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Woody encroachment decreases diversity across North American grasslands and savannas

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Abstract. Woody encroachment is a widespread and acute phenomenon affecting grasslands and savannas worldwide. We performed a meta-analysis of 29 studies from 13 different grassland/savanna communities in North America to determine the consequences of woody encroachment on plant species richness. In all 13 communities, species richness declined with woody plant encroachment (average decline = 45%). Species richness declined more in communities with higher precipitation ($r^2 = 0.81$) and where encroachment was associated with a greater change in annual net primary productivity (ANPP; $r^2 = 0.69$). Based on the strong positive correlation between precipitation and ANPP following encroachment ($r^2 = 0.87$), we hypothesize that these relationships occur because water-limited woody plants experience a greater physiological and demographic release as precipitation increases. The observed relationship between species richness and ANPP provides support for the theoretical expectation that a trade-off occurs between richness and productivity in herbaceous communities. We conclude that woody plant encroachment leads to significant declines in species richness in North American grassland/savanna communities.

Key words: biodiversity; bush encroachment; ecosystem structure; global change; primary productivity; productivity–richness relationship; shrub encroachment; species richness; tree encroachment; tree–grass coexistence; woody release.

INTRODUCTION

Over the last century, the cover and dominance of native trees, shrubs, and bushes has increased dramatically in grasslands and savannas globally (Archer 1995, Scholes and Archer 1997, Roques et al. 2001, Briggs et al. 2005)—a phenomenon referred to as woody encroachment. Potential causes of woody encroachment are many, including increasing atmospheric CO_2 (Bond and Midgley 2000, Wigley et al. 2010), climate change (Shaver et al. 2001, D'Odorico et al. 2010), nitrogen deposition (Kochy and Wilson 2001), fire-suppression, and over-grazing (Scholes and Archer 1997, Van Auken 2000, Roques et al. 2001, Briggs et al. 2005). Understanding the consequences of woody encroachment is important because grassland and savanna communities are undergoing widespread degradation worldwide (Hoekstra et al. 2005) and woody encroachment is further reducing grassland cover through difficult-to-reverse state transitions (Schlesinger et al. 1990, Scheffer et al. 2001, Ratajczak et al. 2011). Here, we present a meta-analysis of how woody encroachment affects species richness in grass-dominated ecosystems of North America (grasslands and tree/shrub savannas), exploring the relationships between woody encroachment, plant species richness, climate, and productivity.

Woody encroachment alters light, water, and nutrient availability (Schlesinger et al. 1990, Archer 1995, Scholes and Archer 1997, Knapp et al. 2008, Brantley and Young 2009)—key resources for many herbaceous grassland/savanna species (Chapin 1980, Knapp and Smith 2001, Clark et al. 2007, Harpole and Tilman 2007). Moreover, woody encroachment has been shown to mitigate the intensity and frequency of disturbances, such as grazing and fire (Riginos and Grace 2008, Ratajczak et al. 2011, Staver et al. 2011), which are integral to maintaining grassland and savanna diversity (Collins et al. 1998). Woody encroachment also increases aboveground net primary productivity (ANPP) far above existing levels (Knapp et al. 2008), which is often correlated with a decline in plant species diversity in many herbaceous communities (Grime 1973, Tilman

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and Pacala 1993, Clark et al. 2007, Harpole and Tilman 2007).

Alternatively, woody encroachment could have a neutral or positive impact on species richness in some plant communities. In some semiarid ecosystems, shrubs create "islands of fertility" where increased nutrient availability below shrubs provides refugia for species sensitive to low nutrient availability (Maestre et al. 2009, Pugnaire et al. 2011). Indeed, shrub establishment in the Mediterranean Basin and Australia has been shown to increase species richness by stabilizing soil and attenuating water stress (Thompson and Eldridge 2005, Maestre et al. 2009, Pugnaire et al. 2011). In North American grasslands, however, resource island formation is also accompanied by a decrease in resources in inter-shrub spaces, which might outweigh the positive effects of shrub dominance (Schlesinger et al. 1990).

Recently, Eldridge et al. (2011) conducted a comprehensive analysis of the consequences of woody encroachment into a number of grasslands around the world. They concluded that woody encroachment had no net effect on species richness globally. However, a zero net effect on richness could result from strong regional positive and negative patterns. We focused our analysis on woody encroachment in North America because North America has a unique evolutionary, disturbance, and human history. Additionally, more data are available for North America across a diverse array of grassland communities because many theses and government reports have been digitized.

For our analysis, we investigated (1) whether encroachment increased, decreased, or had no net effect on species richness and (2) if the effects of woody encroachment on species richness were moderated by mean annual temperature or precipitation, and/or changes in productivity. Our meta-analysis included data from sites that differ in edaphic conditions (e.g., coastal dunes, interior plains, montane grasslands), dominant forms of graminoid vegetation (C_3 vs. C_4 graminoids), ecosystem types (grasslands, savannas, and grassland–shrubland mixes), and climate (mean annual temperature and precipitation ranges of 33°C and 800 mm, respectively). Our analysis is unique in that we (1) had high levels of replication, (2) weighted all communities equally, allowing for more general interpretation, and (3) developed a conceptual framework based on physiological and demographic release of woody plants, which reconciles parallel changes in diversity and ecosystem function with current ecological theory.

METHODS

Literature search and meta-analysis criteria

For this analysis, we performed searches on Scopus, Web of Knowledge, and Google Scholar using relevant combinations of the words encroachment, invasion, thicket, thicketization, succession, shrub, woody, tree, bush, cover, diversity, richness, grass, grassland, and savanna. We also followed citations within published articles and sought papers on ecosystems where encroachment has been reported. For grassland/savanna communities with richness data available, we attempted to find data for differences in ANPP between graminoid and woody dominated patches.

All studies had to meet the following a priori criteria in order to be included in this meta-analysis: (1) they must occur in a North American grassland or savanna; (2) species richness or raw data to calculate species richness must be presented; (3) the study site must not be a grassland created by recent forest clearing or removal of encroaching trees/shrubs, because community recovery can be long (Lett and Knapp 2005) and probably varies considerably between ecosystems; (4) there must be evidence that native woody plants have become more numerous within the ecosystem over the last 150 years (the period when documented encroachment began; Van Auken 2000); (5) the study site must not receive >1100 mm of precipitation, because these areas are commonly forested (Hirota et al. 2011, Staver et al. 2011) making it difficult to discern between woody encroachment and naturally occurring patch dynamics. Following Scholes and Archer (1997), an ecosystem was considered a grassland or savanna if graminoid species were a dominant component of the community (this includes ecosystems co-dominated by grasses and trees/shrubs, such as savannas and big-sagebrush communities).

In all, our search resulted in 225 studies that were initially considered in part or in full for inclusion in the meta-analysis. Of those, 29 papers met our criteria for inclusion in this study. These papers covered 13 grassland/savanna communities and 21 different encroaching species (see Supplement for raw data and site information; Appendix A for citations). ANPP data were readily available for 10 communities that also measured species richness and 2 communities without richness data (Appendix A). Appendix B is a list of studies that met most of our criteria for inclusion, but were eventually rejected for violating one of our inclusion criteria.

Meta-analysis metrics

Studies varied considerably in their design and analysis. Therefore, we used the log response ratio (RR), where $\mathrm{RR} = \ln(X_e/X_c) = \ln(X_e) - \ln(X_e)$, and X_e and X_c are the mean values of experimental and controls groups, respectively. Negative RR values indicate a decline in the variable of interest following encroachment, positive values indicate an increase and 0 indicates no change. Following Clark et al. (2007), we refer to this metric as "richness response." We chose this metric because it accommodates many different experimental designs, as well as differing degrees of statistical reporting (Hedges et al. 1999). Taking the natural log of a fraction also has the beneficial property of making the resulting metric equally responsive to changes in the numerator and denominator. This was especially important because the denominator (measured unen-

TABLE 1. Site attributes and changes in richness and annual net primary productivity (ANPP) following encroachment.

Biome (no. studies)	MAP (mm)	MAT (°C)	Richness response	Encroached ANPP (g/m^2)	Changes in comm. comp.
Pinyon–oak savanna (2)	599	8.0	−0.67		F, I
Barrier island (1)	1050	14.8	−1.11	1471	F, I
Big sagebrush (4)	277	7.4	−0.31		F, I
Chihuahuan Desert (5)	248	14.5	−0.42	134	D, F, I, O
Coastal mesic grassland (1)	1028	10.2	−0.85	1340	NA
Edwards Plateau (2)	549	18.4	−0.60		F, I
Mediterranean grassland (1)	598	13.8	−0.86	1125	I
Mixed-grass prairie (3)	380	0.3	−0.49	325	D, F, I
Oak savanna (2)	782	6.8	−0.66	950	F, I
Sonoran Desert (1)	304	20.8	−0.45	140	D
Subtropical thorn-woodland (1)	682	22.2	−0.72	551	F
Tallgrass prairie (5)	871	14.0	−1.11	1104	D, F, O
Tussock tundra (1)	225	−11.3	−0.32	507	F, I

Notes: Abbreviations are: MAP, mean annual precipitation; MAT, mean annual temperature. For changes in community composition (comm. comp.), F indicates composition changes within and/or between functional groups; D indicates changes in composition as measured by detrended correspondence or ordination analysis; I indicates that the frequency of individual species changes; O indicates change in composition through a miscellaneous methodology; NA indicates that no measurements of composition were reported. Empty cells are cells for which data are not available.

croached richness) varies with both species richness and plot size (e.g., Adler et al. 2005), and our analysis included studies with different plot sizes. The use of this metric and the inclusion criteria above follows Hedges et al. (1999) and Whittaker (2010). Information on how data were obtained from individual studies is presented in Appendix C.

For grasslands/savannas that had multiple studies published on encroachment, we averaged the richness response of all studies for each community. This minimized bias toward grassland/savanna communities that have been studied more extensively than others (see Table 1 for levels of replication). Usually, replicates within communities showed similar responses even if study designs and plot sizes differed (Supplement) and the relationship between plot size and richness response explained little of the overall variability ($r^2 = 0.05$). Therefore, we feel confident that differences in study design do not substantially alter our results. Tallgrass prairie had the most variable results and the highest number of studies ($n = 5$).

Reporting of climatic data varied across studies, therefore we used the WorldClim GIS database to obtain standardized monthly and annual temperature and precipitation for each site (Supplement). WorldClim precipitation values were highly similar to those reported in the subset of papers that included local climate data ($r^2 = 0.96$, $n = 10$ sites). Prior to statistical analysis, temperature and precipitation were averaged within communities in the same way as richness response (Table 1). We analyzed richness response and ANPP data using a mixed-effects model ANOVA where climate variables (precipitation, temperature) were fixed effects fit with a random intercept. Climate variables and ANPP were strongly correlated, therefore we performed separate analyses for richness response with either climate data or ANPP as fixed effects. Because ANPP can be scaled from different plot sizes, analysis was performed on the reported values of ANPP and on the RR transformation of ANPP, when data from both encroached and un-encroached grasslands were available. Unfortunately, comparable data on soil characteristics were not available at many sites and a recent analysis suggests that global soil databases are inadequate for such analyses (Staver et al. 2011). Therefore, we did not include soil variables in our analysis.

RESULTS

Woody encroachment was associated with a significant decline in species richness in the 13 grassland/savanna communities with available data (Table 1). The average richness response for all communities was −0.65 and the average proportional decline in species richness ($[(SR_u - SR_e)/SR_u] \times 100$; where SR is species richness and u and e stand for un-encroached and encroached, repectively) was 45%. Richness response decreased with mean annual precipitation (MAP; Fig. 1a, $r^2 = 0.81$, $P < 0.001$). Richness response was also negatively correlated with the ANPP following encroachment ($r^2 = 0.69$, $P < 0.05$, data not shown) and the magnitude of change in ANPP following encroachment (Fig. 1b, $r^2 = 0.69$, $P < 0.05$). Relationships between richness response and the response ratio of ANPP (RR_{ANPP}) were weaker ($r^2 = 0.48$), suggesting that species richness responds more closely to the magnitude of change in ANPP, rather than the proportional change in ANPP. The ANPP of encroached patches was directly related to precipitation ($r^2 = 0.87$, $P < 0.001$, data not shown), as was the difference in ANPP between encroached and un-encroached patches (Fig. 1c, $r^2 = 0.81$). For both richness response and ANPP of encroached patches, April precipitation was the best monthly predictor ($r^2 = 0.71$ and 0.86, respectively). Temperature was not a significant predictor of richness response or ANPP. After removing one statistical outlier, all reported relationships were also significant when studies are

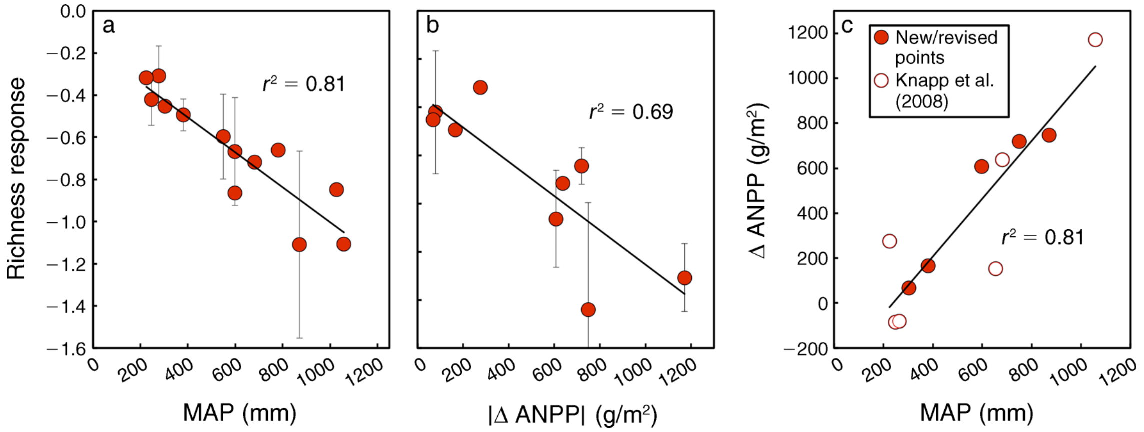

FIG. 1. (a) The relationship between richness response (ln[species richness in encroached plot]/[species richness in unencroached plot]) and mean annual precipitation (MAP). Negative values indicate a greater decline in richness following encroachment. (b) The relationship between "richness response" and the absolute value of changes in annual net primary productivity (ANPP) following encroachment (i.e., ΔANPP). (c) The relationship between ΔANPP and MAP. For panels (a) and (b), all error bars denote ±SE. Points without bars did not have enough replicates to calculate SE or error bars were too small to be seen.

considered as single data points, rather than community type averages (Appendix C).

DISCUSSION

As a whole, woody encroachment consistently resulted in a significant decline in species richness in North America grassland/savanna communities (Table 1). Moreover, most of the studies included here found that encroachment altered community composition as well (Table 1). Species richness often reflects microsite environmental conditions and the traits of species available to colonize an area (Chapin 1980, Shipley et al. 2006). The observed declines in richness, taken together with the noted impacts of woody encroachment on key resources and disturbance mechanisms (Schlesinger et al. 1990, Archer 1995, Scholes and Archer 1997, Knapp et al. 2008, Riginos and Grace 2008, Brantley and Young 2009, D'Odorico et al. 2010, Eldridge et al. 2011, Ratajczak et al. 2011), suggest that few species from the pre-existing grassland/savanna community are well adapted to woody plant dominance in North America.

In contrast to these results, a meta-analysis by Eldridge et al. (2011) found that across continents (~18 equivalents of the "communities" in our study), woody encroachment tended to have a positive or neutral effect on species richness. The analysis by Eldridge et al. (2011) included less than half of the North American communities used in our analysis and this handful of shared communities comprises many of the examples of negative encroachment impacts in their analysis. Thus, the available evidence suggests that the effects of woody encroachment in North America differ from the neutral or positive effects usually observed in other regions. Region-specific variation in evolutionary history (disturbance, grazing, climate, species radiation) and anthropogenic activity (pre- and post-industrial) may account for differences between North America and other continents. For instance, in Mediterranean and Australian grasslands, woody encroachment has been initiated by a discontinuation of pastoral activities and/or wood collection and has been followed by increases in species richness (Thompson and Eldridge 2005, Maestre et al. 2009). Whereas, in North America, intensifying human activity tends to be the primary cause of woody encroachment (Van Auken 2000, Kochy and Wilson 2001, Briggs et al. 2005) and the impact on species richness is negative (Table 1). Together, these studies demonstrate that species richness is consistently greater when anthropogenic impacts are less intense.

Interrelations between richness, productivity, and precipitation across North America

Woody encroachment in North America occurs over a large climatic and productivity gradient. We found that woody encroachment had a greater impact on species richness at sites with higher precipitation (Fig. 1a) and when encroachment resulted in a greater change in ANPP (Fig. 1b). Also, ANPP and changes in ANPP following encroachment were positively related to precipitation (Fig. 1c; see Knapp et al. 2008, Barger et al. 2011). These results mirror other observations that the performance of woody plants in grasslands is moderated by water availability. Precipitation is correlated to maximum woody cover in Africa, Australia, and South America (Williams et al. 1996, Sankaran et al. 2005, Hirota et al. 2011, Staver et al. 2011) and in encroached grasslands globally (Eldridge et al. 2011). Likewise, encroachment-related changes in light interception and litter cover are directly related to precipitation (Knapp et al. 2008, Eldridge et al. 2011). Together, these studies demonstrate that both the impact per unit area and the spatial extent of woody encroachment scale directly with precipitation.

We suggest that the parallel relationships between species richness, ANPP and MAP exist because precipitation determines the magnitude of "woody release" that occurs with woody encroachment (Fig. 2). Through competition for resources in the upper soil layers and as a fuel source for fires, grass dominance negatively impacts woody seedling survival and growth, which can suppress woody vegetation even if resource availability is adequate to support adult shrubs and trees (Higgins et al. 2000, Sankaran et al. 2004, 2005, Bond 2008, Staver et al. 2011). When factors limiting woody vegetation are attenuated by fire suppression, overgrazing, or increased resource availability, water-limited woody plants undergo a release and reach a level of dominance that is determined predominately by precipitation (Figs. 1 and 2; Sankaran et al. 2005, Knapp et al. 2008, Barger et al. 2011, Eldridge et al. 2011, Hirota et al. 2011, Staver et al. 2011) and to a lesser extent, local edaphic factors or grazing (e.g., Williams et al. 1996, Roques et al. 2001, Staver et al. 2011). This release is both physiological (affecting individual plants) and demographic (affecting overall cover). Since there is a greater release at sites with higher precipitation, woody encroachment also has a greater effect on resource availability and ecosystem processes, resulting in stronger declines in species richness.

This woody release hypothesis assumes that the impact of encroachment on key processes increases with woody cover and woody biomass (i.e., that per-mass competitive effects do not vary among North American grasslands). A woody-release interpretation does not tie the observed relationship between precipitation and richness response to changes in any single resource or disturbance across sites, just the magnitude of overall change, which is captured in the various metrics discussed previously. This is important because light, water, nutrients, grazing, and fire are differentially affected by woody encroachment and have divergent effects across grassland communities (Knapp and Smith 2001, Clark et al. 2007, Knapp et al. 2008, Peters et al. 2011, Staver et al. 2011).

The relationship between changes in species richness and changes in ANPP also matches general theoretical expectations. In herbaceous plant communities, the relationship between diversity and productivity is hypothesized to be a unimodal, hump-shaped curve (Grime 1973, Tilman and Pacala 1993). While recent work has found that the unimodal curve might not be appropriate across the natural range of productivity found in grasslands (Adler et al. 2011), several global change experiments suggest that an increase in productivity leads to a decline in species richness (Suding et al. 2005, Clark et al. 2007, Harpole and Tilman 2007). This relationship may scale up from changes within the herbaceous community, to changes in the dominant vegetation type as well. Woody encroachment has similar effects on species richness and productivity (Fig. 1a–c) and is also stimulated by a decrease in disturbance (Van Auken 2000, Briggs et al. 2005, D'Odorico et al. 2010) and/or the fertilization effects of nitrogen deposition/CO_2 emissions (Bond and Midgley 2000, Kochy and Wilson 2001, Wigley et al. 2010). Moreover, the magnitude of changes in species richness scale with the changes in aboveground productivity (Fig. 1b), which is the expected relationship as increasing dominance by an individual species or functional group, in this case a strong aboveground competitor, leads to increased productivity, but decreased diversity (Tilman and Pacala 1993, Clark et al. 2007). In the one case where woody encroachment decreased productivity (Chihuahuan Desert), the theoretical patterns and mechanisms still held. In herbaceous communities, increasing abiotic stress is associated with a decrease in both productivity and diversity: this is the left half of the unimodal curve (Grime 1973, Tilman and Pacala 1993). In the northern Chihuahuan desert, shrub encroachment has facilitated desertification, which intensifies both water and nutrient limitation (Schlesinger et al. 1990). These impacts, in turn, result in a concomitant decline in productivity and diversity (Baez and Collins 2008, Barger et al. 2011), as theory predicts.

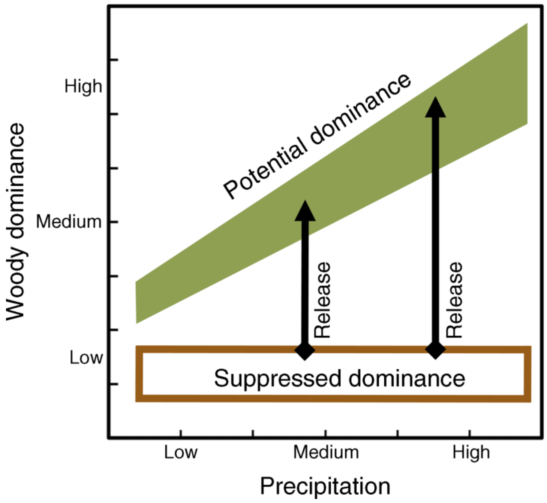

FIG. 2. A conceptual framework of woody release that explains related changes in richness response and ANPP along the North American precipitation gradient. This framework depicts two population states, which differ in their degree of woody plant dominance. The demographically suppressed population is the level of woody dominance when a combination of grass competition and resource availability prevents recruitment of adult woody plants. The potential dominance line represents the climatic potential of woody plants when demographic barriers are attenuated. Woody release is both demographic (more individuals reach the adult stage) and physiological (individual plants become larger). The "potential dominance line" is thick to reflect the potential role of local edaphic factors and grazing as moderators of the level of woody release.

The results of this meta-analysis suggest that in North America, species richness consistently declines following woody encroachment and that the magnitude of impact varies along a large-scale precipitation–productivity gradient. The woody release framework (Fig. 2) explains these patterns based on observations from demographic theory and measured responses of encroachment to precipitation (Fig. 1a–c). We also found preliminary evidence that changes in species richness are related to annual net primary productivity, which represents a scaling up of potential trade-offs between richness and productivity (Fig. 1b). On a global scale, our results suggest that the impacts of woody encroachment vary regionally. Given that woody plant encroachment is a relatively recent global phenomenon, it is possible that species richness may gradually increase over time following encroachment (e.g., Adler et al. 2005). However, woody encroachment currently leads to altered plant communities and a loss of grassland/savannas ecosystems. Because woody encroachment generally reflects a transition to an alternative stable state (Schlesinger et al. 1990, Scheffer et al. 2001, D'Odorico et al. 2010, Ratajczak et al. 2011) and efforts to reverse encroachment have had limited success (Lett and Knapp 2005), continued encroachment will likely lead to further decreases in species richness and changes in community structure throughout grasslands and savannas in North American.

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SUPPLEMENTAL MATERIAL

Appendix A

Citations for all studies used to derive data for meta-analysis (*Ecological Archives* E093-060-A1).

Appendix B

List and description of studies that met many, but not all of our inclusion criteria (*Ecological Archives* E093-060-A2).

Appendix C

Description of how data were obtained from individual studies (*Ecological Archives* E093-060-A3).

Supplement

Richness response, ANPP, and climate data for all studies included in the meta-analysis (*Ecological Archives* E093-060-S1).