored font.

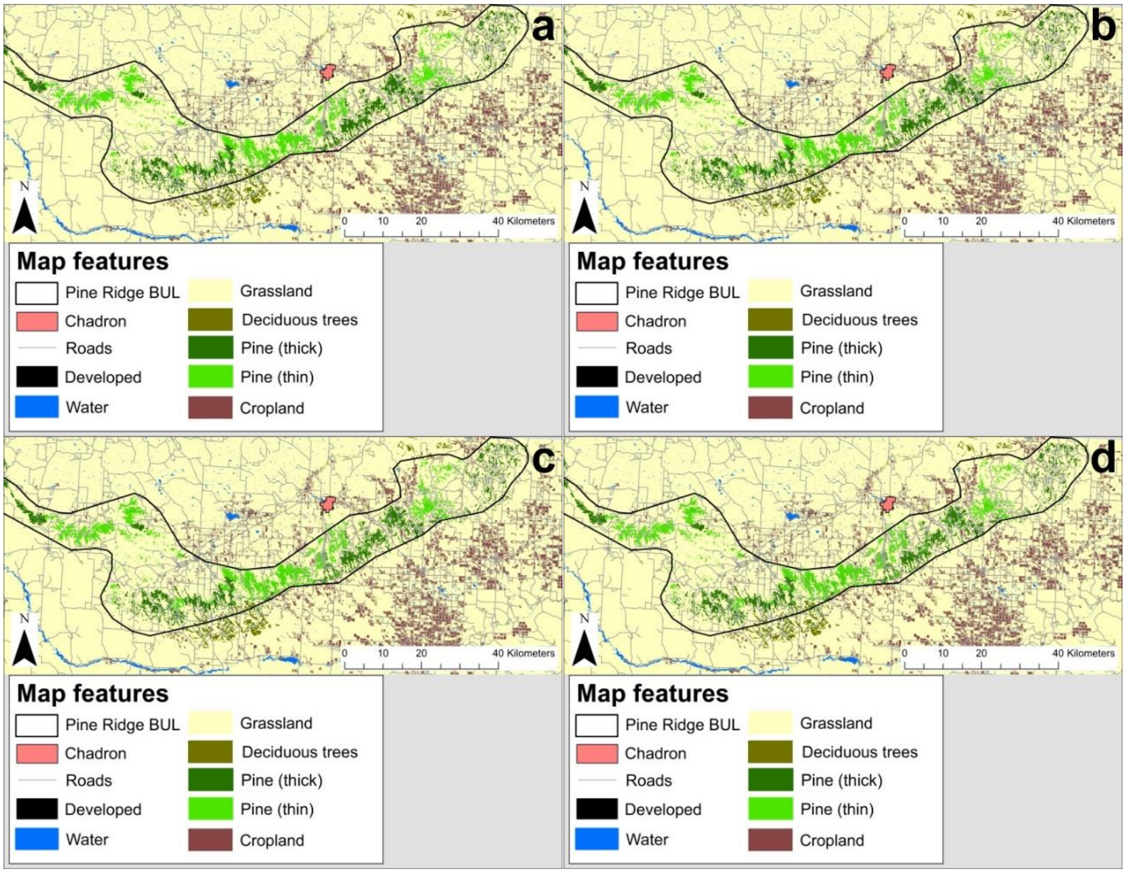
a
b
c
d
N
0 10 20 40 Kilometers
Map features
Pine Ridge BUL
Chadron
Roads
Developed
Water
Grassland
Deciduous trees
Pine (thick)
Pine (thin)
Cropland

Figure 14: Landcover in the Pine Ridge Biologically Unique Landscape (BUL) under the Wood Commodities Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045.

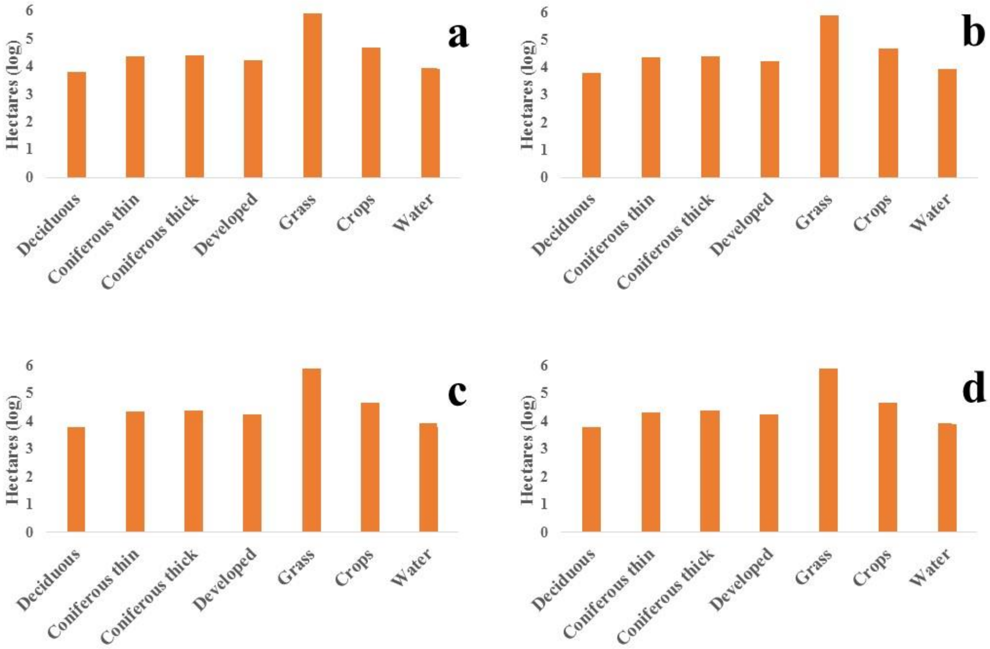

Figure 15: Major landcover class areas (log-transformed hectares) under the Wood Commodities Scenario in the years a) 2015, b) 2025, c) 2035, and d) 2045. Landcover class areas were log-transformed to reduce the influence of the dominant landcover class (i.e., grass) and facilitate visual comparisons among classes.

CHAPTER 8: SUMMARY AND SYNTHESIS

Landcover change is an important global change process affecting social–ecological system(s) (SES) worldwide (Lambin et al. 2006; Lindenmayer & Fischer 2013). Human activities may directly and indirectly drive landcover change, and human populations may be directly and indirectly affected by it (DeFries et al. 2004; Foley et al. 2005; Chhabra et al. 2006; Lambin & Meyfroidt 2011). Although uncertainties exist about the future of landcover change, uncertainties can be engaged strategically in the context of SESs thinking. One such means of strategic engagement involves evaluating and comparing case studies of regional human-driven landcover change—past, present, and potential future—in order to obtain a more holistic and place-based understanding of its social–ecological trajectories, causes, and consequences. Improved understanding of these aspects of regional landcover change could inform decisions and actions that increase the resilience of SESs to landcover change and related global change processes.

In this dissertation, I assessed trajectories, causes, and consequences of past, present, and potential future landcover change in landscapes of Nebraska, U.S.A. in the context of SESs thinking. In these case studies, a variety of methodological approaches—historical literature review, statistical modeling, machine learning, graph theory, and cellular automata—were utilized to increase understanding of past, present, and potential future landcover change in Nebraska landscapes, the direct and indirect relationships between landcover change and people, and the social–ecological tradeoffs associated with alternative landcover change trajectories.

In Chapter 2, I reviewed historical accounts of human energy use in landscapes of the Central and Northern Great Plains—including those of present-day Nebraska, U.S.A.—focusing on the utility, renewability, and geographic distributions of herbaceous biomass, woody biomass, and buffalo chips. Results demonstrated that the geographic distributions of these important organic fuels ebbed and flowed over the course of the 19th century as a result of changes in and interactions among various factors, including environmental conditions, human harvest, and human disturbance regime manipulation. In other words, landcover changes in 19th century SESs of present-day Nebraska and the surrounding Great Plains were both directly and indirectly human-driven and occurred as Native and Euro-Americans simultaneously shaped and responded to their environments. However, differences in these responses across cultures, time, and space set Great Plains SESs on alternative trajectories characterized by unique short-term and long-term landcover-based tradeoffs that extend to present-day.

In Chapter 3, I used generalized linear mixed model(s) (GLMM) to compare brown-headed cowbird (*Molothrus ater*), dickcissel (*Spiza americana*), eastern kingbird (*Tyrannus tyrannus*), and western meadowlark (*Sturnella neglecta*) abundances (i.e., counts) with proportions of land area enrolled in cropland in seven Nebraska, U.S.A. counties in seven years between 1969 and 2007. I found that although statistically significant relationships were evidenced between avian counts and county cropland proportion in the final GLMM for all four avian species, the GLMMs differed in their abilities to explain variability in avian counts along BBS routes, with the best-performing model being for dickcissels and the worst-performing model being for brown-headed cowbirds. This chapter illustrated one approach to assessing the long-term ecological consequences of conversion to cropland and related forms of landcover change in the context of SESs thinking, which emphasizes interconnections and interdependencies between human social systems and ecosystems. In this context, results of this and similar studies could contribute to contemporary and future evaluations of the social–ecological tradeoffs associated with alternative trajectories of human-driven landcover change.

In Chapter 4, I modeled and mapped the geographic distributions of mature individuals of 14 tree species in Indian Cave State Park (ICSP) in southeastern Nebraska in an ensemble modeling approach. Results indicated that no modeling technique within the ensembles consistently outperformed any other; however, predictive performance was consistently better for certain species, particularly American basswood (*Tilia americana*), red oak (*Quercus rubra*), chinkapin oak (*Quercus muehlenbergi*), black oak (*Quercus velutina*), and bur oak (*Quercus macrocarpa*), the predicted distributions of which largely correspond with existing descriptions in the scientific literature. The results of this chapter could contribute useful information to ongoing oak restoration activities in ICSP, and in a broader sense, illustrate how social–ecological memory (SEM) can confer SESs with resilience amidst indirectly-driven landcover change and its drivers.

In Chapter 5, I used graph theory to assess functional connectivity and modularity for herpetofauna in wetland networks of three Nebraska landscapes that have experienced different intensities of conversion to cropland over the past several centuries. I also assessed the level of clustering in wetland geographic distributions in each landscape. Among the three landscapes, wetland connectivity, modularity, and clustering were greatest in the Cherry County Wetlands, a landscape embedded in the large, relatively unbroken grasslands of the Nebraska Sandhills. Compared to the Cherry County Wetlands, connectivity and modularity are lower in the Central Loess Hills, a grass-dominated landscape that is presently experiencing landcover change via the conversion of grasslands and wetlands to rowcrop fields and woodland, and lowest in the Rainwater Basin, a landscape characterized by 20th century conversion to intensive rowcrop production. Thresholds in network-level connectivity are evidenced in the Rainwater Basin and Central Loess Hills between certain assumed species dispersal distances; however, the majority of the Cherry County Wetlands are already functionally connected at the shortest assumed dispersal distance, making any connectivity thresholds unapparent, and therefore, likely more resilient to perturbations at multiple scales than the Central Loess Hills or Rainwater Basin. Evaluations of aerial imagery in the portion of each landscape with the densest wetland clusters reveal relatively unbroken grassland in the Cherry County Wetlands, rowcrop production in the Central Loess Hills, and industrial activity in the Rainwater Basin. Considering the combined influences of changes in habitat quality and functional connectivity for metapopulations of herpetofauna and other wetland-dependent species may assist with the representation of social–ecological tradeoffs associated with conversion to cropland and other forms of directly human-driven landcover change.

In Chapter 6, I applied Uden et al.'s (2015) 10-step framework for adaptive invasive species distribution model(ing) (iSDM) to develop a landcover-based iSDM for the Chinese mystery snail in Lancaster County, Nebraska. Within the framework, a random forests model was trained with presence/absence data from 13 surveyed water bodies, validated with a comparison of predicted *versus* observed Chinese mystery snail presence/absence, and then extrapolated to predict Chinese mystery snail presence/absence in 1,791 additional water bodies in Lancaster County. Predictor variables used to explain variability in Chinese mystery snail presence/absence were water body area, road density, and the Euclidian distance to the City of Lincoln, with the last two landcover-based predictors serving as proxies for human activity and movement. Road density was the most important variable for describing variability in snail presence/absence, and was followed by water body area, and distance from Lincoln, respectively. Model predictive ability was relatively poor, based on the area under the curve statistic of 0.58 from the comparison of predicted and observed presence/absence values. Nevertheless, this chapter represents an important first step for informing Chinese mystery snail management and for improving iSDM predictive ability. Comparative iSDM exercises in eastern Nebraska and elsewhere in the Chinese mystery snail's novel and native ranges could increase understanding of the landcover change-based factors driving its distribution and help inform management decisions and actions.

Finally, in Chapter 7, I reported on a participatory scenario planning exercise conducted in the Pine Ridge Biologically Unique Landscape (BUL) of northwest Nebraska, U.S.A., in which local stakeholders identified and ranked factors they perceived as being important drivers of future change in the Pine Ridge BUL. Drivers about which uncertainty was high and control was low were aggregated to produce alternative, plausible scenario storylines of landcover change in the Pine Ridge from

2015–2045. Storylines then informed the parameterization of cellular automata landcover change simulations, which along with scenario storylines, were iteratively refined, according to stakeholder feedback. In addition to tangible products of uncertainty ranks and simulated future landcover maps, the scenario planning exercise may have produced intangible benefits, such as broadened perspectives and stronger partnerships between individuals and agencies. In the context of SESs thinking, participatory scenario planning could not only be used to consider future trajectories of landcover change, but also to increase the resilience of SESs to landcover change and related global change processes and to facilitate SES adaptation and transformation under their influences.

Individually, the findings of the chapters of this dissertation are useful for increasing understanding of landscape- and SES-specific landcover change causes and consequences and for informing current and future landscape management. In such SES-specific contexts, emphasis on the short- and long-term effects of landcover change for human populations and ecosystems, as well as increasing awareness of the interdependencies between human populations and ecosystems, could assist decision-making through the consideration of the social–ecological tradeoffs associated with alternative landcover-based decisions and actions. For example, the results of Chapter 4 could assist land managers with decisions related to the spatial and temporal application of prescribed fire and tree-thinning in ICSP and surrounding landscapes; the results of Chapter 5 could provide additional landscape-scale information (i.e., functional connectivity) to conservation planners evaluating the social–ecological tradeoffs of landcover-based decisions on wetland-dependent species; and the results of Chapter 6 could help identify landcover-based factors that contribute to the introduction, establishment, and spread of aquatic invasive species.

In a broader sense, the utility of this dissertation's findings lies in the promotion and illustration of the engagement of social–ecological challenges like landcover change—and uncertainties about them—through the lens of SESs thinking.
Indeed, analyzing and comparing case studies of past, present, and potential future landcover change in SESs of a region promotes more holistic understanding of what regional landcover change was, is, and could be. This improved understanding could assist with the management of short- and long-term social–ecological tradeoffs, and could inform landcover-based adaptations under the pressures of landcover change and related global change processes. For example, the results of Chapters 2 and 3 reaffirm basic tents of SESs thinking, such as the interconnectedness and interdependencies of human social systems and ecological systems, the tendency of people to simultaneously shape and respond to their environments, and the potential for different human responses to environmental conditions to set SESs on alternative landcover change trajectories with unique sets of social–ecological tradeoffs. The results of Chapter 4 demonstrate that even when SESs have progressed along certain trajectories for extended periods of time—decades and centuries in the case oak forests—sources of SEM in the SES may preserve the potential for a return to prior stable states, and thereby confer the SES with high levels of resilience to perturbations of directly and indirectly human-driven landcover change. Finally, the results of Chapter 7 show how the strategic engagement of collective uncertainties about future landcover changes can broaden perspectives and increase

preparation and cooperation on social–ecological challenges. In light of the dynamic nature of SESs and global change processes, one of the greatest utilities of this dissertation is perhaps its potential for promoting place-based understanding of landcover change and adaptive responses to it and related social–ecological challenges (e.g., landcover change–climate change interactions) about which uncertainties can be high and control can be low.

Future research

There are a number of avenues for the extension of the findings of this dissertation in future studies. In a broad sense, there are numerous additional comparisons of past, present, and potential future regional landcover change that could contribute to the understanding of landcover change in the context of SESs thinking in general. These region-specific assessments lend themselves to evaluations of region-specific social–ecological tradeoffs in landcover-based decisions and actions. Additional explorations into the associations between past, present, and future landcover change and resilience, adaptation, and transformation in SESs could also be undertaken.

In regard to explorations of the relationships between human-driven landcover change and energy use (i.e., Chapter 2), future studies could apply a similar framework to exploration of the relationships between landcover change and the procurement of food, water, shelter, and other ecosystem services. Historical landcover change–energy use assessments could also be made in different locations and over different timeframes. The inclusion of the effects of fossil fuel use—which was not included in Chapter 2—could provide valuable insights from the late 19th century to present-day.

Future studies related to the social–ecological effects of land conversion (i.e., Chapter 3) could be conducted in different locations, particularly those where the availability of data on large-scale landcover change and avian counts are better matched. In addition, statistical relationships between bird counts and proportions of land area enrolled in specific crop types, or combinations of crop types (Jorgensen et al. 2014), could be explored.

For tree distributions amidst indirectly human-driven landcover change, the ensemble modeling approach adopted in Chapter 4 could simply be extended to species in other size classes (e.g., medium and small), developmental stages (e.g., saplings and seedlings), and forest canopy levels (e.g., canopy and subcanopy). Furthermore, the same data could be analyzed in a community (i.e., multivariate) instead of single-species framework. The comparisons of results from these different analytical approaches—based on the same data—could itself make for interesting comparisons.

For assessments of relationships between landcover change and functional connectivity (i.e., Chapter 5), potential future studies include conducting similar analyses for additional wetland-dependent species, with different wetland datasets, and different forms of dispersal paths beside Euclidian (i.e., straight-line) distance. The incorporation of the difficulties (i.e., resistances) of traversing different landcover classes could provide more realistic assessments of functional connectivity, as could the incorporation of known barriers.

Future explorations of the utility of landcover change-based predictor variables in adaptive iSDMs could simply involve the implementation of steps 8 and 9 of Uden et al.'s (2015) framework, which would ideally produce updated data for application to management and improvement of models. A more robust dataset of Chinese mystery snail occurrence, in particular, would support the utilization of modeling techniques other than random forests, which are likely more interpretable. In addition, predictor variables that are more representative of the relationships between landcover change and Chinese mystery snail spread could be incorporated into future studies. The approach of Chapter 6 could certainly also be extended to other species and locations.

Finally, future studies in landcover-based participatory scenario planning (i.e., Chapter 7) could entail the combination of the alternative scenarios from Chapter 7 into a super-scenario, as suggested by land managers, as well as the improved parameterization of the Pine Ridge landcover change simulations. The participatory scenario planning approach could be extended to other regional landscapes, so that multiple futures from multiple locations can be incorporated into regional landcover change assessments. Finally, repeats of participatory scenario planning exercises in the same landscapes with the same participants could provide insights into how scenario planning exercises affect participant perceptions of impact, uncertainty, and control in drivers of potential future landcover change.

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