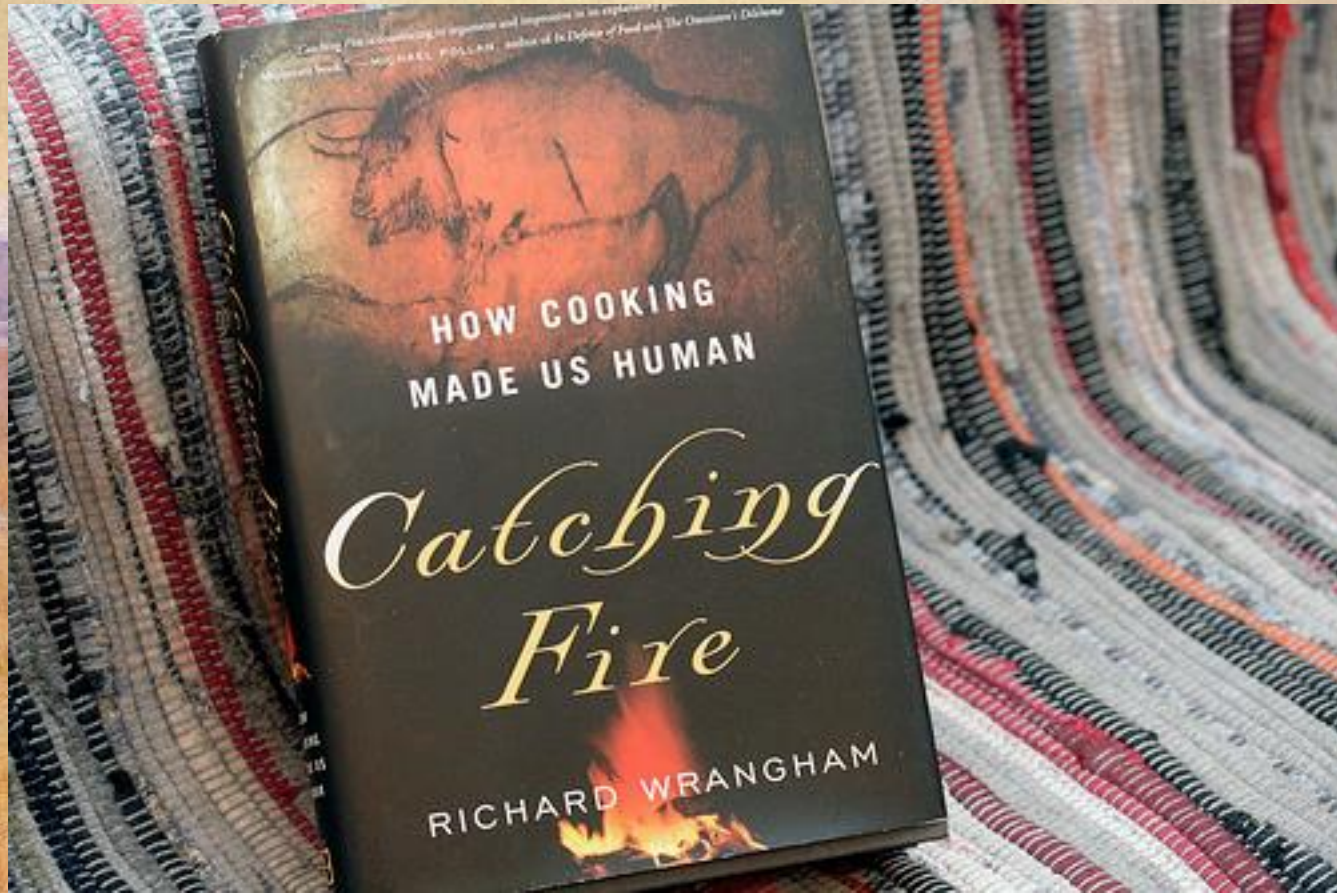
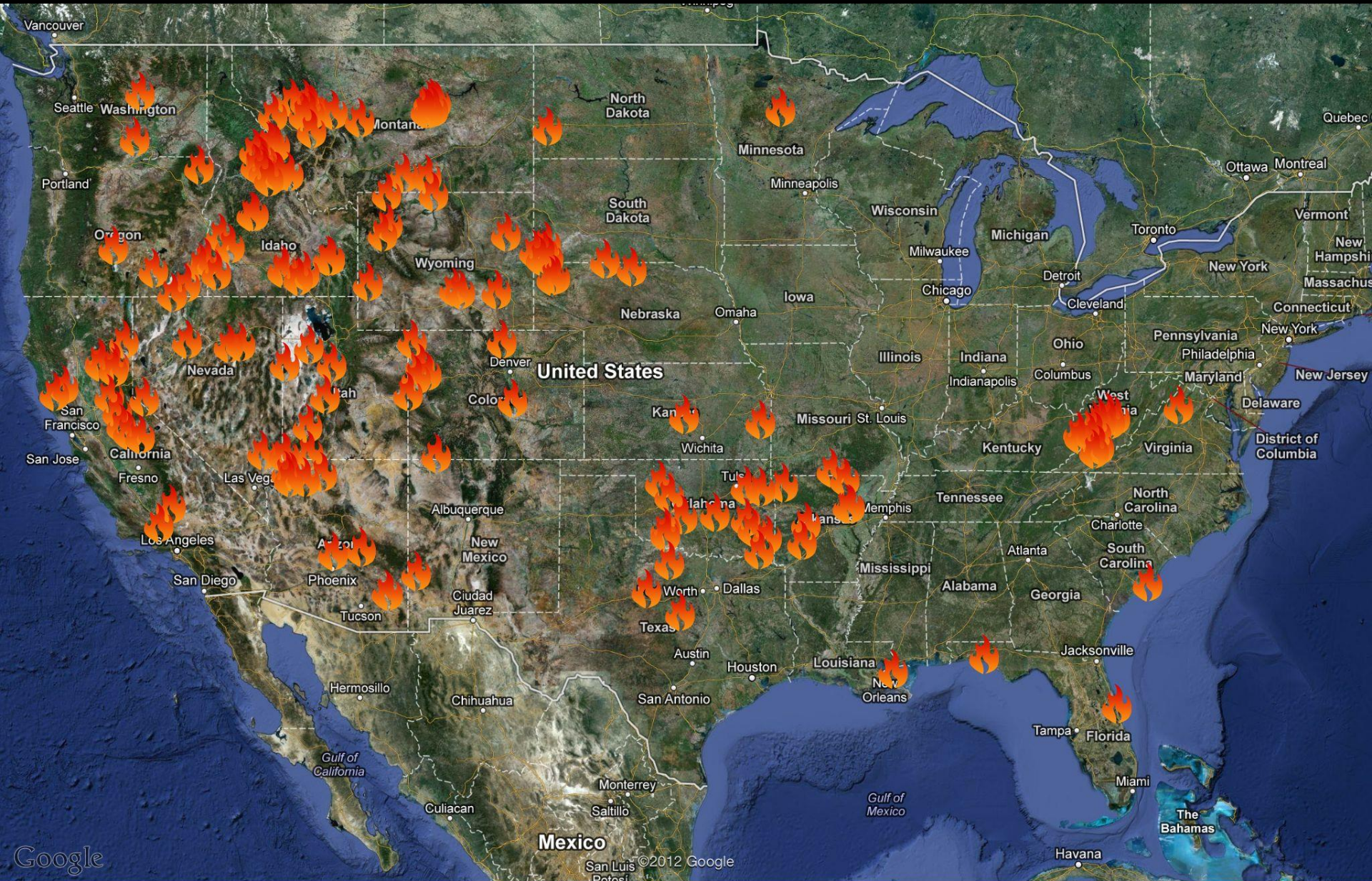


Humans and Fire

courtesy of www.charlesmarionrussell.org



Incidents





Three-fourths of US lands dominated by native vegetation show moderate or high departure from reference conditions as a result of altered fire regimes (TNC 2009).



USDA Forest Service
Rocky Mountain
Research Station
Fire Science Lab
Missoula, MT



DOI USGS
Earth Resources
Observation Systems
(EROS) Data Center
Sioux Falls, SD



The Nature
Conservancy
Global Fire Initiative
Boulder, CO



FRCC Team
Fire & Aviation
Management
Washington DC

Fire cycles in North American interior grasslands and their relation to prairie drought

K. J. Brown^{1*5}, J. S. Clark^{1†}, E. C. Grimm[‡], J. J. Donovan^{**}, P. G. Mueller[‡], B. C. S. Hansen^{**}, and I. Stefanova^{**}

¹Department of Biology and ²Nicholas School of the Environment, Duke University, P.O. Box 90338, Durham, NC 27708; ³Department of Quaternary Geology, Geological Survey of Denmark and Greenland, 10 Øster Voldgade, DK-1350 Copenhagen K, Denmark; ⁴Illinois State Museum, Research and Collections Center, 1011 East Ash Street, Springfield, IL 62703; ⁵Department of Geology and Geography, West Virginia University, 425 White Hall, P.O. Box 6300, Morgantown, WV 26506; and ^{**}Limnological Research Center, University of Minnesota, 220 Pillsbury Hall, 310 Pillsbury Drive Southeast, Minneapolis, MN 55455

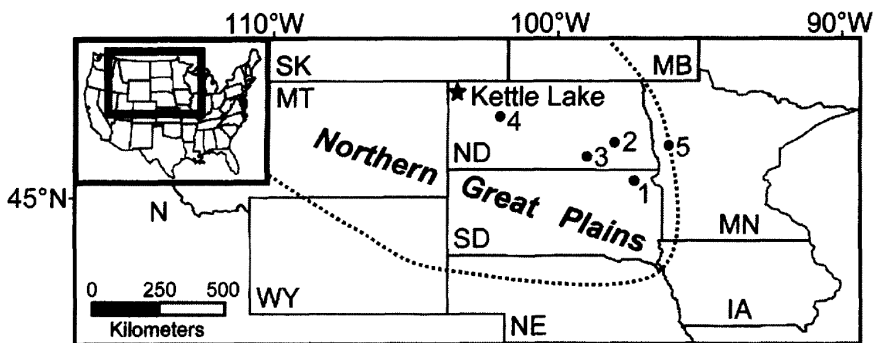


Fig. 1. Study location (*Inset*) and study site map. The dotted line defines the approximate boundary of the NGP. Kettle Lake is marked by a star. Sites numbered 1–4 correspond to other locations where aridity cycles have been detected: 1, Pickerel Lake (South Dakota) and Spring Lake; 2, Moon Lake (North Dakota); 3, Coldwater Lake; 4, Rice Lake. Location 5 is West Olaf Lake.

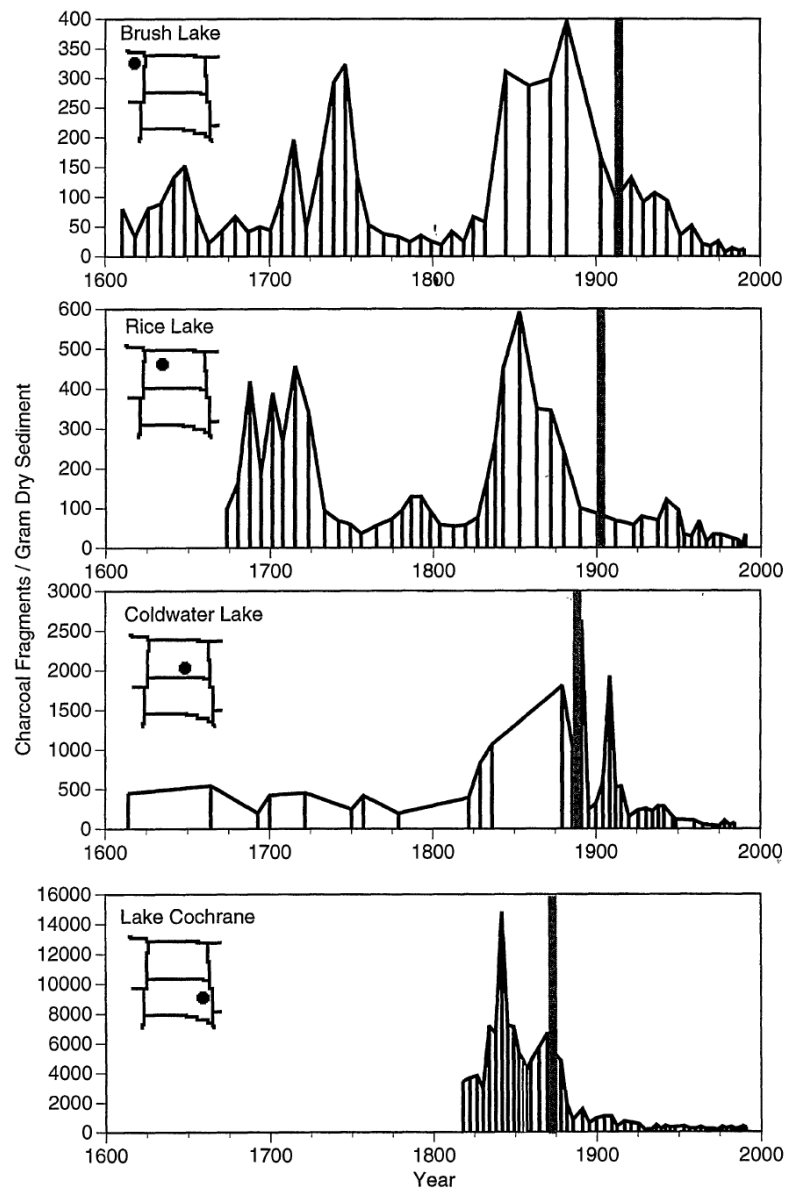


FIG. 1.—Charcoal concentration [fragments/gram (dry weight)] in sediments from four northern Great Plains lakes. Bar indicates approximate time of European settlement. Dot on map indicates location (*see* text for exact coordinates) of lakes

History of fire and Douglas-fir establishment in a savanna and sagebrush–grassland mosaic, southwestern Montana, USA

Emily K. Heyerdahl^{a,*}, Richard F. Miller^{b,1}, Russell A. Parsons^a

Fire History at the Forest-Grassland Ecotone in Southwestern Montana

STEPHEN F. ARNO AND GEORGE E. GRUELL

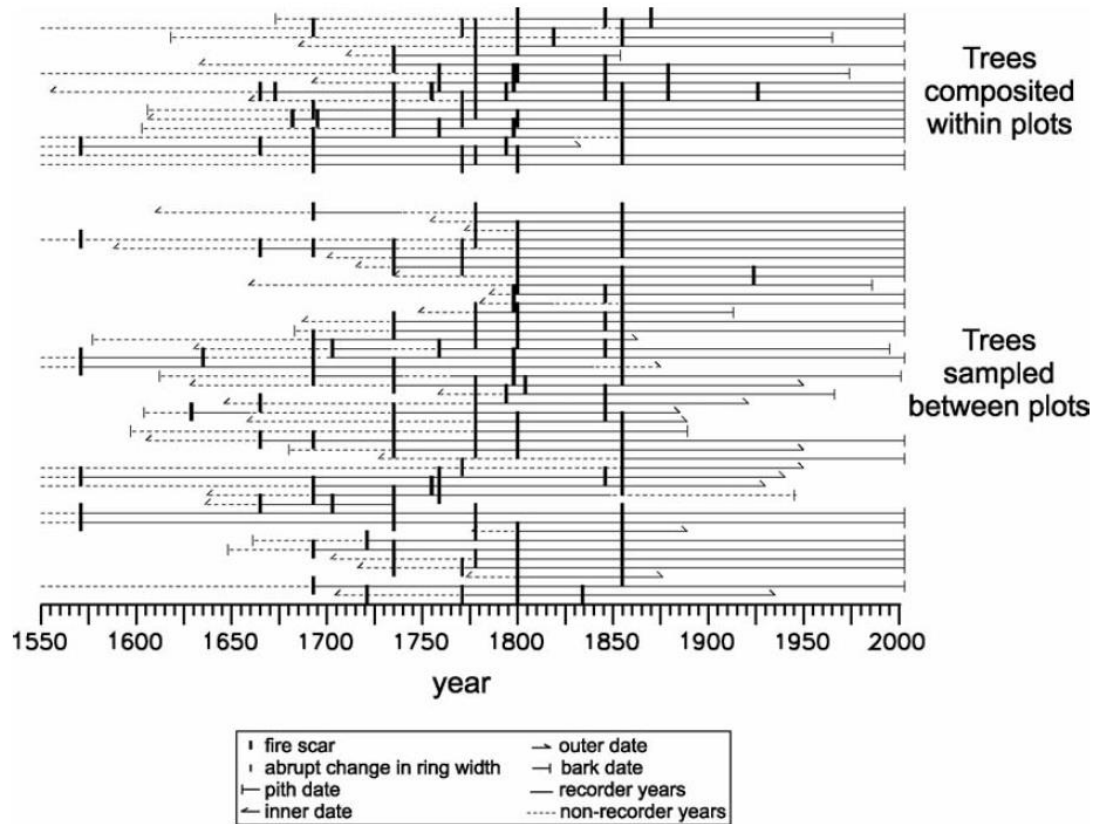


Fig. 2. Chronology of surface fire occurrence in the study area. Each horizontal line shows either the composite fire-scar record for a plot (i.e., fire-scar dates composited for all trees within a plot, specifically one to four trees sampled over approximately 2 ha), or the record from a single tree sampled opportunistically between plots. Non-recorder years precede the formation of the first scar on each tree but also occur when subsequent fires or rot consume that record. Inner and outer dates are the dates of the earliest or latest rings sampled for trees where pith or bark was not sampled.

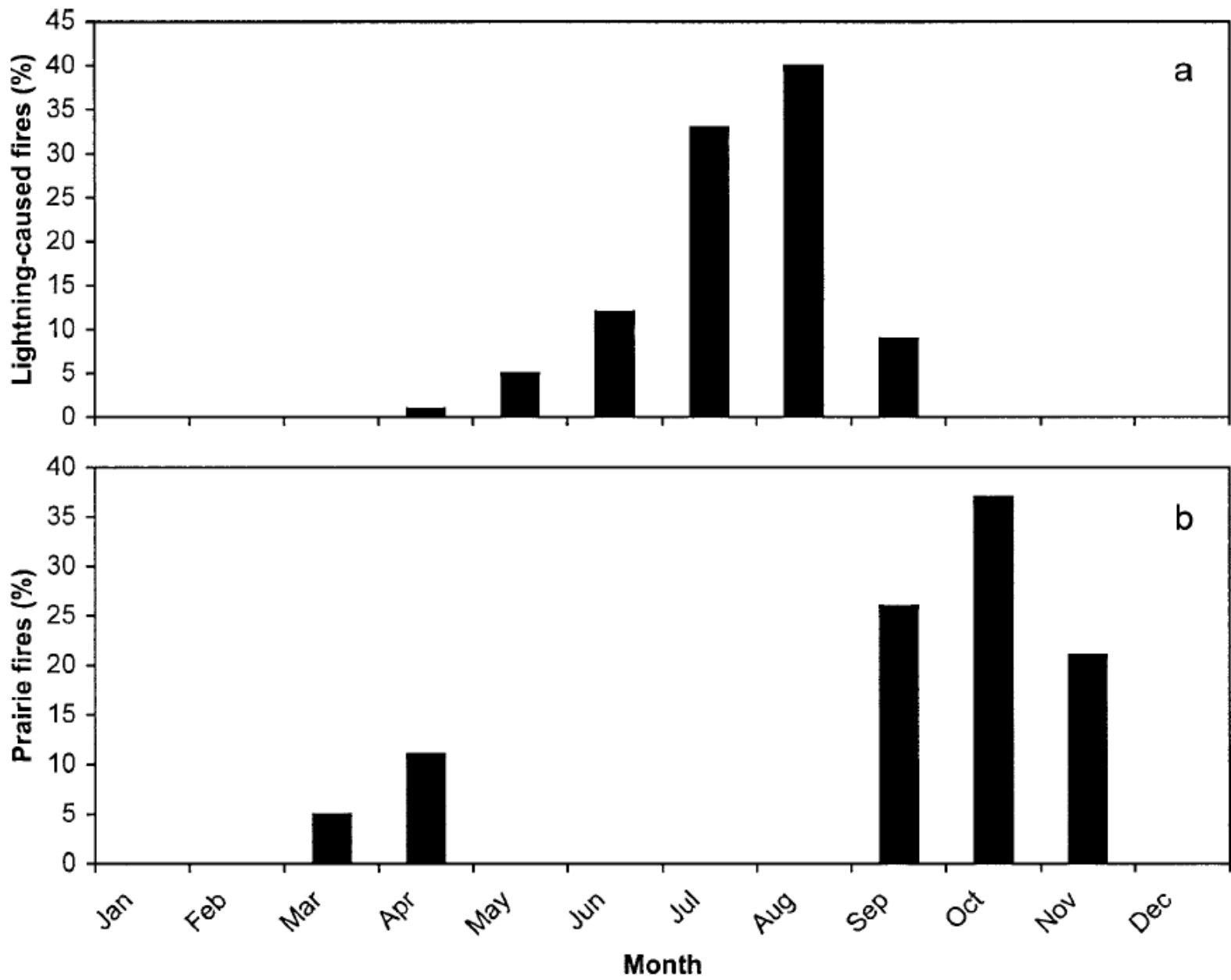
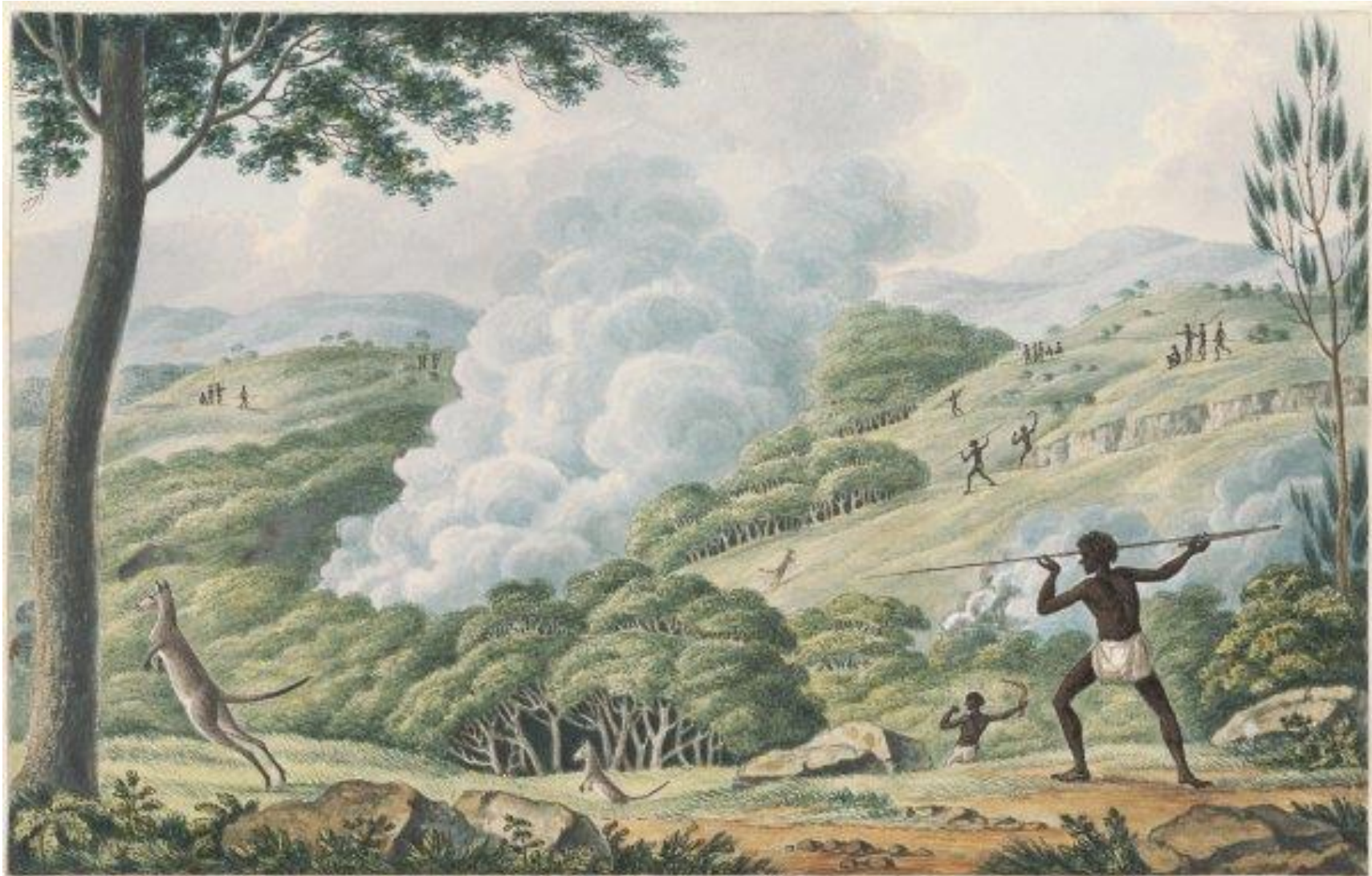


Fig. 4. The distribution of fires on the northern Great Plains. (a) The distribution of lightning fires that occurred from 1940 to 1981, as reported by Higgins (1984). There are few lightning fires during spring or fall because there are very few lightning strikes during those periods. (b) The distribution of prairie fires as reported by Alexander Henry the Younger from 1800 to 1807 when the northern Great Plains were under aboriginal control (Gough 1988).



Pyric Herbivory: What is the role of fire in grazed landscapes?

Sam Fuhlendorf
Oklahoma State University

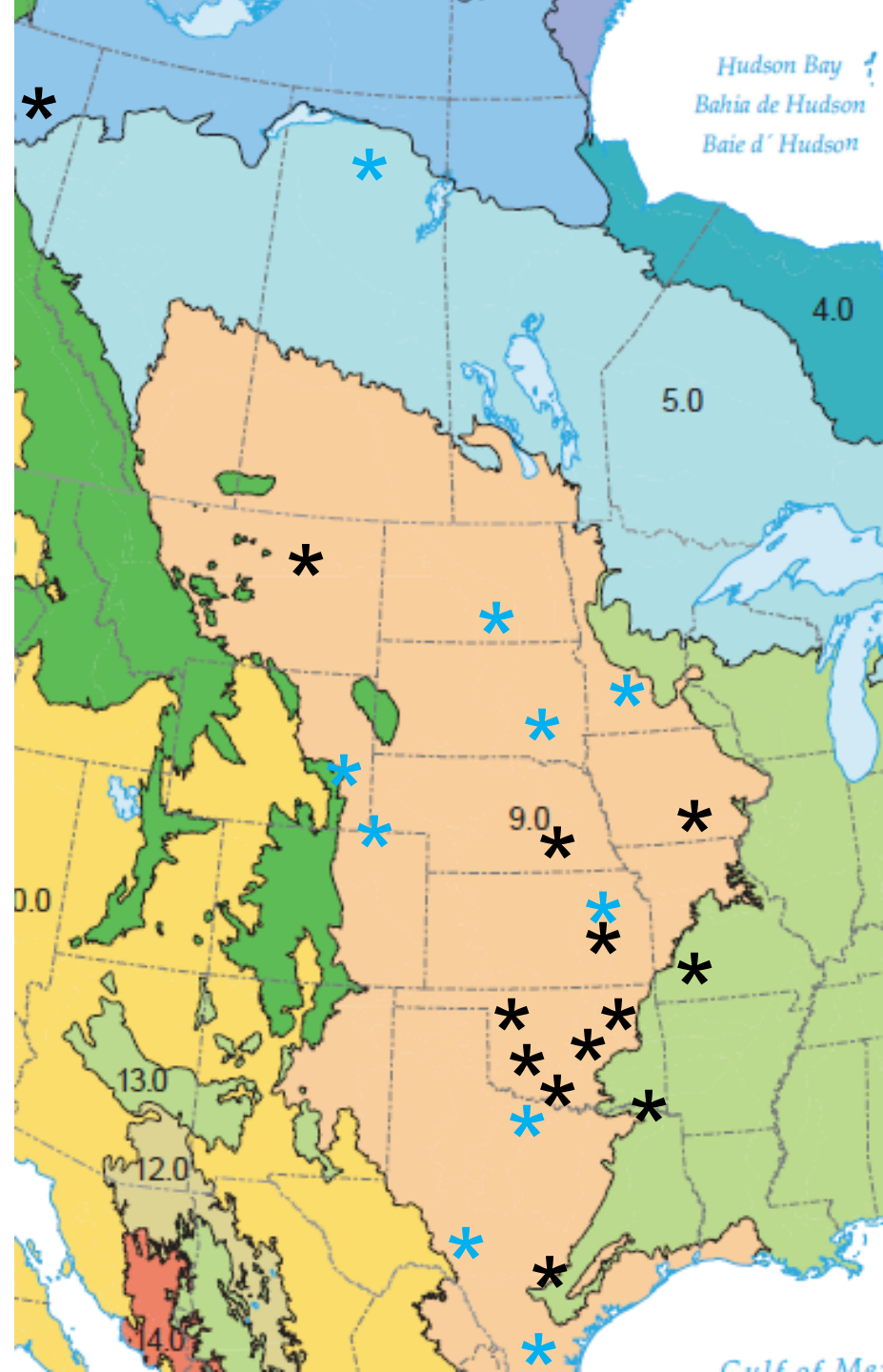


Other important questions:

1. How do fire and grazing interact on landscapes?
2. How can we manipulate the interaction to achieve specific objectives?
3. What is “excellent rangeland condition”?
4. What if bison could carry a drip torch?

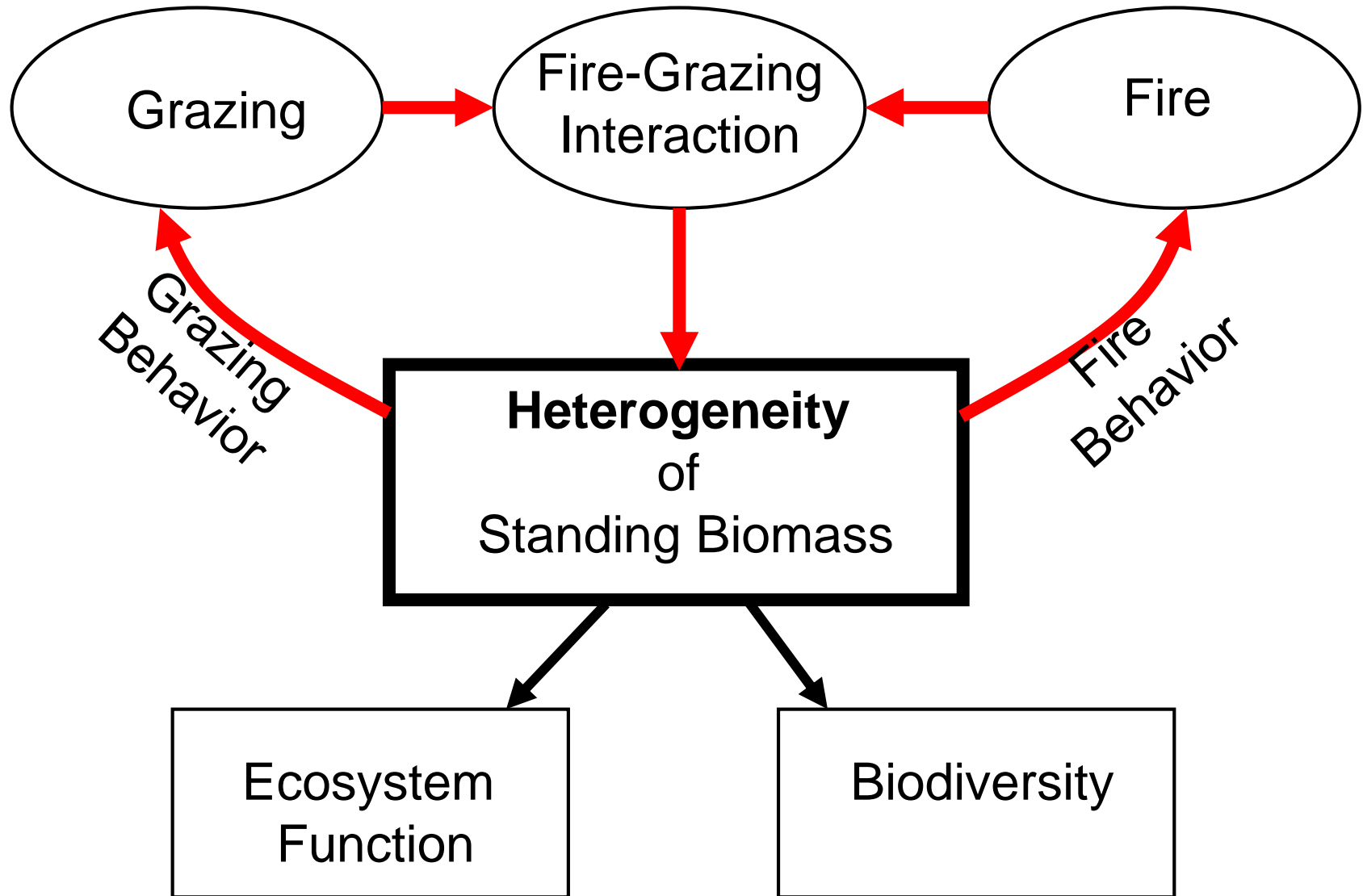
Study Locations

- * Fuhlendorf et al
- * Other studies



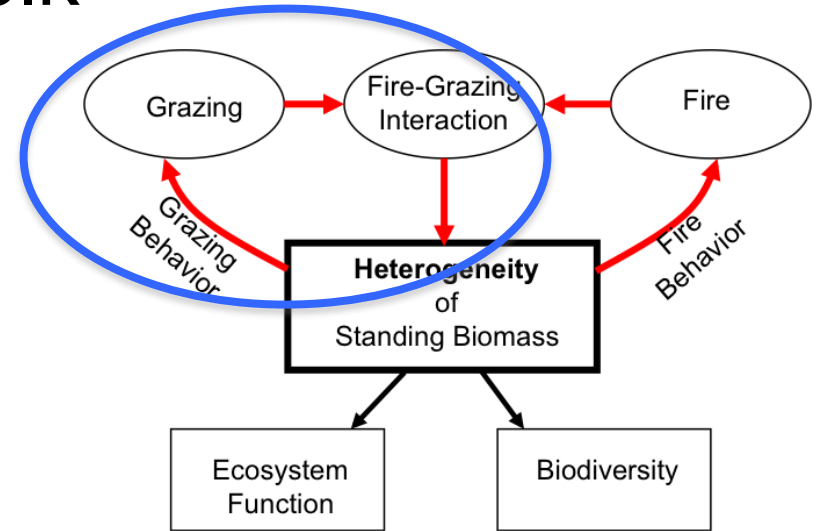
Heterogeneity Paradigm

Pyric Herbivory, Patch Burning, Patch Burn Grazing



Does fire alter grazing behavior?

- Bison, cattle, horses, elk
- Pasture size
- Patch size
- Time since fire
- Variable regions



Fire-grazing interaction (pyric herbivory) as a critical ecosystem process- Global perspective

Africa

Moe, Wegge, & Kapela 1990; Wilsey 1996; Salvatori et al. 2001; Gureja & Owen-Smith 2002; Tomor & Owen-Smith 2002; Archibald & Bond 2004; Archibald et al. 2005; Klop, van Goethem, & de Iongh 2007; Savadogo, Sawadogo, & Tiveau 2007; Archibald 2008; Hassan et al. 2008; Klop & van Goethem 2008; Waldram, Bond, & Stock 2008; Parrini & Owen-Smith 2010

Asia

Moe & Wegge 1994; Moe & Wegge 1997; Sankaran 2005

Australia

Kirkpatrick, Marsden-Smedley, & Leonard In press; Kutt & Woinarski 2007; Murphy & Bowman 2007; Leonard, Kirkpatrick, & Marsden-Smedley 2010

Europe

Kramer, Groen, & van Wieren 2003; Vandvik et al. 2005; Onodi et al. 2008; Davies et al. 2010

North America

Duvall & Whitaker 1964; Hobbs & Spowart 1984; Vinton et al. 1993; Turner et al. 1994; Pearson et al. 1995; Wallace et al. 1995; Coppedge & Shaw 1998; Biondini, Steuter, & Hamilton 1999; Smith, Hardin, & Flinders 1999; Fuhlendorf & Engle 2004; Schuler et al. 2006; Van Dyke & Darragh 2007; Bleich et al. 2008; Meek et al. 2008

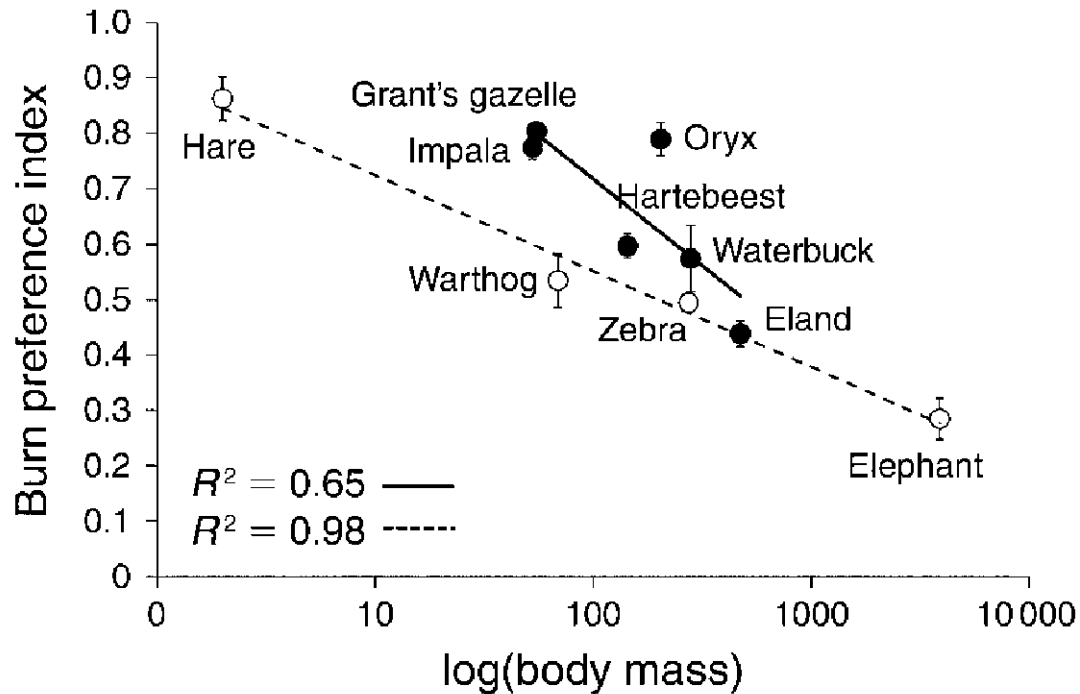


FIG. 2. Grazer preference for burned areas negatively scales to body mass (originally measured in kg) for both hindgut fermenters (open circles) and foregut fermenters (solid circles). Burn preference indices (mean \pm SE) are from 18 burned plots where “burn preference” is $\frac{\text{dung in burned areas}}{\text{dung in burned areas} + \text{dung in control transects}}$. Regression equations for the full linear mixed model on a log–log scale are: $y = 1.24x^{-0.12}$ and $y = 2.17x^{-0.19}$ for hindgut (dotted line) and foregut grazers (solid line), respectively. Fitted lines and R^2 values are for uncorrected means. The burn preference index ranges from 0 to 1, where 0 equals complete avoidance of burned areas and 1 indicates complete preference for burned areas.

Gureja & Owen-Smith 2002
Archibald & Bond 2004
Archibald et al. 2005





The Nature Conservancy's Tallgrass Prairie Preserve

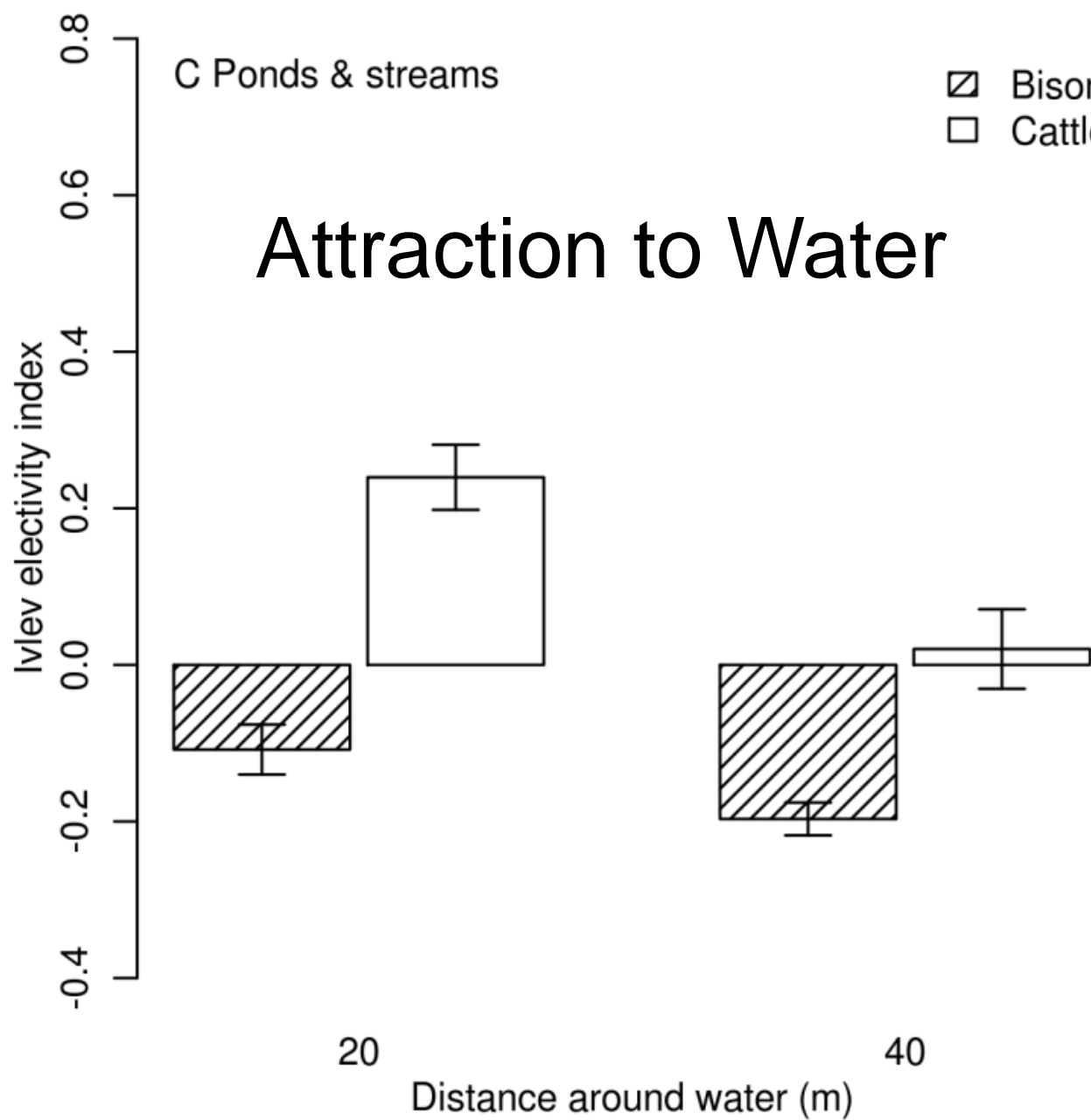
- Bison Unit
24,000 ac
no cross-fences
- Experimental
cattle pastures

- <http://www.youtube.com/watch?v=L5eTmVQxtEM>

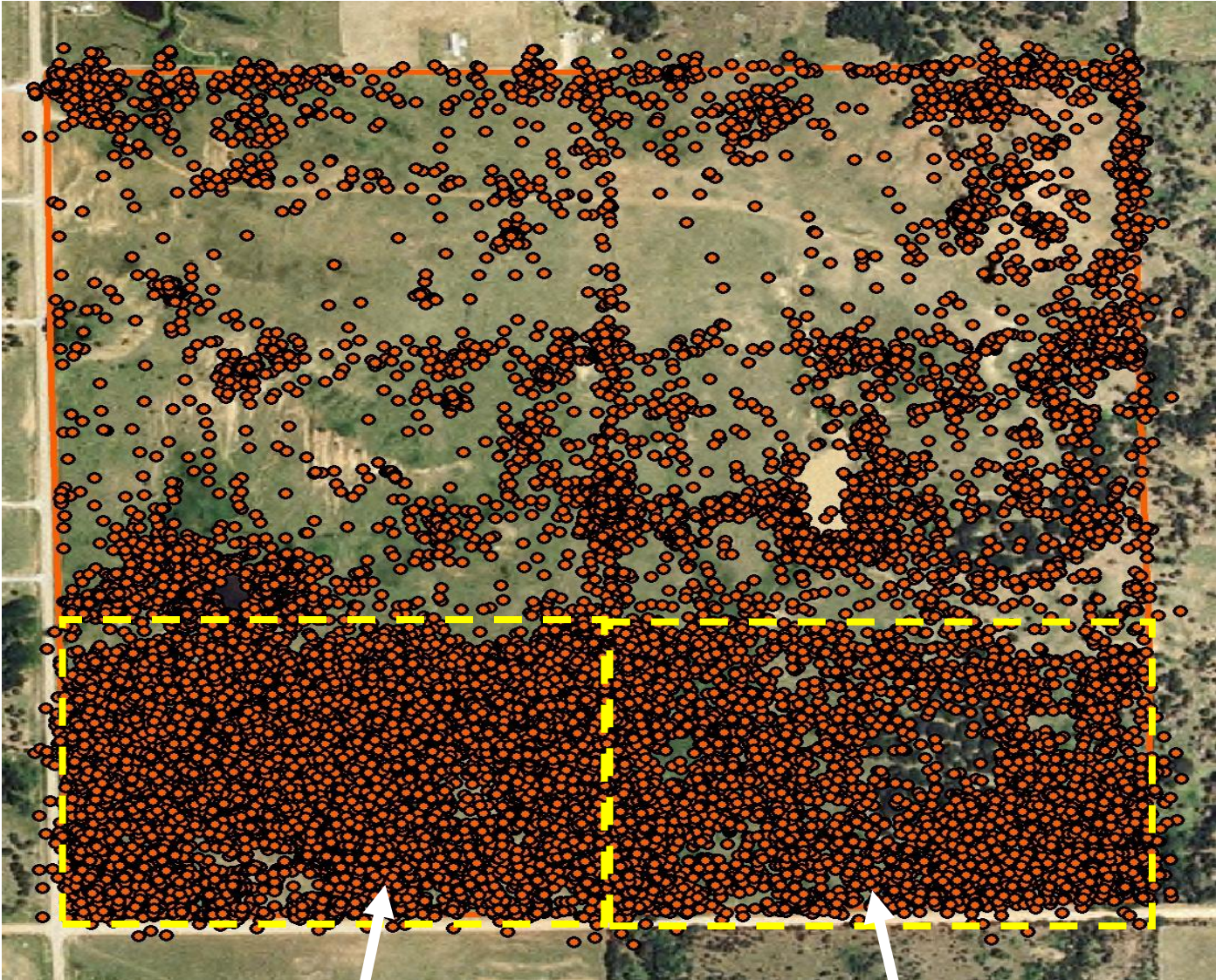
C Ponds & streams

▨ Bison
□ Cattle

Attraction to Water



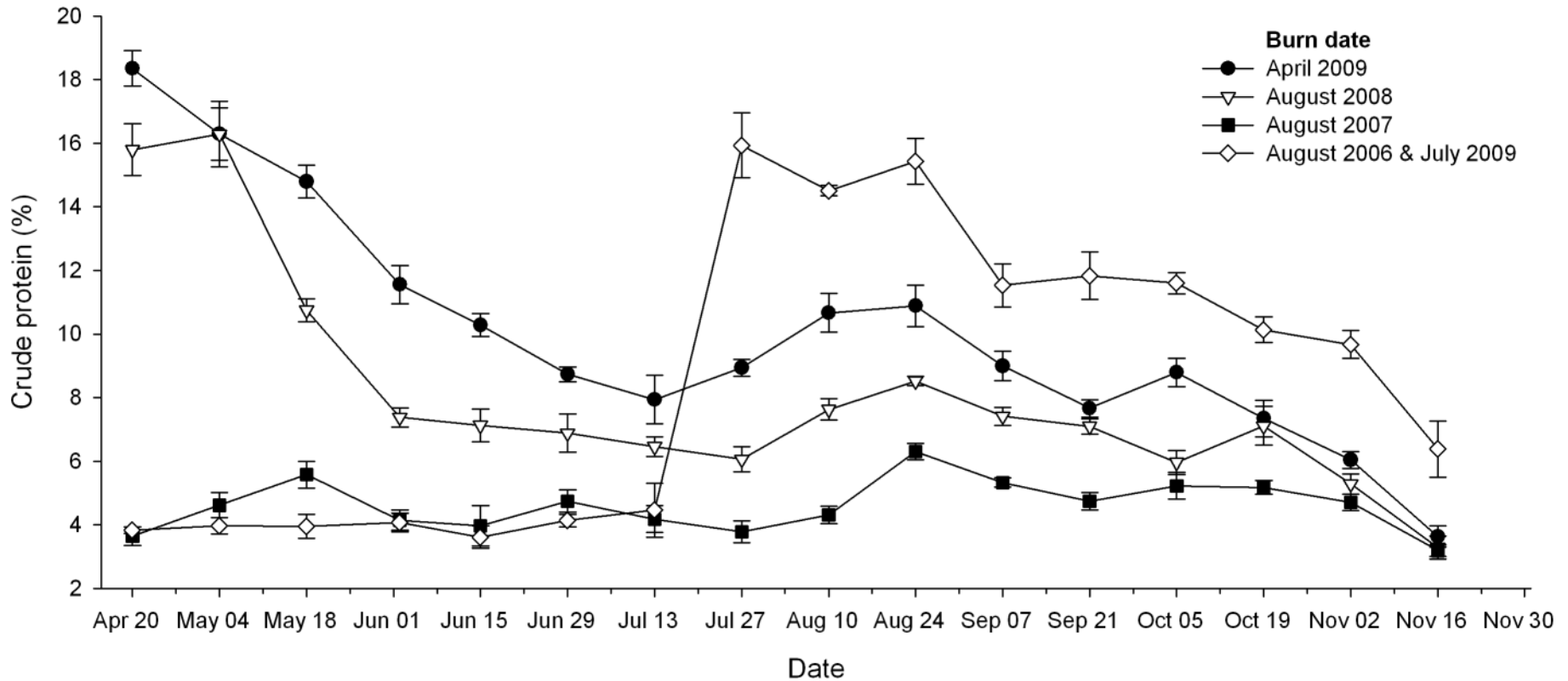
Grazing Site Selection in Heterogeneous Treatment Growing Season 2008



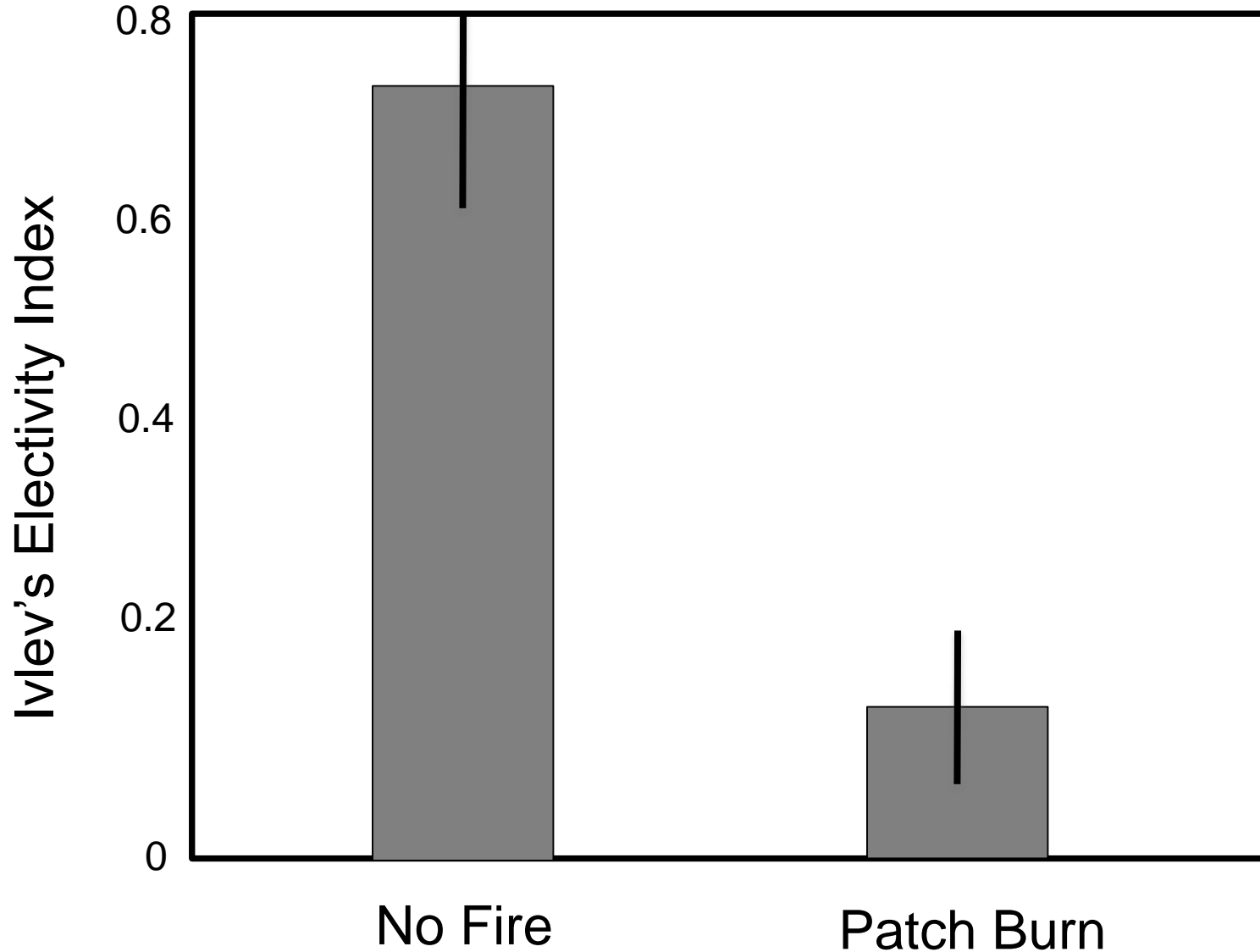
Burned Spring 2008

Burned Summer 2007

Forage quality



Preference by Cattle for Riparian Areas in Western OK



Allred, Fuhlendorf, Engle and Elmore (2011). *Ecology and Evolution*

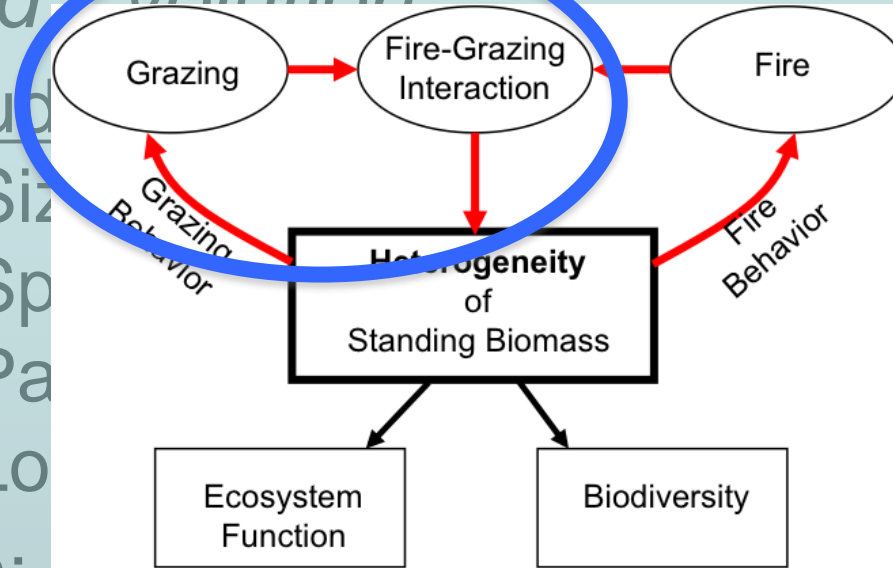
Study

1. Size

2. Sp

3. Pa

4. Lo



cattle)

Conclusion:

1. Time since

influencing

2. The stren

significantly

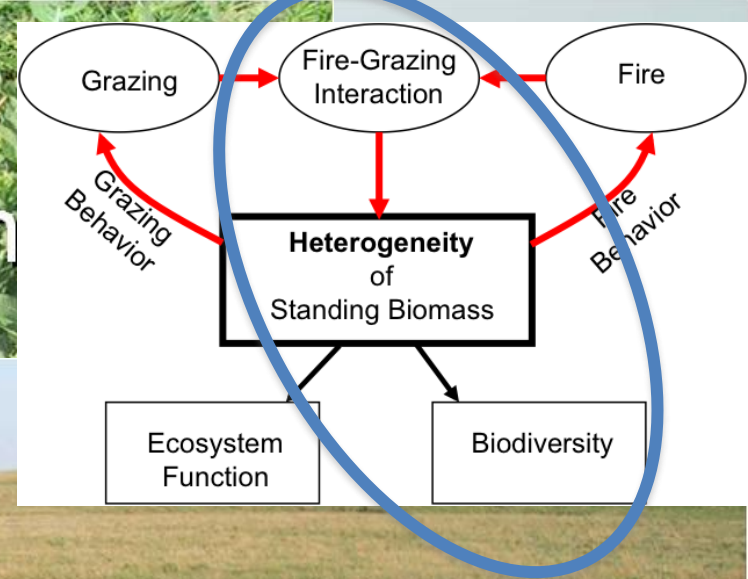
variables.

3. Analysis of grazing without fire is incomplete.

Allred et al. 2011, 2012, 2013
Fuhlendorf et al. 2010
Fuhlendorf and Engle 2004
Etc.

Burned Patch Heterogeneity Treatment Cover

Tallgrass-
Forb- 35%
Litter- 3%
Bare Gro



Unburned Patch Heterogeneity Treatment Cover

Tallgrass- 76% (4)
Forb- 25% (2)
Litter- 91% (2.5)
Bare Ground- 4% (3)

Photo taken 9/24/03

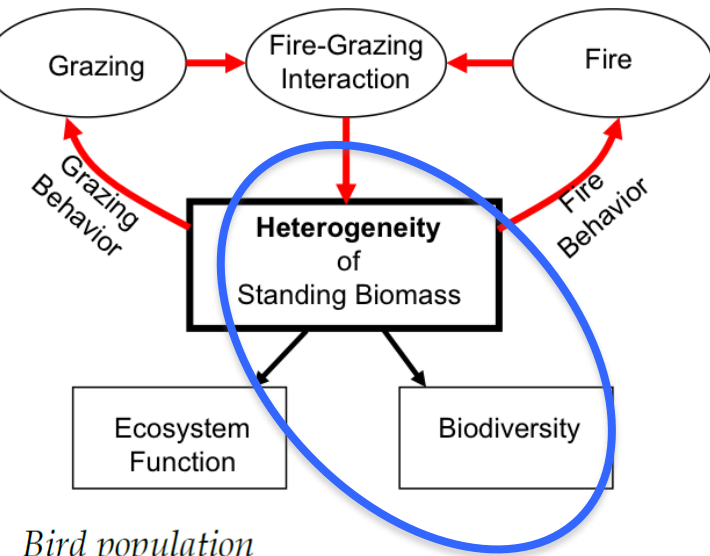
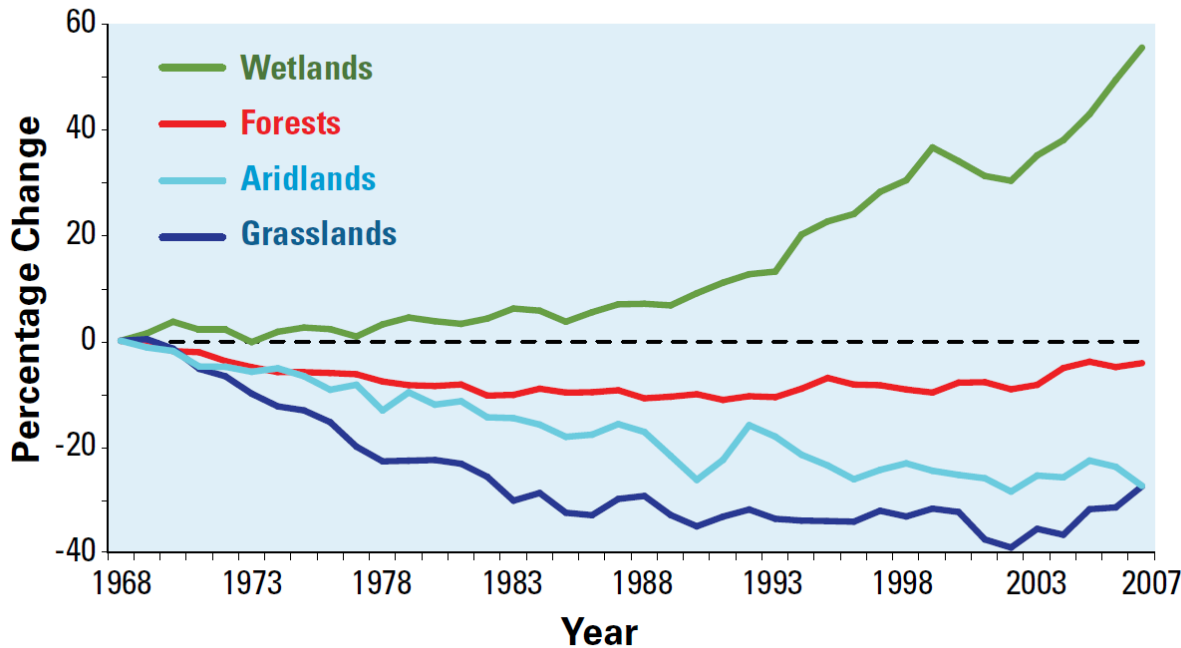
Burned 9/10/02

Burned 3/22/03



Is biodiversity dependent on heterogeneity that is driven by pyric herbivory?

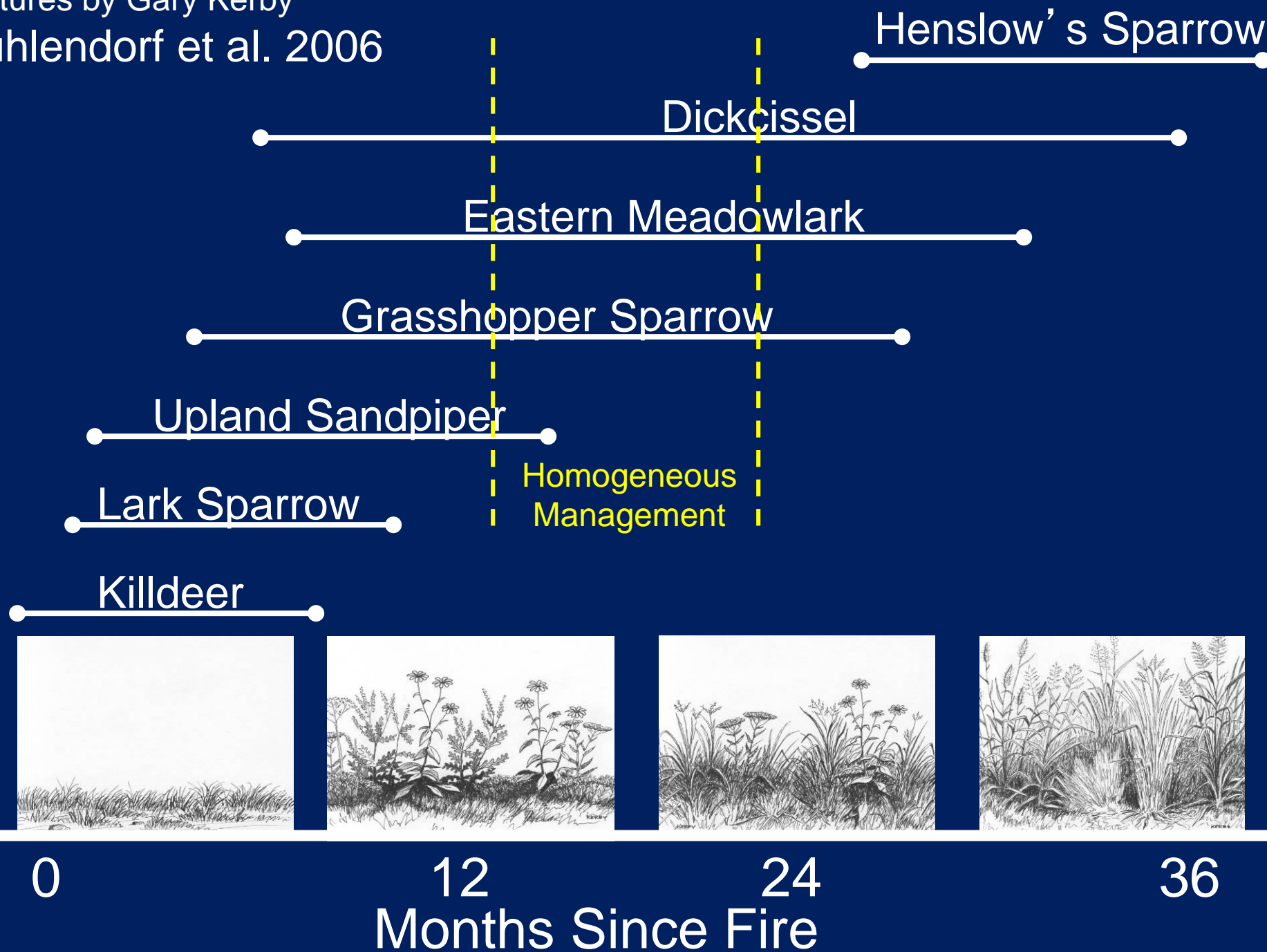
Bird Population Indicators



Bird population indicators based on trends for obligate species in four major habitats.

North American Bird Conservation Initiative, U.S. Committee, 2009. *The State of the Birds, United States of America, 2009.* U.S. Department of Interior: Washington, DC. 36 pp
http://www.stateofthebirds.org/pdf_files/State_of_the_Birds_2009.pdf

Pictures by Gary Kerby
Fuhlendorf et al. 2006



Excessive ← Heavy ————— Moderate ————— Light → None



|—— Mountain Plover ——|

|—— McCown's Longspur ——|

|—— Ferruginous Hawk ——|

|—— Long-billed Curlew ——|

|—— Lark Bunting ——|

|—— Chestnut-collared Longspur ——|

|—— Sprague's Pipit ——|

|—— Baird's Sparrow ——|

|—— Cassin's Sparrow ——|



Bare ← Short ————— Mixed ————— Mixed/Shrub →

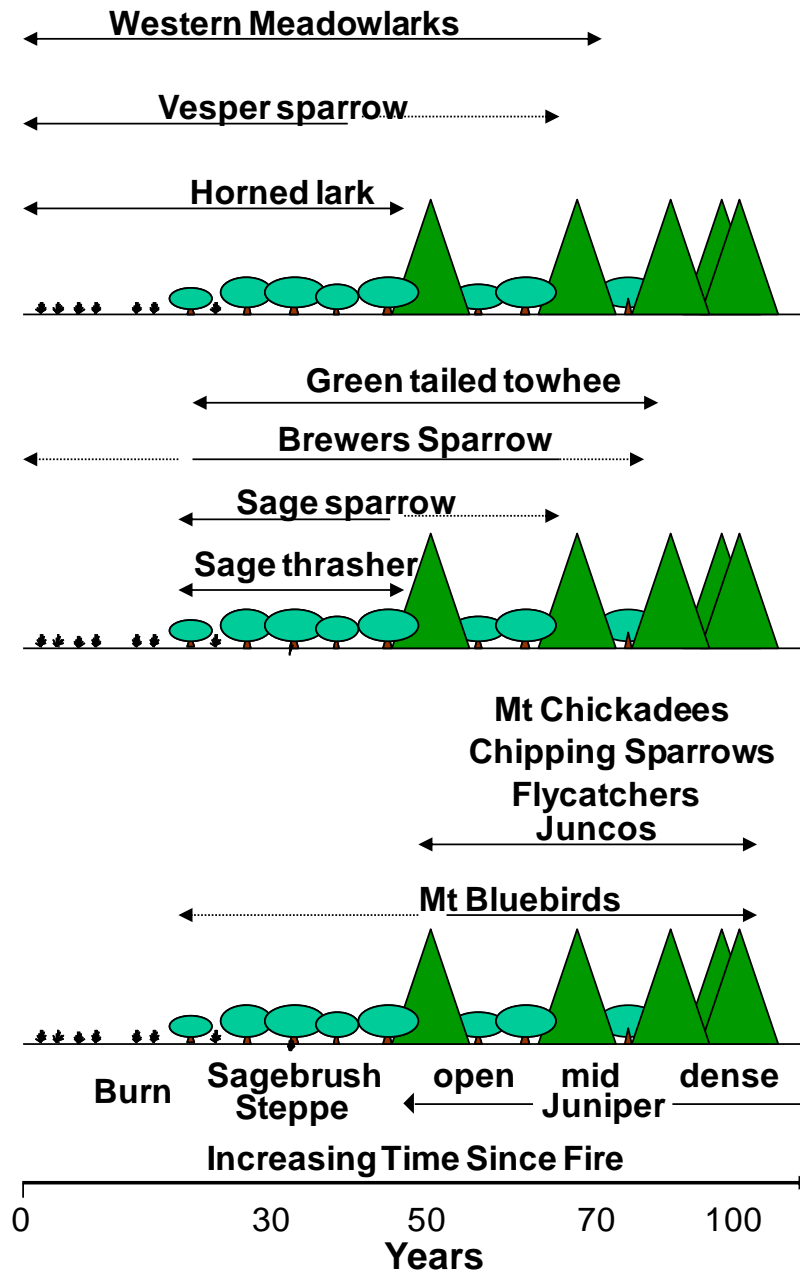
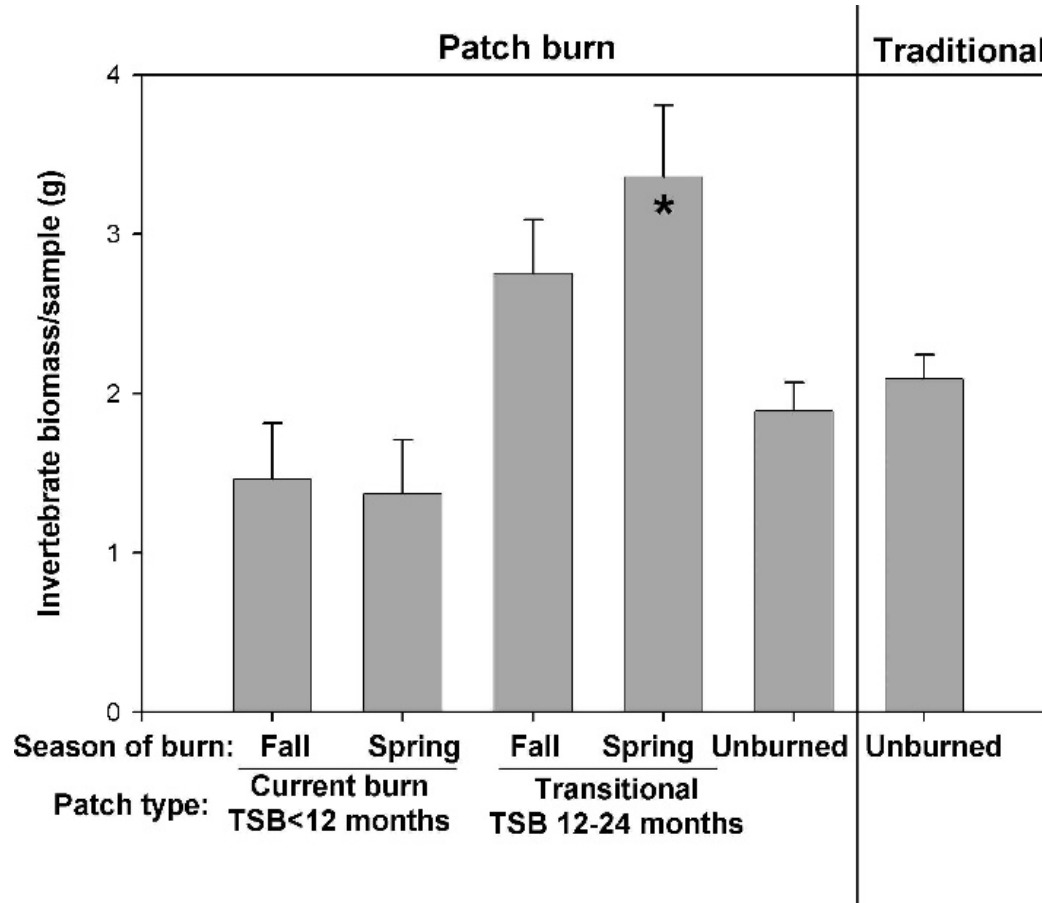


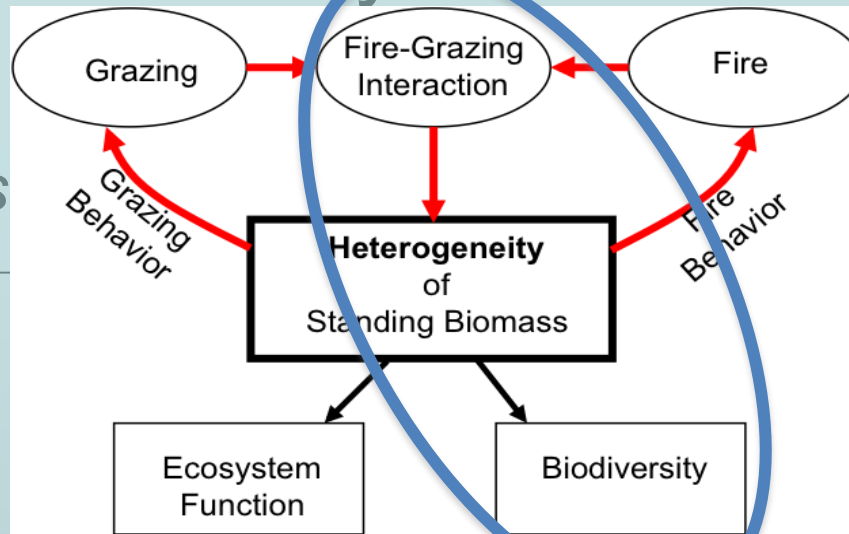
Figure 8. Response of birds to time since fire on Great Basin rangelands (Reinkensmeyer et al. 2007).

Pyric Herbivory and Insects

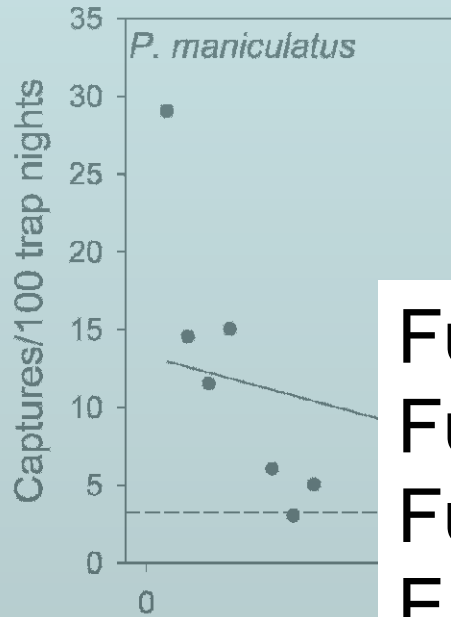


Engle et al. 2008
Doxon et al. 2011

Pyric Herbivory and Small Mammals

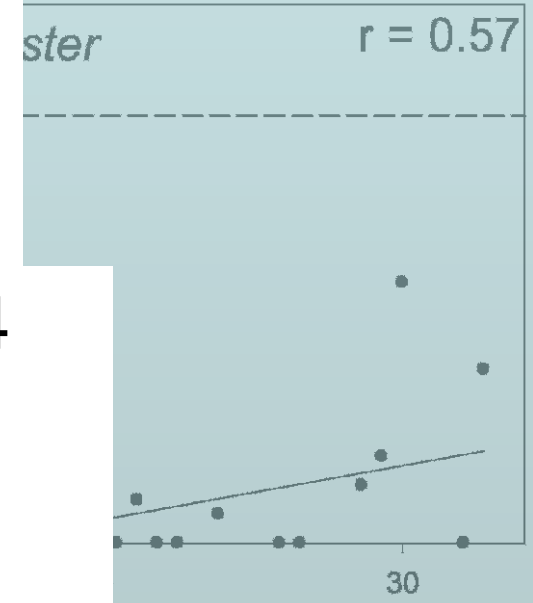


Peromyscus



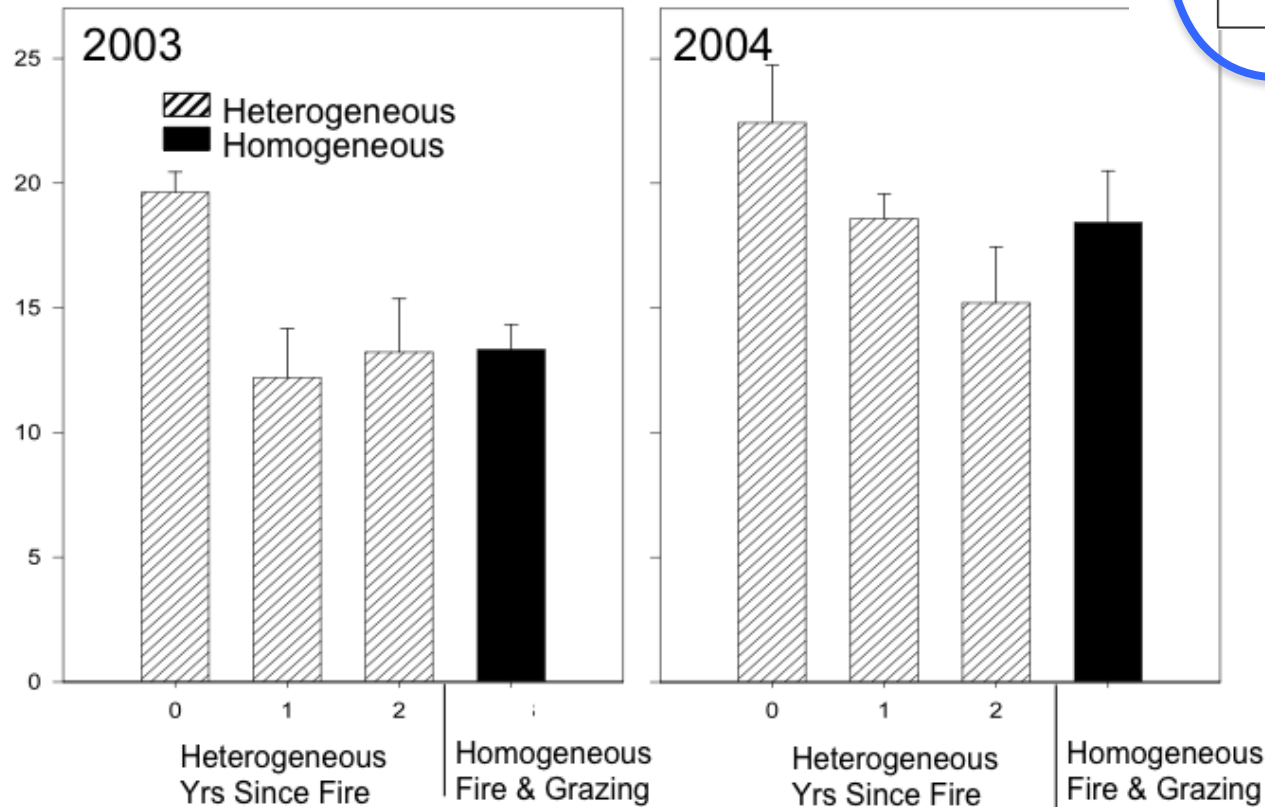
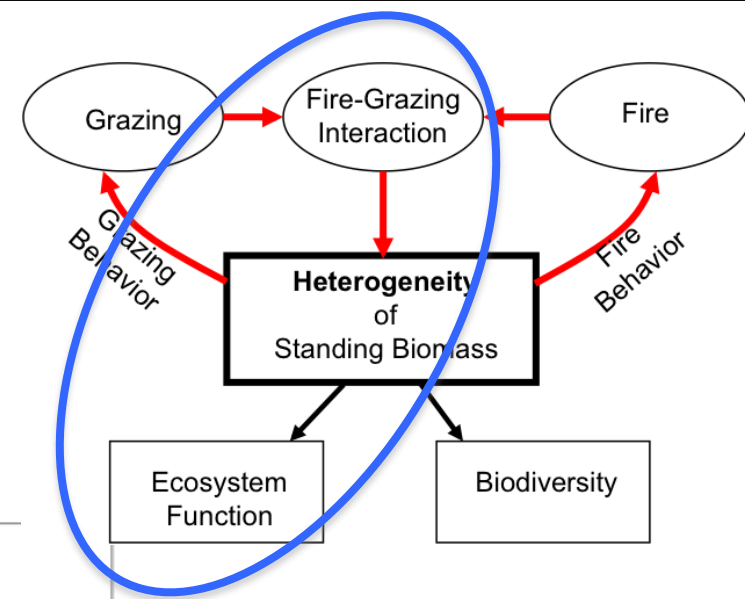
Peromyscus leucopus

Peromyscus leucopus

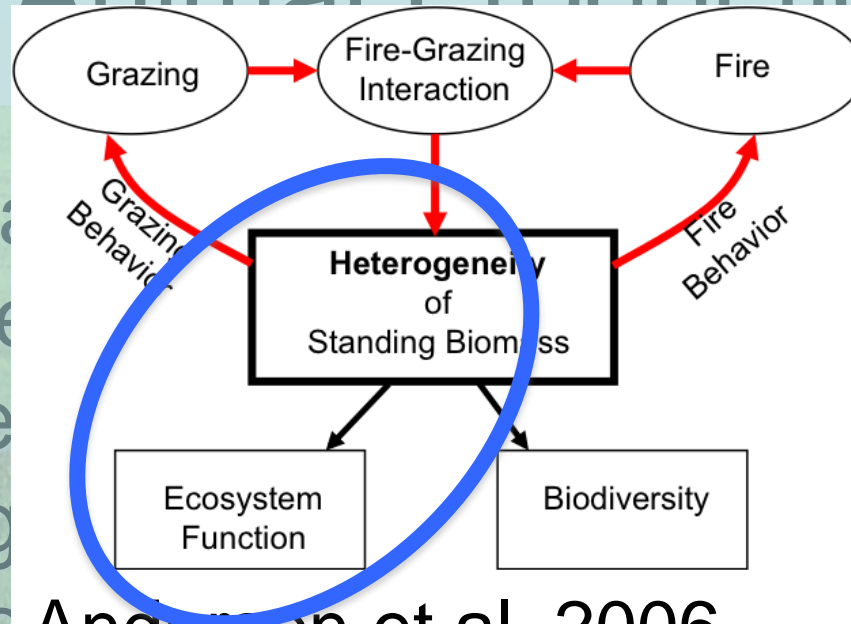


Fuhlendorf and Engle 2004
 Fuhlendorf et al. 2006
 Fuhlendorf et al. 2009
 Engle et al. 2008
 Fuhlendorf et al. 2010
 Doxon et al. 2011
 Etc.

Greater nitrogen available on recently burned patches that attract greater densities of grazers



Animal Production



Anderson et al. 2006

Fuhlendorf et al. 2009

Cummings et al. 2006

Vermeire et al. 2005

Limb et al. 2011

Etc.

1. Bison &

a. Sites

are

b. High

allo

c. Food

tha

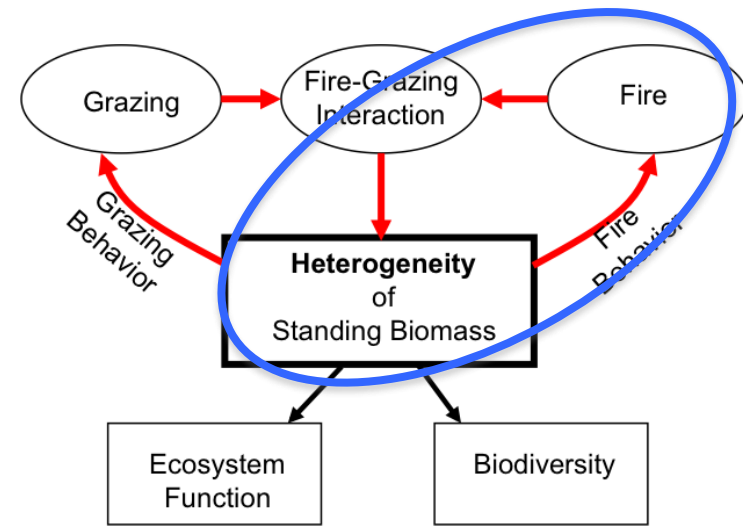
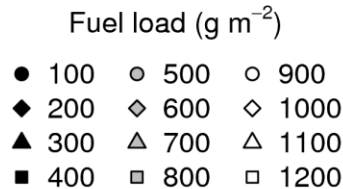
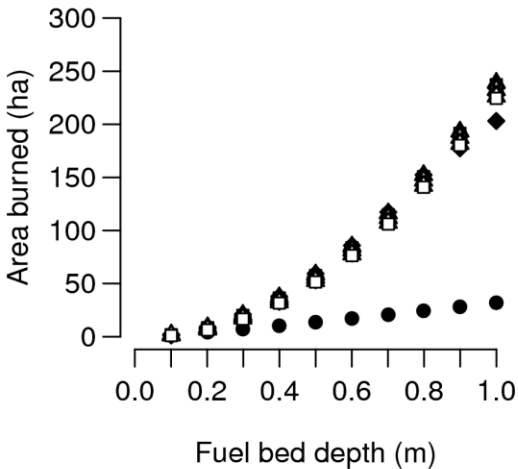
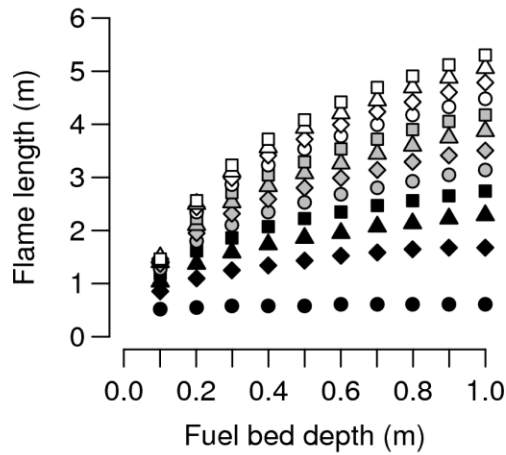
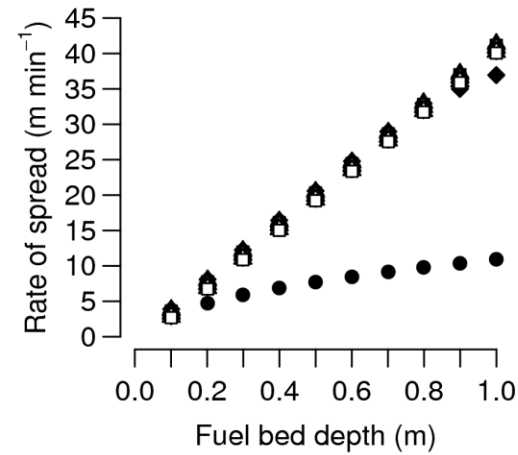
ava

2. Cattle-

years- no negative effects and some

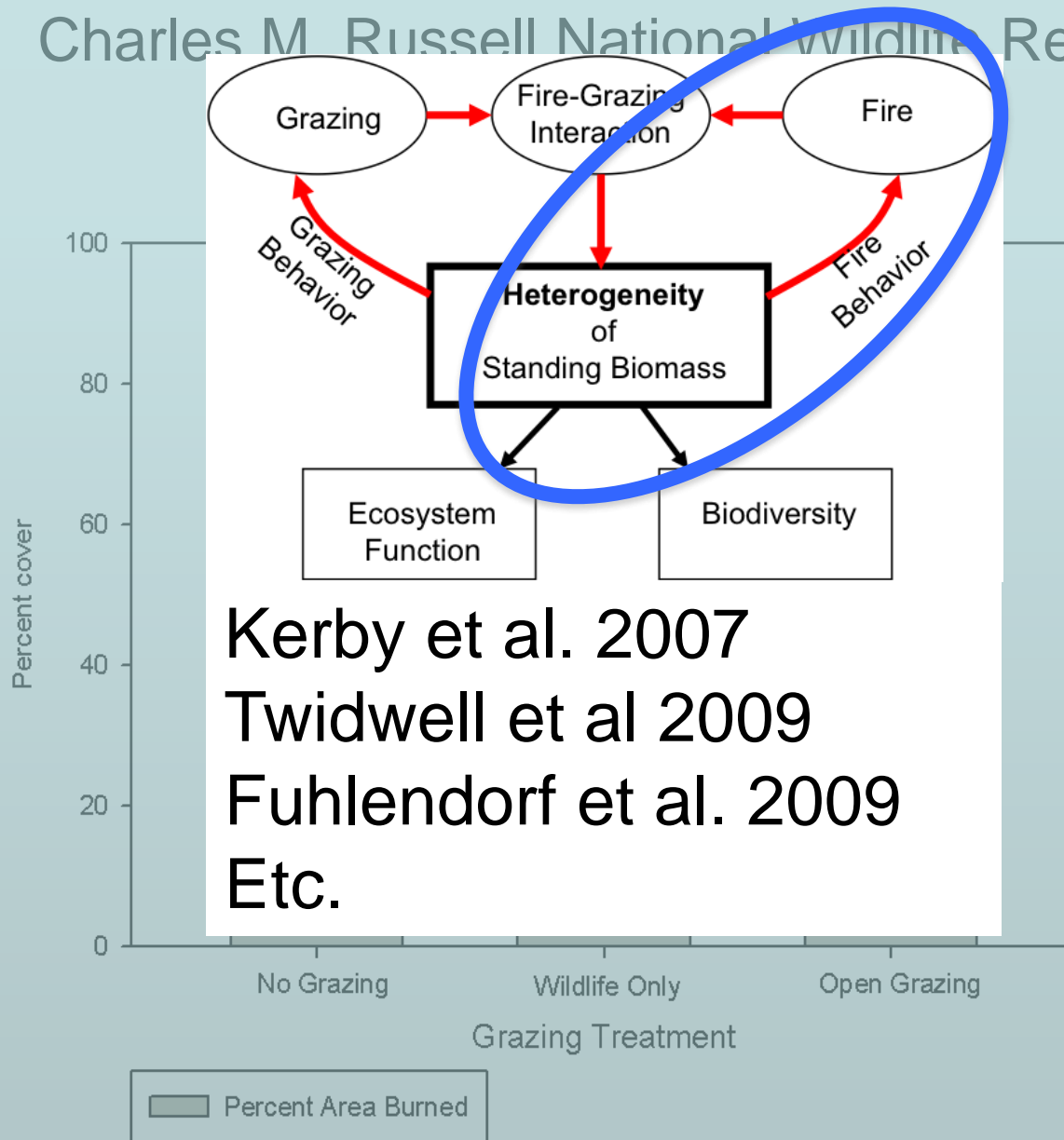
positive effects

Does grazing effect fire behavior?



Kerby et al. 2007, Fuhlendorf et al. 2009

Charles M. Russell National Wildlife Refuge



Fire in Bambi





George Catlin on his 1832 Missouri River voyage:

“Every acre of these vast prairies burns over during the fall or early in the spring, . . . the fire slowly creeps with a feeble flame... **where the wild animals often rest in their lairs until the flames almost burn their noses, when they will reluctantly rise, and leap over it,** and trot off amongst the cinders, where the fire has passed and left the ground as black as jet.”

(Catlin, *Letters and Notes*, vol. 2, no. 33, 1841; reprint 1973)







Fire in Stillwater OK

Conclusions

1. All ecosystems are heterogeneous
2. Fire and herbivory are critically linked
3. Biodiversity requires heterogeneity- in grasslands that means highly variable fire and grazing distribution in space and time
4. Most management is single objective and reduces heterogeneity
5. Considering grasslands as shifting mosaics can simultaneously
 - Enhance biodiversity
 - Sustain ecosystem services
6. This interaction operated anywhere with fire and herbivory
7. The strength is dependent on the relationships among grazing site selection, fire intensity, herbaceous biomass and forage quality- How much heterogeneity is possible?

Fuhlendorf and colleagues . *30 peer-reviewed publications in 8 different journals.* Many other publications from other authors.

A photograph of several wood bison resting in a forest clearing at sunset. The sun is low on the horizon, creating a warm, golden glow and long shadows. The bison are dark against the lighter background of the trees and sky. The ground is covered in dry grass and some snow.

Pyric Herbivory in Action on Boreal Rangelands? The Fire-Grazing Interaction of Wood Bison in NE BC, Canada

S. Leverkus,^{1,2} S. Fuhlendorf,¹ M. Gregory,¹ and N. Elliot²

¹ Oklahoma State University ² Range Program, BC Provincial Government

Boreal rangelands and fire

- Most intact terrestrial ecosystem in the world
- Natural and anthropogenic fire dominant driver
- Boreal fire creates mosaics (landscape) = heterogeneity
- Evidence of fire in the Boreal : charcoal and pollen, oral





09.07.2008 10:05



Boreal Forest

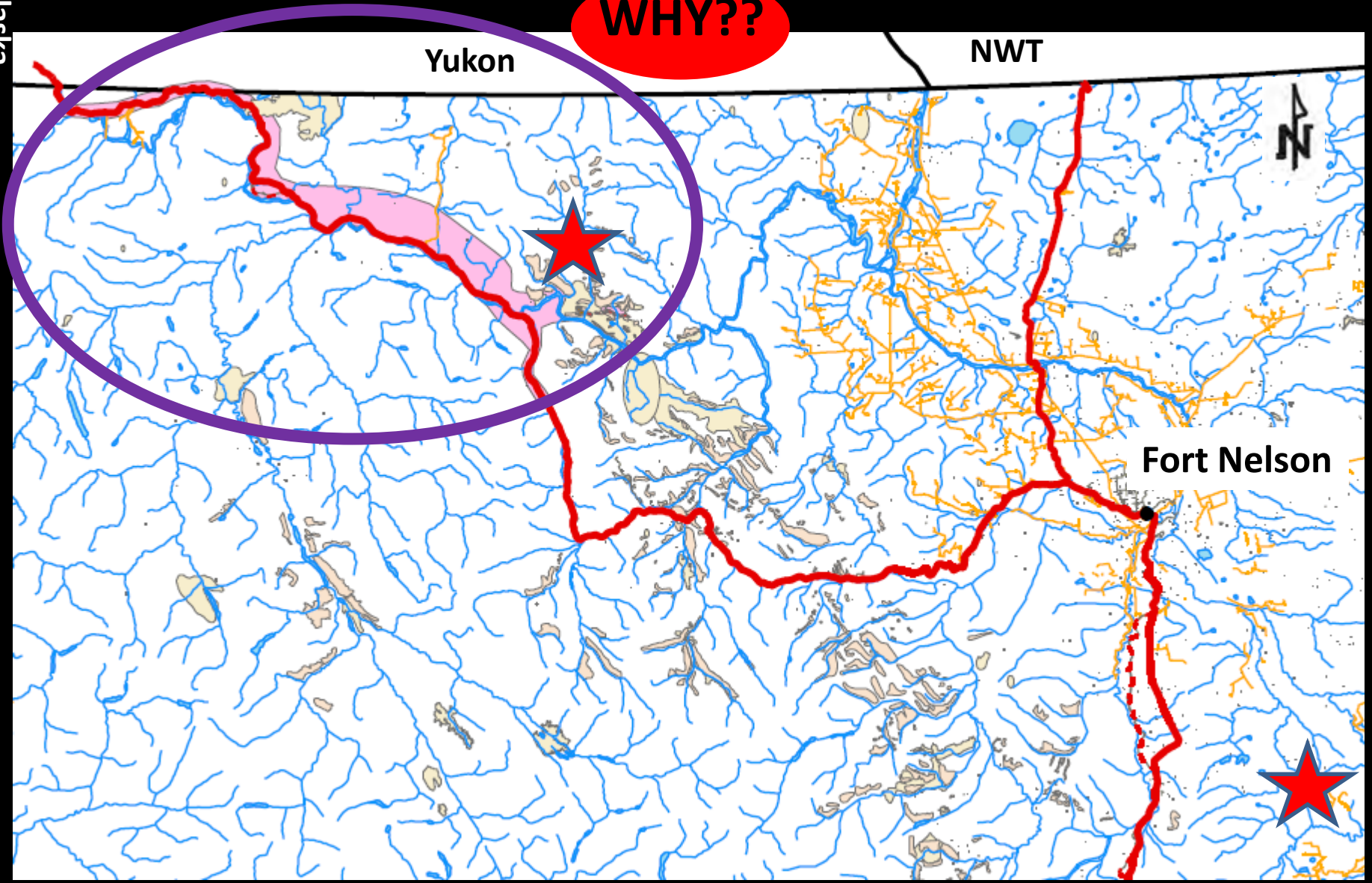


★ Reintroduced 49 head @ Nordquist (1995) on Liard River and 40 head @ Etthithun (1999) on the Fontas River

→ Herd size has remained low since reintroduction

WHY??

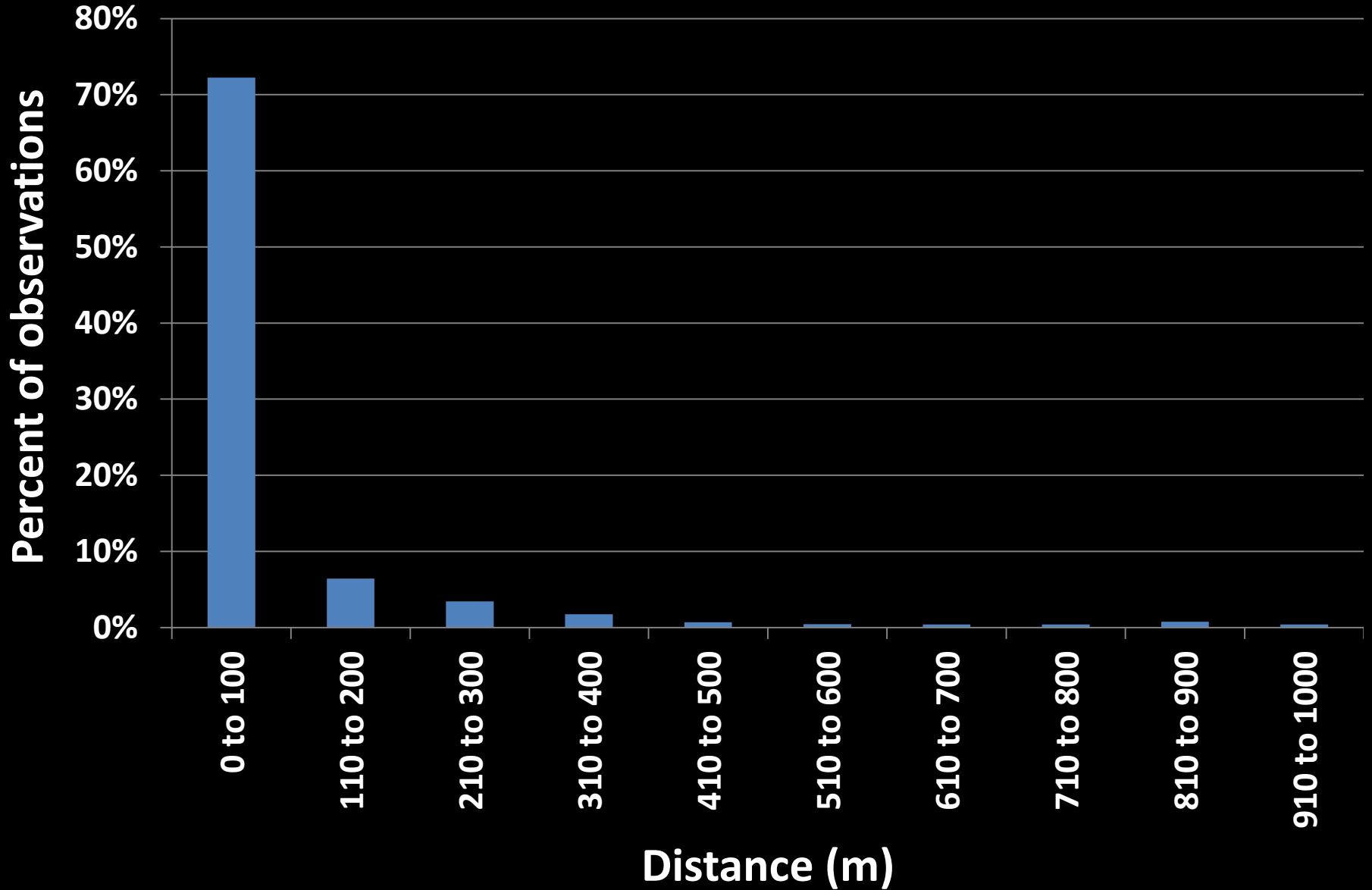
Alaska



Alberta

Alaska Highway

Actual percent observations by distance from highway (1km)



Actual bison distribution of 3 collared animals

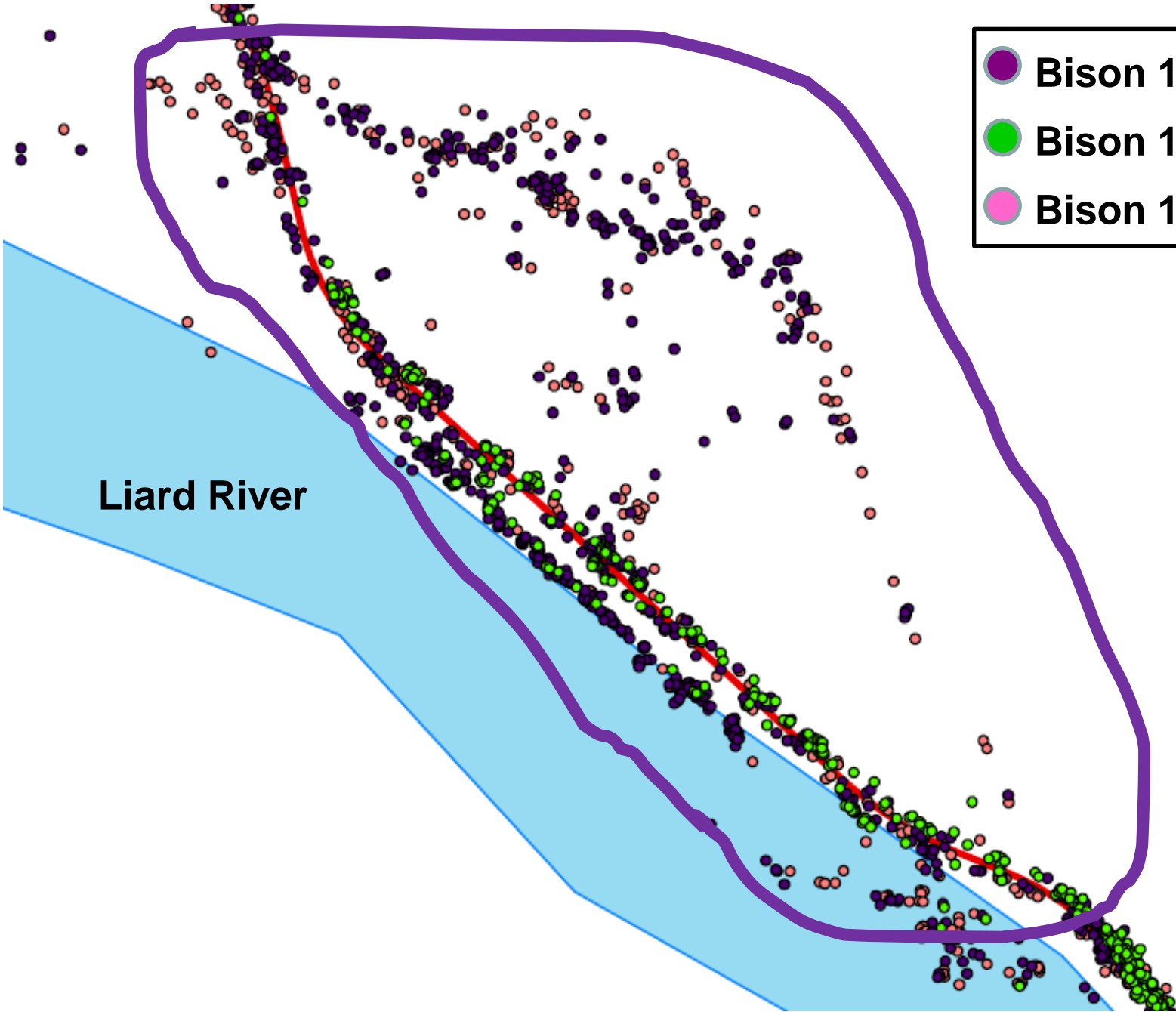




Alaska Highway






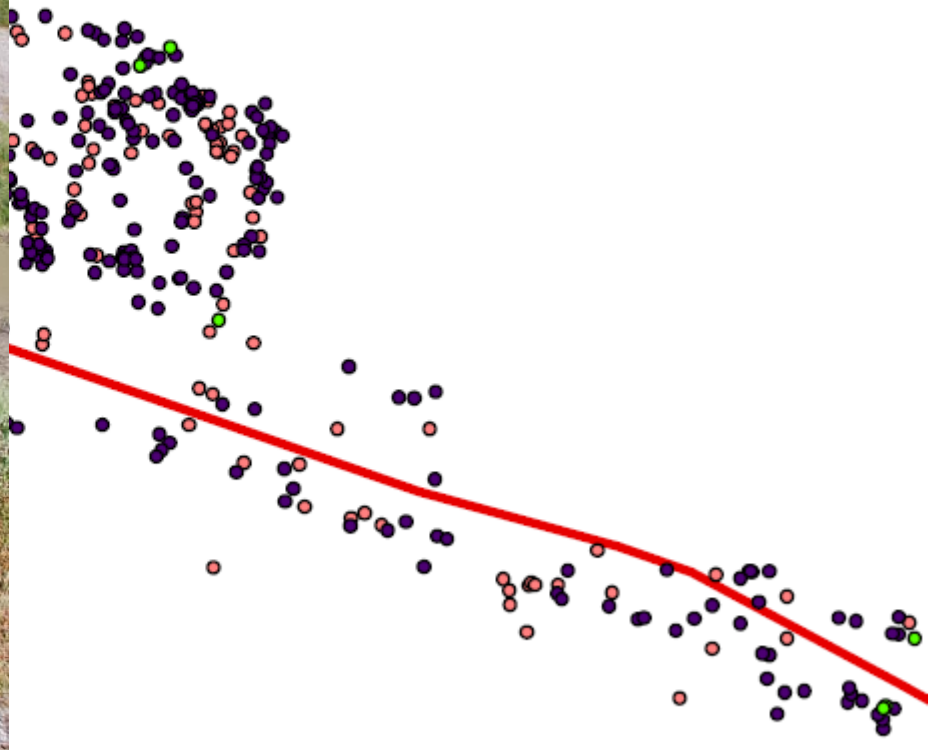
Liard River



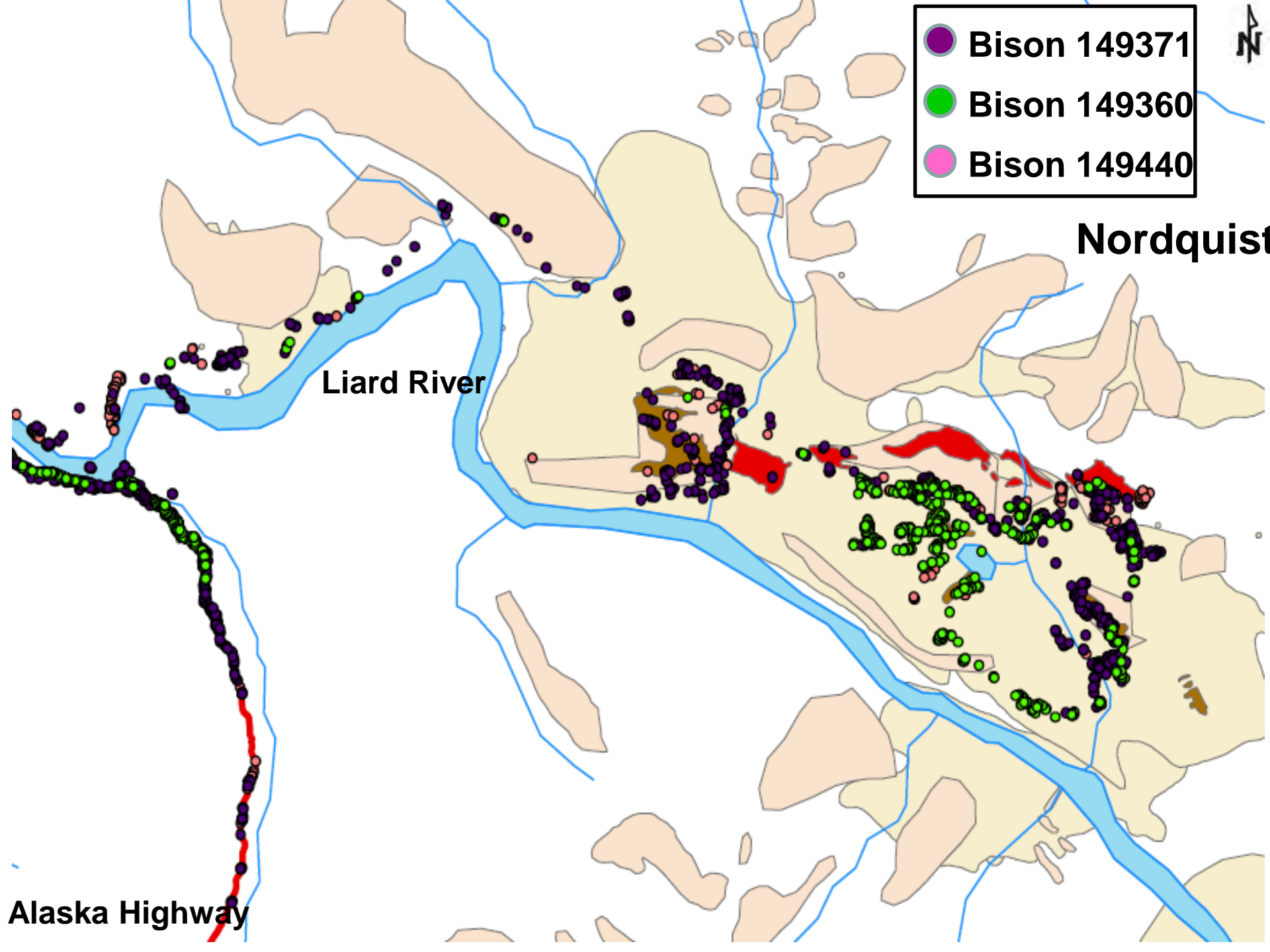




-  **Bison 149371**
-  **Bison 149360**
-  **Bison 149440**



Alaska Highway





21.05.2009 17:14

Lana Lowe, Lands Director, Fort Nelson First Nation













So, is IT a silver bullet?

- Pyric herbivory vs. Patch burning vs. need for heterogeneity
- Scale dependence or landscape context
- What about other herbivores?
- Regional/site differences
- Are there negative effects on some species?
- Interactions with climate and other disturbances (e.g. prairie dogs)

The Prairie Butterfly Paradox



The Regal Fritillary,
For example



07/20/2009

Interactions of climate and fire at two sites in the northern Great Plains, USA

Charles E. Umbanhowar Jr.

Department of Biology, St. Olaf College, 1520 St. Olaf Avenue, Northfield, MN 55057, USA

Received 10 April 2003; received in revised form 12 December 2003; accepted 5 March 2004

Abstract

The relationship of fire and climate in explaining the origin and maintenance of the grassland has long been of interest. I examined the hypothesis that burning was more frequent during reconstruct fire histories near Coldwater Lake in southcentral ND, and Rice Lake in northcentral ND. Ostracod Mg/Ca ratios as a proxy for climate at these same two sites. Over the past 10 000 y, Coldwater ($0.04\text{--}5.68\text{ mm}^2\text{ cm}^{-2}\text{ year}^{-1}$) greatly exceeded influx rates for Rice ($<0.01\text{--}1.91$). Both sites showed strong, significant periodicities of $\sim 1500\text{--}1800$, $\sim 800\text{--}900$ and $\sim 130\text{--}140$ year minima were only similar at ~ 4200 cal years BP. Charcoal influx during the past 2000 years also of between 310–400 and 140 years at both sites. Comparison of smoothed charcoal influx suggests that both proxies are responding to changes in climate. When smoothed with a 320–4 year charcoal influx typically preceded rises in ostracod Mg/Ca ratio by $\sim 50\text{--}100$ years, and further of the residuals suggested a variable relationship between Mg/Ca ratios and charcoal influx. These or reject the fuel limitation hypothesis, and this lack of clear support may result from (a) climate and C_4 grasses resulting in maximum productivity at intermediate moisture levels, (b) possibly C_3 and Mg/Ca ratios to summer vs. winter precipitation, or (c) ground-water driven lags in the response. Comparison of the results from this study with other studies suggests that links between scales (0–100 years) may be broadly constrained by longer term ($\sim 500\text{--}2000$ years) patterns in the Northern Plains.

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Keywords: charcoal; grasslands; fire; C_3/C_4 productivity; northern Great Plains; paleoenvironment

Fire cycles in North American interior grasslands and their relation to prairie drought

K. J. Brown^{†‡§}, J. S. Clark^{†¶}, E. C. Grimm^{||}, J. J. Donovan^{**}, P. G. Mueller^{||}, B. C. S. Hansen^{**}, and I. Stefanova^{**}

[†]Department of Biology and [¶]Nicholas School of the Environment, Duke University, P.O. Box 90338, Durham, NC 27708; [‡]Department of Quaternary Geology, Geological Survey of Denmark and Greenland, 10 Øster Voldgade, DK-1350 Copenhagen K, Denmark; [§]Illinois State Museum, Research and Collections Center, 1011 East Ash Street, Springfield, IL 62703; ^{||}Department of Geology and Geography, West Virginia University, 425 White Hall, P.O. Box 6300, Morgantown, WV 26506; and ^{**}Limnological Research Center, University of Minnesota, 220 Pillsbury Hall, 310 Pillsbury Drive Southeast, Minneapolis, MN 55455

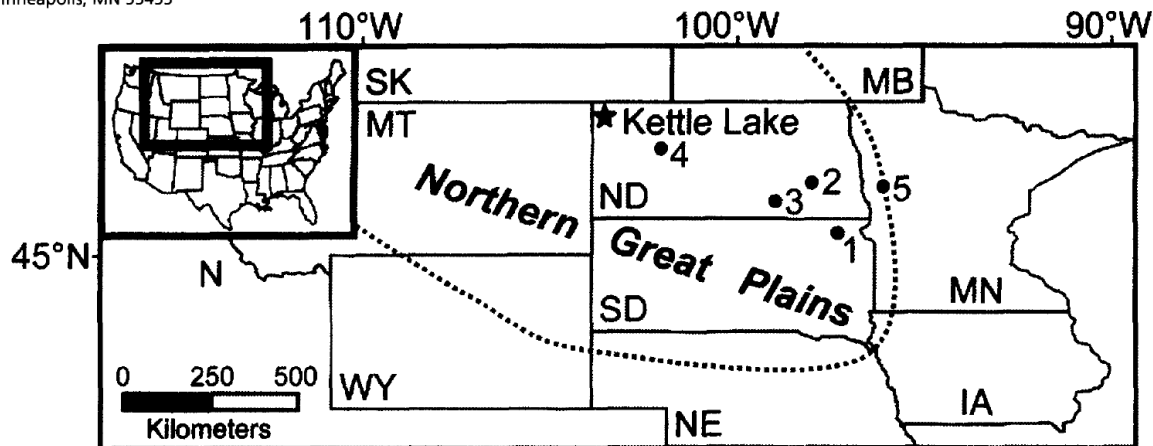


Fig. 1. Study location (*Inset*) and study site map. The dotted line defines the approximate boundary of the NGP. Kettle Lake is marked by a star. Sites numbered 1–4 correspond to other locations where aridity cycles have been detected: 1, Pickerel Lake (South Dakota) and Spring Lake; 2, Moon Lake (North Dakota); 3, Coldwater Lake; 4, Rice Lake. Location 5 is West Olaf Lake.

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- Scale dependence or landscape context
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- Regional/site differences
- Are there negative effects on some species?
- Interactions with climate and other disturbances (e.g. prairie dogs)

Name: Amber Breland

Date of Degree: December 2010

Institution: Oklahoma State University

Location: Stillwater, Oklahoma

Title of Study: **BLACK-TAILED PRAIRIE DOG AND LARGE UNGULATE
RESPONSE TO FIRE ON MIXED-GRASS PRAIRIE**

Pages in Study: 118

Candidate for the Degree of Master of Science

Major Field: Natural Resource Ecology and Management

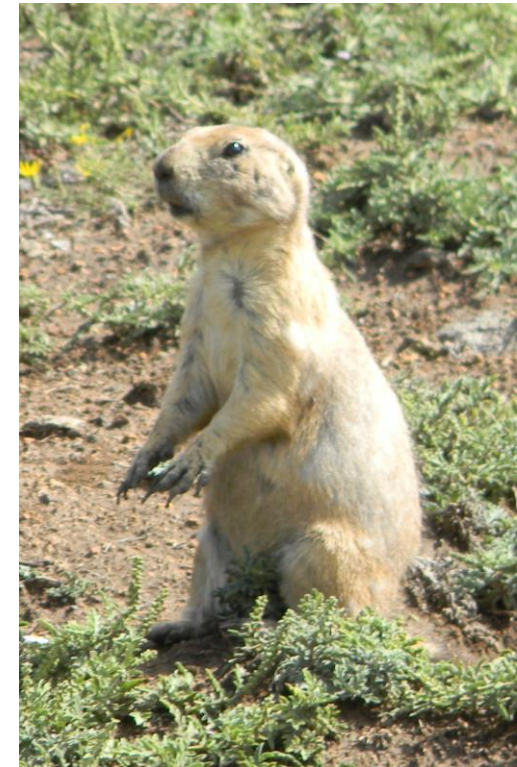
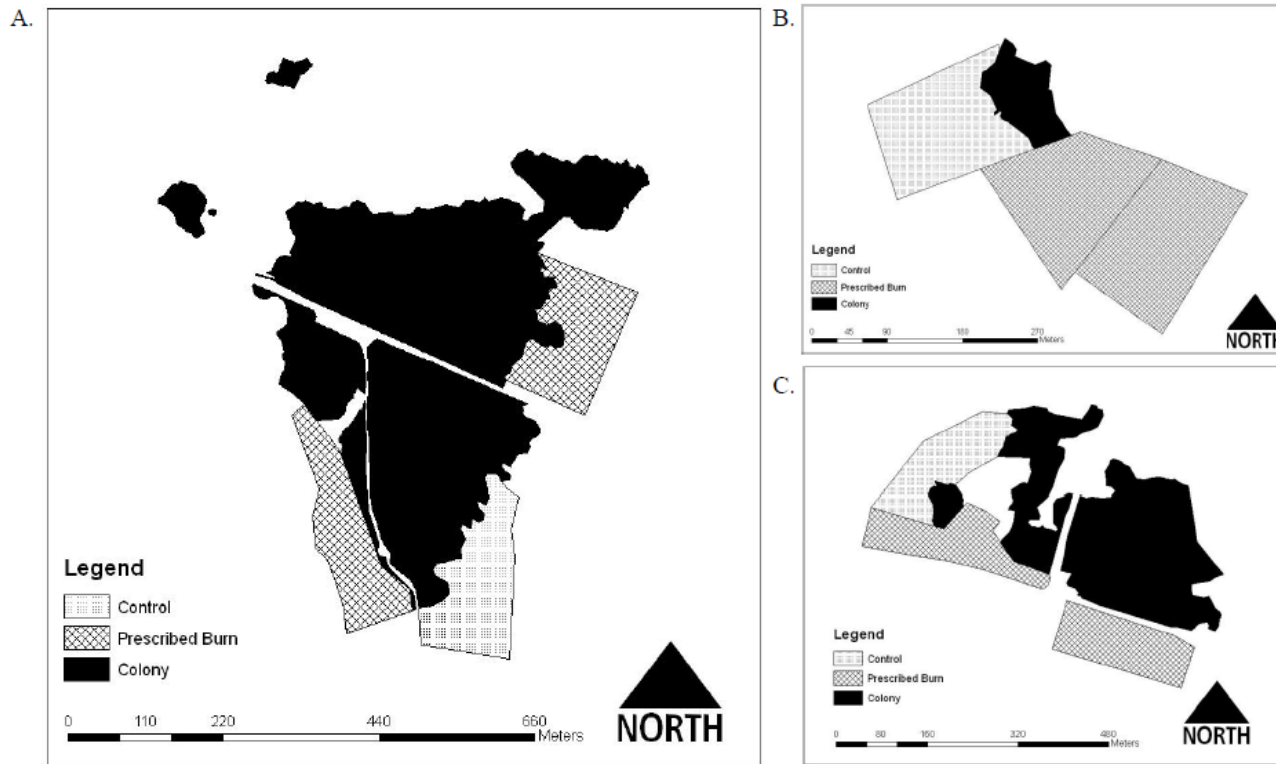
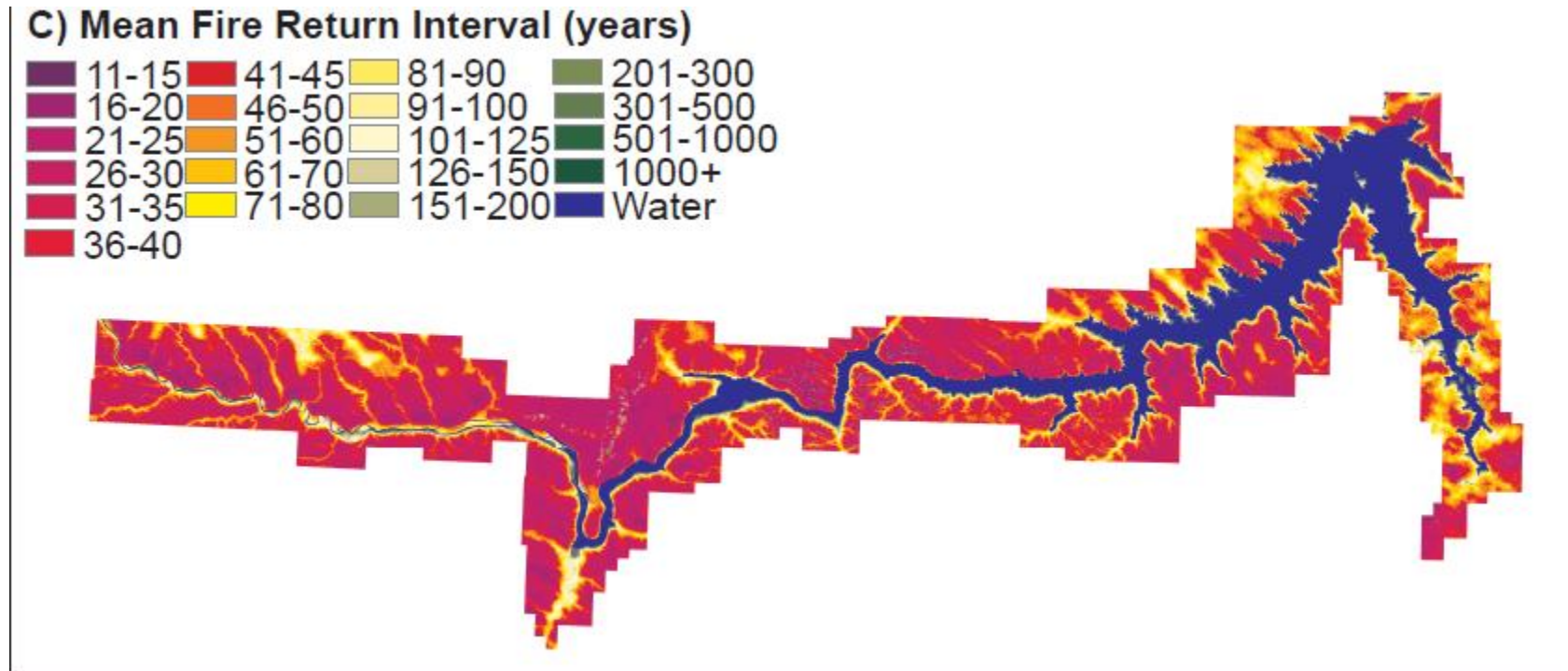


Figure 1.3. (A) Turkey Creek, (B) Quanah Parker, and (C) Holy City colony treatment locations at Wichita Mountains Wildlife Refuge, Oklahoma in 2009 and 2010.

Do we know IT works?

1. We do know that heterogeneity is important for multiple objectives.
2. In grasslands we do know that the fire-grazing interaction was a dominant disturbance.
 - Fire influences grazing
 - Grazing influences fire
 - Biodiversity and ecological processes respond
3. We do know that some species increase while others decrease with disturbance.
4. Should pyric herbivory be used for management of grazed ecosystems?
 - Depends on objectives
 - There is no silver bullet
 - Most important decisions are fire and stocking rate

Part II: HISTORICAL FIRE REGIME



- MFRI is the number of years between successive fire events
- Most of CMR has MFRI of < 45 years and much < 20

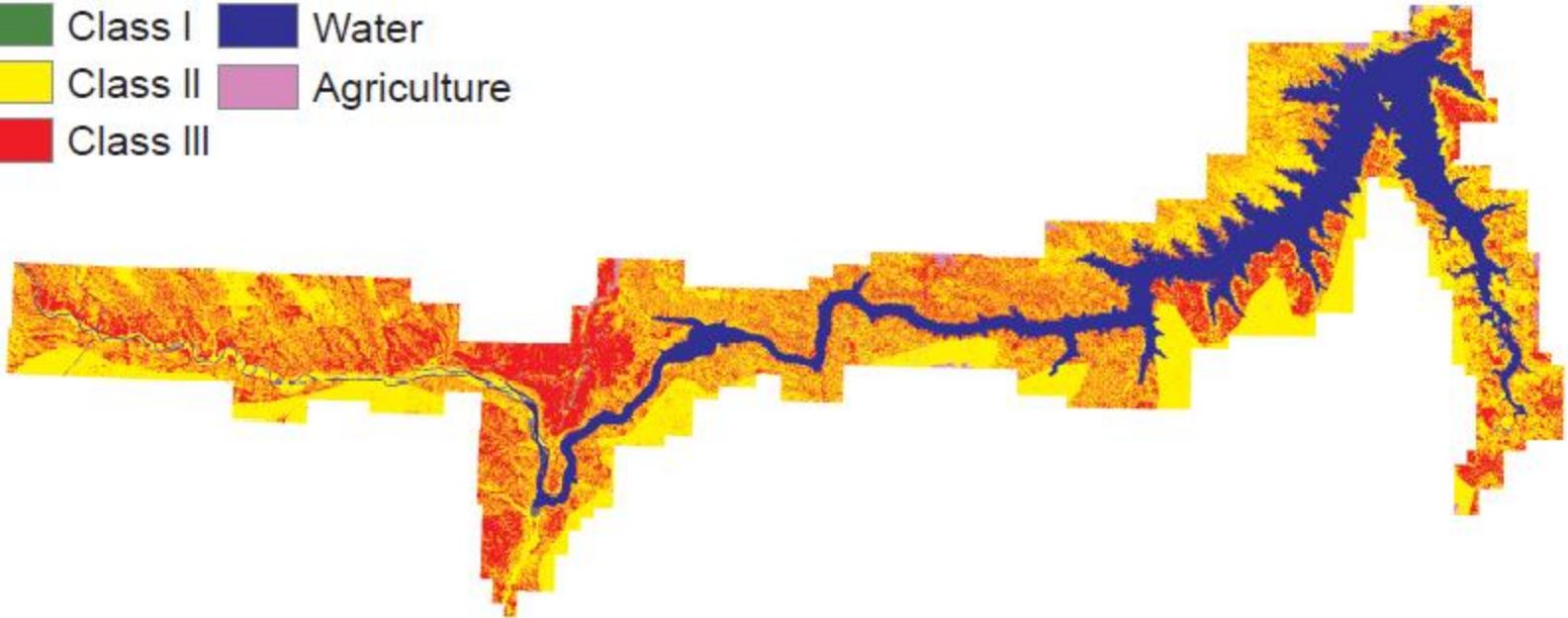
Part II: CURRENT FIRE REGIME

Years	Area burned (ha)	% of Total Refuge Area ¹	No. of fires	Min. Fire Size (ha)	Max. Fire Size (ha)	Ignition Source (% of total)			
						Lightning	Human-caused	Prescribed Fire	Other ²
1980-1984	4163.0	1.3	49	3.81E-03	4007.1	93.9	4.1	0.0	2.0
1985-1989	2829.5	0.9	75	1.64E-05	1214.0	92.0	4.0	1.3	2.7
1990-1994	5823.0	1.8	49	0.07	4478.7	63.3	30.6	4.1	2.0
1995-1999	7751.1	2.3	29	5.71E-04	4061.5	93.1	3.5	0.0	3.5
2000-2004	10509.9	3.2	36	0.04	26918.5	83.3	13.9	0.0	2.8
2005-2008	40579.9	12.3	38	0.03	13345.2	79.0	5.3	13.2	2.6
1980-2008	71656.4	21.6	276	1.64E-05	26918.5	84.4	10.1	2.9	2.5

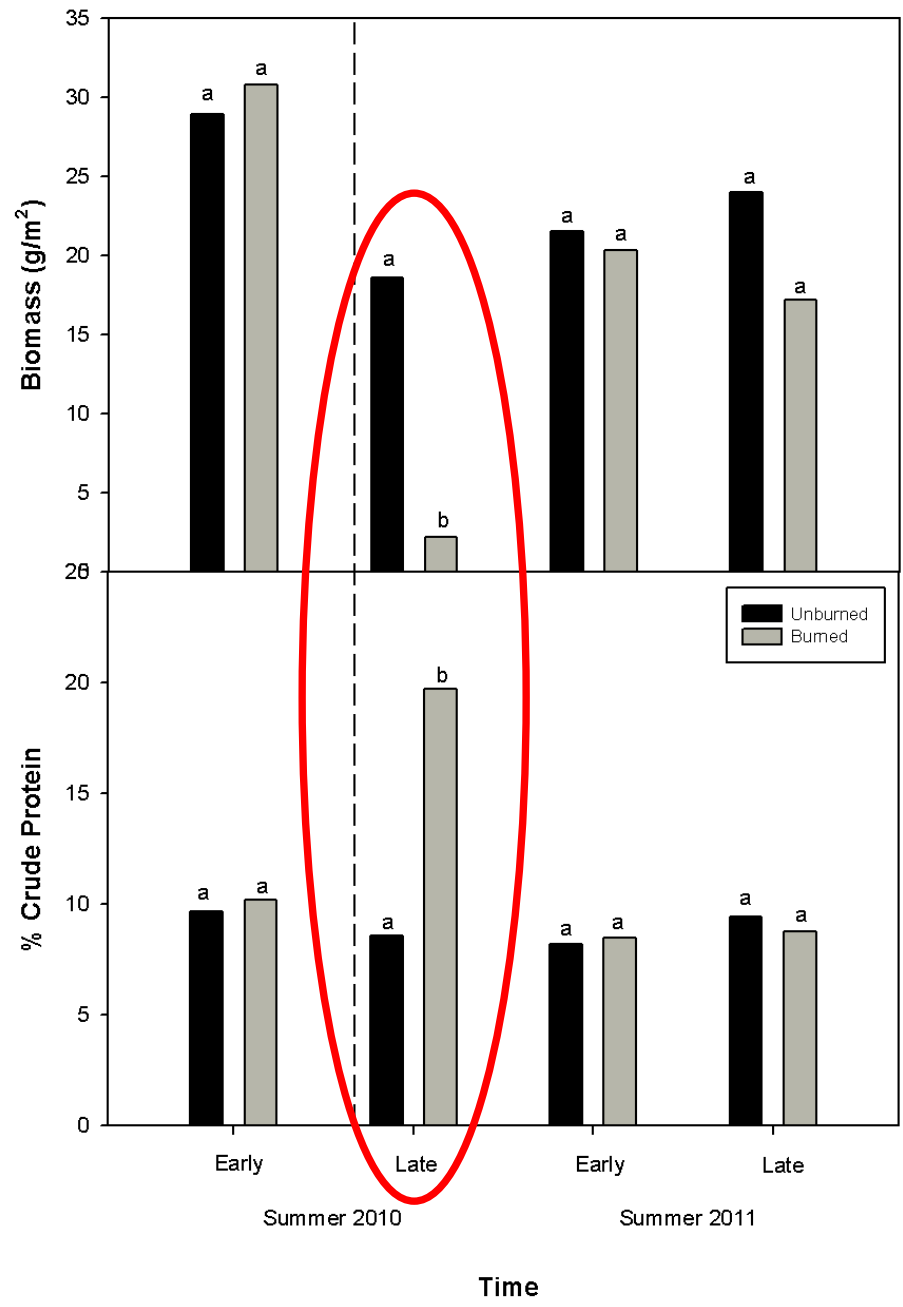
- Trend of increasing area burned
- Only 21.6 % of refuge burned in 29 years
- Recently, there are fewer but larger fires
- Most fires are ignited by lightning
- Fire rotation of 134 years

Part II: HISTORICAL FIRE REGIME

A) Fire Regime Condition Class



- FRCC represents departure from the natural fire regime
- Medium to high departure is dominant on CMR



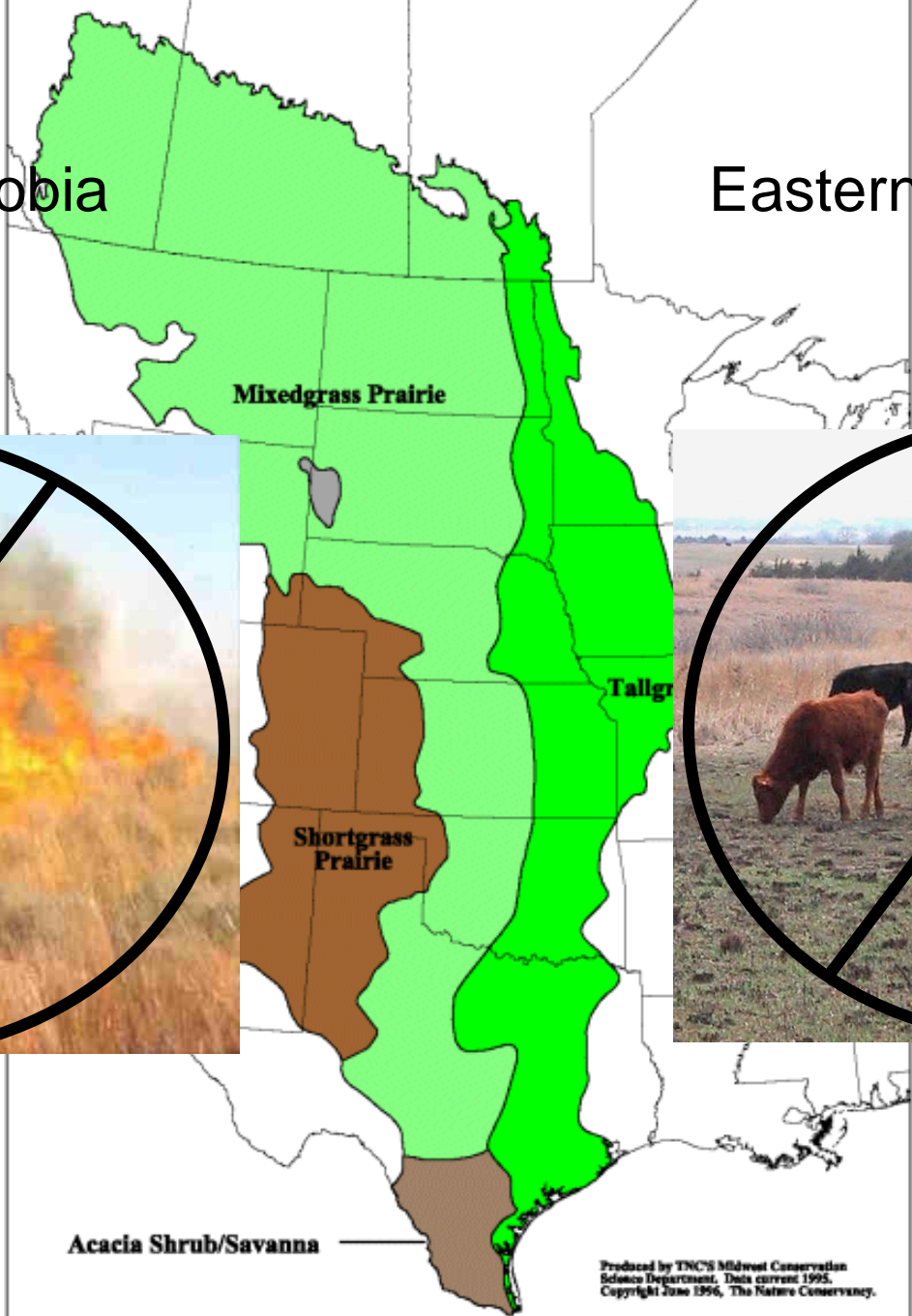
Post-Burn Vegetation Cover

		2011					
		No Grazing		Wildlife Only		Open Grazing	
Group	Species	Unburned	Burned	Unburned	Burned	Unburned	Burned
GRASS	<i>Bouteloua gracilis</i>	1.76 ± 0.38	3.13 ± 0.49	3.41 ± 0.57	4.03 ± 0.59	7.64 ± 0.91	6.37 ± 0.73
	<i>Bromus japonicus</i>	18.53 ± 1.39	8.01 ± 0.93	9.58 ± 0.93	3.66 ± 0.53	10.38 ± 1.20	9.42 ± 1.05
	<i>Pascopyrum smithii</i>	13.15 ± 0.79	12.71 ± 0.94	11.34 ± 0.89	11.26 ± 0.90	12.08 ± 0.92	9.38 ± 0.71
	<i>Stipa viridula</i>	2.00 ± 0.36	1.67 ± 0.38	5.65 ± 0.72	3.86 ± 0.68	3.12 ± 0.61	2.81 ± 0.48
FORB	<i>Melilotus officinalis</i>	2.97 ± 0.66	5.75 ± 1.13	2.28 ± 0.46	2.92 ± 0.56	2.15 ± 0.61	0.99 ± 0.26
SHRUB	<i>Artemisia frigida</i>	1.66 ± 0.33	0.47 ± 0.20	2.13 ± 0.37	1.04 ± 0.27	4.51 ± 0.63	2.22 ± 0.51
	<i>Artemisia tridentata</i>	9.02 ± 1.35	0.65 ± 0.42	7.02 ± 1.06	2.81 ± 0.63	10.42 ± 1.32	4.18 ± 0.92
	<i>Opuntia polyacantha</i>	1.51 ± 0.36	0.96 ± 0.31	0.95 ± 0.26	0.64 ± 0.23	1.28 ± 0.32	1.26 ± 0.36



Western Fire Phobia

Eastern Grazing Phobia



Acacia Shrub/Savanna

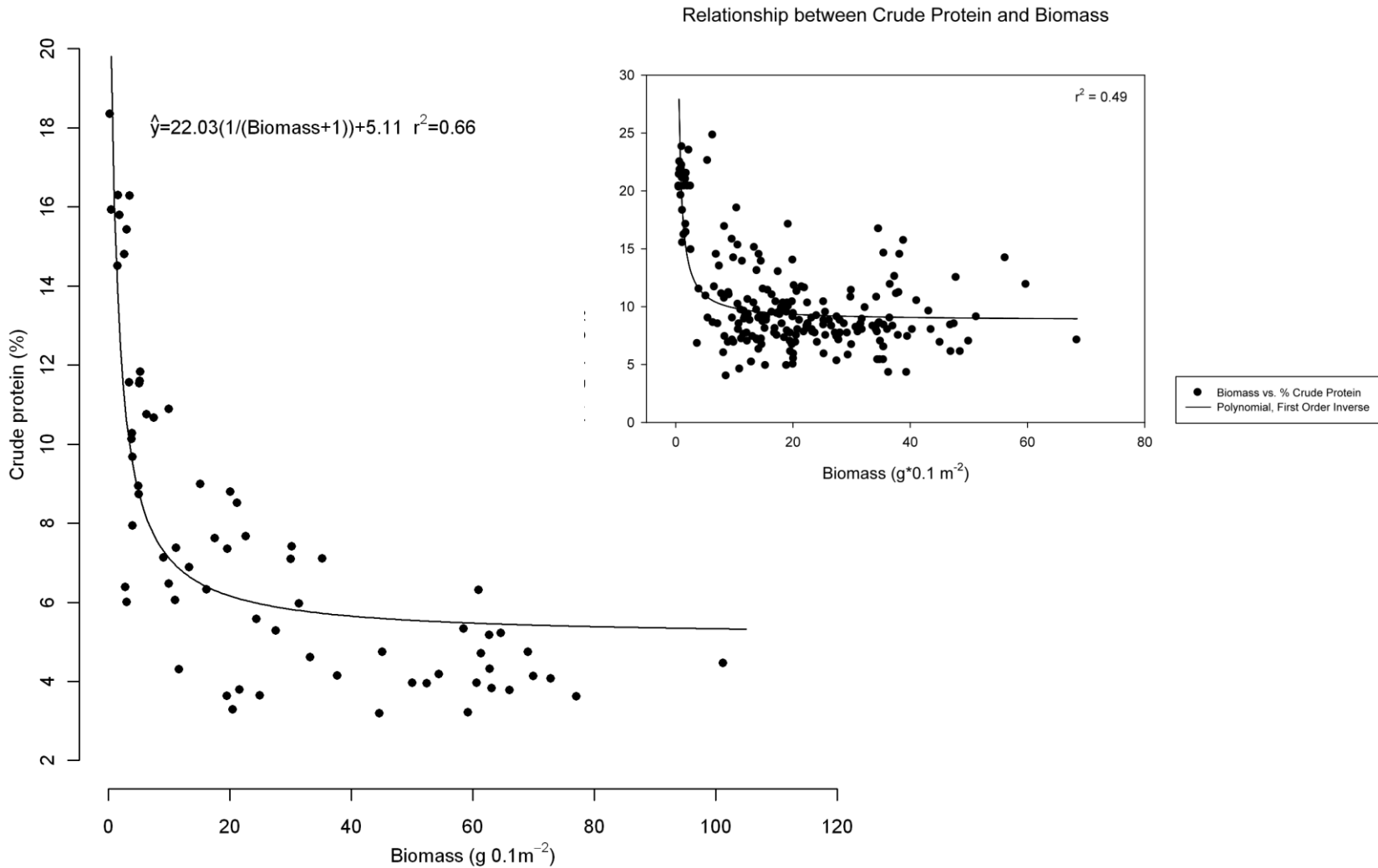
Produced by TNC's Midwest Conservation Science Department. Data current 1995. Copyright June 1996, The Nature Conservancy.

Grasslands of the Great Plains

“... the most important resources of Indian hunter-gatherers are the early succession species commonly found in recently burned areas: bison, moose, deer, elk, rabbits, grouse, grass seeds, legumes, berries, bulbs. However, natural fires are too irregular in occurrence and distribution to be completely relied upon.”

Henry Lewis, ethnohistorian
As quoted by Alston Chase,
Playing God in Yellowstone [pp. 93-94]

Forage quality and quantity paradox



55%

75%

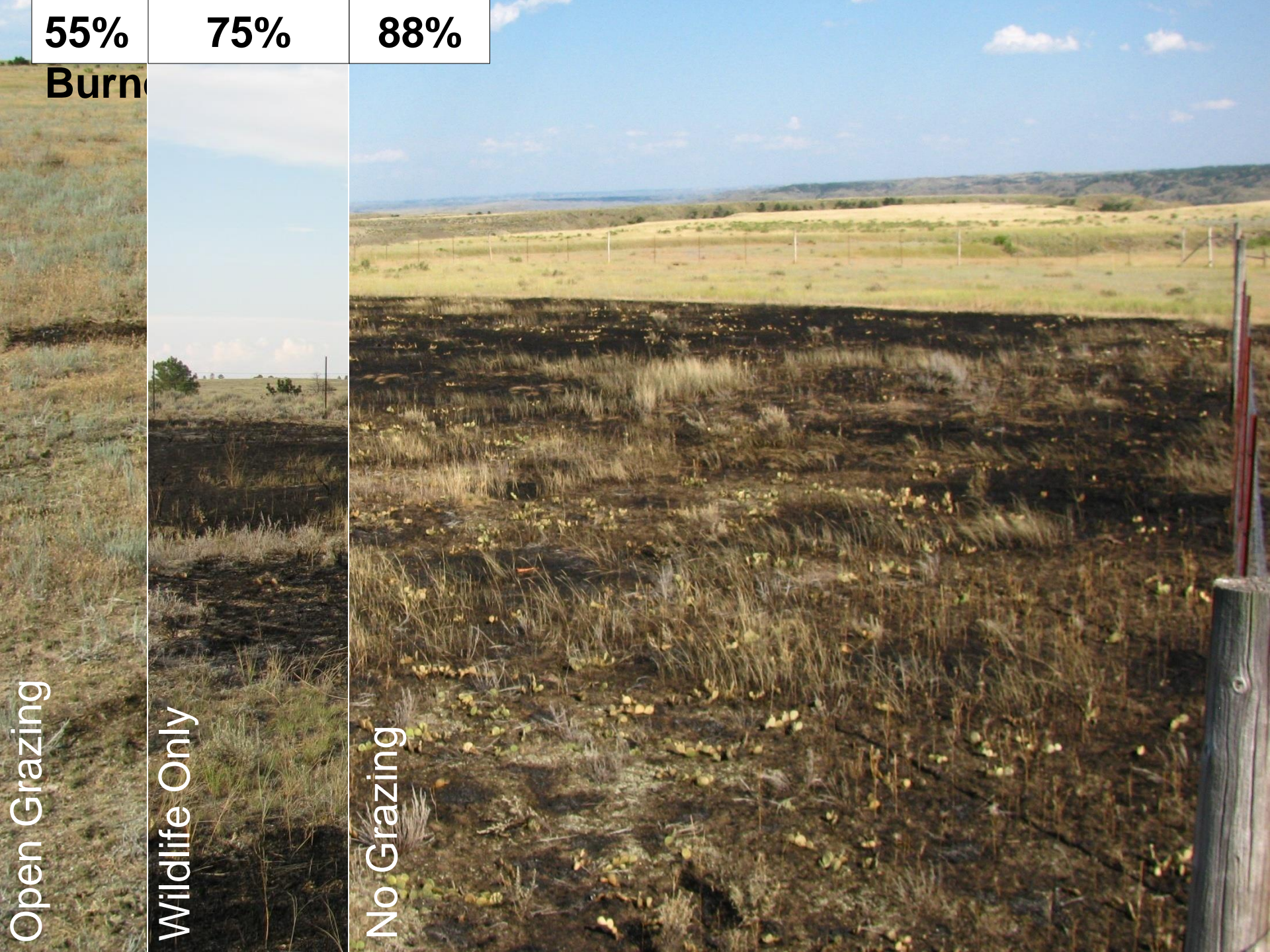
88%

Burn

Open Grazing

Wildlife Only

No Grazing



Fire history of the Rochelle Hills Thunder Basin National Grasslands

BARRY L. PERRYMAN AND W.A. LAYCOCK

Authors are assistant professor, School of Veterinary Medicine, University of Nevada, Reno, Nev. 89557, and professor emeritus, Department of Renewable Resources, University of Wyoming, Laramie, Wyo. 82071. Research was funded by the McIntire-Stennis Ecosystem Management Program and the Department of Rangeland Ecology and Watershed Management, University of Wyoming, Laramie, Wyo.

A fire scar chronology was constructed from ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) trees within the 70 km² Rochelle Hills Area of the Thunder Basin National Grasslands, in north-east Wyoming. A total of 65 fire scars occurred in 48 crossdated samples, and a master fire chronology was constructed for the period 1565 to 1988. No trees recorded more than 3 fires and most (26 of 42) recorded only one. For this reason, fire frequency intervals were considered as fire-free intervals in the Rochelle Hills Area. The Weibull Median Probability Interval (WMPI) for the entire period of record was 7.4; 7.9 for the non suppression period (1565 to 1939); and 6.7 for the suppression period (1940 to 1988). Infrequent occurrence of multiple scars, rough topography, and low potential substrates suggest that understory fuel loads were limited in amount and spatial consistency during most fire years. Position of scars within annual growth rings suggests that most fires (80%) occurred during the latter stages of the growing season or during the dormant period.



What about more arid, more complex and different herbivores?

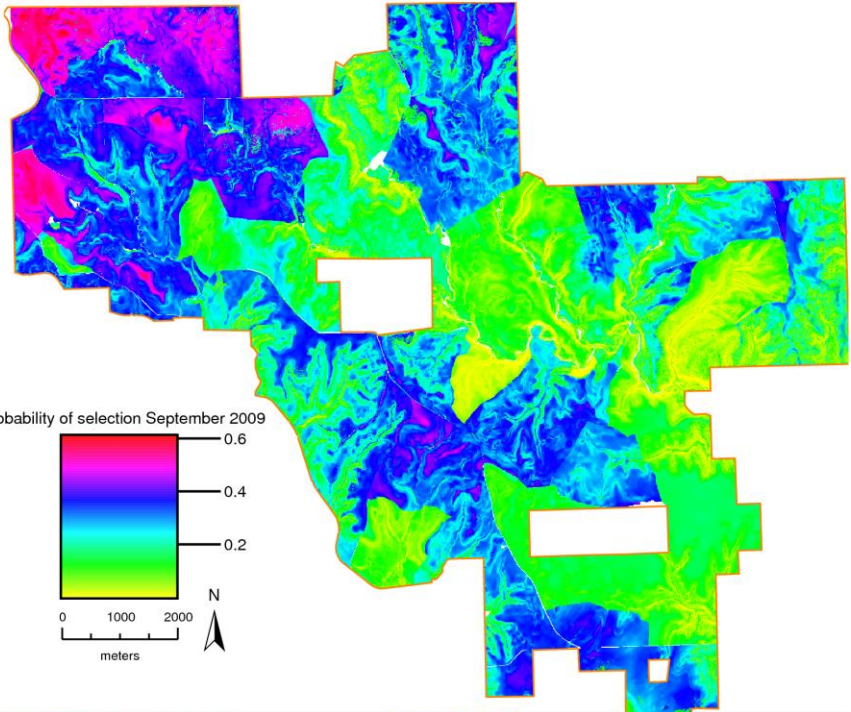
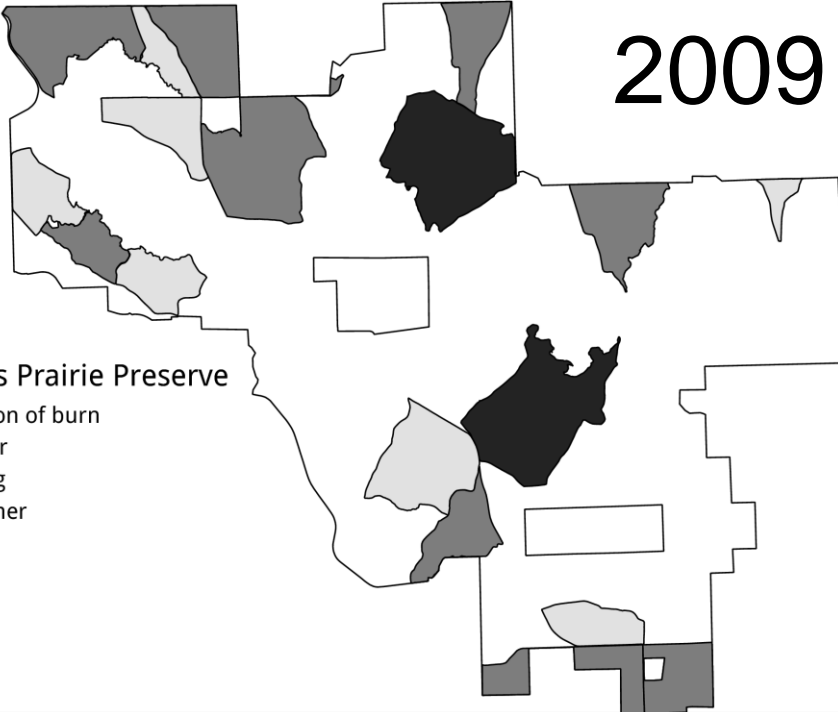


2009

Tallgrass Prairie Preserve

2009 Season of burn

- Winter
- Spring
- Summer

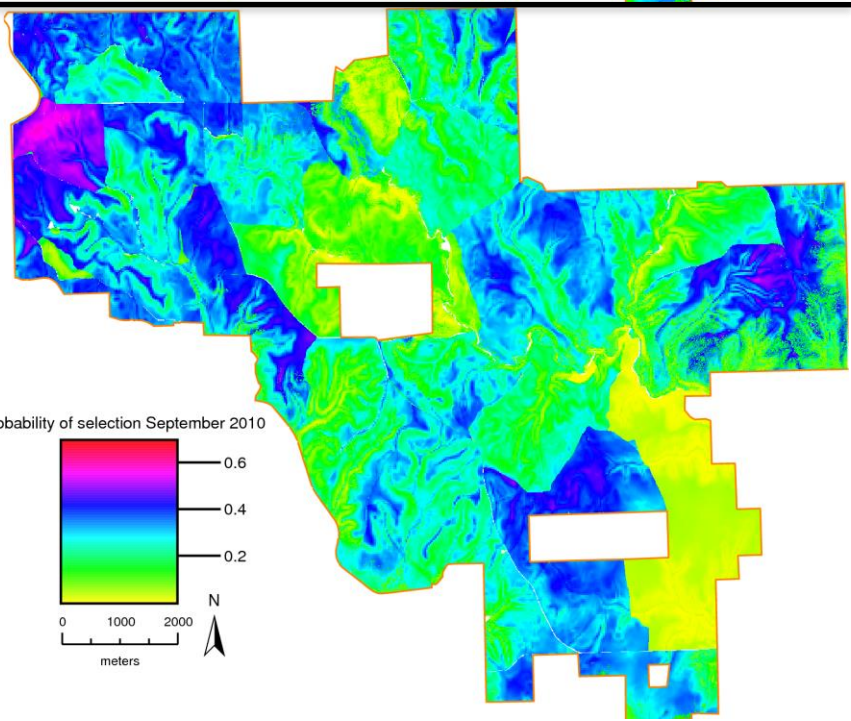
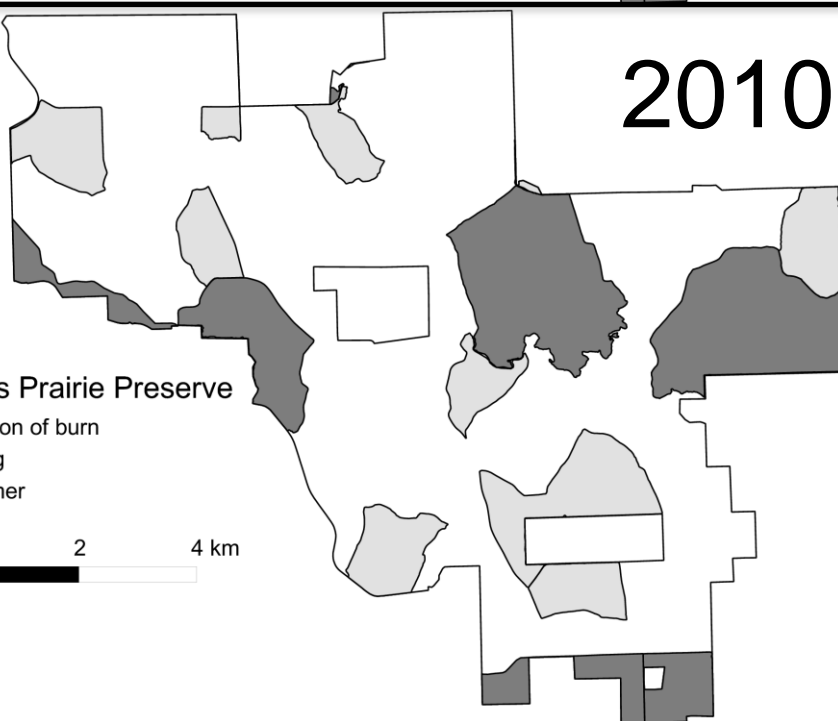


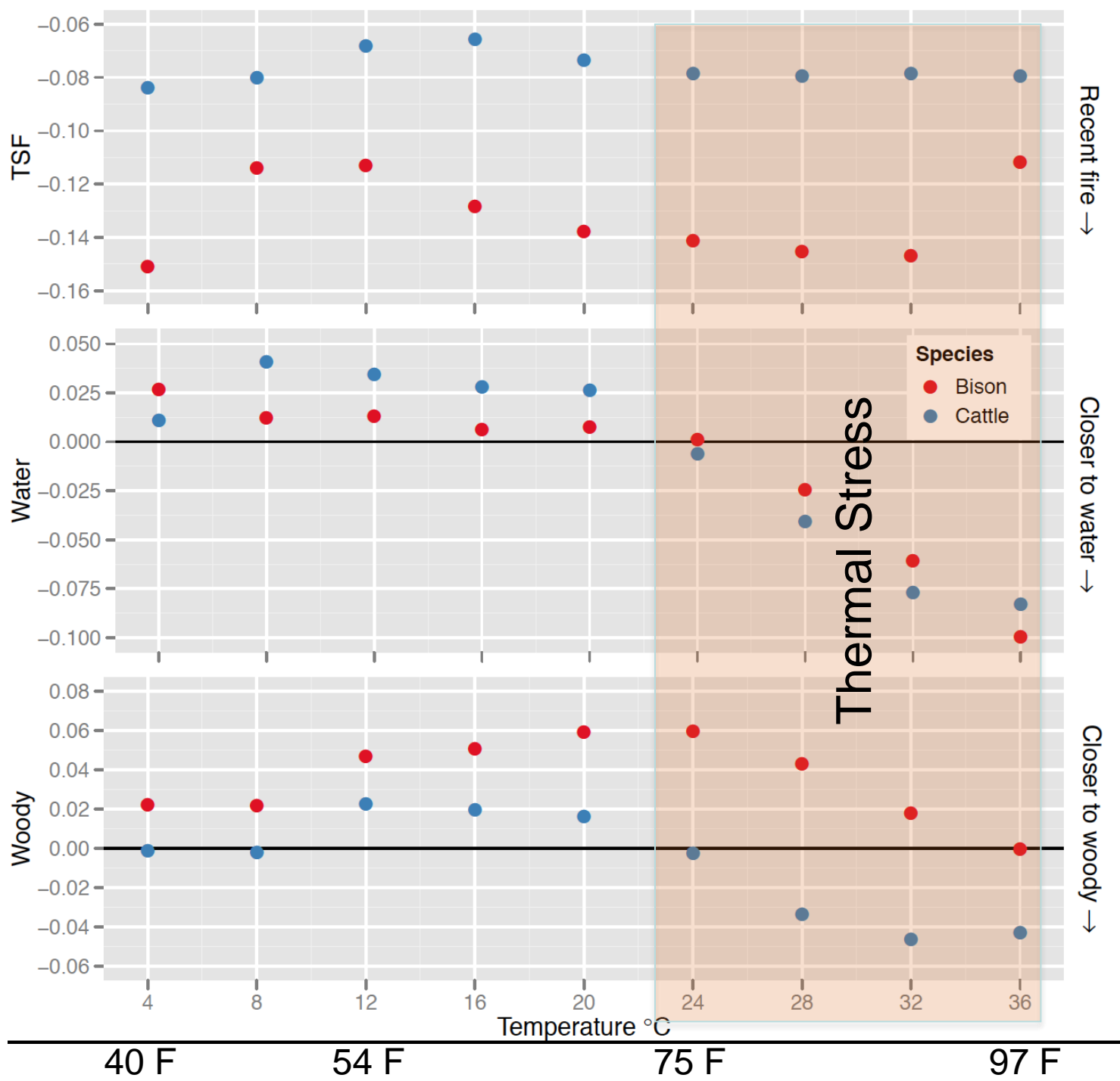
2010

Tallgrass Prairie Preserve

2010 Season of burn

- Spring
- Summer





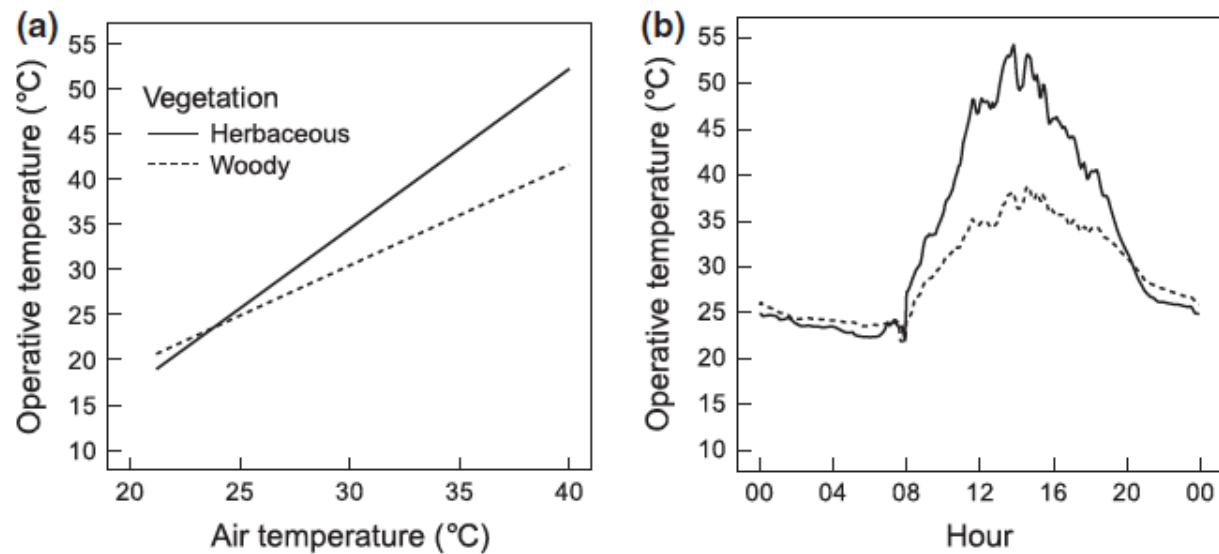


Fig. 1 Thermal representation of a tallgrass prairie ecosystem. Operative temperature as a function of (a), air temperature (T_{air}) separated by vegetation type, herbaceous ($\hat{y} = 1.91T_{air} - 22.33$; $r^2 = 0.72$, $P < 0.05$) and woody ($\hat{y} = 1.13T_{air} - 3.45$; $r^2 = 0.84$, $P < 0.05$) and (b), hour of day (values are averaged over summer sampling periods). Operative temperature is relatively more stable in woody than herbaceous vegetation. Woody vegetation is also significantly cooler at warmer air temperatures and during the heat of the day.

