

Shrub encroachment and vertebrate diversity: A global meta-analysis

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Funding information

University of Florida's School of Natural Resources and the Environment; University of Florida's Center for African Studies; German Federal Ministry of Education and Research, Grant/Award Number: FKZ 01LL1302A

Editor: Thomas Gillespie

Abstract

Aim: Across the planet, grass-dominated biomes are experiencing shrub encroachment driven by atmospheric CO₂ enrichment and land-use change. By altering resource structure and availability, shrub encroachment may have important impacts on vertebrate communities. We sought to determine the magnitude and variability of these effects across climatic gradients, continents, and taxa, and to learn whether shrub thinning restores the structure of vertebrate communities.

Location: Worldwide.

Time period: Contemporary.

Major taxa studied: Terrestrial vertebrates.

Methods: We estimated relationships between percentage shrub cover and the structure of terrestrial vertebrate communities (species richness, Shannon diversity and community abundance) in experimentally thinned and unmanipulated shrub-encroached grass-dominated biomes using systematic review and meta-analyses of 43 studies published from 1978 to 2016. We modelled the effects of continent, biome, mean annual precipitation, net primary productivity and the normalized difference vegetation index (NDVI) on the relationship between shrub cover and vertebrate community structure.

Results: Species richness, Shannon diversity and total abundance had no consistent relationship with shrub encroachment and experimental thinning did not reverse encroachment effects on vertebrate communities. However, some effects of shrub encroachment on vertebrate communities differed with net primary productivity, amongst vertebrate groups, and across continents. Encroachment had negative effects on vertebrate diversity at low net primary productivity. Mammalian and herpetofaunal diversity decreased with shrub encroachment. Shrub encroachment also had negative effects on species richness and total abundance in Africa but positive effects in North America.

Main conclusions: Biodiversity conservation and mitigation efforts responding to shrub encroachment should focus on low-productivity locations, on mammals and herpetofauna, and in Africa. However, targeted research in neglected regions such as central Asia and India will be needed to fill important gaps in our knowledge of shrub encroachment effects on vertebrates. Additionally, our findings provide an impetus for determining the mechanisms associated with changes in vertebrate diversity and abundance in shrub-encroached grass-dominated biomes.

KEYWORDS

biodiversity, global change, grasslands, grazing, pastoral abandonment, savannas, shrub encroachment, shrub thinning, species richness, woody encroachment

1 | INTRODUCTION

Across the planet, grass-dominated biomes are experiencing largely unprecedented increases in woody biomass attributable to short-statured plants (< 6 m, i.e., shrub encroachment; Eldridge et al., 2011), driven by increasing atmospheric CO₂ and land use (Cabral, De Miguel, Rescia, Schmitz, & Pineda, 2003; Stevens, Erasmus, Archibald, & Bond, 2016; Van Auken, 2000; Wigley, Bond, & Hoffman, 2010). Grass-dominated biomes experiencing shrub encroachment include grassland and savanna, tundra, Mediterranean *dehesas*, and savanna maintained by seasonal flooding (e.g., South American Pantanal; Assine & Soares, 2004; Naito & Cairns, 2011; Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014; Stevens et al., 2016; Van Auken, 2000). We define a biome as grass-dominated if it is characterized by a layer of grass and herbaceous plants (a physiognomic approach sensu Whittaker, 1962). According to this definition, at least six of the world's 14 terrestrial biomes are grass-dominated, and shrub encroachment is occurring in all of them (Olson, Dinerstien, & Wikramanayake, 2001; Parr et al., 2014; Supporting Information Table S1). Shrub encroachment is promoted by land use, such as pastoralism, because disturbance regimes change (e.g., fires and grazing), whereas atmospheric CO₂ contributes to shrub encroachment by favouring woody plants over grasses (Stevens et al., 2016). Shrub encroachment affects cover and other resources known to be critical to many vertebrates, which may lead to important and consistent effects of encroachment on communities across grass-dominated biomes (Parr et al., 2014; Pausas & Keeley, 2009; Ricklefs, 2004). Indeed, shrub encroachment can change the structure and composition of terrestrial vertebrate communities (Blaum, Rossmannith, & Jeltsch, 2007; Chown, 2010; Sirami & Monadjem, 2012). However, the effects of shrub encroachment on vertebrates have not been synthesized to determine if they are consistent or how they vary across climate conditions, continents, and vertebrate groups (i.e., birds, mammals and herpetofauna).

There are several reasons why shrub encroachment effects on vertebrate communities may vary across global climatic and disturbance gradients, amongst continents, and across taxa. Grass-dominated biomes maintained by limited and variable precipitation are less productive than biomes maintained by fire and herbivory and often have lower vertebrate diversity (Bond, Woodward, & Midgley, 2005; Murphy & Bowman, 2012). Additionally, spatial and temporal differences in available cover, food and nesting substrates between arid and mesic conditions can be particularly striking (Collins et al., 2014; Radford & Andersen, 2012). For example, vegetation in desert grasslands and arid savannas is temporally stable and patchy compared to mesic grasslands and savannas, which are temporally dynamic and characterized by continuous vegetative cover (Briske, Fuhlendorf, & Smeins, 2003; Parr et al., 2014). Shrub encroachment may create more novel cover dynamics in drier grass-dominated biomes, where shrub cover has historically been uncommon, resulting in greater reductions in vertebrate diversity (Morton et al., 2011; Scholes & Archer, 1997). In contrast, mesic grass-dominated biomes have historically exhibited dynamic and variable shrub cover that pre-dates recent encroachment, and therefore may contain species for which shrub cover is not novel (Morton

et al., 2011; Scholes & Archer, 1997). Vertebrates within a continent also share common evolutionary and ecological histories that may lead to different responses to shrub encroachment amongst continents. For example, most savannas are maintained by either limited precipitation or disturbance, but some are maintained by seasonal flooding and infrequent fire, such as the Pantanal in South America (Assine & Soares, 2004; Beerling & Osborne, 2006; Murphy & Bowman, 2012). Vertebrate groups may also differ in their responses to shrub encroachment because of underlying differences that are globally consistent. Birds build nests in species-specific locations and types of vegetative cover and simplified vegetation structure can limit their diversity (Slagsvold, 2001). Therefore, birds could increase in richness and diversity with shrub encroachment as new nest substrates become available. Responses of mammals and herpetofauna to shrub encroachment are more difficult to predict. Shrub encroachment could reduce the diversity of mammals and herpetofauna by removing specialist taxa adapted to grassy cover or bare ground (Ceballos et al., 2010), or responses driven by different habitat associations might lead to compositional shifts but no change in diversity (Leynaud & Bucher, 2005).

We conducted a systematic review and global meta-analysis of shrub encroachment effects on vertebrate communities (birds, mammals and herpetofauna), focusing on whether impacts vary across global climatic gradients driving historical disturbance regimes, amongst continents, and across vertebrate groups (Hurlbert & Haskell, 2003). Our objectives were to (a) estimate the magnitude of relationships between shrub cover and vertebrate community structure, and (b) identify associations between global climatic gradients, continents, and the magnitude of shrub encroachment effects on vertebrates. We predicted that reductions in vertebrate diversity and abundance with shrub encroachment would be greatest in grass-dominated biomes with the lowest productivity. We also predicted that vertebrate groups would exhibit specific shrub-encroachment responses. We expected birds to increase in richness, diversity and abundance with shrub encroachment owing to a wider variety of nesting and foraging options, whilst mammals and herpetofauna would decrease in richness and diversity (Kutt & Martin, 2010). Finally, we predicted that mammals and herpetofauna would exhibit no change in abundance because food availability should not increase with shrub encroachment.

2 | METHODS

2.1 | Study design

Meta-analysis is an established method of synthesizing quantitative research by taking effect sizes from multiple studies weighted according to their respective variances (Cooper, Hedges, & Valentine, 2009; Gurevitch, Curtis, & Jones, 2001). Meta-analyses are also useful for modelling variation in effect sizes amongst studies using covariates, and are consequently well suited for synthesizing research that is global in scope (Stewart & Schmid, 2015). Further, meta-analysis can account for the lack of independence amongst and within studies, and be structured to permit inference beyond the existing literature, by the use of

appropriate random-effects models (Cooper et al., 2009; Koricheva, Gurevitch, & Mengersen, 2013).

2.1.1 | Literature search

We systematically searched the Web of Science, ProQuest and Google Scholar databases to locate studies of terrestrial vertebrate diversity across shrub-encroachment gradients in space or time using multiple keyword combinations (see Supporting Information Table S2 for details; Eldridge, Maestre, Maltez-Mouro, & Bowker, 2012). We located unpublished studies by searching grey literature such as dissertations, theses and government reports indexed by Google Scholar and ProQuest, as well as contacting researchers directly, and including studies located by checking the reference sections of relevant articles. We contacted the corresponding authors of all relevant papers with incomplete data and removed those studies if we did not receive a positive response to our data request within 3 weeks. Finally, we assessed the assembled studies for geographic gaps in coverage. We noted an absence of suitable studies from India, Asia and Australia, so we contacted researchers working in those regions if a Google Scholar search indicated they had recently (since 2006; Supporting Information Table S2) published on shrub encroachment or vertebrate diversity in a grass-dominated biome in the region. Each e-mail inquiry included a request to provide contact information for other researchers that might have suitable expertise (Biernacki & Waldorf, 1981).

2.1.2 | Inclusion criteria

When conducting our literature search, we included studies if the authors collected vertebrate community data across a standardized area, indicated shrub encroachment had occurred, and measured percentage shrub cover or shrub density at one or more spatial scales. Further, we required that all included studies either: (a) report one or more measures of species richness, Shannon diversity or total abundance for ≥ 5 species of at least one vertebrate group, or (b) indicate that species richness, Shannon diversity or total abundance of each vertebrate group studied could be computed from the underlying data. In the latter case, we computed effect sizes if we could extract or acquire sufficient data. We separated studies that measured the effects of experiments and before-after, control-impact studies of shrub reduction by mechanical thinning, fire, and herbicides from observational studies of shrub encroachment and analysed them separately because we expected their respective effects to be of opposite sign.

2.1.3 | Data collection

We recorded data from each study to quantify the effects of shrub encroachment on vertebrate communities. For each study, we recorded: geographic coordinates, continent, and vertebrate group considered (herpetofauna, small mammals, ungulates, mammalian carnivores or birds). We also recorded study design, i.e., longitudinal or space-for-time substitution, because the space-for-time-substitution design could yield different, and possibly unreliable, results (Pickett, 1989). Likewise, few shrub encroachment studies cover the entire possible gradient of percentage shrub cover (0–100%) and vertebrate responses to encroachment may not be linear, so we recorded ranges,

means and standard deviations of percentage shrub cover, study-wide for each article and between author-defined groups where relevant (Brook, Sodhi, & Bradshaw, 2008; Burkett, Wilcox, Stottlemeyer, Barrow, & Fagre, 2005). We recorded shrub density where the authors did not record percentage shrub cover. Finally, we recorded whether live-stock grazing occurred during the study because it is a putative driver of both shrub encroachment and vertebrate community structure in grass-dominated biomes (D'Odorico, Okin, & Bestelmeyer, 2012; Ricketts & Sandercock, 2016; Waters, Orgill, Melville, Toole, & Smith, 2016).

Reporting of climatic data is frequently incomplete and data sources used vary across studies. We therefore used global databases to quantify mean annual precipitation and net primary productivity at the geographic coordinates of each study we identified. Specifically, we extracted historic mean annual precipitation and net primary productivity from WorldClim Version 1.4 (Figures 1 and 2; 1950–2000 and 1981–2000 for precipitation and net primary productivity, respectively; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), and historic normalized difference vegetation index (NDVI) values from the Global Land Cover Facility's Earth Science Data Interface (2001–2006; <http://glcfapp.umd.edu:8080/esdi/index.jsp>; Pettorelli et al., 2005). We used the MOD09A1 eight-day surface reflectance product, which sampled using a 500 m² pixel (<http://glcfapp.glcf.umd.edu:8080/esdi/product?productID=16>). We collected these measures because they provide similar but potentially distinct information about ecological conditions amongst sites and no measure is clearly superior (Pettorelli et al., 2005). For example, precipitation should regulate community structure at smaller spatial scales than productivity and NDVI (Harrison & Grace, 2007). Likewise, the correlation between precipitation and NDVI is lower at higher levels of precipitation and can be moderated by soil conditions (Fabricante, Oesterheld, & Paruelo, 2009; Nicholson & Farrah, 1994). We also used a global database to assign each study to a biome and ecoregion (ecoregions are nested within biomes and delineated based on distinctive species assemblages; Olson et al., 2001) to facilitate placing the studies in a detailed biogeographic context and permit testing for differences in shrub encroachment effects amongst biomes (Olson et al., 2001).

2.2 | Analysis

2.2.1 | Effect size calculations

We calculated Fisher's z -transformed r (r hereafter), a transformation of the correlation coefficient that facilitates model fitting and treated it as the effect size for all analyses (Cooper et al., 2009; Koricheva et al., 2013). We chose r because it provides directly interpretable estimates of shrub cover effects on species richness, Shannon diversity or total abundance in terms of standard deviations and it was readily estimated from studies where these shrub cover effects were modelled directly. We calculated r from model partial coefficients, unstandardized coefficients and their respective standard errors, sample sizes, t -statistics, R^2 values, F -statistics and χ^2 -square statistics, or directly from raw data (Cooper et al., 2009; Nakagawa & Cuthill, 2007). When authors compared two groups with different mean shrub cover, such as control and

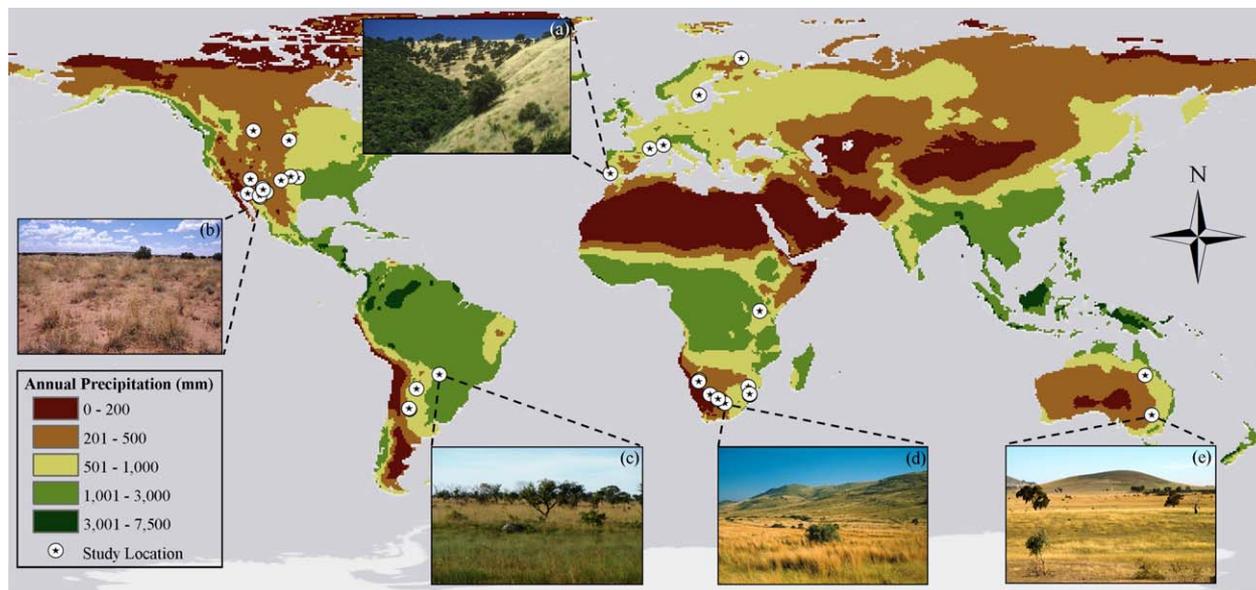


FIGURE 1 Locations and mean annual precipitation associated with studies of shrub-encroachment effects on vertebrate community structure worldwide, 1978–2016. Inset photographs illustrate typical vegetation structures amongst continents, in (a) a European steppe-like community (<http://www.bbc.co.uk/education/guides/zmyj6sg/revision/4>); (b) a North American semi-desert grassland (from Brown, Reichenbacher, & Fran-son, 1998); (c) a South American wet grassland (photograph by Alessandra Fidelis); (d) a South African Highveld grassland (photo by Gerald Cubitt – Bruce Coleman Ltd.); and (e) an Australian grassland (photograph by Geoff Park)

experimental plots in thinning experiments (Koricheva et al., 2013; Lipsey & Wilson, 2001), we first calculated Hedge's g values (Lipsey & Wilson 2001) and then converted them to correlation coefficients for Fisher's z -transformation. We calculated Hedge's g using group means (e.g., control and treatment), sample sizes, and standard deviations (Koricheva et al., 2013).

Studies of shrub encroachment effects have employed diverse designs and analytical methods, often comparing several models. We selected effect sizes from each study based upon the simplest relevant model, that is, the univariate model if reported, and the best multivariate

model otherwise, as determined by the authors' chosen information-theoretic or hypothesis-testing criteria. We collected multiple measures from the same study when data were not suitably aggregated, such as when reporting effects of mesquite, *Prosopis glandulosa*, and creosote bush, *Larrea tridentata*, separately (Boeing, Griffis-Kyle, & Jungels, 2014). However, we only collected results from the most recent sampling period or the most contrasting group (i.e., maximum Δ shrub) when authors disaggregated their data into ≥ 3 groups according to year, season, range condition or grazing intensity but did not provide the F -statistics required to calculate Hedge's g directly (Lipsey & Wilson 2001).

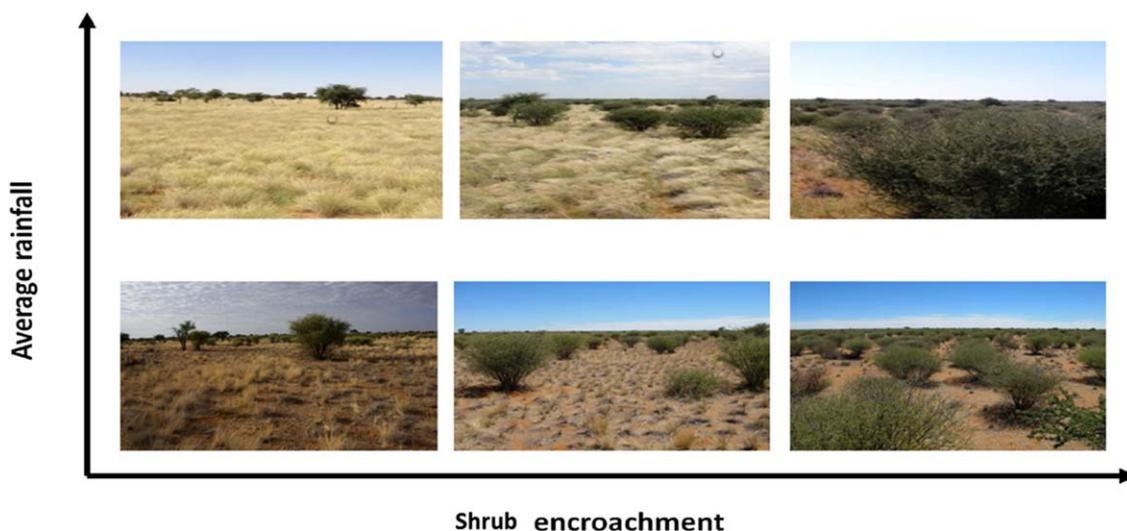


FIGURE 2 Variation in vegetation structure across gradients of annual precipitation and shrub encroachment in a semi-arid savanna: the Kalahari rangelands of South Africa. The sites in each column are the same, photographed in either a wet year (top row) or a dry year (bot-tom row)

2.2.2 | Modelling approach

We determined the relationships between shrub encroachment and vertebrate diversity by treating species richness, Shannon diversity (Shannon 1948) and total abundance, that is, the total number of birds, herpetofauna (reptiles or amphibians) or mammals reported, as response variables. We built separate models for observational and experimental studies to determine if removal of shrubs by fire, herbicide or mechanical means reverses the effects of encroachment – that is, were the effects of thinning on vertebrates of opposite sign and similar magnitude? We also fit random-effects meta-regressions in R's 'metafor' package to determine if methodological or ecological conditions explained heterogeneity in the effect of shrub encroachment on vertebrate communities (R Core Team, 2016; Viechtbauer, 2010). We treated study as a random effect because we extracted more than one effect from some studies and wanted to make inferences beyond the population of studies sampled (Viechtbauer, 2010). There were a priori reasons to expect that shrub-cover-vertebrate-diversity relationships may be nonlinear. Shrub encroachment effects could also vary according to differing percentage shrub cover considered amongst studies. We therefore fitted a model with a linear and a quadratic term for shrub cover for richness, Shannon diversity, and community abundance in the metafor package and two-part piecewise regressions of Fisher's z -transformed r on study-wide mean percentage shrub cover in R's 'segmented' package (Muggeo, 2003). We weighted each study in a piecewise regression by its respective precision (1/variance), akin to a meta-regression. These tests complemented meta-regressions testing if mean shrub cover effects on species richness, Shannon diversity and community abundance were different from zero (R Core Team, 2016; Viechtbauer, 2010). We focused on the meta-regression results unless the piecewise regressions were significant, in which case we reported and drew inference from the piecewise regression results.

2.2.3 | Candidate models

We assessed global effect sizes and confidence intervals without moderators or control variables to determine the overall effects of shrub encroachment on vertebrate community structure (Koricheva et al., 2013). We then fit models accounting for several potential sources of effect size heterogeneity from a candidate set (Supporting Information Appendix S4). We initially planned to test for the effects of mean annual precipitation, net primary productivity, NDVI, vertebrate group, continent, biome, whether the dominant encroaching shrub species was native or introduced, land-use type and study design (longitudinal or not). We collapsed some categorical variables into fewer groups and removed some variables from consideration because the available data were insufficient for our planned analyses. We found that 95% of relevant studies involved encroachment by native shrub species so we decided not to test whether invasive shrubs had different effects on vertebrates. We collapsed land-use types into grazed or ungrazed by cattle during the study period because most studies occurred on rangelands and protected areas. We also pooled all mammalian taxa into a single group because most mammalian orders were poorly represented in the data. We found articles with useable effect sizes distributed

across eight biomes but only three biomes were studied in > 5 articles, so we only considered those biomes when testing for differences amongst biomes. The biomes we considered included: (a) deserts and xeric woodlands; (b) temperate grasslands, savannas and shrublands; and (c) tropical and subtropical grasslands, savannas and shrublands (Olson et al., 2001). There were also cases where a planned model could not be fit because there was no variation in the sample, for example, all observational studies reporting Shannon diversity also employed space-for time substitution designs. We therefore ultimately fit 43 models (Supporting Information Appendix S4). We interpret significance from the p values for each parameter estimates from each respective model ($p < .05$) but note where we found weak evidence for an effect, that is, $.05 < p < .10$.

2.2.4 | Model goodness-of-fit and possible publication bias

We estimated the amount of unmodelled heterogeneity remaining for each model using the I^2 statistic, which ranges from 0 to 100% (Higgins, Thompson, Deeks, & Altman, 2003). The I^2 statistic can provide a heuristic aid for judging whether sources of heterogeneity in effects have meaningful explanatory power (Higgins et al., 2003). We also plotted effect size against precision overlain with a 95% distribution expected in the absence of bias (i.e., funnel plots), and inspected them for apparent asymmetry (Cooper et al., 2009; Egger, Smith, Schneider, & Minder, 1997). Asymmetry in funnel plots can indicate bias attributable to selective publication and other factors (Sterne, Sutton, & Ioannidis, 2011).

3 | RESULTS

3.1 | Literature search

Our literature searches identified 1694 results comprising 255 unique articles. We selected 188 articles for further scrutiny after scanning titles and abstracts. We ultimately reduced the 188 potentially relevant articles to 43 that met our inclusion criteria (A list of the data sources is found in Appendix 1; see also Table S3). The articles we included were published between 1978 and 2016. We extracted 114 r values effects from the 43 articles (Supporting Information Table S3). We extracted 15 effects from 6 experiments and 99 effects from 38 observational studies. Common reasons we removed studies from consideration included: (a) ordination methods were used that rendered the data uninterpretable for our purposes; and (b) no relevant tests of shrub cover effects on vertebrate community structure were reported or could be computed even though suitable data were collected.

We found differences in apparent research effort amongst vertebrate groups, with 61, 31 and 22 effects pertaining to birds, mammals and herpetofauna, respectively. Amongst mammals, we identified 19, 8 and 4 articles allocated to rodents, carnivores and ungulates, respectively. Likewise, the effects we included were concentrated in North America and Africa (27 and 43 effects, respectively), whereas we collected few effects from Australia, Europe and South America (4, 13 and 12 effects, respectively) and no effects from Asia. The coverage of vertebrate groups differed across continents. We collected effects from all groups in North America, effects from birds and mammals in Africa,

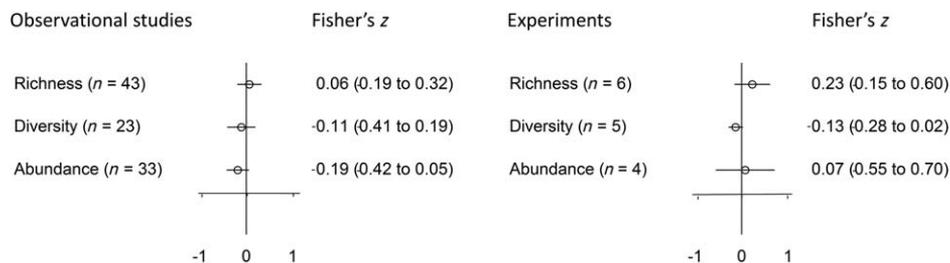


FIGURE 3 Shrub encroachment had no overall effect on the species richness, Shannon diversity, and abundance of vertebrate communities, nor does experimental thinning by fire, herbicides, or mechanical removal. Plotted values are standardized correlation coefficients, that is, Fisher's z-transformed r . Each value of r is reported under the "Fisher's z" column with its corresponding 95% confidence interval in parentheses

data from birds only in Europe and Australia, and data from herpetofauna alone in South America (Supporting Information Table S3). Finally, we extracted effects from studies across eight biomes. Five biomes were the subject of one or two articles and the remaining three biomes were the subject of five or more articles (Supporting Information Table S3).

3.2 | Meta-analyses

Meta-analysis did not reveal general, consistent effects of shrub encroachment on the species richness, Shannon diversity or total abundance of vertebrate communities in either observational or experimental studies ($p > .05$; Figure 3). Likewise, neither adding a quadratic

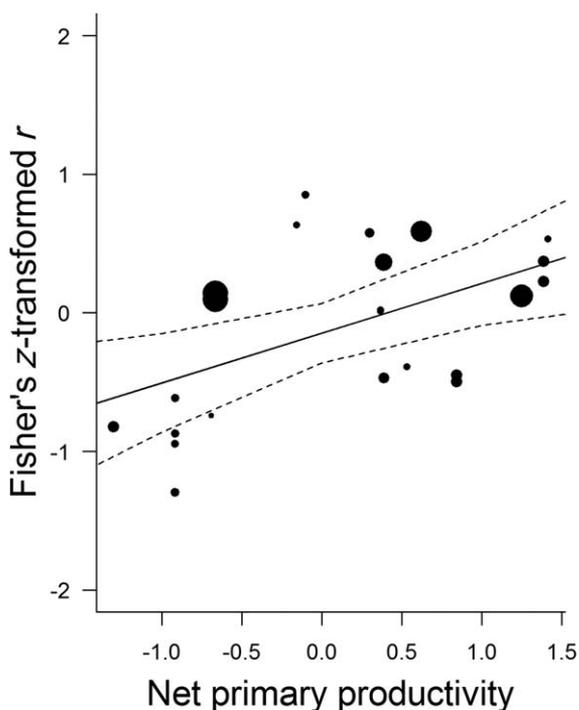


FIGURE 4 Shrub encroachment reduced vertebrate Shannon diversity at low net primary productivity (standardized) but had no effect at high net primary productivity across observational studies ($p = .0019$). We obtained similar but non-significant results for the effects of mean annual precipitation and the normalized difference vegetation index ($p = .1154$ and 0.0657 , respectively). Points are displayed at different sizes proportional to their respective precisions

shrub cover term nor piecewise regression indicated any nonlinear effect of mean shrub cover amongst studies ($p > .05$). Shrub encroachment effects on species richness, Shannon diversity and community abundance also did not differ amongst biomes ($p > .05$; Supporting Information Figure S1). Univariate meta-regressions did indicate, however, that shrub encroachment effects in observational studies varied with net primary productivity, amongst vertebrate groups, and across continents (Figure 4).

The effect of shrub encroachment on vertebrate diversity was negative at the lowest net primary productivity in observational studies, with no effect in the most productive locations [$\hat{\beta} = 0.44 \pm 0.14$ SE, $p = .0019$, number of effects (k) = 23; Figure 4]. We also found positive but non-significant relationships of shrub encroachment effects on diversity with mean annual precipitation and NDVI in observational studies ($\hat{\beta} = 0.23 \pm 0.15$ SE and 0.30 ± 0.16 SE, $p = .12$ and $.07$, respectively, $k = 23$; Supporting Information Table S4) and a non-significant positive relationship with species richness and mean annual precipitation in thinning experiments ($\hat{\beta} = 0.35 \pm 0.19$ SE, $p = .06$, $k = 6$; Supporting Information Table S4). We found no other relationships between productivity, precipitation and vertebrate richness or total abundance ($p > .05$; Supporting Information Table S4).

Shrub encroachment effects varied amongst vertebrate groups. Shannon diversity of mammals and herpetofauna was negatively correlated with shrub encroachment ($\hat{\beta} = -0.75 \pm 0.31$ SE and -0.90 ± 0.26 SE, $p = .02$ and $.0007$, respectively, $k = 23$; Supporting Information Table S4). Further, total abundance was also negatively correlated with shrub encroachment amongst herpetofauna and mammals ($\hat{\beta} = -0.51 \pm 0.23$ SE and -0.55 ± 0.22 SE, $p = .02$ and $.01$, respectively, $k = 33$; Figure 5). We found weak evidence of shrub encroachment effects on bird Shannon diversity and community abundance, which were of the predicted sign ($\hat{\beta} = 0.30 \pm 0.16$ SE, $p = .06$, $k = 23$ for Shannon diversity and 0.13 ± 0.17 SE, $p = .45$, $k = 33$ for total abundance). The effects of shrub encroachment on species richness did not differ amongst groups (minimum $p = .17$; Supporting Information Table S4).

Distributions of r differed amongst continents but not amongst the three most-studied biomes across observational studies ($p > .05$; Supporting Information Table S4). In Africa, relationships between shrub encroachment and vertebrate species richness were negative ($\hat{\beta} = -0.28 \pm 0.14$ SE, $p = .04$, $k = 43$; Figure 5). Studies in Australia, Europe and North America, however, exhibited positive relationships

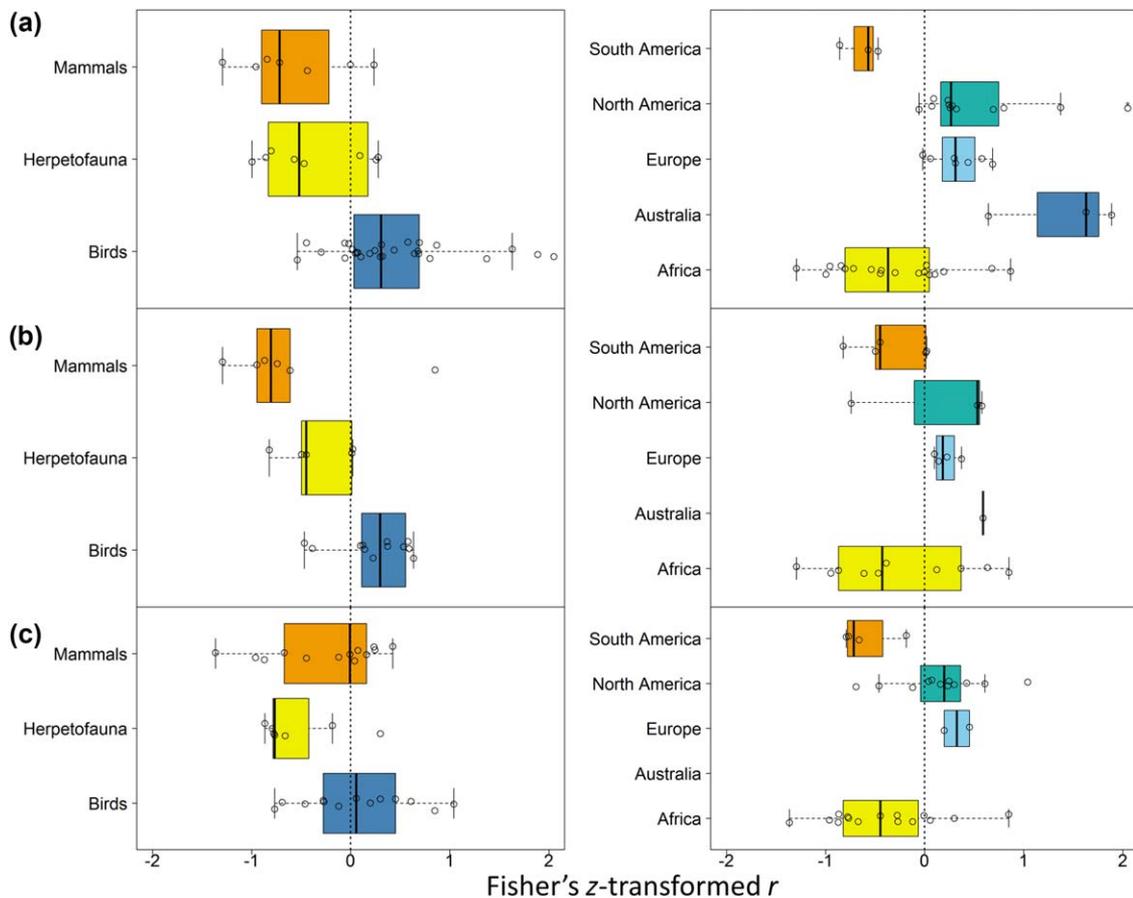


FIGURE 5 Shrub encroachment effects (r) on vertebrate community structure amongst groups and across continents. Bird (a) species richness, (b) Shannon diversity and (c) total abundance ($n = 28, 12$ and 13 , respectively) responses to encroachment were positive or neutral whereas those of herpetofauna ($n = 8, 5$ and 7) and mammals ($n = 7, 5$ and 13) were negative. Median shrub encroachment effects on vertebrates were negative in Africa ($n = 18, 10$ and 15) and South America ($n = 3, 5$ and 4) but generally positive in Australia ($n = 3, 1$ and 0), Europe ($n = 7, 4$ and 2) and North America ($n = 12, 3$ and 12)

between shrub encroachment and species richness ($\hat{\beta} = 1.48 \pm 0.38$ SE, 0.57 ± 0.29 SE and 0.81 ± 0.25 SE, $p = .0001, .05$ and $.0012$, for Australia, Europe and North America, respectively, $k = 43$; Figure 5). Similarly, shrub encroachment was associated with reduced total abundance in Africa but increased total abundance in North America ($\hat{\beta} = -0.36 \pm 0.15$ SE and 0.53 ± 0.25 SE, $p = .02$ and $.05$, for Africa and North America, respectively, $k = 33$; Figure 5). However, we found no effects of shrub encroachment on Shannon diversity amongst continents (all $p > .05$). There was evidence of unmodelled heterogeneity in all of the meta-regressions as determined by I^2 (range: 0.62 – 0.96 ; Supporting Information Table S3). Funnel plots also indicated that substantial heterogeneity in effects across studies did not indicate any systematic bias (Supporting Information Figure S2).

4 | DISCUSSION

4.1 | Shrub encroachment effects across climatic gradients and taxa

We found no consistent effect of shrub encroachment on vertebrate diversity across the planet. Yet we identified variability in shrub

encroachment effects on vertebrate communities amongst continents and vertebrate groups as well as with net primary productivity. Specifically, shrub encroachment effects on vertebrate communities were negative (a) in arid environments where shrub encroachment is novel and can precipitate a biome switch (Knapp et al., 2008), (b) amongst mammals and herpetofauna, and (c) in Africa. Collectively, these results provide a basis for focusing conservation efforts in arid grass-dominated biomes and an impetus for determining the mechanisms associated with reduced diversity and abundance of mammals and herpetofauna in shrub-encroached grass-dominated biomes.

Our finding that the diversity and abundance of mammals and herpetofauna declined with shrub encroachment was surprising but explicable considering the traits of each vertebrate group. Mammals and herpetofauna may exhibit less variation in use of cover and foraging modes than birds, for example, leading to increased sensitivity to shrub encroachment (Eldridge et al., 2011; Slagsvold, 2001). Also, mammal studies are generally limited to similar species, for example, carnivores or rodents, which might magnify these effects. There may be encroachment effects amongst mammalian taxa along these lines that warrant further exploration. For example, the only available evidence indicated that carnivore richness and abundance was highest at intermediate

shrub cover and lowest at high shrub cover, but this was based on studies from a single ecoregion (Blaum, Rossmanith, & Jeltsch, 2007; Blaum, Rossmanith, Popp, & Jeltsch, 2007; Blaum, Tietjen, & Rossmanith, 2009).

4.2 | Shrub encroachment effects amongst continents

We expected to find differences in shrub encroachment effects on vertebrates amongst continents but the pattern we observed did not conform to a common biogeographic theme. For example, we did not observe consistent effects between biomes, which were delineated largely on the basis of coarse differences in precipitation and temperature (i.e., desert and xeric shrubland versus temperate or non-temperate grassland, savanna and shrubland). We suspect this occurred in part because the prevailing biome classifications were not developed with a focus on vertebrate biology, but rather on abiotic controls driving plant distributions (Olson et al., 2001). Further, there were not consistent effects between the New World and the Old World, with their distinctive common fauna, nor between the Northern and Southern Hemispheres, which have distinct climate histories (Hays, Imbrie, & Shackleton, 1976). Rather, Africa was markedly different from North America, Europe and Australia. We expect that more recent events such as land-use intensification and species invasions have had different trajectories in Africa than the other continents (Ellis & Ramankutty, 2008; Lonsdale, 1999), and that the increased diversity and abundance seen in North America, Europe and Australia may therefore be driven by widespread, generalist species invading grass-dominated biomes (Dukes & Mooney, 1999). Species traits might explain variation in the effects of shrub encroachment we found, suggesting mechanisms for shrub encroachment's effects.

4.3 | Data gaps and limitations

There were striking geographic gaps in available studies of shrub encroachment effects on vertebrates in Asia, India and Australia. Further, some biomes in these areas may be misclassified as forest despite extensive grass cover maintained by herbivory and fire (Parr et al., 2014; Ratnam, Tomlinson, Rasquinha, & Sankaran, 2016). This collection of neglected "tropical grassy biomes" faces several threats yet we found no data about the effects of shrub encroachment on vertebrate diversity for them. The extant studies have additional noteworthy imbalances in geographic and taxonomic coverage. For example, we found no data for Australia's extensive arid grasslands (Fensham, Fairfax, & Archer, 2005; Tassicker, Kutt, Vanderduys, & Mangru, 2006). Likewise, we found no data from the vast steppes of continental Asia, and limited data on herpetofauna and mammals across continents. Altogether, these gaps limit our ability to discuss the effects of shrub encroachment on vertebrates across a substantial portion of the world's grass-dominated biomes. Future research in these regions would help fill these important data gaps.

4.4 | Implications for ecology, conservation and management

We found that increased net primary productivity was associated with reduced impact of shrub encroachment on vertebrate diversity.

Our results suggest that reducing factors that facilitate shrub encroachment, such as overgrazing, would be most effective in maintaining historic vertebrate diversity in desert grasslands and semi-arid savannas. Our results also indicate that shrub thinning has been ineffective in reversing shrub encroachment effects on vertebrate communities, at least at the spatial and temporal scales studied to date. Therefore, prevention and mitigation measures may be more effective than restoration. Grass-dominated biomes maintained by human livelihoods, on the other hand, generally have high net primary productivity, so vertebrate community structure in such biomes should be less sensitive to shrub encroachment and a lower priority for mitigation efforts (e.g., Laiolo, Dondero, Ciliento, & Rolando, 2004). Finally, as global CO₂ concentration appears to be the most consistent driver of shrub encroachment (Stevens et al., 2016; Wigley, Bond, & Hoffman, 2009), conserving vertebrate biodiversity in grass-dominated biomes should be treated as a global-scale problem, and detailed prioritization schemes developed based on the available evidence.

Our results show how climate and land-cover change can contribute to community assembly in ways that could not be predicted from studying global change drivers in isolation. We found no general effect of shrub encroachment encompassing all taxa and across the world, yet there were important differences in vertebrate responses to shrub encroachment that appear to be driven by climatic factors associated with different disturbance dynamics amongst the world's diverse grass-dominated biomes. Surprisingly, we also uncovered evidence that the structure of bird communities has been resilient in the face of shrub encroachment while other taxa have not. Thoughtful synthesis paired with experimentation will ultimately yield more refined answers about why these differences exist. Our results provide a valuable heuristic basis for global-scale conservation prioritization of vertebrate communities in the interim.

ACKNOWLEDGMENTS

We gratefully acknowledge The University of Florida's School of Natural Resources and the Environment and Center for African Studies for funding support. M. Leonard at the University of Florida's Marston Science Library provided research assistance. J. Fonderflick, P. Pereira, A. Kutt, J. Santana, F. Keesing and L. O'Reilly shared valuable data. N. Blaum is grateful for support from the German Federal Ministry of Education and Research (BMBF) in the framework of the SPACES project OPTIMASS (FKZ 01LL1302A).

DATA ACCESSIBILITY

We have included the .csv file we used as Supporting Information Table S1.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Stanton RA, Boone WW, Soto-Shoemaker J, Fletcher RJ, Blaum N, McCleery RA. Shrub encroachment and vertebrate diversity: A global meta-analysis. *Global Ecol Biogeogr*. 2018;27:368–379. <https://doi.org/10.1111/geb.12675>

APPENDIX : DATA SOURCES

Alford, A. L., Hellgren, E. C., Limb, R., & Engle, D. M. (2012). Experimental tree removal in tallgrass prairie: variable responses of flora and fauna along a woody cover gradient. *Ecological Applications*, 22, 947–958.

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