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Amphibian responses to livestock use of wetlands: new empirical data and a global review

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Abstract. Pastureland currently occupies 26% of Earth's ice-free land surface. As the global human population continues to increase and developing countries consume more protein-rich diets, the amount of land devoted to livestock grazing will only continue to rise. To mitigate the loss of global biodiversity as a consequence of the ever-expanding amount of land converted from native habitat into pastureland for livestock grazing, an understanding of how livestock impact wildlife is critical. While previous reviews have examined the impact of livestock on a wide variety of taxa, there have been no reviews examining how global livestock grazing affects amphibians. We conducted both an empirical study in south-central Florida examining the impact of cattle on amphibian communities and a quantitative literature review of similar studies on five continents. Our empirical study analyzed amphibian community responses to cattle as both a binary (presence/absence) variable, and as a continuous variable based on cow pie density. Across all analyses, we were unable to find any evidence that cattle affected the amphibian community at our study site. The literature review returned 46 papers that met our criteria for inclusion. Of these studies, 15 found positive effects of livestock on amphibians, 21 found neutral/mixed effects, and 10 found negative effects. Our quantitative analysis of these data indicates that amphibian species that historically occurred in closed-canopy habitats are generally negatively affected by livestock presence. In contrast, open-canopy amphibians are likely to experience positive effects from the presence of livestock, and these positive effects are most likely to occur in locations with cooler climates and/or greater precipitation seasonality. Collectively, our empirical work and literature review demonstrate that under the correct conditions well-managed rangelands are able to support diverse assemblages of amphibians. These rangeland ecosystems may play a critical role in protecting future amphibian biodiversity by serving as an "off-reserve" system to supplement the biodiversity conserved within traditional protected areas.

Key words: Anura; cattle; Caudata; climate; community; conservation; land-use; rangeland.

Introduction

Livestock production occupies 26% of Earth's ice-free land surface, employs 1.3 billion people, and accounts for 40% of the world's agricultural gross domestic product (Steinfeld et al. 2006, Robinson et al. 2014). Understanding how this massive land-use change has affected native ecosystems has been the topic of hundreds of papers and several reviews (see Fleischner 1994, Holechek et al. 1999, 2006, Howland et al. 2014, Schieltz and Rubenstein 2016). Despite the extensive body of literature on this widespread land use and data showing that effects are taxon specific, there have been no reviews of livestock's impacts on amphibians, one of the most globally endangered taxonomic groups (WWF 2018).

Livestock grazing affects community structure and ecosystem function in a variety of ways, including changes in hydrology, water temperature, nutrient cycling, stream morphology, soil characteristics, and effects on riparian plant, upland plant, invertebrate, and wildlife communities (See Fleischner 1994, Jones 2000, and Schieltz and Rubenstein 2016 for reviews). Fleischner (1994) grouped these processes into three main categories: (1) changes in community composition, (2) disruption of ecosystem functioning, and (3) alteration of ecosystem structure. These changes may result from direct nutrient input into ecosystems, grazing and browsing, and/or trampling of substrate (see reviews by Hobbs 1996, Bakker 1998, and Austrheim and Eriksson 2001). By affecting these ecological processes, grazers act as

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ecosystem engineers and impact multiple trophic levels (Gordon et al. 2004, Mysterud 2006). In areas where cattle heavily graze, these processes may lead to biodiversity loss, nutrient loss, and high levels of erosion and subsequent sedimentation (Milchunas et al. 1988, Gordon et al. 2004, Mysterud 2006). Previous literature reviews have examined the effects of livestock grazing across a variety of taxa and recorded primarily negative responses. For example, the studies reviewed by Fleischner (1994) showed declines in groups as diverse as mammals, fish, birds, and squamates due to livestock grazing in Western North America. Similarly, 11 of 16 studies on the impact of grazing on a diverse set of taxa in arid North American ecosystems revealed significant negative impacts of cattle grazing (Jones 2000).

More recent literature reviews suggest that responses to livestock grazing are highly dependent on specific grazing regimes and the taxa examined. Schieltz and Rubenstein (2016) recorded 34 negative responses, 18 neutral responses, and only 8 positive responses of community-level small mammal abundance to livestock grazing. Wild ungulates exhibited similar mixed responses to livestock grazing (86 negative, 35 neutral, and 34 positive responses; Schieltz and Rubenstein 2016). In certain habitat types and with livestock operations designed to prevent overgrazing and habitat degradation, grazing can positively impact native rangeland vegetation (Fuhlendorf and Engle 2004, Holechek et al. 2006), species adapted for open habitats (Schieltz and Rubenstein 2016), herpetofauna communities (Kay et al. 2017, Neilly et al. 2018), and biodiversity (Dorrough et al. 2004). Briske et al. (2011) found that the response of birds to livestock grazing was dependent upon the stocking rate of cattle, Neilly et al. (2018) found that reptile abundance was not negatively impacted by sustainably managed grazing treatments, and Rotem et al. (2016) found that, in mesic conditions, reptile diversity increased with grazing treatments. Since there is no clear consensus across wildlife taxa and environmental contexts on the impact of livestock, examining how they affect amphibian communities will provide insight on how to best predict and manage their potential positive and negative impacts on this sensitive taxonomic group.

Understanding why cattle have differential impacts on various species and communities is a challenging task. Studies have attempted to address these issues by examining effects of livestock on plant communities through the lenses of the intermediate disturbance hypothesis (Grime 1973, Horn 1975, Fox 1979), predator–prey interactions (Paine 1966, 1971), and models accounting for both evolutionary grazing history and environmental moisture (Milchunas et al. 1988). Despite these efforts, it remains unclear what constitutes “well-managed” livestock production (Schieltz and Rubenstein 2016), or the mechanisms by which livestock drive shifts in community composition (Kay et al. 2017). Clear results are further stymied by the lack of baseline data prior to the introduction of domesticated livestock to much of the world and a lack of specific data examining critical covariates, such as the phenological intensity and duration of grazing, the synergistic impacts of other forms of management (e.g., burning or mowing), and environmental gradients (e.g., precipitation, elevation, water chemistry).

Amphibians are in a state of global decline caused in part by habitat loss, habitat fragmentation and degradation, introduced diseases, and climate change (Houlahan et al. 2000, Collins and Storfer 2003, Blaustein et al. 2011, Scheele et al. 2019). Widespread conversion of forested land into either grazing land or feedstock farming, especially in the Tropics, is a leading cause of amphibian decline in regions where rates of active deforestation and land-use conversion continue to increase (Murgueitio et al. 2011, Armenteras et al. 2017). While deforestation as a result of land-use change is clearly detrimental to amphibians and wildlife as a whole, it is less clear how livestock grazing impacts areas that have already been converted to grassland or were historically open-canopy habitats grazed by large ungulates.

The unique physiology and varied life histories of amphibians make it difficult to predict their responses to livestock grazing. Amphibians are generally sensitive to water quality parameters such as levels of dissolved oxygen (DO), nitrate concentration (Hecnar 1995, Rouse et al.1999), and sediment loads (Lefcort et al. 1997, Carter 2001). Heavy browsing can exacerbate these problems by increasing nitrate levels, sediment loads, and rates of DO consumption (Kauffman and Krueger 1984, Anderson et al. 2001, Corn et al. 2003). Livestock may also affect amphibians directly through mortality of egg masses, juveniles, or adults by trampling through breeding ponds or streams. Despite these potential negative effects, livestock grazing may also confer some positive benefits in areas with naturally low levels of nutrient inputs or regions with an evolutionary history of large grazers. In low-nutrient systems, grazing can be a primary contributor to increasing ecosystem productivity (Plăiasu et al. 2010). The combination of increased fertilization and removal of senescent vegetation stimulates new plant growth, which may provide extra habitat and foraging opportunities for amphibian communities in oligotrophic aquatic ecosystems (Denton et al. 1997, Plăiasu et al. 2010). Additionally, the compacting of soil coupled with reduced vegetation (i.e., reduced evapotranspiration) may increase the hydroperiod of wetlands, which could be critical in arid areas where hydroperiods are naturally short and amphibians often fail to reach metamorphosis before wetlands dry (Marty 2005, Pyke and Marty 2005).

Previous reviews (Fleischner 1994, Schieltz and Rubenstein 2016) examining how livestock grazing affects ecosystems and wildlife have excluded analyses of amphibian responses to livestock grazing. In light of the mixed empirical results regarding amphibian responses to livestock (briefly outlined in the preceding paragraph), we sought to quantify the impacts of livestock grazing on amphibian abundance and diversity and synthesize the results of prior studies to discern broader patterns with respect to taxonomic group, habitat type, geography, and climate. Here we present the results of our own empirical study on the impacts of livestock on an amphibian assemblage in south-central Florida, USA and provide a quantitative literature review of the global impacts of livestock production on amphibians.

Materials and Methods

Empirical study design and implementation

Study site.—Research was conducted in seasonally inundated wetlands at the MacArthur Agro-Ecology Research Center (MAERC; 27°20′ N, 81°20′ W), a division of Archbold Biological Station. MAERC (also known as Buck Island Ranch) is a 4,086-ha cattle ranch located in south-central Florida, USA. MAERC produces more than 3,000 head of cattle annually and is one of the top 20 beef producers in the state (Swain et al. 2013). The ranch consists of improved pasture (40%), semi-native prairie (38%), seasonally inundated wetlands (14%), and oak–cabbage-palm hammocks (6%; Babbitt et al. 2009). Improved pastures are intensively grazed and ditched, consist mainly of exotic Bahia grass (*Paspalum notatum*), and are supplemented with nitrogen and phosphorous fertilizer. While stocking densities vary based on annual rainfall and temperature patterns, the improved pastures have been historically stocked at a higher rate (~0.57–1.7 cows/ha) than the semi-native pastures (~0.15–1.12 cows/ha; Boughton et al. 2015). Most of the more than 500 wetlands at MAERC are characterized as emergent freshwater marshes having sandy substrates (Baber et al. 2002). In deeper wetlands, grasses and other emergent, herbaceous species (e.g., *Pontederia cordata*, *Sagittaria lancifolia*) dominate the central part of the wetland, with low-growing species (e.g., *Bacopa caroliniana*, *Hydrochloa carolinensis*) forming a distinct outer vegetation band in shallower water (Baber et al. 2002, Babbitt et al. 2006).

Data collection.—Forty wetlands at MAERC were previously included in a study examining the interactive effects of cattle grazing, fire, and pasture type on wetland plant communities (Boughton et al. 2015). We focused our sampling around 20 of these wetlands (ranging in area from 0.3 to 1.3 ha) that were fenced to exclude cattle starting in 2007. We identified all other wetlands within the same size range that occurred in the same pastures as these 20 to control for spatial effects. This resulted in a list of 139 wetlands (20 fenced and 119 grazed). We visited these 139 wetlands during July 2017 (approximately eight weeks after the typical onset of the wet season) and sampled 49 that were inundated; the remaining wetlands filled unusually late in 2017 due to drought conditions. Two of these wetlands later had to be dropped because they could not be resampled in August 2017 due to accessibility issues. Thus, the full data set on amphibian community composition for this study consisted of 47 wetlands (6 fenced and 41 open to grazing).

We sampled each wetland twice, once in July and once in August 2017. Each sampling occasion entailed one round of dip netting and one night of trapping. Steel minnow traps (9 × 17.5 inches [1 inch = 2.54 cm]; Memphis Net and Twine, Memphis, Tennessee, USA) and crayfish traps (54 inch circumference; Nets and More, Jonesville, Louisiana, USA) were deployed overnight to target larger amphibians (e.g., metamorphosed anurans and large aquatic salamanders; Shaffer et al. 1994, Adams et al. 1998, Wilson and Pearman 2000, McKnight et al. 2015). The traps were baited with glow sticks to increase capture rates (Grayson and Roe 2007, Bennett et al. 2012). We deployed three minnow traps and one crayfish trap for every 1000 m^2 of wetland area, which was estimated by multiplying the length and width of the inundated portion of the wetland. To increase catch rates, trap deployment was non-random. Larval and metamorphosing amphibians were collected by dip netting around the perimeter of the wetland (one 1-m sweep every 10 m using a 3-mm mesh net; Bull et al. 2001, Watson et al. 2003, Marty 2005, Babbitt et al. 2006). We also recorded the abundance of all fish, crayfish, and predatory macroinvertebrates (Anisoptera, Belostomatidae, and Dytiscidae) caught in dip nets or traps.

We measured a set of environmental variables at a single point within each wetland, including conductivity, nitrate concentration, DO, pH, and temperature using a YSI Professional Plus Handheld Multiparameter Water Quality Instrument (YSI, Yellow Springs, Ohio, USA). Maximum water depth was determined using a meter stick in the deepest part of each wetland. As a measure of the intensity of cattle use, we recorded the total number of cow pies (i.e., dung) per wetland found within a meter of the wetland perimeter (Cole and North 2014). The total number of cow pies was standardized by dividing by the perimeter of the wetland.

Statistical analyses of MAERC Data.—To standardize data across wetlands, we calculated a total catch per unit effort (CPUE) for each of the three capture techniques by taking the total number of individual amphibians collected by each technique and dividing it by the total number of dip net sweeps performed or the total number of traps deployed. We then calculated a weighted trapping effort for each wetland by multiplying the number of each sampling technique performed by its respective CPUE, and summing all three values. When creating the community matrix, each row (wetland) was standardized by its total trapping effort, and each column (species) was standardized by its total abundance in order to upweight rare species.

We conducted community composition analyses to determine how cattle and other environmental variables affect amphibian communities at MAERC. Wetlands from which no amphibians were collected were excluded from these analyses, and amphibian species that were collected from only a single wetland were dropped. We first performed a PERMANOVA to determine whether the amphibian community differed between cattle excluded and cattle non-excluded wetlands. Second, we used a distance-based redundancy analysis (db-RDA) with the Bray-Curtis distance metric to determine whether our continuous measure of cattle use intensity (cow pie density) affected amphibian community composition while simultaneously accounting for other environmental factors. The other environmental factors considered were maximum depth, wetland surface area, fish abundance, crayfish abundance, predatory macroinvertebrate abundance, conductivity, nitrate concentration, DO, pH, and water temperature. We used Monte Carlo tests to determine which of the individual environmental factors were significantly associated with amphibian community composition. All community analyses were run using the vegan package (Oksanen et al. 2018) in R version 3.4.0 (R Core Team 2017). We then used JMP Pro 13 (SAS 2013) to identify the set of environmental variables that best predicted total amphibian abundance and richness. We created all possible models consisting solely of main effects and selected the one with the lowest AIC_c.

Scope and inclusion criteria for literature review

The goal of our review was to synthesize all available literature on impacts of livestock grazing on amphibians. We searched Web of Science and Google Scholar using a series of keywords (Table 1) derived from reviews by Winter et al. (2018) and Schieltz and Rubenstein (2016). Each combination of these search terms was used to search both databases. Searches were conducted between 1 April 2018 and 28 May 2018. For all combinations of terms, we examined the first 100 query results in both databases. If it was obvious from the title that the study did not include information pertinent to the search terms it was excluded. After the first round of exclusion based on article titles, the abstracts of the remaining articles were examined to exclude any that were not pertinent to the search terms. Upon reading the remaining articles we excluded two more studies that did not have enough replicates to provide statistical power for their results ($N < 4$ per treatment), three studies that only analyzed the effects of grazing with other management strategies (e.g., burning) or land use change (e.g., coffee plantations, sugar cane fields), and five studies/reports that recorded direct mortality events of individual amphibians but did not have control sites or did not attempt to examine the effects of livestock on amphibian abundance, diversity, or richness. Finally, we examined the literature cited of the included papers to garner further studies that might have been missed during the original literature search. Only sources that had at least their title and abstract published in English were used in this review, likely geographically biasing our results.

Table 1. List of keywords used in the Web of Science and Google Scholar literature searches.

Livestock-related words	Amphibian-related words
Livestock	Frog
Cattle	*amphib*/amphibian
Sheep	Toad
Goat	Newt
graz/grazing	Salamander
ranch/ranching	*anura*/Anuran
	Caudata
	Gymnophiona
	Caecilian

Data extraction for literature review.—Conducting a formal meta-analysis would require information regarding the means and variances of paired grazed and un-grazed sites from studies that used similar methodologies. These data could be used to calculate the magnitude as well as the direction of the effect recorded by each study to more accurately compare the effects of livestock exclusion on amphibians. Out of the 46 papers included in our literature review, only 9 (20%) recorded the data necessary to calculate the magnitude of the effect of livestock on a common response variable (amphibian richness). Previous reviews have also been unable to conduct formal meta-analyses on the impacts of cattle grazing due to a lack of unified methodologies and response variables (Fleischner 1994, Jones 2000, Schieltz and Rubenstein 2016). As a result of these limitations, we instead focused solely on the direction of effects, categorizing the impact of cattle on each response variable as either positive, neutral, or negative.

In order to categorize effects in this manner, we searched the Results section of each study for changes in species abundance, species survivorship rates, species presence/absence, or community richness. If studies reported positive effects for one species and negative effects for another species, then the results for the study as a whole were considered to be neutral. We further extracted effect scores at the species level by recording the impact that all studies reported on individual species as a 1 (positive), 0 (neutral), or −1 (negative) effect. To compare effect scores based on species' preferred habitat type, we extracted habitat information for each species from the IUCN website (https://www.iucn.org/commissions/ssc-groups/amphibians-reptiles/amphibian; see Appendix S1: Table S1 for a list of species' habitat classifications and sources). We then categorized the species' preferred habitat into open canopy (e.g., lakes, marshes, flooded grasslands, ponds), closed canopy (e.g., swamps, wooded areas, pine savannas, cloud forests), or mixed (where both habitat types were listed). For a list of all the data extracted from each paper included within the literature review see Appendix S2: Table S2.

Statistical analysis for literature review.—If multiple studies reported results on a single amphibian species, we averaged the effect scores to get a single species mean score that was used in all further analyses. There were no cases in which separate studies reported both positive and negative effects of grazing on the same amphibian species. When studies conflicted, the results were either a mix of neutral and positive effects or neutral and negative effects. We used a Kruskal-Wallis test to determine if preferred habitat type (open, closed, or mixed), sampling method, continent, or phylogenetic clade were predictive of species' mean effect scores. Sampling method categories were: passive collection (drift fences, cover boards, minnow traps, etc.), active collection (visual encounter surveys, vocalization surveys, egg mass counts, etc.), or a mix of both active and passive methods.

To investigate the potential influence of climate on the effect of livestock grazing on amphibians, we used the 19 Bioclim variables retrieved from the WorldClim database (Hijmans et al. 2005), which represent combinations of temperature and precipitation variables, and extracted the values of each variable from the georeferenced locality of each study. We then conducted a series of multinomial logistic regressions between each climate variable and the effect scores to test for a relationship between climate and livestock impact on amphibians. To reduce the likelihood of a Type I error from multiple comparisons we applied a Bonferroni correction. All data were analyzed using JMP Pro 13 (SAS 2013).

Results

Results from MAERC

In total we collected 725 individuals of 12 amphibian species in the 47 sampled wetlands at MAERC. Species richness averaged 2.3 ± 0.25 (mean ± SE), and ranged from 0 to 7 species per wetland. The amphibian community composition largely overlapped with the composition detected by other studies at this site (Babbitt et al. 2009, Medley et al. 2015). Mean amphibian abundance across wetlands was 15 ± 2.8 (SE) and ranged from 0 to 70 individuals. The most abundant species was the squirrel treefrog (*Hyla squirella*), with a mean abundance of 8.7 ± 2.5 individuals. Six wetlands having zero amphibian captures were excluded from the community composition analysis, as were three amphibian species found in only a single wetland. This resulted in a final community matrix consisting of 40 wetlands, nine species, and 30% matrix fill. According to PERMANOVA, amphibian community composition did not differ between cattle excluded and grazed wetlands ($P = 0.08$) or between semi-native and improved pastures ($P = 0.21$). From the db-RDA we found that overall, the environmental variables had a significant effect on species composition ($P = 0.002$; Fig. 1). Individual variables that had significant effects were fish abundance ($P = 0.006$), depth ($P = 0.01$), and nitrates ($P = 0.04$; Fig. 2). Model selection identified fish abundance ($P < 0.001$) and nitrates ($P = 0.08$) as the most important environmental factors explaining amphibian abundance. Abundance was positively related to nitrates and negatively related to fish abundance (Abundance = 0.03 − 0.56 (Fish) + 0.21(Nitrates)). Model selection identified area ($P = 0.002$), depth ($P = 0.008$), nitrates ($P = 0.08$), and fish ($P = 0.11$) as the most important environmental factors explaining amphibian species richness. Richness was positively related to depth and area and negatively related to nitrates and fish (Richness = −0.02 + 0.41 (Area) + 0.35(Depth) − 0.21(Nitrates) − 0.20(Fish)).

Literature review

Forty-six papers met our criteria for inclusion in the review. Of these, 15 found positive effects of livestock on amphibians, 21 found neutral/mixed effects, and 10 found negative effects (for a list of citations see Table 2). From these studies, we retrieved data on 47 species of amphibians (see Appendix S1: Table S1).

Geographical bias.—We retrieved studies from five of the six continents where amphibians occur. However, the majority of these studies (59%) were conducted in the United States alone, and 74% were conducted in either North America or Europe. The two largest geographical areas lacking studies include the entire continent of Africa and the area between longitudes 25° E and 103° E (Fig. 3). There was a significant effect of continent on mean effect scores ($\chi^2_3 = 15.77$, $P = 0.0025$; we did not include Asia or Africa in the analysis due to extremely low sample size). Based on pairwise comparisons using the Steel-Dwass Method, only Europe (mean effect score = 1.0) and North America (mean effect score = −0.25) were significantly different from each other ($P = 0.0035$).

Taxonomic bias.—Studies included effects on a total of nine anuran families and three caudate families (Table 3). Within the nine anuran families, the majority of species (78%) were from just three families (Bufonidae, Hylidae, and Ranidae). While hylids had slightly lower effect scores (−0.3) than either bufonids (0.28) or ranids (0.19), these differences were not significant ($\chi^2{}_2 = 2.55$, $P = 0.28$). There was also no significant difference in effect scores of anurans vs. caudates ($\chi^2{}_1 = 0.79$, $P = 0.37$).

Collection bias.—Of the 46 studies, 12 utilized some type of collection method (pitfall traps, cover boards, drift fences, dip-netting, etc.), 17 studies utilized some type of encounter method (either time-constrained or transect visual encounter or auditory surveys), and 16 studies used a combination of these techniques (we were unable to determine the methodology of Jian-hong et al. (2005) because the main text was written in Chinese). We found no significant difference in mean effect score between sampling methods ($\chi_2{}^2 = 3.89$, $P = 0.14$).

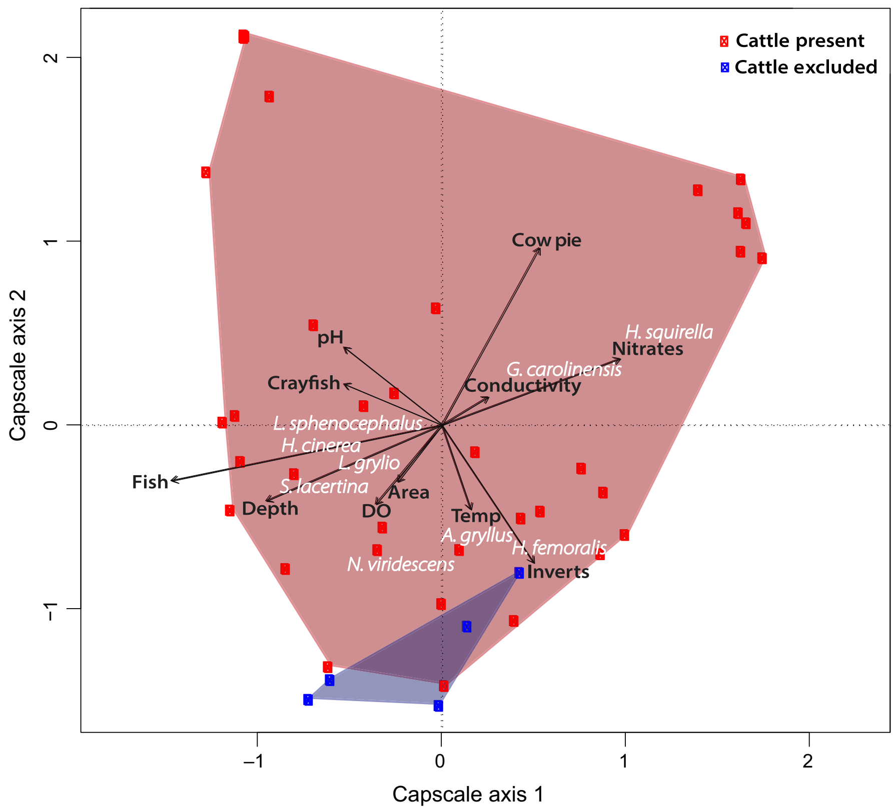

FIG. 1. Ordination plot from a dbRDA showing the relationship between habitat variables and amphibian community composition in a south-central Florida, USA rangeland. Red dots represent ponds that were open to grazing and blue dots represent ponds where cattle were excluded, with each set surrounded by a minimum convex hull. Arrows illustrate the correlation between individual environmental variables and the ordination space. Species names are central to the ponds where that species was most likely to be found see Appendix S1: Table S1.

Parameter	Community composition	Amphibian abundance	Amphibian richness
Fish abundance	0.006	**-0.56** 0.00003	**-0.20** 0.11
Cattle presence	0.08		
Depth	0.01		**0.35** 0.008
Area			**0.41** 0.002
Nitrates	0.04	**-0.21** 0.08	**0.21** 0.08

P > 0.11
P = 0.1
P = 0.005

FIG. 2. Heat map displaying the habitat variables most predictive of amphibian community composition (PERMANOVA and dbRDA) and amphibian abundance and richness (model selection). Values in boldface type are parameter estimates for each of the variables, while lightface type illustrates P values, which are color coded according to the color ramp on the right. Seven variables (conductivity, DO, pH, temp, Cow pie, invertebrates, and crawfish) are not included in the figure, because they did not appear in any of the top models.

Habitat type.—There was a significant relationship between amphibian habitat type and the effect of livestock grazing ($\chi_2^2 = 11.53$, $P = 0.0031$), with species adapted to open and mixed canopy types having similar mean effect scores of 0.39 and 0.36 (positive effect), respectively, whereas species adapted to closed canopies had a mean effect score of –0.78 (negative effect; Fig. 4).

TABLE 2. List of studies finding negative, positive, and mixed effects of livestock grazing on amphibians.

Studies finding negative effects	Studies finding mixed/no effects	Studies finding positive effects
Arkle and Pilliod (2015)	Adams et al. (2009)	Buckley et al. (2014)
Babbitt et al. (2009)	Babbitt et al. (2006)	Cabrera-Guzmán et al. (2013)
Hoverman et al. (2011)	Badillo-Saldana et al. (2016)	Cogălniceanu et al. (2012)
Jansen and Healey (2003)	Bower et al. (2014)	Fellers and Guscio (2004)
Jofre et al. (2007)	Bull and Hayes (2000)	González-Bernal et al. (2012)
Knutson et al. (2004)	Bull et al. (2001)	Hartel and von Wehrden (2013)
Muenz et al. (2008)	Burton et al. (2009)	Hartel et al. (2014)
Pilliod and Scherer (2015)	Cole and North (2014)	Jian-hong et al. (2005)
Reidel et al. (2008)	Cole et al. (2016)	Marty (2005)
Schmutzer et al. (2008)	Gray et al. (2007)	Mester et al. (2015)
	Homyack and Giuliano (2002)	Moreira et al. (2016)
	Howard and Munger (2003)	Pelinson et al. (2016)
	Kay et al. (2017)	Plăiasu et al. (2010)
	Larson (2014)	Pyke and Marty (2005)
	McIlroy et al. (2013)	Rannap et al. (2007)
	Munger et al. (1998)	
	Roche et al. (2012*a*)	
	Roche et al. (2012*b*)	
	Shovlain (2005)	
	Verga et al. (2012)	
	Watson et al. (2003)	
N = 10	N = 21	N = 15

Climatic context.—Of the 19 Bioclim variables, Bio2 (mean diurnal temperature range; $P = 0.0002$), Bio5 (maximum temperature of the warmest month; $P = 0.021$), Bio8 (mean temperature of the warmest quarter; $P = 0.029$), and Bio15 (precipitation seasonality; $P = 0.0055$) were significantly correlated with the effect of livestock on amphibians. Bio2 and Bio5 were negatively correlated with the effect of livestock on

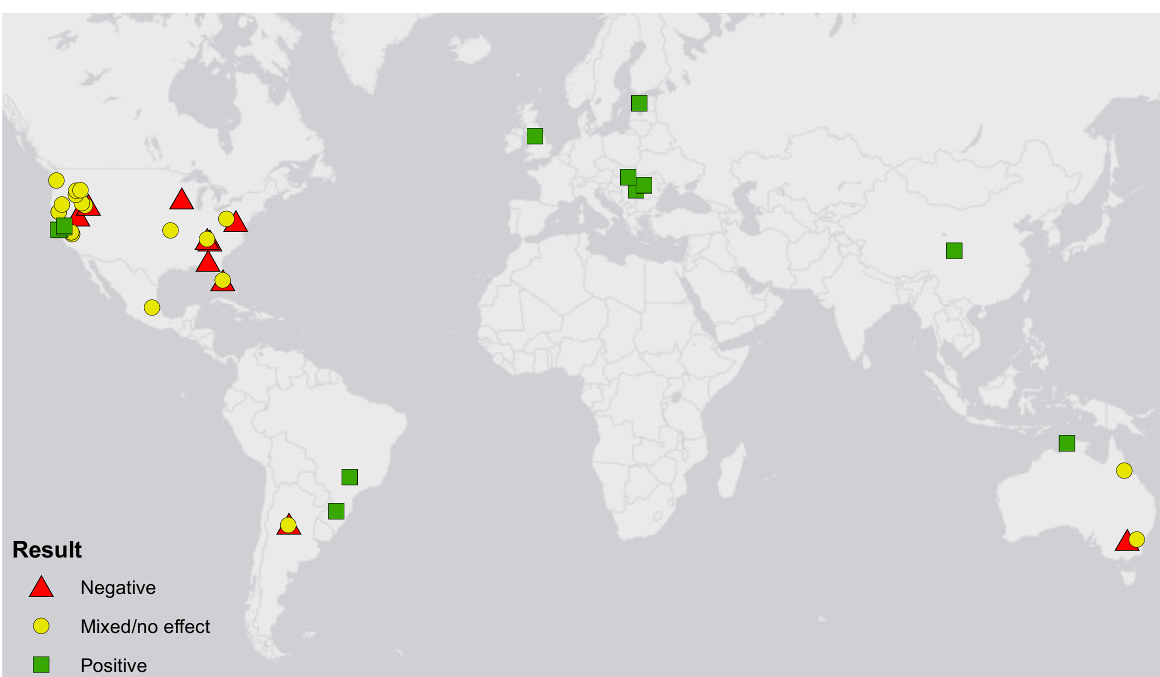

FIG. 3. Locations of the reviewed studies examining the impacts of livestock grazing on amphibian abundance and richness. Of the 47 studies, 28 were conducted in the United States and 7 were conducted in Europe.

Table 3. Amphibian orders and taxonomic biases of the reviewed studies.

Order	Number of families	Number (%) of families studied	Number of species studied	Number of studies
Anura	55	9 (16%)	41	43
Caudata	10	3 (30%)	6	8
Gymnophiona	10	0	0	0

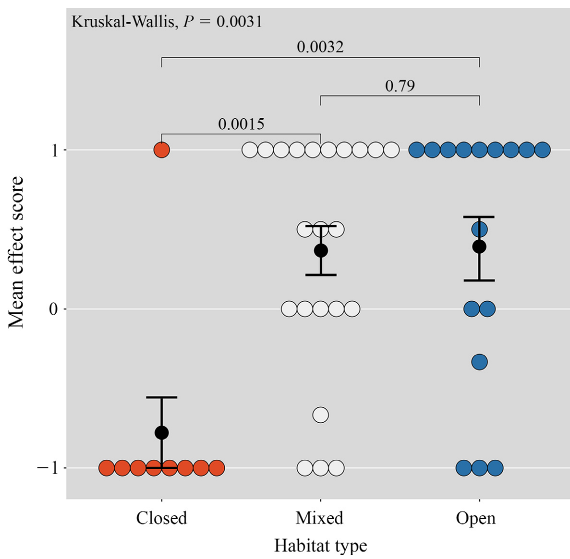

Fig. 4. Strip plot displaying amphibian species' response to livestock. Amphibians that prefer closed-canopy habitat are more negatively affected by livestock than are amphibians that prefer open-canopy or mixed habitats types. Each white, red, or blue circle represents an amphibian species; black circles are means for each habitat type ± SE.

amphibians (i.e., as the Bioclim values increase, the effect of livestock on amphibians became more negative). Bio15 was positively correlated with the effect of livestock on amphibians (i.e., as precipitation seasonality increased, the effect of livestock on amphibians became more positive), and Bio8 was positively correlated with studies that had neutral/mixed effects. However, after correcting the α value with a Bonferroni correction for multiple comparisons, only Bio2 remained significant ($P < 0.0026$).

Discussion

Our empirical data, collected in a subtropical rangeland in south-central Florida, corroborate other studies demonstrating that well-managed rangelands (those carefully managed to prevent overgrazing) can support robust amphibian communities. Our analyses detected the same drivers of amphibian richness (depth) and amphibian abundance (fish) as previous studies at this site (Babbitt et al. 2006, 2009), indicating that our sampling effort was sufficient to detect the primary factors influencing amphibian community composition, and cattle were not among them. We analyzed amphibian community responses to cattle as both a binary (presence/absence) variable and as a continuous variable based on cow pie density. Neither approach indicated that cattle were a significant factor influencing amphibian community composition, richness, or abundance.

The results from our quantitative review provide additional evidence that the impact of livestock on amphibians is highly variable and dependent on both species' habitat type and climatic context. Since previous reviews on other taxa have recorded mostly negative effects of livestock grazing, we expected to find similar results. However, 45% of the examined studies reported mixed/no significant impact and 34% of the studies reported positive effects of livestock. Additionally, our results demonstrate that the known habitat preference of each species is a useful predictor of how that species will respond to livestock grazing. Species that preferred open-canopy habitat had a mean effect score of 0.39, whereas species that preferred closed-canopy habitat had a mean effect score of −0.78. This result supports the hypothesis that responses to livestock activity are a function of evolutionary history and how much a species' niche is impacted by grazing pressure (Milchunas et al. 1988, Neilly et al. 2018). For species that have a long evolutionary history of existence in open-canopy habitat subject to grazing or other frequent disturbance, cattle presence at stocking densities that avoid overgrazing and subsequent habitat degradation may not only be harmless but beneficial.

Negative amphibian responses

In studies that found negative responses to livestock (21%), researchers documented lower dissolved oxygen, increased rates of sedimentation, loss of valuable riparian habitat, direct mortality through trampling of eggs and adults, increased nitrate levels, and increased temperature (see Table 2 for a list of citations). Jansen and Healey (2003), Schmutzer et al. (2008), and Babbitt et al. (2009) all reported lower amphibian species richness in grazed wetlands compared to non- or lightly grazed wetlands. Other studies have reported depressed population sizes and occupancy rates, increased juvenile and adult mortality, and increased prevalence of diseases (Gray et al. 2007, Jofre et al. 2007, Arkle and Pilliod 2015, Pilliod and Scherer 2015). Some of these negative impacts are dependent on grazing intensity, duration, timing, and frequency. Amphibian responses likely become more pronounced as stocking rates become high enough to cause overgrazing and subsequent wetland degradation. Watson et al. (2003) reported that moderate grazing removed dense stands of reed-canary grass (*Phalaris arundinacea*) and created habitat for the Oregon spotted frog (*Rana pretiosa*); however, heavy grazing removed too much emergent vegetation and resulted in unsuitable habitat. Munger et al. (1998) found that short-term grazing did not significantly affect the presence of either Columbia spotted frogs (*Rana luteiventris*) or Pacific treefrogs (*Hyliola regilla*), but that long-term overgrazing led to a lower water table and loss of critical riparian habitat.

Our literature review focused on the direct consequences of livestock grazing and consequently we did not attempt to consider or quantify the indirect impacts of deforestation or general land-use change that normally preface the transition to rangeland (Nicholson et al. 1994, Angelsen and Kaimowitz 2001). Numerous studies have shown a positive correlation between amphibian diversity and abundance and the amount of surrounding forest cover (see Cushman 2006 for a review). As overall habitat destruction is a major component of global amphibian declines (Kiesecker and Blaustein 1995, Collins and Storfer 2003, Blaustein et al. 2011), the conversion of any closed-canopy habitat into rangeland through wide-scale deforestation will likely cause a substantial decline in the amphibian biodiversity of an area (Cushman 2006).

Neutral/mixed amphibian responses

In contrast to other reviews assessing the impact of livestock, we recorded more studies with no/mixed effects than either positive or negative effects. Studies have shown that some amphibian species either select for different habitat than livestock (Roche et al. 2012*a,b*) or complete their annual breeding cycle before water quality degradation becomes severe enough to affect reproduction (Canals et al. 2011). It is also likely that the presence of livestock often has simultaneously negative (decreased water quality and increased direct mortality) and positive (decreased emergent vegetation and increased hydroperiod) impacts on amphibian communities, making detection of a purely positive or negative net effect less likely. Additionally, some effects may be highly dependent on the environmental context. For example, the increase in wetland hydroperiod as a result of soil compaction and reduced evapotranspiration has positive impacts in arid environments where hydroperiods are generally very short, but in some landscapes may increase the probability that a wetland will contain predatory fish and ranavirus (Pyke and Marty 2005, Hoverman et al. 2011, Richter et al. 2013). Furthermore, studies undertaken during stressful environmental conditions (e.g., drought, very cold winters) hypothesized that the additional stress of extreme weather coupled with the impact of the cattle may have exacerbated the negative impacts of livestock (Bower et al. 2014, Pilliod and Scherer 2015).

It also appears that, in some cases, other local abiotic and biotic variables are more important factors in determining amphibian community composition than livestock grazing. For example, in six out of nine studies that analyzed the importance of predatory fish (mainly introduced trout species), researchers found that the presence of fish was more important than livestock for predicting amphibian abundance and/or richness. The results from our empirical study mirror this finding from the literature. The results from our dbRDA and PERMANOVA show that fish and depth are far more important drivers of amphibian abundance and richness than either a categorical or continuous measure of livestock presence. Species that are adapted to reproducing in permanent water bodies (e.g., pig frog [*Lithobates grylio*], greater siren [*Siren lacertina*]) were more likely to occur in ponds with greater depth and more fish, whereas other amphibian species are unable to tolerate these conditions. Thus, the primary axis influencing amphibian community composition is the gradient from permanent hydrology/with fish to temporary hydrology/fishless, rather than factors related to livestock grazing.

Positive amphibian responses

We recorded 16 studies that documented positive responses of amphibians to livestock, either by preventing succession or by increasing the hydroperiod of wetlands through soil compaction and/or a reduction in evapotranspiration. In areas of Europe, the use of livestock grazing to prevent ecological succession has been a successful management strategy for the natterjack toad (*Epidalea calamita*; Rannap et al. 2007, Buckley et al. 2014), the common toad (*Bufo bufo*; Hartel and von Wehrden 2013, Hartel et al. 2014), and the common frog (*Rana temporaria*; Plăiasu et al. 2010, Cogălniceanu et al. 2012). In the arid environments of California and the mountains of eastern Europe, decreased rates of evapotranspiration and soil compaction from cattle trampling increases hydroperiod enough for amphibians to complete their annual breeding cycles in ephemeral wetlands (Marty 2005, Pyke and Marty 2005, Cogălniceanu et al. 2012). For species like the natterjack toad (*Epidalea calamita*), California tiger salamander (*Ambystoma californiense*), and California red-legged frog (*Rana draytonii*), the species' continued persistence is now likely tied to livestock activity maintaining early successional habitat at breeding sites (Fellers and Guscio 2004, Marty 2005, Pyke and Marty 2005, Rannap et al. 2007, Buckley et al. 2014). In these instances, livestock are replacing the ecological role lost by the disappearance of native megafaunal grazers (Rannap et al. 2007, Buckley et al. 2014).

In other cases, the transition to rangeland increases the number of ephemeral wetlands dispersed across a landscape (Babbitt et al. 2006, 2009, Hartel and von Wehrden 2013). These ephemeral wetlands generally lack predatory fish and increase the availability of suitable breeding habitat for amphibians (Babbitt et al. 2006, 2009, Hartel and von Wehrden 2013). In our field study, both narrow-mouthed toad (*Gastrophryne carolinensis*) and squirrel treefrog (*Hyla squirella*) were negatively associated with fish and wetland depth, and positively associated with nitrates, which have been previously tied to cattle (Hack-ten Broeke et al. 1996, Rouse et al. 1999; Fig. 1). Perhaps generalist amphibian species such as the narrow-mouthed toad and squirrel treefrog (Carr 1940, Dodd and Cade 1997) are those most likely to benefit from the proliferation of livestock-associated wetlands.

Role of climatic variables

Our review also provides insight into how environmental factors, such as climate, may mediate effects of livestock grazing on amphibians. The negative correlation between Bioclim variables 2 (mean diurnal range) and 5 (max temperature of warmest month) and the effect of livestock grazing suggests that colder temperatures with less daily temperature fluctuations may mitigate the effect of livestock on amphibians. Colder water stores more dissolved oxygen, is less likely to have detrimental algal blooms, and has lower electrical conductivity. Because overgrazing is known to contribute to increased rates of oxygen consumption, increased nitrate levels (leading to increased conductivity), and eutrophication leading to algal blooms, cooler climates may provide a buffer against negative impacts from livestock's use of wetlands. Of the 10 study sites with the lowest mean diurnal temperature range, 9 detected positive effects and one detected no/mixed effects of livestock. Seven of those studies were in Europe, where all reported effects of cattle grazing were positive (Fig. 3). We also observed a positive correlation between precipitation seasonality (Bio15) and positive effects of livestock grazing. Areas that have high precipitation seasonality (distinct wet and dry seasons) will generally have shorter hydroperiod wetlands. Under these conditions, having cattle increase the hydroperiod of a wetland through soil compaction and a reduction in evapotranspiration rates may allow ephemeral wetlands to persist for longer periods and turn once unsuitable habitat into suitable breeding sites (Marty 2005, Pyke and Marty 2005).

Review limitations

There were several issues with the accumulated studies used in the review that preclude us from identifying clearer management recommendations. First, many studies categorized grazing into a binary variable consisting of "grazed" and "ungrazed" sites. This lack of a continuous measure of cattle use has also been noted as an issue in previous reviews (Barrett et al. 1999, Briske et al. 2011, Schieltz and Rubenstein 2016). Studies that attempted to experimentally control frequency, duration, or intensity of cattle grazing generally had low levels of replication. Our review was also limited to papers that had at least an English language abstract; if papers were published entirely in another language the search terms would not have returned them as a result. Consequently, there may be some published results that we were unable to include in this review.

Our quantitative review also highlights several geographic and taxonomic biases in the collated studies. The majority (75%) of studies were conducted in North America and Europe, despite South America and Asia harboring both higher diversity and a larger proportion of threatened amphibian species (Jenkins et al. 2013). These high-diversity areas often coincide with regions of high mean temperature, which our analyses suggest may exacerbate negative effects of livestock grazing. This is alarming, as the developing world is currently undergoing a massive expansion in the amount of meat products produced and consumed (Steinfeld et al. 2006, Bruinsma 2009, Kastner et al. 2012, Laurance et al. 2014). As the demand for meat products increases, habitat that was previously considered marginal will be slowly converted into pastureland to increase meat production. It is more critical than ever that we have studies that provide robust understanding of amphibian responses to livestock production in these developing areas. Even in countries where multiple studies have been conducted, the focal taxa were often restricted to just three anuran families (i.e., Bufonidae, Hylidae, and Ranidae). The Columbia spotted frog (*Rana luteventris*) alone has had six separate studies (13% of all studies included in our literature review) assessing the impact of livestock grazing on their populations. Future studies should address this taxonomic bias by focusing on understanding the impact of livestock on either unstudied amphibian species or on amphibian communities as a whole.

Interestingly, our review also points out potential biases in the citation of literature examining the impact of livestock on amphibians. Studies that recorded negative effects of livestock on amphibians were cited approximately twice as frequently (mean = 35 citations) as papers that found either neutral (mean = 12) or positive (mean = 17) effects of livestock on amphibians (citation numbers aggregated from Web of Science Citation Database as of 26 August 2018). While these differences were not statistically significant, even when controlling for date of publication ($F_{2,36} = 1.49$, $P = 0.24$), it is concerning to see that papers finding neutral or positive impacts are cited less. To this end, Jones (2000) criticized Fleischner's (1994) highly cited review of grazing in western North American ecosystems as being biased toward using only studies reporting negative impacts of livestock. Future authors should make a concerted effort to position their findings within the total scope of the literature and not within a subset of papers that reflect the results of their study.

Rangelands as "off-reserve" management areas

A global target of 17% of land being set aside as protected areas has been proposed to limit the global loss of biodiversity (Convention on Biological Diversity 2011). While preventing habitat loss is an obvious necessity in preventing the loss of global amphibian biodiversity, several authors have raised concern about the quality of the lands set aside as reserves (Mora and Sale 2011, Venter et al. 2014). Indeed, several studies have detected declines of amphibians within protected areas, raising questions about their efficacy to protect biodiversity in the long term (Fellers and Drost 1993, Knapp and Matthews 2000, Bosch et al. 2001). Using a system of carefully managed, "off-reserve" areas to supplement the biodiversity of protected areas may allow for the maintenance of greater biodiversity at a landscape or regional scale (Mora and Sale 2011). Because rangeland ecosystems tend to be more compatible with wildlife use than other more intensive forms of agriculture, they may be able to contribute to an "off-reserve" system designed to reduce global biodiversity losses (Delaney and Linda 1994, Morrison and Humphrey 2001, Babbitt et al. 2009). The results of our literature review and empirical data set support the notion that for at least some amphibian species, particularly ones with an evolutionary history tied to open-canopy habitats, a well-managed rangeland is compatible with maintaining amphibian species richness and may act either as a compliment to protected areas or in special cases serve as a stand-alone reservoir of viable populations (Homyack and Giuliano 2002, Burton et al. 2009, Verga et al. 2012, Mester et al. 2015). In peninsular Florida, the high number of seasonally inundated wetlands (Babbitt and Tanner 2000, Baber et al. 2002) and intact woodlands present on many ranches provide enough habitat to maintain high amphibian diversity while simultaneously being used for commercial cattle production (Babbitt et al. 2006, 2009, this study). Furthermore, off-reserve habitat on private lands managed by livestock grazing is critical for some imperiled species, such as the natterjack toad, California tiger salamander, and California red-legged frog (Fellers and Guscio 2004, Marty 2005, Pyke and Marty 2005, Rannap et al. 2007, Buckley et al. 2014).

Management recommendations

We are limited in our ability to provide management recommendations given the lack of data on stocking rates and rotation schedules in many of the studies examined by our literature review. As noted in other reviews, even some studies that reported "overgrazing" did not define the criteria used to merit this classification (Schieltz and Rubenstein 2016). Studies have shown that, in some instances, maintaining cattle at an intermediate stocking density, that reduces the potential for overgrazing, can return the greatest profit margin while still providing adequate habitat for reptiles (Neilly et al. 2018), rangeland vegetation (Holechek et al. 2006), ungulates (Schieltz and Rubenstein 2016), and lepidopterans (Weiss 1999). This growing body of evidence suggests that a well-managed rangeland ecosystem can maintain high levels of biodiversity and provide necessary income for landowners, though it remains a task for future researchers to clarify which grazing regimes produce these benefits.

The results of our analysis show that species adapted to closed-canopy ecosystems are generally negatively impacted by the presence of livestock. As an example, the Hylidae (tree-frog) family, a group generally adapted to closed canopy ecosystems, had the most negative effect score out of the three amphibian families with adequate sample sizes. Additionally, the results of our climate analyses provide support to the management recommendations of Neilly et al. (2018) and Smith et al. (2012) that stocking rates and management strategies need to be adapted to specific landscape types and ecoregions. Areas with cooler overall temperatures and less diurnal fluctuations may be buffered from some of the negative impacts of livestock grazing. While it would be optimal from the perspective of amphibian biodiversity to prevent any further deforestation in the pursuit of increased livestock production, global demand for meat products continues to rise and the inevitable consequence will be a rising need for additional rangeland. While the loss of high quality natural habitat to rangeland will undoubtedly result in a loss of amphibian biodiversity, understanding how to best use rangelands to manage amphibian biodiversity will be a critical component of mitigating long-term amphibian biodiversity declines.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1976/full

Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.q15p9d0