Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America

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1   Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the

2   Central Great Plains of North America

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9   Running Header: Tri-Stability of Grasslands, Shrublands, and Woodlands

10

11   Summary

12   1. This review synthesizes evidence that altered fire frequency drives discontinuous ecosystem

13   transitions from mesic grasslands to shrublands or woodlands in the Central Great Plains, U.S.A.

14   2. Long-term fire manipulations reveal that grassland to shrubland transitions are triggered when

15   fire-free intervals increase from 1-3 years to $\geq$ 3-8 years and longer fire returns (~10 years or

16   more) result in transitions to woodlands. Grazing and soil properties alter these fire thresholds.

17   3. Grassland to shrubland transitions are abrupt and exhibit non-linear relationships between

18   driver and state variables. Transitions to shrublands and woodlands exhibit hysteresis, where

19   reintroducing frequent fires does not reverse transitions in management-relevant time-scales

20   (decades).

21   4. Non-linear transitions and hysteresis emerge because grasses generate positive feedbacks with

22   fire that create strong demographic barriers for shrub and tree establishment. Fire-free intervals

23   allow shrubs and trees to reach a size sufficient to survive fire, reproduce, and disrupt the fire

24   feedback loop through competition.

25   5. *Synthesis*: Mesic grasslands, shrublands, and woodlands constitute self-reinforcing states

26   (alternative attractors) separated by critical fire frequency thresholds. Even without major shifts

27   in climate, altered fire frequency can produce dramatic state-changes, highlighting the

28   importance of fire for predicting future ecosystem states. Local management should focus on

29   prevention of unwanted transitions rather than post-hoc restoration.

30 **Key-words:** alternative stable states, bi-stability, bush encroachment, critical transitions, plant

31 population and community dynamics, positive feedbacks, resilience, restoration, stability,

32 tallgrass prairie, tipping points, woody encroachment

33

34 **Introduction**

35 Woody encroachment—the increasing extent and dominance of woody plants in grass-dominated

36 systems—is occurring across most North American grassland ecosystems (Archer *et al.* 1988,

37 Briggs *et al.* 2005, Van Auken and McKinley 2008, Barger *et al.* 2011, Ratajczak, Nippert &

38 Collins 2012), and in many other grasslands globally (Eldridge *et al.* 2011). This recent

39 widespread increase in shrub and tree cover in grasslands and savannas can lead to states of co-

40 dominance by shrubs and grasses or complete conversions of grasslands to shrublands or tree-

41 dominated woodlands, often referred to as an ecosystem transition.

42   The ramifications of these ecosystem transitions are multifarious, with impacts on

43 community composition and vegetation structure (Eldridge *et al.* 2011, Ratajczak *et al.* 2012),

44 ecosystem function (Barger *et al.* 2011), ecohydrology (Huxman *et al.* 2005, Brunsell, Nippert &

45 Buck 2014*)* and long-term conservation of biodiversity (Gray & Bond 2012). Woody

46 encroachment into mesic grassland can impact regional economies by reducing forage for large

47 grazers (Hoch, Briggs &Johnson 2002, Briggs *et al.* 2005, Limb *et al.* 2010), hindering

48 economically-important livestock production (Limb *et al.* 2011).

49   Woody encroachment into grasslands has been attributed to a variety of drivers operating

50 at global (elevated CO_2, climate change; Bond & Midgley 2012, Kulmatiski & Bear 2013),

51 regional (nitrogen deposition, fragmentation; Kochy & Wilson 2001, Briggs *et al.* 2005) and

52 local scales (over-grazing, fire; Walker *et al.* 1981, Roques *et al.* 2001, Fuhlendorf *et al.* 2008,

53   Van Auken & McKinley 2008). Within mesic grasslands, including North American tallgrass

54   prairie, changes in the timing, intensity and frequency of fire have been implicated as important

55   proximate drivers of transitions from grasslands to shrubland or woodland (Briggs *et al.* 2005,

56   Fuhlendorf *et al.* 2008, Bond 2008, Gibson 2009, Twidwell *et al.* 2013a).

57   As with many grasslands and savannas globally (Archibald, Staver & Levin 2012), fire

58   frequency in the North American Central Great Plains (CGP) is largely controlled by the number

59   of ignition events, which occur via lightning strikes or by humans (Allen & Palmer 2011,

60   Stambaugh, Guyette & Marschall 2013, Twidwell *et al.* 2013b). The best estimates of pre-

61   settlement fire regimes in CGP grasslands suggest that fire-free intervals generally ranged from

62   3-5 years (Wright & Bailey 1982, Allen & Palmer 2011, Desantis, Hallgren & Stahle 2010,

63   Strambaugh *et al.* 2013). Fire frequency now varies across the region (Mohler and Goodin 2012)

64   from annual or biennial in many grasslands managed primarily for cattle production (Smith &

65   Owensby 1978), to 3-4 years in areas managed to balance cattle production and biodiversity

66   (Fuhlendorf *et al.* 2009, Allred *et al.* 2011), to long-term fire suppression of 20 years or more

67   associated with a cessation of ranching and sub-urban development (e.g. Hoch *et al.* 2002,

68   Briggs *et al*. 2005, Mohler & Goodin 2012). A critical question is if and how this landscape will

69   respond to changes in fire frequency.

70   This review synthesizes and expands upon recent research on fire as a driver of woody

71   encroachment in mesic grasslands (i.e., tallgrass prairies) of the North American CGP. For this

72   review, we define the CGP as the ecoregion bounded to the south by the Cross-Timbers region,

73   to the north by transition from C_4 grass dominance to C_3 grass dominance, to the west by the

74   transition to mixed grass prairie, and to the east by deciduous forest (similar to Barger *et al.*

75   2011). The focus on temperate mesic grassland transitions is timely, given the need for increased

76 conservation of this grassland (Hoekstra et al. 2005) and widespread manipulation of fire in

77 grasslands (Mohler & Goodin 2012, Twidwell et al. 2013b). We review the mechanistic and

78 experimental evidence for whether fire frequency creates tipping points that separate grasslands,

79 shrublands and woodlands as alternative attractors. We build on >30 years of extensive research

80 manipulating fire frequency and grazing in a North American tallgrass prairie at the Konza

81 Prairie Biological Station (KPBS), as well as data from other tallgrass prairie sites in the region.

82

83 **Conceptual Framework**

84 Woody encroachment of grasslands has been described using many different conceptual

85 frameworks, including succession (Archer *et al.* 1988), gradual linear dynamics (Roques *et al.*

86 2001), state and transition models (Westoby, Walker & Noy-Meir 1989, Briske *et al.* 2005,

87 Briske, Fuhlendorf, & Smeins 2006), alternative attractors (or alternative stable states) (Walker

88 *et al.* 1981, Frehlich *et al.* 1999, Anderies et al. 2002, Folke *et al.* 2004, Bestelmeyer *et al.* 2011),

89 demographic models (Higgins & Schieter 2012), rapid changes in ecosystem drivers

90 (Bestelmeyer *et al.* 2013), physiological thresholds (Hoffman *et al.* 2012, Twidwell *et al.* 2013a)

91 and others (Scholes & Archer 1997, Bond 2008, Briggs *et al.* 2005). Here we focus on

92 comparing linear and alternative attractor models, because ecosystems with alternative attractors

93 are susceptible to rapid and difficult to foresee regime shifts (Holling 2001, Folke *et al.* 2004,

94 Walker & Salt 2006, Scheffer 2009) and knowledge of potential alternative attractors is also key

95 for successful ecosystem restoration (see Briske et al. 2008, Suding & Hobbs 2009).

96   Different fire frequencies could generate non-linear transitions that are difficult to reverse

97 (i.e. tipping points, critical thresholds). Non-linear responses occur when an ecosystem state is

98 initially resistant to external forcing, but has a point(s) where gradual forcing precipitates non-

99   linear changes in state (threshold systems) (Fig 1, Noy-Meir 1975, May 1977, Holling 2001,

100   Walker 1981, Folke 2006, Briske *et al.* 2008, Scheffer 2009, Bestelmeyer *et al.* 2011). In more

101   extreme cases, threshold transitions also exhibit hysteresis, where eliminating the external

102   forcing or returning driving variables to their pre-transition levels is insufficient to reverse the

103   state transition (Noy-Meir 1975, May 1977, Walker *et al.* 1981). When a system exhibits

104   threshold transitions and hysteresis, we refer to the two potential states as alternative attractors

105   (similar to the concept of alternative stable states and critical transitions), "critical thresholds"

106   refer to non-reversible thresholds, and "regime shifts" refer to transitions from one alternative

107   attractor to another (Scheffer 2009).

108   Determining if systems have alternative attractors requires multiple lines of inference,

109   including but not limited to mechanistic studies and studies relating salient driver variables with

110   ecosystem state (Scheffer & Carpenter 2004, Schroder *et al.* 2005, Bestelmeyer *et al.* 2011,

111   D'Odorico *et al.* 2012). Mechanistic studies of ecological thresholds typically focus on

112   demography and feedback processes (Archer *et al.* 1988, Roff & Mumby 2012, Higgins &

113   Scheiter 2013), because ecological thresholds occur primarily in systems with demographic

114   barriers and/or strong feedback mechanisms (De Roos and Persson 2002, Walker & Salt 2006,

115   D'Odorico *et al.* 2012, Boerlijst, Oudman, & Roos 2013, Higgins & Schieter 2013, Huss *et al.*

116   2013). Demographic bottlenecks are establishment barriers or low population growth rates for a

117   life stage, resulting from evolved life history traits and/or ecological constraints (Grime 1979).

118   Demographic bottlenecks can suppress a potentially dominant functional group through priority

119   effects and other mechanisms (De Roos & Persson 2002, Higgins & Schieter 2012, Huss *et al.*

120   2013). Distinguishing between feedbacks and demographic bottlenecks can be difficult because

121   feedbacks by one group or species can create demographic bottlenecks for other one or more

122   other species. However, feedbacks generally refer to interactions that amplify (positive

123   feedbacks) or dampen (negative feedbacks) pressures (Walker & Salt 2006, D'Odorico *et al.*

124   2012). Experimental and observational approaches can identify thresholds by determining

125   whether a system exhibits linear or threshold relationships between driver and state (Scheffer &

126   Carpenter 2004, Bestelmeyer *et al.* 2011). Reversing the change in drivers that precipitated a

127   threshold transition can identify hysteresis (Fig. 1). For transitions from grasslands to shrublands

128   and woodlands, we first review the mechanistic evidence for feedbacks and demographic

129   barriers, followed by evidence for fire frequency thresholds, abrupt ecological shifts and

130   hysteresis.

131

132   **Grassland to shrubland transitions**

133   *Mechanistic Background*: Historically, much of the CGP was tallgrass prairie, an herbaceous

134   plant community dominated by rhizomatous C_4 (i.e. warm-season) grasses with a diverse

135   subdominant community of C_3 grasses, forbs, and legumes (Collins & Adams 1983, Gibson &

136   Hulbert 1987, Collins & Calabrese 2012). In this region, the balance of precipitation and

137   evapotranspiration can support woody vegetation (Borchert 1950, Hayden 1998) and yet, woody

138   plant cover was historically low, except along riparian corridors and certain other landscape

139   features (e.g., outcrops, seeps, etc.) (Weaver 1954, Wells 1970, Axelrod 1985, Abrams 1985).

140   The dominant grasses of this region are well-adapted to fire and drought, but poorly adapted to

141   light limitation (Knapp 1993, Scholes and Archer 1997, Bond 2008, Nippert et al. 2011, Schieter

142   & Higgins 2012) and they generate self-reinforcing feedbacks that promote these conditions and

143   demographic barriers that inhibit other plant growth forms by: 1) leaving little open space for

144   colonization by other species, even in post-fire windows (Weaver 1954, Briggs & Knapp 2001,

145 Benson & Hartnett 2006); 2) producing large concentrations of fibrous roots in the upper 30 cm

146 (Jackson *et al.* 1996, Nippert & Knapp 2007, Nippert *et al.* 2012) that can rapidly utilize water

147 and nutrients at this soil depth (Knapp 1993, Epstein *et al.* 1997, Knapp *et al.* 2001,

148 Bredenkamp, Spada, & Kazmierczak 2002, Ocheltree *et al.* 2013, 2014); and 3) generating large

149 amounts of herbaceous biomass that facilitates frequent and intense fires, resulting in direct

150 mortality of unprotected meristems (Gibson, Hartnett, & Merrell 1990, *sensu* Van Wilgen *et al.*

151 2002, Bond 2008, Scheiter & Higgins 2012). As a result, the establishment of shrub seedlings in

152 frequently burned grasslands is rare (Benson & Hartnett 2006, Ratajczak *et al.* 2011).

153   However, once shrubs establish in grasslands, the competitive dynamics between grasses

154 and shrubs change dramatically. Initially, shrub seedlings recruit as single-stemmed ramets that

155 are highly susceptible to top-kill by fire. Given sufficient time and resource availability

156 encroaching shrub species in CGP tallgrass prairie, such as *Cornus drummundii* and *Rhus*

157 *glabra*, form clonal multi-stem clusters in the grassland matrix ("shrub islands") that increase in

158 both height and radial extent over time (Petranka & McPherson 1979, Collins & Adams 1983,

159 Anderson *et al.* 2000, Harrell *et al.* 2001, McCarron & Knapp 2003, Brudvig *et al.* 2007,

160 Ratajczak, Nippert & Ocheltree *in press*). Increasing shrub cover leads to light limitation for

161 grasses, along with concomitant decreases in grass cover, grass biomass, and the fine fuels that

162 carry fire (Heisler *et al.* 2004, Lett & Knapp 2005). While the reductions in grass biomass are

163 greatest at the center of shrub clusters, even the edges have significantly lower fine fuels,

164 allowing new clonal recruits to benefit from shrub-mediated fire suppression (Ratajczak *et al.*

165 2011). If fire kills the above-ground portion of large shrubs, they typically resprout and reach

166 their former height in as little as one or two years (Heisler *et al.* 2004, Hajny, Hartnett & Wilson

167 2011). In the even rarer instances where fire kills shrubs completely, the potential for C_4 grasses

168   to recover their pre-transition productivity in short time frames (2 years or less) has usually

169   eroded (Lett & Knapp 2005), leaving windows of opportunity for shrub seedlings to establish in

170   a low-competition environment. Thus, while frequent prescribed fires might inhibit shrub

171   establishment, they may no longer be a viable filter for prohibiting shrub expansion once shrub

172   establishment is initiated.

173   The effects of resource competition and availability also change as shrubs reach larger

174   size-classes. Mature clonal shrubs are deep-rooted and obtain a larger percentage of their water

175   from deeper soils (> 50 cm depth), reducing competition for water with the dominant grasses,

176   which rely primarily on shallow soil water (McCarron & Knapp 2001, Ratajczak *et al.* 2011).

177   Use of deeper water sources by shrubs mitigates susceptibility to summer drought and climate

178   variability (Nippert *et al.* 2013). Crucially, deep-rooted parent stems can also transfer water to

179   developing clonal stems in the grassland matrix, allowing them to avoid competition with grasses

180   and increase in size until they can access deep soil moisture, suppress grass growth via shading,

181   and begin developing their own clonal recruits (Ratajczak *et al.* 2011, Killian 2012). The clonal

182   growth form and rooting properties of these shrubs, combined with their effects on fire

183   suppression, creates a positive feedback loop with low fire intensity and alters the demographic

184   bottleneck related to shrub recruitment, both of which facilitate shrub cluster survival and

185   expansion (Petranka & McPherson 1979, Yao *et al.* 1999, Ratajczak *et al.* 2011, similar to De

186   Roos & Persson 2002, D'Odorico *et al.* 2012, Huss *et al.* 2013), but only if shrubs are allowed to

187   increase in size by fire-free intervals.

188   *Experimental and observational evidence for fire thresholds:*

189   The mechanistic evidence presented thus far indicates that decreasing fire frequency

190   should facilitate a transition to shrublands. The presence of feedback mechanisms and

191 demographic potential associated with clonal life history traits in both grasses and shrubs,

192 suggests that this transition may be non-linear and capable of hysteresis (Walker & Salt 2006).

193 A synthesis of fire frequency studies (Fig 4-5) shows that fire return intervals ≤ 2 years prevent

194 shrub expansion in CGP grasslands (Bragg & Hulbert 1976, Briggs & Gibson 1992, Kettle *et al*.

195 2001, Bowles & Jones 2013, Ratajczak *et al. in press*; Fig. 2), 3 year fire returns sometimes

196 maintain grasslands, but can also allow transitions to shrublands, and fire returns >3 years

197 consistently result in rapid shrub expansion (Brudvig et al. 2007, Bowles *et al.* 2013, Ratajczak

198 *et al. in press*). This non-linear relationship between fire and shrubland formation is consistent

199 with alternative attractor theory. Moreover, the transition from grassland to shrubland has the

200 hallmarks of a threshold transition (e.g. Scheffer & Carpenter 2004, Bestelmeyer *et al.* 2011):

201 abrupt shifts in shrub cover over time, spatiotemporal bi-modality of system state, and non-linear

202 correlations between state and drivers variables (Fig. 2; Ratajczak *et al. in press*). The transition

203 to shrub-grass co-dominance typically takes 20 years, with gradual increases in shrub cover at

204 first, and rapid rates of clonal expansion later in the process, as illustrated by long-term

205 measurements at KPBS (Fig 2B; Collins & Adams 1983, Ratajczak *et al. in press*). Analysis of

206 28 years of plant composition at KPBS indicates that abrupt shifts in shrub cover are not related

207 to abrupt shifts in climate or fire (i.e. pulses), but instead are correlated with gradual changes in

208 grass cover (a proxy for fire intensity and the effects of grasses on resource availability;

209 Ratajczak et al. *in press*). This suggests that the abrupt transition from grassland to shrubland

210 represents the crossing of a threshold, rather than a response to abrupt changes in salient driver

211 variables (Bestelmeyer *et al.* 2011). Demographic rates, in particular the high survival and rapid

212 rate of clonal expansion, might also contribute to the abruptness of grassland to shrubland

213 transitions. The importance of demographic bottlenecks (e.g. Huss *et al.* 2013) is further

214   evidenced by the 8-fold faster expansion rates by clonal shrubs, compared to non-clonal wood

215   plants (Fig 2A-C).

216   For grasslands and shrublands to be alternative attractors they must also show hysteresis

217   with respect to fire frequency and grass dominance (Fig 1C). The clonal shrub *Rhus glabra* has

218   the capacity to withstand annual fires once established (Hajny *et al*. 2011) and although exposing

219   clonal oak shrublands to biennial fires initially lowers cover, it returns to previous levels within 2

220   years and shrubs that survive increase in size, reducing long-term fire susceptibility (Harrell *et*

221   *al.* 2001, Boyd & Bidwell 2002). Data from KPBS also show hysteresis. Directly after a

222   transition to shrubland, ungrazed grasslands were burned twice in 4 years, but failed to return a

223   grassland state (Ratajczak *et al. in press*). We attribute these examples of hysteresis to the ability

224   of shrubs to both suppress grasses and resist fire, and to resprout when top-killed.

225   Similar to other alternative attractors (Staver *et al.* 2011, Roff & Mumby 2012), critical

226   thresholds in CGP grasslands appear to be context-specific. Fire intensity and frequency play an

227   interactive role, whereby less frequent but more intense fires can exclude woody plants

228   (Fuhlendorf *et al.* 2008, Twidwell *et al.* 2013a) and vise versa (Ratajczak *et al*. *in press*).

229   Resource availability and other disturbance processes are also important. For instance, most

230   establishment and expansion of shrub species at KPBS and elsewhere occurs in areas with deeper

231   soils, while uplands with thin soils are rarely colonized by shrubs, despite long-term fire

232   suppression (Fig 2D, Bragg & Hulbert 1976, Ratajczak *et al.* 2011, Bowles & Jones 2013). This

233   is surprising, because upland fires are less intense (Gibson et al. 1990). The inability of shrubs to

234   reach a fire resistant size in uplands is most likely due to greater run-off, coarser soils, and

235   shallower soil depth, which collectively results in lower available soil moisture (Nippert *et al.*

236   2011) and forces shrubs to compete directly with grasses in upper soil layers (Nippert & Knapp

237   2007, Ratajczak *et al.* 2011).

238   Herbivory alters grass-shrub competition in many systems (Holdo *et al.* 2013). Browsing

239   in CGP grasslands does not appear to play a major role in shrubland transitions, considering that

240   the species most preferred by browsers have increased the most in cover (Van Der Hoek *et al.*

241   2002 *vs.* Heisler, Briggs & Knapp, 2003, Ratajczak *et al*. 2011). However, introducing more

242   diverse or larger browsers could potentially have an effect, as seen in similar systems on other

243   continents (Staver et al. 2012). In many grasslands globally, grazing has shifted grassland-

244   shrubland thresholds in favor of shrubs by reducing grass dominance (Walker *et al.* 1981,

245   Scholes &Archer 1997, Fuhlendorf *et al.* 2008). Recent research in the CGP does not support

246   this paradigm. If anything, grazing appears to suppress dominant shrub establishment (Kettle *et*

247   *al.* 2000, Brudvig *et al.* 2007, Ratajczak *et al. in press*), perhaps because native grazers

248   physically damage woody species (Coppedge & Shaw 1997) and create more bare ground which

249   increases sensible heat and reduces surface soil moisture (Walker *et al.* 1981, Nippert *et al.*

250   2013). More research is needed on how grazing affects grass-shrub interactions, considering the

251   predominance of grazing in the CGP and mesic grasslands globally.

252

253   **Transitions to woodlands**

254   *Mechanistic Background***:** The final state of woody plant expansion that we consider is

255   conversion to woodlands. We focus primarily on *Juniperus virginiana* (eastern red cedar)

256   woodlands (subsequently referred to as Juniper woodlands) rather than deciduous woodlands,

257   because Juniper woodlands exhibit the greatest expansion in the CGP (Twidwell *et al.* 2013b).

258   As with shrubs, the pyrogenic traits of C_4 grasslands impose limits on Juniper trees. In

259   fact, Juniper woodland expansion should be acutely constrained by fire because unlike grasses

260   and shrubs, *J. virginiana* does not resprout when top-killed and *J. virginiana* develops bark

261   slowly, leaving it poorly insulated against fires until older ages (Vanderweide & Hartnett 2011).

262   As a result, smaller *J. virginiana* (<2 m tall) suffer high mortality rates during fires (Hoch, *et al.*

263   2002, Fuhlendorf *et al.* 2008, Vanderweide & Hartnett 2011). For these reasons, greater fire

264   suppression should be needed for Juniper woodland formation, compared to shrublands.

265   Once *J. virginiana* reaches a larger size its response to fire may exhibit hysteresis. *J.*

266   *virginiana* suppresses grass growth with dense canopies that intercept the majority of sunlight

267   (Hoch *et al.* 2002, McKinley *et al.* 2008, Myster 2009, Limb *et al.* 2010, Van Els *et al.* 2010).

268   With time, this disruption of fuel continuity decreases fire transmission (Abades *et al.* this issue),

269   creating a positive feedback between *J. virginiana* and fire suppression. With long-term fire

270   suppression *J. virginiana* can also over-top and replace shrubs, as shown in long-term vegetation

271   surveys and the inability of shrubs seedlings to regenerate under older *J. virginiana* canopies

272   (Myster 2009, Van Els *et al.* 2010). Thus, while the fires typical of grasslands and shrublands

273   might prohibit tree establishment, exposing mature woodland trees to fires should have little

274   effect.

275   Unlike transitions to shrubland, low water availability and thin soils are less important

276   constraints for *J. virginiana* expansion (Volder *et al.* 2010, 2013). Evergreen trees are at least, if

277   not more, drought resistant than grasses under most drought scenarios (Awada *et al.* 2012). As a

278   result, *J. virginiana* seedlings in fire-free locations have high survivorship in both high-diversity

279   and grass-dominated patches (Ganguli *et al.* 2008), shallow soils, and through droughts (Yao *et*

280 *al.* 1999, Eggemeyer *et al.* 2006, Engle *et al.* 2006, Volder *et al.* 2010, 2013)—conditions that

281 typically exclude trees and most invasive species (Bond 2008, Seabloom *et al.* 2013).

282

283 *Theoretical Description & Empirical Support*

284 Statistical indications of regime shifts (e.g. abrupt shifts, state bi-modality) require experiments

285 and observational data-sets with frequent sampling events and replicates that are scaled with the

286 life span and spatial footprint of organisms involved (van Nes & Scheffer 2005, Bestelmeyer *et*

287 *al.* 2011). Given the long generation time of *J. virginiana*, observing a threshold transition to

288 woodland would require an experiment that increases fire returns slowly, allowing tree species to

289 equilibrate with their changing carrying capacity until a potential threshold is crossed. Instead,

290 most observations of woodland transitions have large gaps between samples (~a decade, Fig. 4,

291 5- references therein), which are not suitable for tests of abrupt shifts between states. Moreover,

292 most examples of woodland transitions take place when fire frequency is altered from frequent

293 fires (1-3 yrs) to complete fire suppression. This effectively pushes the driver variable (fire) far

294 past any potential thresholds. The ecological response to this change in driver variables should

295 be loss of grasses and a pattern of logistic growth by trees and shrubs as they reach their new

296 carrying capacity (May 1977, Hughes *et al.* 2012); this result is evident over 30 to 50 year

297 observations in areas with fire suppression (Fig. 2, 3) (Anderson *et al*. 2000, Hoch *et al.* 2002,

298 Peterson, Reich & Wrage 2007, Limb *et al*. 2010, Van Els *et al*. 2010, Twidwell *et al.* 2013,

299 Ratajczak *et al. in press*).

300   While we lack the data to identify "abrupt shifts" during woodland transitions we can

301 identify management thresholds by asking: is there a fire frequency threshold that prohibits

302 transitions from shrubland to woodland? And if so, does increasing fire frequency in woodlands

303   reverse the transition or does the ecosystem show hysteresis? Detailed mapping of tree

304   establishment and analyses of shrub cover at KPBS shows that 30 years of prescribed fire at 3-4

305   year frequencies allows establishment of shrubs, but not trees (Fig. 2). The lack of tree

306   establishment over a 30-year period with 3-4 year fire intervals and the prevalence of clonal

307   shrublands throughout the region (Petranka & McPherson 1979, Collins & Adams 1983,

308   Anderson *et al*. 2000, Harrell *et al*. 2001, Brudvig *et al*. 2007, Ratajczak *et al*. 2011), suggests

309   that shrublands are a separate alternative attractor from woodlands and that longer fire-free

310   intervals are needed to precipitate a transition to woodland. Less frequent burning (~ 20 year fire

311   returns) or complete fire suppression allows tree establishment (Fig 3) and eventual formation of

312   closed-canopy woodland (Bragg & Hulbert 1976, Kettle *et al.* 2000, Norris *et al.* 2001, Hoch *et*

313   *al.* 2002, Engle *et al.* 2006, Twidwell et al. 2013a).

314   A process-based approach suggests that woodland transitions may be possible at lower

315   fire frequencies than the 20-year fire experiment presented here (Fig 4). To resist typical

316   grassland fires, *J. virginiana* must reach a height of ~2.5 m and diameter of 17.5 cm at breast

317   height (1.4 m) (Owensby, Eaton, & Russ 1973, Hoch *et al.* 2002, Vanderweide & Hartnett 2012).

318   Connecting these thresholds to reported *J. virginiana* growth rates (Owensby *et al.* 1973, Engle

319   & Kulbeth 1992, Schmidt & Wardle 2002), we estimate that fire free intervals of 15-20 years

320   would allow consistent tree establishment, although this interval may be as short as 6-10 years

321   for locations with abundant tree seed sources and heavy grazing (Owensby *et al.* 1973, Hoch *et*

322   *al.* 2002, Fuhlendorf *et al.* 2008). These estimates closely match modeling by Fuhlendorf and

323   colleagues (2008), as well as historical observations that *J. virginiana* is more common in

324   pyrrhic woodlands with a fire frequency >5 years (Batek *et al.* 1999, Stambaugh *et al.* 2013).

325   Similarly, a fire following 15 years of fire suppression at KPBS killed ~3/4 of Juniper trees, but

326   did not stop the transition to woodland when it was followed by further fire suppression (Fig

327   2C). This indicates that transitions to Juniper woodland are possible at 15 year fire return

328   intervals. However, the rate of transition will be significantly suppressed with more frequent

329   fires (Fig 2C).

330   Expansion of *J. virginiana* can decrease fire intensity, which could create hysteresis in

331   response to fire. In mixed deciduous/Juniper woodlands, re-introduction of 3-year fire returns

332   and aerial chemical controls allows *J. virginiana* to maintain ~20% cover (Engle *et al.* 2006). In

333   both the southern and northern CGP, reintroducing fire returns of ~2-3 years for a duration of 20

334   to 30 years had only marginal effects on tree cover and increased grass cover to only 10-20%

335   (Peterson *et al*. 2007, Burton, Hallgren & Palmer 2010, Burton *et al.* 2011). In historical records

336   (dendrochronology) Juniper woodlands persisted in areas with fire returns ranging from 2 to 6

337   years (Batek *et al.* 1999, Desantais *et al.* 2010, Strambaugh *et al.* 2013). However, studies by

338   Burton *et al.* (2010, 2011) and Peterson *et al.* (2007) were performed in primarily deciduous

339   woodlands, and results may not apply to Juniper woodlands.

340   A more rapid reversion of woodlands to grasslands typically requires physical or

341   chemical removal of *J. virginiana* trees, combined with frequent burning to foster grass

342   dominance and fire promoting feedbacks (Engle *et al*. 2006, Pierce & Reich 2010, Alford *et al.*

343   2012). To achieve this, tree removal and reintroduction of fire should coincide, or the legacy

344   effects of woodland dominance can facilitate a rapid return to the woodland state (Kettle *et al.*

345   2000). It also may be possible to achieve faster reversals to grasslands using novel burning

346   techniques that stimulate high-intensity (Twidwell *et al.* 2013a).

347   Woodland fire thresholds are context specific in ways that differ from thresholds

348   differentiating grasslands and shrublands. A unique attribute of woodland trees, relative to

349   shrubs, is their ability to establish in more xeric and thin soils with sufficient fire suppression

350   (Fig 4B: Engle *et al*. 2006, Eggemeyer *et al*. 2006, Knapp *et al*. 2008, McKinley *et al.* 2008).

351   Conventional cattle grazing generally favors greater tree establishment by reducing fuel loads,

352   and thereby, fire intensity (Hoch *et al*. 2002, Fuhlendorf *et al*. 2008, Twidwell *et al.*2013a).

353   Grazing can also create microsite conditions that facilitate woodland seedling establishment

354   (Owensby *et al.* 1973). In contrast, native grazers such as bison (*Bos bison*) can significantly

355   restrict woodland development. At moderate densities at KPBS, bison physically damage *J.*

356   *virginiana* trees (personal observations) and these behavioral traits have been observed in *Bos*

357   *bison* from other North American grasslands (Bork *et al*. 2013, but see Coppedge & Shaw 1997).

358   At KPBS, this effect is so strong that *J. virginiana* is asbent from *Bos bison* grazed areas, and

359   instead other trees are more prevalent, such as the thorned tree *Gleditsia triacanthos*

360   (Unpublished data, Z. Ratajczak). These observations indicate the importance of considering

361   grazer impacts as a whole in grassland to woodland transitions, and not just their indirect effects

362   on trees via grass abundance and soil characteristics.

363

364   **Synthesis and Opportunities**

365   Based on the data presented here and our synthesis of results from other fire frequency studies

366   (Fig 4), we propose a conceptual framework of tri-stability for the CGP that treats grasslands,

367   shrublands and woodlands as alternative attractors moderated by critical fire frequency

368   thresholds. Based on experimental and observational studies of fire and ecosystem state we have

369   constructed complementary catastrophe fold (Fig 4) and state and transition models that illustrate

370   the positions of critical thresholds and the system's capacity for hysteresis (Fig. 5). In areas with

371   lower water holding capacity or thin soils that restrict access to deep soil moisture, shrubs cannot

372   establish and grasslands and woodlands are the only viable alternative attractors. Starting with

373   grasslands as the baseline state, fire return intervals of 3-8 years result in transitions to

374   shrublands, and fire frequencies of 8-10 years lead to transitions to woodlands (Fig 5). Once a

375   shrubland or woodland state is established, self-reinforcing feedback mechanisms and altered

376   demographic sensitivity to fire result in hysteresis, such that decreasing the fire return interval to

377   pre-transition levels does not readily return the ecosystem to a grassland state.

378   The tri-stability framework presented here is novel on two fronts. First, evidence for

379   alternative attractors with descriptive mechanisms *and* non-linear transitions and hysteresis in

380   response to changes in driver variables are rare in terrestrial ecosystems (Schroder *et al.* 2005).

381   Identifying ecosystem thresholds, hysteresis, and the mechanisms behind these processes are

382   major challenges in adaptive management and governance (Walker & Salt 2006) and ecosystem

383   and community ecology (Sutherland *et al.* 2013). Second, in a single region (CGP) and climate

384   zone, we provide evidence for three distinct ecosystem states depending on human management

385   of fire, soil type, and to some extent, grazer identity and abundance. In light of the growing

386   control of fire by humans, we argue that predictions of future vegetation shifts cannot rely solely

387   on climate, and should incorporate fire frequency and social factors that determine fire

388   management plans.

389   Our conceptual framework provides testable hypotheses that can be applied to other sites

390   and in experimental settings. Spatial analyses of tree cover would provide evidence for whether

391   transitions to woodland constitute a regime shift (using methods described in Hirota *et al.* 2011,

392   Staver *et al.* 2011). Other avenues for future research include testing competition models

393   (Chesson 2000), theoretically derived "generic leading indicators" of impending thresholds

394   (Scheffer et al. 2012), and demographic models that have advanced prediction in several

395   ecological systems (De Roos & Perssons 2002, Huss *et al.* 2013). Such research might also help

396   identify opportunities for reversing transitions (Fig. 5; Holmgren & Scheffer 2001, Twidwell et

397   al. 2013b).

398   In the CGP and similar systems the tri-stability framework may serve as a valuable

399   management tool, allowing landowners to employ fire frequency to avoid unwanted state

400   changes. Given the economic and conservation priorities in the CGP (Hoekstra *et al*. 2005), the

401   tri-stability framework suggests that preventing transitions to shrublands and woodlands is more

402   cost effective than post-encroachment restoration, because returning fire will not necessarily

403   facilitate the transition back to a grassland state on management-relevant time scales. Therefore,

404   reversing unwanted transitions will likely require costly inputs, such as physical and chemical

405   removal.

406   Combining theoretical predications and application, we agree with others who have

407   cautioned that critical thresholds can vary over time (Bestelemeyer & Briske 2012). Conditions

408   that facilitate grass growth, greater fire intensity, or reduce tree/shrub growth will favor the

409   grassland state, requiring longer fire-free intervals to facilitate a transition to a shrubland or

410   woodland (Fig. 4C, *sensu* Staver *et al.* 2011, Bond & Midgley 2012, Hoffmann *et al.* 2012, Roff

411   & Mumby 2012). Initial evidence suggests that fire thresholds have already changed in the CGP;

412   prior to European arrival, the estimated fire return interval for the CGP was ~4 years (Wright &

413   Bailey 1982, Allen & Palmer 2011) and that much of the region was devoid of shrublands and

414   woodlands (Weaver 1954, Wells 1970, Axelrod 1985, Abrams 1986). Now, 3 to 4 year fire

415   frequencies are often insufficient to prevent the transition to shrublands (Fig 2). These

416   observations suggest that fire thresholds have responded to global and/or regional pressures, such

417   as elevated CO_2 (Bond & Midgley 2012), loss of larger browsers and native grazers, and exurban

418 expansions that have increased woody plant cover and enhanced woody plant seed sources

419 (Briggs *et al.* 2005). Given this potential flexibility, continued monitoring of grasslands and

420 adaptive management are critical (for examples, see Fuhlendorf *et al.* 2008, Bestelmeyer &

421 Briske 2012, Twidwell *et al.* 2013b).

422   The CGP grasslands share many drivers, feedbacks, and demographic traits for woody

423 encroachment with other grasslands and savannas (Scholes & Archer 1997, Wu & Archer 2005,

424 Bond 2008, Staver *et al.* 2011, D'Odorico *et al.* 2012, Higgins & Schieter 2013, Holdo *et al.*

425 2013), contributing fertile ground for cross-site syntheses and development of more sustainable

426 grassland management. One major research opportunity is elucidating the role of grazers and

427 browsers on woody encroachment in the CGP. Identifying system-specific roles of grazers and

428 browsers on ecosystems transitions will improve our ability to identify patterns and generalize

429 across ecosystems, resulting in better *a priori* detection of ecosystem thresholds and enhanced

430 opportunities to avoid critical thresholds.

431 **Acknowledgements**

438 **References**

439 Abades, S.R., Gaxiola, A., & Marquet, P.A. (*this issue*) Fire, percolation thresholds and the

440 savanna forest transition: a neutral model approach. *Journal of Ecology*.

441 Abrams, M.D. (1985) Effects of Prescribed Fire on Woody Vegetation in a Gallery Forest

442 Understory in Northeaster Kansas. *Transactions of the Kansas Academy of Science*, **91**, 63-70.

443 Alford, A.L, Hellfren, E.C., Limb, R. & Engle, D.M. (2012) Experimental tree removal in

444 tallgrass prairie: variable responses of flora and fauna along a woody cover gradient. *Ecological*

445 *Applications*, **22**, 947-958.

446 Allen, M.S., & Palmer M.W. (2011) Fire history of a prairie/forest boundary: more than 250

447 years of frequent fire in a North American tallgrass prairie. *Journal of Vegetation Science*, **22**,

448 436-444.

449 Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011) Ungulate preference for

450 burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, **1**, 132–44.

451 Anderies, J.M., Janssen, M.A., & Walker, B.H. (2002) Grazing management, resilience, and the

452 dynamics of a fire-driven rangeland system. *Ecosystems*, **5**, 23-44.

453 Anderson, R.C., Schwegman, J.E., & Anderson, M. R. (2000) Micro-Scale Restoration: A 25-

454 Year History of a Southern Illinois Barrens. *Society for Ecological Restoration*, **8**, 296-306.

455 Archer, S., Scifres, C., Bassham, C. R., & Maggio, R. (1988) Succession in a Subtropical

456 Savanna: Conversion of Grassland to Thorn Woodland. *Ecological Society of America*, **58**, 111-

457 127.

458 Archibald, S., Staver, A.C. & Levin, S.A. (2012) Evolution of human-driven fire regimes in

459 Africa. *Proceedings of the National Academy of Science U.S.A.,* **109**, 847-852.

460   Axelrod, D. I. (1985) Rise of the Grassland Biome, Central North-America. *Botanical Review*,

461   **51**, 163–201.

462   Awada, T., El-Hage, R., Geha, M., Wedin, D.A., Huddle, J.A., Zhou, X., Msanne, J., Sudmeyer,

463   R.A., Martin, D.L. & Brandle, J.R. (2012) Intra-annual variability and environmental controls

464   over transpiration in a 58-year-old stand of invasive woody *Juniperus virginiana* L. in the

465   Nebraska Sandhills, USA. *Ecohydrology*, **6**, 731-740.

466   Barger, N.N., Archer, S.R., Campbell, J.L., Huang, C., Morton, J.A., & Knapp, A.K. (2011)

467   Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem

468   carbon balance. *Journal of Geophysical Research*, **116**, 1-17.

469   Batek, M.J., Rebertus, A.J., Schroeder, W.A., Haithcoat, T.L., Compas, E., & Guyette, R.P.

470   (1999) Reconstruction of early nineteenth-century vegetation and fire regimes in the Missouri

471   Ozarks. *Journal of Biogeography*, **26**, 397-412.

472   Benson, E.J. & Hartnett, D.C. (2006) The role of seed and vegetative reproduction in plant

473   recruitment and demography in tallgrass prairie. *Plant Ecology*, **187**, 163-177.

474   Bestelmeyer, B.T., Ellison, A.M., Fraser, W.R., Gorman, K.B., Holbrook, S.J., Laney, C.M.,

475   Ohman, M.D., Peters, D.P.C., Pillsbury, F.C., Rassweiler, A., Schmitt, R.J., & Sharma, S. (2011)

476   Analysis of abrupt transitions in ecological systems. *Ecosphere*, **2**, 1-26.

477   Bestelmeyer, B.T. & Briske, D.D. (2012) Grand challenges for resilience-based management of

478   rangelands. *Rangeland Ecology and Management*, **65**, 654-663).

479   Bestelmeyer, B.T., Duniway, M.C., James, D.K., Burkett, L.M., & Havstad, K.M. (2013) A test

480   of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience

481   than we thought. *Ecology Letters*, **16**, 339-345.

482   Boerlijst, M.C., Oudman, T., & Roos, A.M. (2013) Catastrophic Collapse Can Occur without

483   Early Warning: Examples of Silent Catastrophes in Structured Ecological Models. *PLOS ONE*,

484   **8**, 1-6.

485   Bond, W.J. (2008) What limits trees in C_4 grasslands and savannas. *Annual Review of Ecology,*

486   *Evolution, and Systematics*, **39**: 641-659.

487   Bond, W.J. & Midgley, G.F. (2012) Carbon dioxide and the uneasy interactions of trees and

488   savannah grasses. *Philosophical Transactions of The Royal Society*, **367**, 601-612.

489   Borchert, J.R. 1950. The climate of the central North American grassland. Annals of the

490   Association of American Geographers 40:1-39.

491   Bork, E.W., Carlyle, C.N., Cahill, J.F., Haddow, R.E. & Hudson, R.J. (2013) Disentangling

492   herbivore impacts on *Populus tremuloides*: a comparison of native ungulates and cattle in

493   Canada's Aspen Parkland. *Oecologia*, **173**, 895-904.

494   Bowles, M.L. & Jones, M.D. (2013) Repeated burning of eastern tallgrass prairie increases

495   richness and diversity, stabilizing late successional vegetation. *Ecological Applications*, **23**, 464-

496   478.

497   Boyd, C.S. & Bidwell, T.G. (2002) Effects of Prescribed Fire on Shinnery Oak (*Quercus*

498   *havardii*) Plant Communities in Western Oklahoma. *Society for Ecological Restoration*, **10**, 324-

499   333.

500   Bragg, T.B. & Hulber, L.C. (1976) Woody Plant Invasion of Unburned Kansas Bluestem Prairie.

501   *Society for Range Management*, **29**, 19-24.

502   Bredenkamp, G., Spada, F., & Kazmierczak, E. (2002) On the origin of northern and southern

503   hemisphere grasslands. *Plant Ecology*, **163**, 209–229.

504   Briggs, J.M & Gibson, D.J. (1992) Effect of Fire on Tree Spatial Patterns in a Tallgrass Prairie

505   Landscape. *Bulletin of the Torrey Botanical Club*, **119**, 300-307.

506   Briggs, J.M. & Knapp, A.K. (2001) Determinants of C_3 forb growth and production in a C_4

507   dominated grassland. *Plant Ecology*, **152**, 93-100.

508   Briggs, J.M., Knapp, A.K., & Brock, B.L. (2002) Expansion of Woody Plants in Tallgrass

509   Prairie: A Fifteen-Year Study of Fire and Fire-Grazing Interactions. *American Midland*

510   *Naturalist*, **147**, 287-294.

511   Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., & McCarron, J.K.

512   (2005) An Ecosystem in Transition: Causes and Consequences of the Conversion of Mesic

513   Grassland to Shrubland. *BioScience*, **55**, 243-254.

514   Briske, D.D., Fuhlendrof, S.D., & Smeins, F.E. (2005) State-and-transition models, thresholds,

515   and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology*

516   *and Management,* **58**, 1-10.

517   Briske, D.D., Fuhlendorf, S.D., & Smeins, F.E. (2006) A unified framework for assessment and

518   application of ecological thresholds. *Rangeland Ecology & Management*, **59**, 225-236.

519   Briske, D.D., Bestelmeyer, B.T., Stringham, T.K., & Shaver, P.L. (2008) Recommendations for

520   development of resilience-based state-and-transition models. *Rangeland Ecology and*

521   *Management*, **61**, 359-367.

522   Brudvig, L.A., Mabry, C.M., Miller, J.R., & Walker, T.A. (2007) Evaluation of Central North

523   American Prairie Management Based on Species Diversity, Life Form, and Individual Species

524   Metrics. *Conservation Biology*, **21**, 864-874.

525   Brunsell, N.A., Nippert, J.B. & Buck, T.L. (*in press*) Impacts of seasonality and surface

526   heterogeneity on water-use efficiency in mesic grasslands. *Ecohydrology.*

527   Burton, J.A., Hallgren, S.W. & Palmer, M.W. (2010) Fire frequency affects structure and

528   composition of xeric forests of eastern Oklahoma. *Natural Areas Journal*, **30**, 370-379.

529   Burton, J.A., Hallgren, S.W., Fuhlendorf, S.D & Leslie, D.M. (2011) Understory response to

530   varying fire frequencies after 20 years of prescribed burning in an upland oak forest. *Plant*

531   *Ecology*, **212**, 1513-1525.

532   Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology*

533   *and Systematics*, **31**, 343-366.

534   Collins, S.L. & Adams, D.E. (1983) Succession in Grasslands: Thrity-Two Years of change in a

535   Central Oklahoma Tallgrass Prairie. *Vegetatio*, **51**, 181-190.

536   Collins, S.L. & Calabrese, L.B. (2012) Effects of fire, grazing and topographic variation on

537   vegetation structure in tallgrass prairie. *Journal of Vegetation Science,* **23**, 563-575.

538 Coppedge, B.R. & Shaw, J.H. (1997) Effects of Horning and Rubbing Behavior by Bison (Bison

539 bison) on Woody Vegetation in a Tallgrass Prairie Landscape. *American Midland Naturalist*,

540 **138**, 189-196.

541 D'Odorico, P., Okin, G.S., & Bestelmeyer, B.T. (2012) A synthetic review of feedbacks and

542 drivers of shrub encroachment in arid grasslands. *Ecohydrology*. **5**, 520-530.

543 De Roos, A.M. & Persson, L. (2002) Size-dependent life-history traits promote catastrophic

544 collapses of top predators. *Proceedings of the National Academy Sciences U.S.A.*, **99**, 12907-

545 12912.

546 Desantis, R.D., Hallgren, S.W., & Stahle, D.W. (2010) Historic fire regime of an uplad oak

547 forest in south-central North America. *Fire Ecology*, **6**, 45-61.

548 DeSantis, R.D., Hallgren, S.W., & Stahle, D.W. (2011) Drought and fire suppression lead to

549 rapid forest composition change in a forest-prairie ecotone. *Forest Ecology and Management*,

550 **261**, 1833-1840.

551 Eggemeyer, K.D., Awada, T., Wedin, D.A., Harvey, F.E., & Zhou, X. (2006) Ecophysiology of

552 Two Native Invasive Woody Species and Two Dominant Warm-Season Grasses in the Semiarid

553 Grasslands of the Nebraska Sandhills. *International Jouranl of Plant Sciences*, **167**, 991-999.

554 Eldridge, D. J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., & Whitford, W.G.

555 (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global

556 synthesis. *Ecology Letters,* **14**, 709–722.

557 Engle, D.M. & Kulberth, J.D. (1992) Growth Dynamics of Crowns of Eastern Redcedar at 3

558 Locations in Oklahoma. *Journal of Range Management*, **45**, 301-305.

559 Engle, D.M., Bodine, T.N., & Stritzke, J.F. (2006) Plant Community in the Cross Timbers over

560 Two Decades of Brush Treatments. *Rangeland Ecology & Management*, **59**, 153-162.

561 Epstein, H. E., Lauenroth, W. K., Burke, I. C., & Coffin, D. P. (1997) Productivity patterns of C-

562 3 and C-4 functional types in the US Great Plains. *Ecology*, **78**, 722–731.

563 Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., & Holling, C.S.

564 (2004) Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review*

565 *of Ecology, Evolution, and Systematics*, **35**, 557-581.

566 Folke, C. (2006) Resilience: The emergence of a perspective for social-ecological systems

567 analyses. *Global Environmental Change*, **16**, 253-267.

568 Frehlich, L.E & Reich, P.B. (1999) Neighborhood effects, disturbance severity, and community

569 stability in forests. *Ecosystems*, **2**, 151-166.

570 Fuhlendorf, S.D., Archer, S.A., Smeins, F.E., Engle, D.M., & Taylor, Jr., C.A. (2008) The

571 Combined Influence of Grazing, Fire, and Herbaceous Productivity on Tree-Grass Interactions.

572 *Western North American Juniperus Communities: A Dynamic Vegetation Type* (ed. O.W. Van

573 Auken), pp. 219-238. Springer, New York.

574 Fuhlendorf, S.D., Engle, D.M., Kerby, J., & Hamilton, R. (2009) Pyric Herbivory: Rewilding

575 Landscapes through the Recoupling of Fire and Grazing. *Conservation Biology*, **23**, 588-598.

576 Ganguli, A.C., Engle, D.M., Mayer, P.M. & Hellgren, E.C. (2008) Plant community diversity

577 and composition provide little resistance to *Juniperus* encroachment. *Botany*, **86**, 1416-1426.

578 Gibson, D.J. & Hulbert, L.C. (1987) Effects of Fire, Topography and Year-to-Year Climatic

579 Variation on Species Composition in Tallgrass Prairie. *Vegetatio*, **72**, 175-185.

580   Gibson, D.J., Hartnett, D.C. & Merrill, G.L.S. (1990) Fire temperature heterogeneity in

581   contrasting prone habitats: Kansas tallgrass prairie and Florida sandhill. *Bulletin of the Torrey*

582   *Botanical Club*, **117**, 349-356.

583   Gibson, D.J. (2009) *Grasses & Grassland Ecology*. Oxford University Press, New York.

584   Gray, E.F. & Bond, W.J. (2013) Will woody plant encroachment impact the visitor experience

585   and economy of conservation areas? *Koedoe*, **55**, 1-9.

586   Grime, P. 1979. "Plant Strategies and Vegetation Processes". John Wiley and Sons Press, New

587   York.

588   Hajny, K.M., Hartnett, D.C & Wilson, G.W.T. (2011) *Rhus glabra* response to season and

589   intensity of fire in tallgrass prairie. *International Journal of Wildland Fire*, **20**, 709-720.

590   Harrell, W.C., Fuhlendorf, S.D., & Bidwell, T.G. (2001) Effects of Prescribed Fire on Sand

591   Shinnery Oak Communities. *Society for Range Management*, **54**, 685-690.

592   Hayden, B.C. (1998) Regional climate and the distribution of tallgrass prairie. *Grassland*

593   *Dynamics* (eds A.K. Knapp, J.M. Briggs, D.C. Hartnettt, & S.L. Collins), pp 193-221, Oxford

594   University Press, New York.

595   Heisler, J.L, Briggs, J.M. & Knapp, A.K. (2003) Long-term patterns of shrub expansion in a C_4-

596   dominated grassland: fire frequency and the dynamics of shrub cover and abundance. *American*

597   *Journal of Botany*, **90**, 423-428.

598   Heisler, J.L., Briggs, J.M, Knapp, A.K., Blair & Seery, A. (2004) Direct and indirect effects of

599   fire on shrub density and above-ground diversity in a mesic grassland. *Ecology*, **85**, 2245-2257.

600   Higgins, S.I. & Scheiter, S. (2012) Atmospheric CO_2 forces abrupt vegetation shifts locally, but

601   not globally. *Nature*, **488**, 209-213.

602   Hirota, M., Holmgren, M., Van Nes, E.H., & Scheffer, M. (2011) Global Resilience of Tropical

603   Forest and Savanna to Critical Transitions. *Science*, **334**, 232-235.

604   Hoch, G.A., Briggs, J.M., & Johnson, L.C. (2002) Assessing the rate, mechanisms, and

605   consequences of the conversion of tallgrass prairie to Juinperus virginiana forest. *Ecosystems*, **5**,

606   578-586.

607   Hoekstra, J. M., Boucher, T. M., Ricketts, T. H. & Roberts, C. (2005) Confronting a biome

608   crisis: global disparities of habitat loss and protection. *Ecology Letters*, **8**, 23–29.

609   Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L.,

610   Haridasan, M., & Franco, A.C. (2012) Ecological thresholds at the savanna-forest boundary: how

611   plant traits, resource and fire govern the distribution of tropical biomes. *Ecology Letters*, **15**, 759-

612   768.

613   Holling, C.S. (2001) Understanding the complexity of economic, ecological, and social systems.

614   *Ecosystems*, **4**, 390-405.

615   Holmgren, M. & Scheffer, M. (2001) El Nino as a Window of Opportunity for the Restoration of

616   Degraded Arid Ecosystems. *Ecosystems*, **4**, 151-159.

617   Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A. & van Nes, E.H. (2012) Living

618   dangerously on borrowed time during slow, unrecognized regime shifts. *Trends in Ecology &*

619   *Evolution*, **28**, 149-155.

620 Huss, M., de Roos, A.M., Van Leeuwen, A., Casini, M. & Gardmark, A. (2013) Cohort dynaics

621 give rise to alternative stable community states. *The American Naturalist*, **182**, 374-392.

622 Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine,

623 K., Pockman, W.T., & Jackson, R.B. (2005) Ecohydrological implications of woody plant

624 encroachment. *Ecology*, **86**, 308-319.

625 Jackson, R.B., Candell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., & Schulze, E.D. (1996) A

626 global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389-411.

627 Kettle, W.D., Rich, P.M., Kindscher, K., Pittman, G.L., & Fu, P. (2000) Land-Use History in

628 Ecosystem Restoration: A 40-Year Study in the Prairie-Forest Ecotone. *Restoration Ecology*, **8**,

629 307-317.

630 Killian, P.D. (2012) Mechanisms driving woody encroachment in the tallgrass prairie: an

631 analysis of fire behavior and physiological integration. MS thesis, Kansas State University,

632 Manhattan.

633 Köchy, M. & Wilson, S.D. (2001) Nitrogen deposition and forest expansion in the northern

634 Great Plains. *Journal of Ecology*, **89**, 807-817.

635 Knapp, A. K. (1993) Gas-Exchange Dynamics in C-3 and C-4 Grasses - Consequences of

636 Differences in Stomatal Conductance. *Ecology*, **74**, 113–123.

637 Knapp, A. K., Briggs, J. M., & Koelliker, J. K. (2001) Frequency and extent of water limitation

638 to primary production in a mesic temperate grassland. *Ecosystems*, **4**, 19–28.

639 Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, Bret-Harte, M.S., Ewers,

640 B.E., Peters, D.P., Young, D.R., Shaver, G.R., Pendall, E., & Cleary, M.B. (2008a) Shrub

641 encroachment in North American grasslands: shifts in form dominance rapidly alters control of

642 ecosystem carbon inputs. *Global Change Biology*, **14**, 615-623.

643 Knapp, A.K., McCarron, J.K, Silletti, A.M., Hoch, G.A., Heisler, J.A., Lett, M.S., Blair, J.M.,

644 Briggs, J.M., & Smith, M.D. (2008b) Ecological consequences of the replacement of native

645 grasslands by *Juniperus virginiana* and other woody plants. *Western North American Juniperus*

646 *Communities: A Dynamic Vegetation Type* (ed. O.W. Van Auken), pp. 219-238. Springer, New

647 York.

648 Kulmatiski, A. & Beard, K.H. (2013) Woody plant encroachment facilitated by increased

649 precipitation intensity. *Nature Climate Change*, **3**, 833-837.

650 Lett, M.S. & Knapp, A.K. (2005) Woody plant encroachment and removal in mesic grassland:

651 production and composition responses of herbaceous vegetation. *American Midland Naturalist*,

652 **153**, 217-231.

653 Limb, R.F., Engle, D.M., Alford, A.L., & Hellgren, E.C. (2010) Tallgrass Prairie Plant

654 Community Dynamics Along a Canopy Cover Gradient of Eastern Redcedar (*Juniper virginiana*

655 L.). *Rangeland Ecology Management*, **63**, 638-644.

656 Limb R.F., Fuhlendorf S.D., Engle D.M., Weir, J.R., Elmore, R.D., & Bidwell, T.G. (2011)

657 Pyric–herbivory and cattle performance in grassland ecosystems. Rangeland Ecology

658 Management, **64**, 659–663.

659   May, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states.

660   *Nature*, **269**, 471-477.

661   McCarron, J.K. & Knapp, A.K. (2001) C3 woody plant expansion in a C4 grassland: are grasses

662   and shrubs functionally distinct? *American Journal of Botany*, **88**, 1818-1823.

663   McCarron, J.K. & Knapp, A.K. (2003) C3 shrub expansion in a C4 grassland: positive post-fire

664   responses in resources and shoot growth. *American Journal of Botany*, **90**, 1496-1501.

665   McKinley, D.C., M.D. Norris, J.M. Blair and L.C. Johnson. 2008. Altered ecosystem processes

666   as a consequence of *Juniperus virginiana L.*encroachment into North American tallgrass prairie.

667   Pages170-187 In *Ecological Studies Series 196 - Western North American Juniperus*

668   *Communities: A Dynamic Vegetation Type* (O.W. Van Auken ed.), Springer-Verlag, NY

669   Mohler, R.R.L. & Goodin, D.G. (2012) Mapping burned area in the Flint Hills of Kansas and

670   Oklahoma, 2000-2010. *Great Plains Research*, **22**, 15-25.

671   Myster, R.W. (2009) Tree seedling survivorship, growth, and allocation in the Cross Timbers

672   ecotone of Oklahoma, USA. *Plant Ecology*, **205**, 193-199.

673   Myster, R.W. (2013) The role of seed predation in the maintenance of the Cross Timbers ecotone

674   Oklahoma, USA. *Journal of Plant Interactions*, **8**, 134-139.

675   Nippert, J.B. & Knapp, A.K. (2007) Linking water uptake with rooting patterns in grassland

676   species. *Oecologia*, **153**, 261-272.

677   Nippert, J.B., Ocheltree, T.W., Skibbe, A., Kangas, L.C., Ham, J.M., Shonkwilder Arnold, K.B.

678   & Brunsell, N.A. (2011) Linking plant growth responses across topographic gradients in tallgrass

679   prairie. *Oecologia*, **4**, 1131-1142.

680   Nippert, J.B., Wieme, R.A., Ocheltree, T.W., & Craine, J.M. (2012) Root characteristics of C_4

681   grasses limit reliance on deep soil water in tallgrass prairie. *Plant and Soil*, **355**, 385-394.

682   Nippert, J.B., Ocheltree, T.W., Orozco, G.L., Ratajczak, Z., Ling, B., & Skibbe, A.M. (2013)

683   Evidence of Physiological Decoupling from Grassland Ecosystem Drivers by an Encroaching

684   Woody Shrub. *PLOS ONE*, **8**, 1-8.

685   Norris, M.D., J.M. Blair, L.C. Johnson and R.B. McKane. 2001. Assessing changes in biomass,

686   productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass

687   prairie. *Canadian Journal of Forest Research* 31:1940-1946.

688   Noy-Meir, I. (1975) Stability of grazing systems: an application of predator-prey graphs. *Journal

689   of Ecology*, **63**, 459-481.

690   Ocheltree, T. W., Nippert, J. B., & Prasad, P. V. V. (2014) Stomatal responses to changes in

691   vapor pressure deficit reflect tissue-specific differences in hydraulic conductance. *Plant, Cell &

692   Environment*, **37**, 132-139.

693   Ocheltree, T. W., Nippert, J. B., & Prasad, P. V. V. (2013) Changes in stomatal conductance

694   along grass blades reflect changes in leaf structure. *Plant, Cell & Environment*, **35**, 1040–1049.

695   Owensby, C.E., Blan, K.R., Eaton B.J., and O.G. Russ (1973) Evaluation of eastern redcedar

696   infestations in the Northern Kansas Flint Hills. *Journal of Range Management*, **26**, 256-260.

697   Peterson, D.W., Reich, P.B., & Wrage, K.J. (2007) Plant functional group responses to fire

698   frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of

699   Vegetation Science*, **18**, 3-12.

700 Petranka, J.W. & McPherson, J.K. (1979) The role of Rhus copallina in the dynamics of the

701 forest-prairie ecotone in north-central Oklahoma. *Ecology*, **60**, 956-965.

702 Pierce A.M. & Reich, P.B. (2010) The effects of eastern red cedar (*Juniperus virginiana*)

703 invasion and removal on a dry bluff prairie system. *Biological Invasions*, **12**, 241-252.

704 Polley, H. W., Briske, D. D., Morgan, J. A., Wolter, K., Bailey, D. W., & Brown, J. R. (2013)

705 Climate Change and North American Rangelands: Trends, Projections, and Implications.

706 *Rangeland Ecology & Management*, **66**, 493–511.

707 Ratajczak, Z., Nippert, J.B., Hartman, J.C., & Ocheltree, T.W. (2011) Positive feedbacks amplify

708 rates of woody encroachment in mesic tallgrass prairie. *Ecosphere*, **2**, 1-14.

709 Ratajczak, Z., Nippert, J.B., & Collins, S.L. (2012) Woody encroachment decreases diversity

710 across North American grasslands and savannas. *Ecology*, **93**, 697-703.

711 Ratajczak, Z., Nippert, J.B., & Ocheltree, T.W. (*in press*) Abrupt transition of mesic grassland to

712 shrubland: evidence for thresholds, alternative attractors, and regime shifts.

713 http://dx.doi.org/10.1890/13-1369.1

714 Roff, G. & Mumby, P.J. (2012) Global disparity in the resilience of coral reefs. *Trends in*

715 *Ecology and Evolution*, **27**, 404-413.

716 Roques, K.G., O'Connor, T.G., & Watkinson, A.R. (2001) Dynamics of shrub encroachment in

717 an African savanna: relative influences of fire, herbivory, rainfall and density dependence.

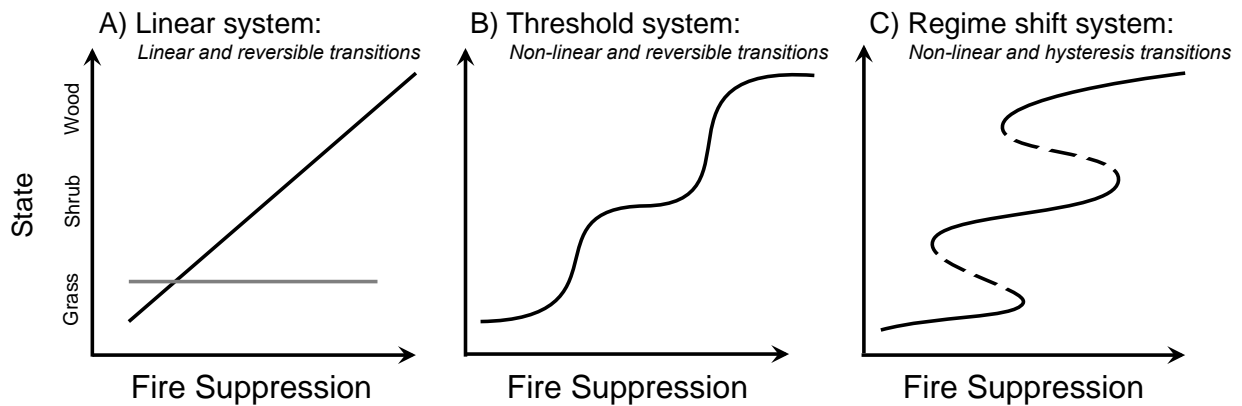718 *Journal of Applied Ecology*, **38**, 268-280.

719   Scheffer, M. & Carpenter, S.R. (2003) Catastrophic regime shifts in ecosystems: linking theory

720   to observation. *Trends in Ecology and Evolution*, **18**, 648-656.

721   Scheffer, M. (2009) *Critical transitions in nature and society*, Princeton University Press,

722   Princeton.

723   Scheffer, M. and 11 others (2012). Anticipating Critical Transitions. *Science,* **338**, 344-348.

724   Scheiter, S., Higgins, S.I., Osborne, C.P., Bradshaw, C., Lunt, D., *et al.* (2012) Fire and fire

725   adapted vegetation promoted C_4 expansion in the late Miocene. *New Phytologist*, **195**, 653-666.

726   Schmidt, T.L. & Wardle, T.D. (2002) Impact of pruning eastern redcedar (*Juniperus virginiana*).

727   *Western Journal of Applied Forestry*, **17**, 189-193.

728   Scholes, R.J. & Archer, S.R. (1997) Tree-grass Interactions in Savannas. *Annual Review of*

729   *Ecology and Systematics*, **28**, 517-544.

730   Schröder, A., Persson, L., & De Roos, A.M. (2005) Direct experimental evidence for alternative

731   stable states: a review. *Oikos*, **110**, 3-19.

732   Seabloom, E.W. & 74 others. (2013) Predicting invasion in grassland ecosystems: is exotic

733   dominance the real embarrassment of richness? *Global Change Biology*, **19**, 3677-3687.

734   Smith, E.F., Owensby, C.E. (1978) Intensive-early stocking and season-long stocking of Kansas

735   Flint Hills Range. *Journal of Range Management*, **31**, 14-17.

736   Stambaugh, M.C., Guyette, R.P. & Marschall, J. (2013) Fire history in the Cherokee nation of

737   Oklahoma. *Human Ecology*, **41**, 749-758.

738   Staver, A.C., Archibald, S., & Levin, S.A. (2011) The Global Extent and Determinants of

739   Savanna and Forest as Alternative Biome States. *Science*, **334**, 230-232.

740   Staver, A.C., Bond, W.J., Cramer, M.D., & Wakeling J.L. (2012) Top-down determinants of

741   niche structure and adaptation among African Acacias. *Ecology Letters*, **15**, 673-679.

742   Suding, K.N. & Hobbs, R.J. (2009) Threshold models in restoration and conservation: a

743   developing framework. *Trends in Ecology and Evolution*, **24**, 271-279.

744   Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J, Beissinger, S.R., Benton, T., Cameron, D.D.

745   *et al*. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, **101**,

746   58-67.

747   Twidwell, D., Fuhlendorf, S.D., Taylor, Jr., C.A., & Rogers, W.E. (2013a) Refining thresholds in

748   coupled fire-vegetation models to improve management of encroaching woody plants in

749   grasslands. *Journal of Applied Ecology*, **50**, 603-613.

750   Twidwell, D., Rogers, W.E., Fuhlendorf, S.D., Wonkka, C.L., Engle, D.M., Weir, J.R., Kreuter,

751   U.P., & Taylor, Jr., T.A. (2013b) The rising Great Plains fire campaign: citizens' response to

752   woody plant encroachment. *Frontiers in Ecology and the Environment,* **11**, 64–71.

753   Van Auken and McKinley (2008) Structure and Composition of *Juniperus* Communities and

754   Factors That Control Them. *Western North American Juniperus Communities: A Dynamic*

755   *Vegetation Type* (ed. O.W. Van Auken), pp. 19-47. Springer, New York.

756   van der Hoek, D., Knapp, A.K., Briggs, J.M., & Bokdam, J. (2002) White-tailed deer browsing

757   on six shrub species of tallgrass prairie. *Great Plains Research*, **12**, 141-156.

758   van Nes, E.H. & Scheffer, M. (2005) Implications of spatial heterogeneity for catastrophic

759   regime shifts in ecosystems. *Ecology*, **86**, 1797-1807.

760   Van Wilgen, B.W., Trollope, W.S.W., Biggs, H.C., Potgieter, A.L.F., & Brockett, B.H. (2002)

761   Fire as a driver of ecosystems variability. *The Kruger Experience: ecology and management of*

762   *savanna heterogeneity* (eds. J.T. Du Toit, K. H. Rogers, and H.C. Biggs), pp. 149-170. Island

763   Press, Washington, D.C.

764   VanderWeide, B.L. & Hartnett, D.C. (2011) Fire resistance of tree species explains historical

765   gallery forest community composition. *Forest Ecology and Management*, **261**, 1530-1538.

766   Volder, A., Briske, D.D., & Tjoelker, M.G. (2013). Climate warming and precipitation

767   redistribution modify tree-grass interactions and tree species establishment in a warm-temperate

768   savanna. *Global Change Biology*, **19**, 843–857.

769   Volder, A., Tjoelker, M.G., Briske, D.D. (2010) Contrasting physiological responsiveness of

770   establishing trees and a C_4 grass to rainfall events, intensified summer drought, and warming in

771   oak savanna. *Global Change Biology*, **16**, 3349-3362.

772   Walker, B.H., Ludwing, D., Holling, C.S., & Peterman, R.M. (1981) Stability of Semi-Arid

773   Savanna Grazing Systems. *Journal of Ecology*, **69**, 473-498.

774   Walker, B. & Salt, D. (2006) *Resilience thinking: sustaining ecosystems and people in a*

775   *changing world*. Islands Press New York.

776   Weaver, J.E. (1954) *Papers of John E. Weaver (1884-1856)*. Johnsen Publishing Company,

777   Lincoln Nebraska.

778   Wells, P.V. (1970) Postglacial history of the Great Plains. *Science*, **167**, 1574-1582.

779   Westoby, M., Walker, B. & Noy-Meir, I. (1989) Opportunistic management for rangelands not at

780   equilibrium. *Journal of Range Management*, **42**, 266-274.

781   Wright H. A. & Bailey, A.W. (1982) Fire Ecology. John Wiley and Sons, Inc., New York.

782   Wu, X.B. & Archer, S.R. (2005) Scale-dependent influence of topography-based hydrologic

783   features on patterns of woody plant encroachment in savanna landscapes. *Landscape Ecology*,

784   **20**, 733-742.

785   Yao, J., Holt, R.D., Rich, P.M & Marshall, W.S. (1999) Woody plant colonization in an

786   experimentally fragmented landscape. *Ecography*, **22**, 715-728.

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789   Fig. 1: A depiction of potential internal ecosystem dynamics in response to fire. For all panels,

790   solid lines denote stable equilibria, and in C) dotted lines delineate unstable repellors. A) shows

791   the null hypothesis where fire does not result in ecosystems transitions (grey line) and a scenario

792   where CGP ecosystems respond gradually to fire (black). B) shows a threshold system where

793   small changes in fire can lead to disproportionate, but reversible change in system state. In

794   systems with alternative attractors (C), shifts between states show threshold behavior as in (B).

795   However, returning drivers to their pre-transition values does not reverse the transition. This

796   figure is based on works by Noy-Meir (1975), Walker *et al.* (1981), Holling (2001), Folke *et al.*

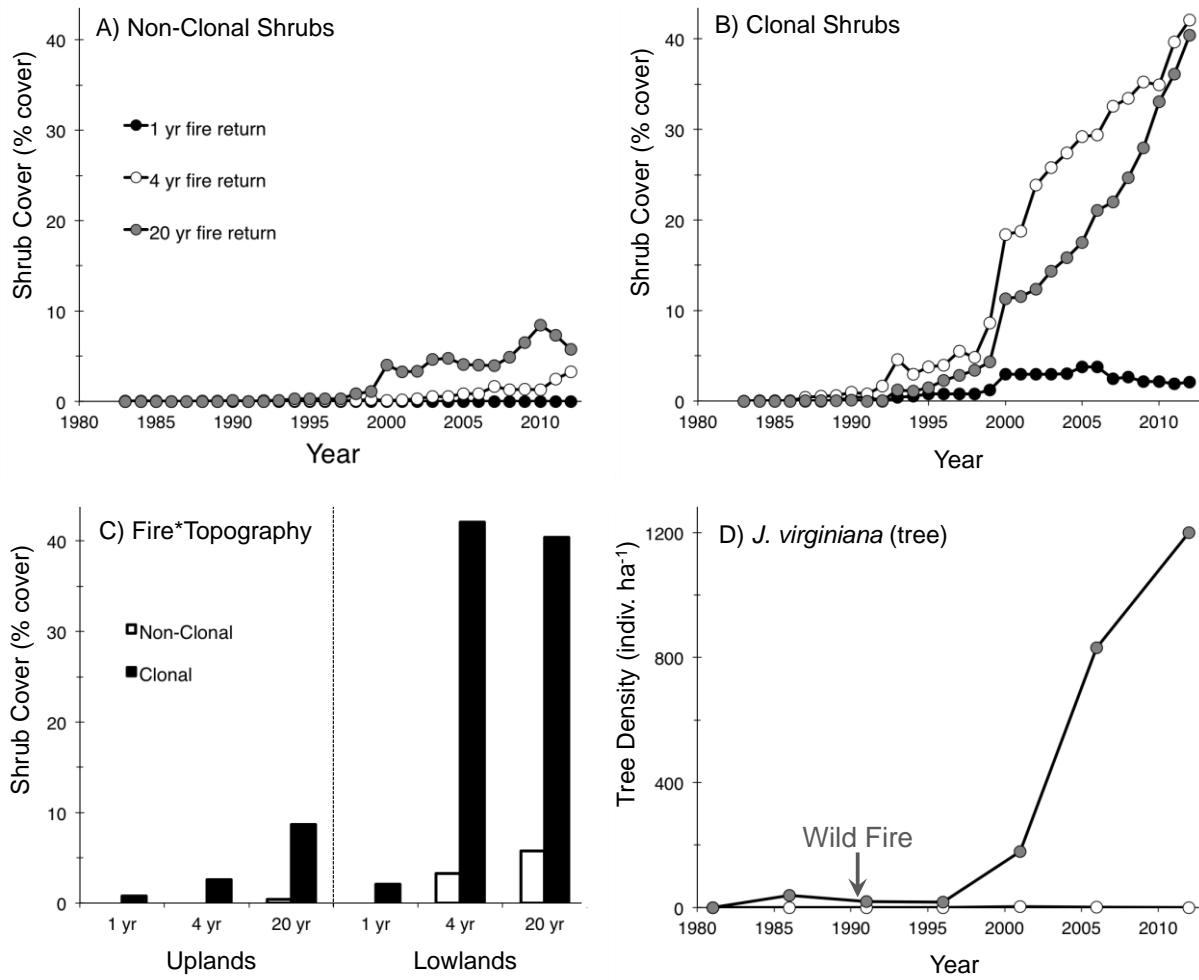797   (2004), Scheffer (2009), and Bestelmeyer *et al.* (2011).

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800 Fig 2. Measurements of shrub and tree dynamics in treatments of Konza Prairie exposed to

801 different prescribed frequencies starting in the late 1970's. "Clonal shrubs" refer to *Cornus*

802 *drummondii*, *Rhus glabra*, and *Prunus americana* cover and "non-clonal shrubs" include all

803 other shrub species with a canopy that exists above the grass layer. (A) and (B) depict changes in

804 shrub cover within lowland topographies for non-clonal (A) and clonal (B) functional groups.

805 Fire free intervals vary from 1 year (black fill), 4 years (white fill) and 20 years (grey fill). (C)

806 depicts the factorial cross of fire frequency and topography (uplands and lowlands) with respect

807 to shrub cover, for non-clonal (white) and clonal shrubs (black) after 30 years of fire frequency

808 manipulation (i.e. the level of shrub cover circa 2012). All shrub cover estimates are averaged

809 across grazed and ungrazed treatments (n = 40, 10 m^2 plots per combination of fire and

810 topography, derived equally from grazed and ungrazed areas). (D) Shows changes in *J.*

811 *virginiana* tree density for ungrazed areas with a fire free interval of 4 years (white fill) and 20

812 years (grey fill). These data come from detailed mapping of catchment basins (see figure 3). The

813 arrow in (D) indicates the timing of a wildfire that affected the 20-year fire treatment.
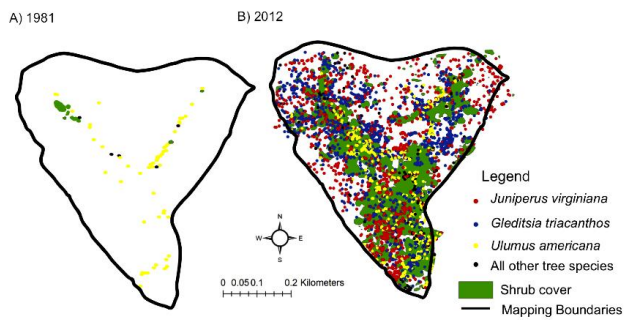
A) Non-Clonal Shrubs

- ● 1 yr fire return
- ○ 4 yr fire return
- ● 20 yr fire return

B) Clonal Shrubs

C) Fire*Topography

- □ Non-Clonal
- ■ Clonal

Uplands

Lowlands

D) *J. virginiana* (tree)

Wild Fire

814

815

816 Fig. 3: Changes in woody species occurrence on an ungrazed catchment basin at Konza Prairie in

817 A) 1981 and B) 2012, with only one fire since 1983. In both 1981 and 2012, coordinates of all

818 tree stems and shrubs above the grass canopy were recorded. Trees were mapped as points and

819 shrubs as polygons (see Briggs et al. 2002 for more details). For symbols, *Juniperus virginiana* =

820 red dots, *Gleditsia triacanthos* = blue dots, *Ulmus americana* = yellow dots, all other tree species

821 = black dots, and shrub cover = green polygon. Note that the watershed boundaries changed

822 between 1981 and 2012, therefore, the original mapping boundaries are delimited with a black
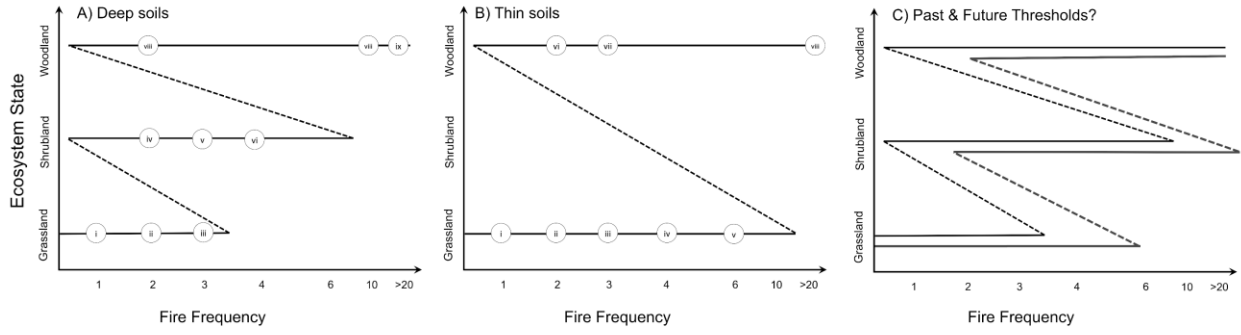
823 line.

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827 Fig. 4: The CGP tri-stability framework for alternative attractors of grasslands, shrublands, and

828 woodlands in (A) deep and (B) thin soils. Horizontal black lines denote alternative attractors and

829 dotted lines denote unstable states. Circles with roman numerals represent contrasting ecosystem

830 states identified by experimental or observational studies showing CGP ecosystem has existed at

831 the respective state and fire frequencies indicated on the x- and y-axes. Following thresholds

832 from Ratajczak *et al. in press*, grasslands were those ecosystems with <10% shrub cover and C_4

833 grasses present, shrublands were 10-60% shrub cover, with minimal trees present, and

834 woodlands were those ecosystems with many trees above the 2.6 m tall, 17 cm diameter at breast

835 height fire-mortality thresholds (Owensby 1973, Hoch *et al.* 2002, Vanderweide & Hartnett

836 2011). C) depicts how thresholds may change (grey lines) relative to current thresholds (black

837 lines), if shrub growth rate is increased more than grass growth rate (e.g. more grazing, elevated

838 CO_2). Factors that favor grass dominance would move the curve in the opposite direction. Note

839 that shifts from grassland to shrubland were discrete (occurring in 2-5 years), whereas transitions

840 are more gradual between grassland and woodland, and shrubland and woodland. Supporting

841 citations: Bowles and Jones 2013: A) i, ii, iii, v, B) i, ii, iii, iv, v; Boyd and Bidwell 2002: A) iv;

842 Bragg and Hulbert 1976: A) ii, ix; Briggs and Gibson 1992, Briggs et al. 2002, Fig 2 & 3 (this

843 review): A) i, ii, v, xi; B) i, iii, viii; Fuhlendorf et al. 2008: A) viii; Fuhlendorf et al. 2009: A) iii;

844 Harrell et al 2001: A) ii; Kettle et al. 2000: A) ii, xi; Hoch et al. 2002: A) ix B) viii; Owensby et

845 al. 1973: A) i, ii; Peterson et al 2007: A) vii, viii, ix; Process-based estimates (described in text):

846 A) viii; Ratajczak et al. 2011, Ratajczak et al. in press, Fig 3: A) i, iv, v, vi; B) i, iv, viii; Engle et

847 al 2006: B) vii, viii; Burton et al. 2010, 2011: B) vi, viii.

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851   Fig 5. State and transition model of grassland, shrubland, and woodland states. Following Westoby *et* al

852   (1989) and Briske *et* al. (2005), squares represent states and arrows represent processes that may or may

853   not elicit a transition to another state. Dashed arrows represent state trajectories that are only possible in

854   lowland and mesic soils. Hysteresis is accounted for by the "selfing" arrows for shrubland and woodland

855   states, where conditions that used to maintain grasslands do not reverse shrubland and woodland

856   transitions once they have occurred. There are few opportunities to reverse transitions to shrublands and

857   woodlands with fire alone, but we have left an arrow labeled "unknown opportunities" in anticipation that

858   new techniques and adaptive management schemes will emerge to return CGP ecosystems to grasslands

859   (e.g. Twidwell *et al.* 2013). Photo Credits: (Grassland: Eva Horne, Shrubland: Zak Ratajczak, Woodland:

860   John Blair).

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