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RESEARCH ARTICLE

A meta-analysis of the effects of habitat aridity, evolutionary history of grazing and grazing intensity on bee and butterfly communities worldwide

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Abstract

1. A variety of habitat-associated factors moderate effects of grazing on insect biodiversity. Here, we examine how aridity, evolutionary history of grazing and grazing intensity individually and interactively mediate the effect of livestock grazing on pollinator biodiversity (native bees and butterflies).
2. Using a meta-analysis of 59 studies published in the primary literature, we characterized the response of pollinator communities to grazing across several continents.
3. In very humid habitats, high grazing intensities generally had negative impacts on pollinator abundance and richness, but these effects were not found in semi-arid habitats, where livestock grazing intensity did not interact with aridity to impact pollinator abundance or richness. However, within semi-arid habitats livestock grazing was associated with reduced pollinator richness in areas with short evolutionary histories grazing.
4. Pollinator life history mediated effects of livestock grazing on pollinator communities: livestock grazing had negative impacts on richness of social bees and butterflies but not solitary bees, though abundances of all three pollinator categories were consistently reduced under livestock grazing.
5. Our synthesis suggests that effects of cattle on pollinators may be driven by impacts on nesting habitats (e.g. soil compaction), rather than consumption or alteration of forb cover. Our collective findings have importance for coordinating grazing management and pollinator conservation efforts and help to distinguish how grazing practices could impact pollinator biodiversity across ecoclimatic regions.

KEYWORDS
butterflies, cattle, grazing effects model, livestock grazing, native bees, rangeland

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1 INTRODUCTION

Rangelands are a globally abundant ecosystem type covering an estimated 54% of terrestrial ecosystems (Estell et al., 2012; Reynolds et al., 2007). Rangelands provide key ecosystem services and support the livelihoods of millions of people by providing subsistence and pastoral opportunities (Derner et al., 2017). In addition to benefitting human well-being, rangelands provide critical habitats and foraging resources to a variety of wildlife, including insects. Insects, especially bees (Hymenoptera) and butterflies (Lepidoptera), are among the most important taxa driving key ecological interactions such as pollination. An estimated 90% of the world's plant species are pollinated by insects, and bees and butterflies are perhaps the most common flower visitors, providing the foundation for pollination services across many ecosystems (Ollerton et al., 2011). Pollination plays a vital role in ecosystem function and is important for maintaining genetic diversity in wild and managed plant populations, promoting biodiversity and enhancing the economic value of many agricultural crops (Chaplin-Kramer et al., 2011). However, some evidence indicates that insect pollinators are declining in rangelands due to anthropogenic disturbances, environmental stressors and ecosystem management practices including grazing by livestock (Potts et al., 2010; Rafferty, 2017). Accordingly, there is a broad need to understand how livestock grazing affects pollinators across different rangeland environments.

Livestock grazing is a common land use practice in rangeland ecosystems, and is an important process for converting plant biomass into animal protein for human consumption (Alkemade et al., 2013; Asner et al., 2004). Livestock grazing practices on rangelands are regarded both critically and favourably by natural resource managers due to their dual nature as potential disturbances and as management tools, respectively, and it is increasingly recognized that appropriate management of rangelands is needed to conserve ecosystem services across large spatial scales. In some cases, livestock grazing practices may conflict with conservation goals and several recent studies demonstrate direct or indirect negative effects of livestock grazing on pollinator biodiversity. For example, direct effects of livestock on pollinators include destroying nesting and foraging habitats through soil compaction or consumption of floral resources (Glaum & Kessler, 2017; Moreira et al., 2019) and the trampling of adult bees and their larvae (Sjödin, 2007; Sugden, 1985). In contrast, indirect effects may be mediated by the plant community response to livestock grazing including altered plant assemblages and floral species composition (Carvell, 2002; Hatfield & LeBuhn, 2007; Smallidge & Leopold, 1997; Roulston & Goodell, 2011). On the other hand, several studies have also demonstrated positive effects of livestock grazing on pollinator diversity (Kruess & Tscharntke, 2002; Sjödin, 2007).

However, the effects of livestock grazing on pollinators are likely mediated by a variety of site-specific as well as global factors. For example, regional differences in the evolutionary history of livestock grazing may interact with grazing pressure (intensity) and ecosystem aridity to drive plant diversity, which could have consequences for plant–pollinator interactions. Earlier conceptual models of plant diversity (i.e. Milchunas et al. 1988) predict that areas with long evolutionary histories of grazing by large native herbivores experience little-to-no reduction in plant biodiversity with increased livestock grazing pressure; however, in areas with short evolutionary histories of grazing by large herbivores, increased livestock grazing pressure is associated with rapid decline in plant biodiversity. In contrast, in humid or mesic regions with long evolutionary histories of large herbivore grazing, livestock grazing tends to maximize plant diversity at intermediate levels, and this relationship is similar but truncated in humid regions with short evolutionary histories of grazing by large native herbivores. Recent meta-analyses (e.g. Gao & Carmel, 2020; Herrero-Jáuregui & Oesterheld, 2018) have tested these interactions for plant communities, with mixed support for the original conceptual model proposed by Milchunas et al. (1988). However, it remains unknown if similar principles may broadly extend to pollinator assemblages, though some authors have recently investigated this idea (Filazzola et al. 2020; Hanberry et al., 2020). An understanding of how relationships between livestock grazing pressure, evolutionary history of large herbivore grazing and ecosystem aridity affect pollinator assemblages carries implications for global pollinator conservation and can help to prioritize rangeland management efforts.

Using a meta-analysis, the goal of the present study is to evaluate variation in pollinator community abundance and richness by describing the response of pollinators to livestock grazing under various grazing pressures, coevolutionary histories, and regional-scale environmental factors (aridity). Specifically, we address the following questions: (1) Does ecosystem aridity mediate effect of livestock grazing pressure on pollinator diversity?; (2) Do ecosystem aridity and evolutionary history of large herbivore grazing interact to affect pollinators?; and (3) Do livestock grazing effects on pollinator communities differ with respect to pollinator life histories? Our study provides new insights into the dynamics of livestock grazing-mediated effects on pollinator assemblages at a worldwide scale, with importance for interpretation of factors driving diversity and distribution of insect communities that provide key ecosystem services.

2 MATERIALS AND METHODS

2.1 Data collection

We collated primary literature that meets our research objectives from an online database (ISI Web of Science, hereafter 'WOS') using the following word combinations: (graz* OR livestock OR cattle OR sheep OR goat) AND (pollina* OR hymenoptera OR bee OR bumblebees OR butterfly OR lepidopteran) (see PRISMA flow chart, Supporting Information 1). Other managed grazers (e.g. alpacas, llamas, reindeer, horses, etc.) were omitted from our final search because too few articles existed from which to draw meaningful conclusions. We only included articles published in English in the field of ecology, plant sciences, environmental sciences, biodiversity conservation and entomology to discard unrelated research to our study and reduce redundancy in the WOS article retrieval process. The literature searches were performed at two different times and results were pooled: a first search was made in June 2020 and second in December 2020. In addition, we used literature cited in previous research syntheses and meta-analyses about the response of pollinators to grazing (e.g. Filazzola et al., 2020; Tonietto & Larkin, 2018; Wang & Tang, 2019; Winfree et al., 2009). In total, our search yielded 1478 articles and this number was subsequently reduced to 106 articles for full-text assessment by manually screening the titles and abstracts (Supporting Information 1).

Our meta-analysis explicitly focuses on studies of wild bees and butterflies (hereafter, referred to as 'pollinators'). Studies focusing on honeybees (*Apis mellifera*) were excluded from analysis. In our meta-analysis, we included those studies that reported the effect of livestock grazing on pollinator abundance and richness and provided statistical parameters that included means, standard deviations or standard errors and sample sizes under conditions of livestock grazing and grazing exclusion, focusing on natural rangeland habitats (i.e. not planted paddocks or pastures). Grazing treatments could include several levels (low, moderate and heavy livestock grazing), if indicated by the authors of the study. Many articles lacked a description of discrete grazing pressure metrics such as animal unit months (AUM)/hectare (ha) or per cent plant biomass consumed (i.e. utilization). Accordingly, grazing pressure categories are unitless and may vary relative to ecosystem productivity (e.g. 'heavy' livestock grazing pressure is likely evaluated differently by studies in low-productivity habitats with high evapotranspiration demands compared to studies from high-productivity mesic habitats with low evapotranspiration). For studies that compared intensive versus extensive livestock grazing practices, intensive grazing was considered as high grazing pressure and extensive grazing was considered as low grazing pressure. We excluded articles that did not report geographic coordinates of study locations or enough details to reliably extract coordinates. Coordinates were applied to a global aridity index to derive aridity of study locations.

After applying the above criteria, 171 study cases (94 reporting pollinator abundance, and 77 reporting richness) were incorporated from 59 articles published in the primary literature (i.e. 59 papers were filtered from the initial 106 possibilities) (Supporting Information 2). Most studies were conducted in Europe ($n = 31$) and North America ($n = 19$), followed by Asia ($n = 3$), the Middle East ($n = 2$), South America ($n = 2$) and Australia and Africa each with a single study (Figure 1). Each study area was subsequently characterized based on aridity and estimated evolutionary history of grazing by large herbivores.

To characterize aridity in each study area, we used provided coordinates to extract Aridity Index Values (UNEP, 1997) from the Global Aridity Index and Potential Evapotranspiration (PET) Climate Database version 2 (Trabucco & Zomer, 2018). Aridity classifications were assigned to each study based on the empirical distribution of extracted PET values: an aridity index value of $\leq$0.598 (1st to 33rd percentile) was used to classify study areas as 'semi-arid', aridity index values of >0.598 and <0.910 (34th to 66th percentile) were classified as 'humid' and areas with an aridity index value of $\geq$0.910 (67th percentile and above) were classified as 'very-humid' (Supporting Information 3). This empirical distribution-based aridity categorization was comparable to already existing categories of aridity (Spinoni et al., 2015; Trabucco & Zomer, 2018), and was necessary to ensure adequate representation of the literature in each category. To characterize the evolutionary history of large herbivore grazing, we follow the recent approach of Gao and Carmel (2020) for the classification of study sites. Studies conducted in Asia, Europe, Africa and the Great Plains of North America including the Eastern part of America were classified as having a 'long' evolutionary history, while western North America, South America and Australia were considered as having comparatively 'short' evolutionary histories of large herbivore grazing. Gao and Carmel (2020) classified all of North America as having a short evolutionary history of grazing, but the Great Plains (Mack & Thompson, 1982; Perryman et al., 2021) and great basin (Perryman et al., 2021) evolved with heavy large ungulate (bison) grazing. Thus, our classification differs slightly from theirs. Although we recognize the limitations of this approach in assigning grazing history to incorporated studies, it was necessary to make some generalizations to test how interactions between aridity and evolutionary grazing history affect pollinators. Due to few available studies of pollinator responses to grazing in mesic habitats with short evolutionary histories of large herbivore grazing, our analysis of evolutionary history × grazing pressure interactions is restricted to arid habitats only. To understand whether livestock grazing differentially affects pollinators, pollinator taxa were categorized into three groups including social bees (primarily bumblebees, *Bombus* spp.), non-*Bombus* wild bees (mainly taxa with a solitary life history) and butterflies.

2.2 | Meta-analysis

In our meta-analysis, we used standardized mean difference (hereafter, 'Hedge's *g*') as the statistic to compare effect sizes between livestock grazing of any level (low, medium or high grazing pressure) or undefined intensity (treatment) and grazing exclusion (control) (Gurevitch et al., 2001). The effect size was calculated using 'escalc' function in the 'metafor' package (Viechtbauer, 2010). Due to the diverse nature of statistical parameters reported in the primary literature, we calculated Hedge's *g* in three ways. First, we calculated effect size directly from the statistical parameters of mean, standard deviation and sample size. These were reported in most included studies. Second, we calculated effect size from correlation coefficients (*r*) and sample size for studies that reported correlations between continuous grazing intensities and pollinator diversity by transforming correlation coefficient into Fischer's *z* and then to Hedge's *g*. Third, we calculated effect size from *t* and *F* statistical scores and reported sample sizes.

We used a multilevel mixed-effect model to estimate the effect size and significance of livestock grazing intensity or aridity effects on each pollinator-related response variable (abundance and richness) using the 'rma.mv' function in 'metafor' (Viechtbauer, 2010). The model includes calculated effect sizes, sampling variance and study identification (study ID) as random factors using the restricted maximum-likelihood estimation method. The effect of livestock grazing over grazing exclusion was considered significant if the 95% confidence interval (CI) did not overlap with zero (Koricheva et al., 2013). We also tested for variability in effect size among the studies for pollinator abundance

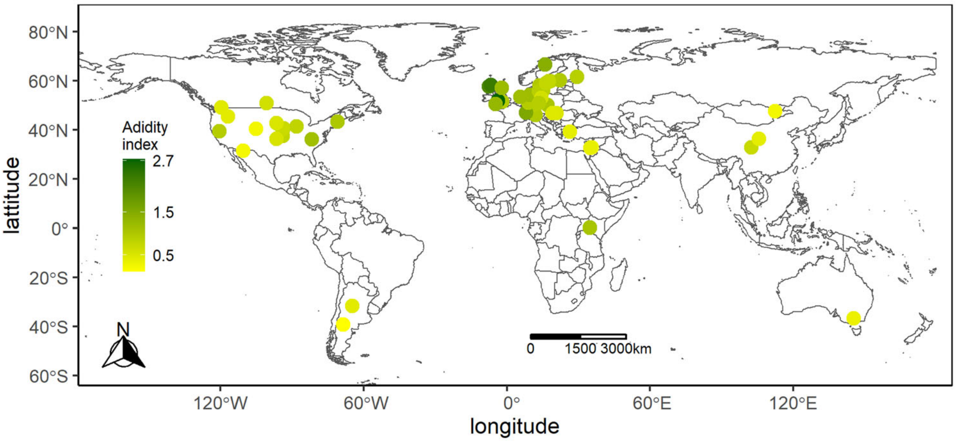

FIGURE 1 Global distribution of livestock grazing study sites incorporated in this meta-analysis, shown relative to a global aridity index (potential evapotranspiration)

and richness using *Q* statistic. A significant (i.e. $P < 0.05$) *Q* statistic indicates high heterogeneity between selected studies. Further, we also re-applied the abovementioned model with the moderator variables of ecosystem aridity (arid vs. moderate vs. mesic), evolutionary history of grazing (short vs. long) and pollinator life history (solitary bees vs. social bees [bumblebees] vs. butterflies) to test if effect sizes differed between groupings. We used *QM* and *P*-values of model results to test effects of moderating variables. All calculations and analyses were conducted in R version 4.0.2 (R Core Team, 2020). We also performed several standard analyses to eliminate the possibility of publication bias and confirmed minimal evidence of publication bias (detailed in Supporting Information 4).

3 | RESULTS

Overall, livestock grazing had significant negative effects on pollinator abundance in humid-aridity ($g = -0.637$, 95% CI -1.037 to -0.236, $P = 0.001$) and very-humid habitats ($g = -0.878$, 95% CI -1.480 to -0.277, $P = 0.004$), but there were no detectable effects of livestock grazing pressure on pollinator abundances in semi-arid habitats ($g = -0.180$, 95% CI -0.487 to 0.125, $P = 0.247$). Similarly, there was evidence for negative effects of livestock grazing pressure on pollinator richness in humid-aridity ($g = -0.443$, 95% CI -0.737 to -0.149, $P = 0.003$) and very-humid habitats ($g = -0.797$, 95% CI -1.270 to -0.323, $P = 0.001$), but no detectable effects of livestock grazing on pollinator richness in semi-arid habitats ($g = -0.063$, 95% CI -0.341 to 0.214, $P = 0.655$; Figure 2).

The effect size of livestock grazing on pollinator richness differed among the three PET classifications ($QM = 7.291$, $df = 2$, $P = 0.026$), but this was not the case for pollinator abundance ($QM = 3.147$, $df = 2$, $P = 0.207$). We detected high heterogeneity in effect size among the studies for both pollinator abundance (very-humid: $Q = 329.847$, $df = 35$, $P < 0.001$; humid: 89.886, $df = 23$, $P < 0.001$; semi-arid: $Q = 42.301$, $df = 23$, $P = 0.008$) and richness (very-humid: $Q = 116.219$, $df = 26$, $P < 0.001$; humid: $Q = 54.002$, $df = 25$, $P < 0.001$; semi-arid: $Q = 79.227$, $df = 23$, $P < 0.001$) across the three PET classifications.

3.1 | Effects of ecosystem aridity × livestock grazing pressure interactions on pollinators

In very-humid habitats, heavy ($g = -0.981$, 95% CI -1.675 to -0.287, $P = 0.005$), moderate ($g = -0.983$, 95% CI -1.607 to -0.360, $P = 0.002$) and undefined ($g = -1.121$, 95% CI -2.367 to 0.125, $P = 0.077$) livestock grazing pressure had significant negative effects on pollinator abundance compared to no grazing, but light ($g = -0.494$, 95% CI -1.506 to 0.516, $P = 0.337$) did not impact pollinator abundance (Figure 2). However, patterns for species richness were variable and suggested that light ($g = -1.234$, 95% CI -2.474 to 0.005, $P = 0.051$), moderate ($g = -1.137$, 95% CI -1.777 to -0.497, $P < 0.001$) and undefined ($g = -0.668$, 95% CI -1.240 to -0.096, $P = 0.022$) livestock grazing pressures have negative effects on pollinator richness but we did not detect a significant negative effect of heavy grazing on pollinator richness in very-humid habitats ($g = -1.105.$, 95% CI -2.819 to -0.607, $P = 0.205$).

In humid-aridity habitats, livestock grazing was negatively associated with pollinator abundance under moderate ($g = -1.096$, 95% CI -1.985 to -0.207, $P = 0.015$) and undefined grazing pressure ($g = -0.769$, 95% CI -1.264 to -0.273, $P = 0.002$), but heavy ($g = -0.453$, 95% CI -1.641 to -0.734, $P = 0.454$) and light grazing pressure ($g = -0.045$, 95% CI -0.898 to 0.988, $P = 0.093$) had no detectable effect on pollinator abundances. Undefined grazing pressure ($g = -0.552$, 95% CI -0.855 to -0.249, $P < 0.001$) was negatively associated with pollinator richness, but no patterns were detected for light ($g = -0.580$, 95% CI -1.580 to 0.420, $P = 0.255$), moderate ($g = -0.348$, 95% CI -1.196 to -0.499, $P = 0.420$) or heavy grazing intensities ($g = 0.281$, 95% CI -0.879 to 1.442, $P = 0.634$), potentially because of low sample sizes.

In semi-arid habitats, variable livestock grazing pressures were not associated with either pollinator abundance or richness (Figure 2).

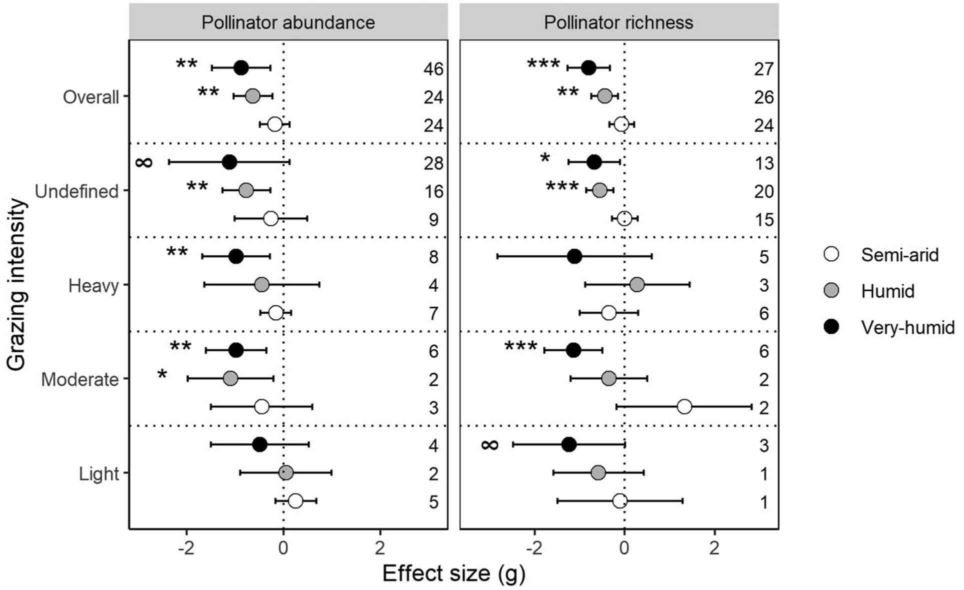

FIGURE 2 Aridity mediates the effects of grazing pressure on pollinator abundance and richness. Comparisons of grazing effects are made against non-grazed control sites, and symbols denote significant deviation from the 'no effect' line shown at zero; $^{\infty}P < 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{**}P < 0.001$. The number of studies incorporated in the analysis is shown at right in each panel

3.2 | Effects of ecosystem aridity × evolutionary history of large herbivore grazing interactions on pollinators in arid habitats

In semi-arid habitats with short evolutionary histories of large herbivore grazing, livestock grazing had a negative effect on pollinator richness ($g = -0.336$, 95% CI -0.463 to -0.210, $P < 0.001$), but this was not observed in semi-arid habitats with long evolutionary histories of large herbivore grazing ($g = 0.157$, 95% CI -0.178 to 0.493, $P = 0.358$). There was a difference in mean effect size due to evolutionary history of large herbivore grazing ($QM = 4.638$, $df = 1$, $P = 0.031$) for pollinator richness. However, there were no detectable effects of livestock grazing on pollinator abundance in habitats with either a short ($g = -0.589$, 95% CI -1.320 to 0.142, $P < 0.001$) or long evolutionary history ($g = -0.066$, 95% CI -0.411 to 0.278, $P = 0.706$) of large herbivore grazing. Effect size was comparable between both groupings ($QM = 1.596$, $df = 1$, $P = 0.206$; Figure 3).

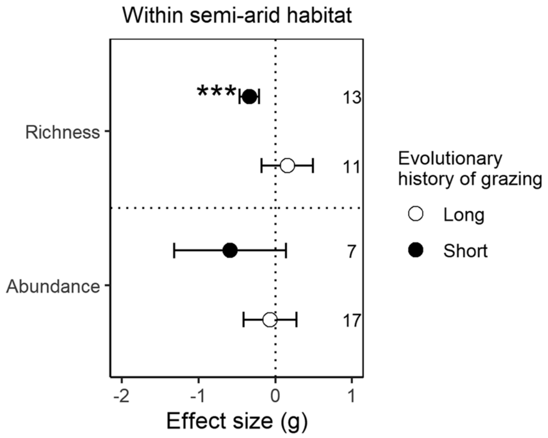

FIGURE 3 Effects of grazing history on pollinator abundance and richness, considered for arid habitats only. Non-grazed sites are treated as controls for the comparison. The number of studied incorporated in the analysis is shown at right, and asterisks denote significant deviation from the 'no effect' line shown at zero; $^{***}P < 0.001$

3.3 | Effects of grazing across pollinator life histories

For all classified pollinator types, livestock grazing was negatively associated with abundance (solitary bees: $g = -0.634$, 95% CI -0.961 to -0.306, $P < 0.001$; bumblebees: $g = -0.671$, 95% CI -1.340 to -0.003, $P = 0.048$; butterflies: $g = -0.593$, 95% CI -1.042 to -0.143, $P = 0.009$). The same was true for butterfly richness ($g = -0.662$, 95% CI -0.958 to -0.367, $P < 0.001$) and bumblebee richness ($g = -0.434$, 95% CI -0.705 to -0.162, $P = 0.001$), but not for solitary bee richness: ($g = -0.212$, 95% CI -0.59 to 0.164, $P = 0.269$; Figure 4). Effect sizes were different across pollinator types for both abundance ($QM = 14.914$, $df = 2$, $P < 0.001$) and richness ($QM = 8.781$, $df = 2$, $P = 0.013$).

4 | DISCUSSION

Few syntheses attempt to describe livestock grazing effects on pollinator communities, and existing analyses that address this subject focus on livestock grazing as a general category in the larger context of anthropogenic impacts (Winfree et al., 2009) and habitat restoration (Tonietto & Larkin, 2018), or consider pollinators (i.e. Hymenoptera,

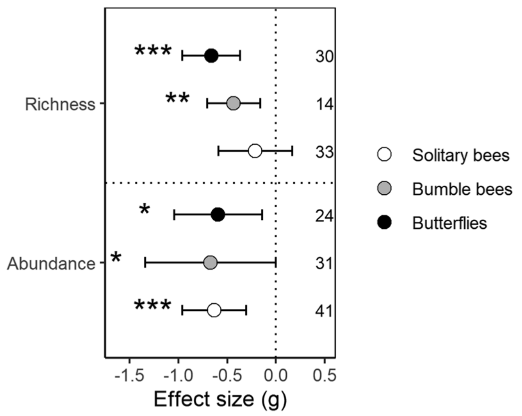

FIGURE 4 Effects of grazing on abundance and richness of different types of pollinators. Asterisks denote significant deviation from the 'no effect' line shown at zero; *$P < 0.05$, **$P < 0.01$, **$P < 0.001$. The number of studies incorporated in the analysis is shown at right

Lepidoptera, etc.) only as a general group within multi-trophic systems (Filazzola et al., 2020; Wang & Tang, 2019). Accordingly, these earlier studies do not parse out effects of different livestock grazing practices or their interactions with habitat variables on pollinators. Our meta-analysis expands on these previous works by directly interpreting such effects at a worldwide scale and to assess the relative contributions of habitat aridity and grazing practices on pollinators, with specific focus on native bee and butterfly communities.

Our results indicate that aridity strongly mediates effects of livestock grazing pressure on pollinator abundance and species richness. In very-humid habitats, increased grazing pressure generally had negative effects on pollinator abundance and species richness, whereas in semi-arid habitats impacts of livestock grazing had no detectable effects on pollinator abundance or richness. Effects of livestock grazing pressure on pollinators were variable in humid habitats (Figure 2). This finding has important implications for grazing management and suggests that grazing pressure × aridity relationships are likely to have effects on ecosystem services provided by native pollinators. Effects of aridity on pollinators are likely indirectly controlled by adaptations of rangeland forb species to grazing (Evju et al., 2009), and raising livestock in arid habitats with short evolutionary histories of grazing is likely to have negative consequences for pollinator richness. The same was not true for pollinators in semi-arid habitats with comparatively long evolutionary histories of grazing by large herbivores, where we detected no effects of livestock grazing on pollinator assemblages (Figure 3). Presently, too few studies exist to make reliable conclusions about pollinator community responses to livestock grazing practices in humid and very-humid habitats with short evolutionary histories of large herbivore grazing. The limited literature investigating grazing effects on pollinators in such habitats indicates a knowledge gap that should be addressed.

Our results for bee and butterfly pollinators match those from empirical studies examining grazing-mediated impacts on arthropod communities in arid landscapes with long evolutionary histories of grazing and suggest a general convergence of findings across an array of studies, taxa and regions. For example, Newbold et al. (2014) found that arthropod communities were relatively insensitive to variable grazing intensities in short grass steppe, which has a long evolutionary history of grazing by bison (and more recently, cattle). Similarly, pioneering work by Coyner (1939), Weese (1939) and Smith (1940) reported positive-to-null effects of high-intensity cattle grazing on various insect communities in tallgrass prairie systems of western North America. Likewise, in eastern Mongolia, heavy grazing pressure was found to be associated with an increase in the number of plant–pollinator interactions, even though overall forb diversity was reduced (Yoshihara et al., 2008). However, a study from the Inner Mongolia region of China (Ma et al., 2017) showed that over-grazing can reduce abundances of primary and secondary (arthropod) consumers over time. So, although a growing body of evidence suggests insect communities tolerate livestock grazing effects in arid rangelands, there likely exist thresholds of grazing pressure that should not be exceeded in the interest of insect conservation.

The larger overall effect size of livestock grazing on pollinators in very-humid habitats is potentially attributable to multiple, non-mutually exclusive factors. First, there is general evidence for a higher diversity and more widespread distribution of pollinators in semi-arid habitats (e.g. Michener, 2007). This could suggest that pollinator communities in semi-arid regions may be able to withstand greater absolute losses before proportionally similar effects on biodiversity (i.e. as compared to mesic areas) are detected. Differences in native bee life-history strategies between semi-arid and very-humid habitats could contribute to this pattern. In very-humid habitats, social bees are more abundant and solitary bees are relatively infrequent by comparison to bee assemblages in semi-arid habitats, where solitary bee taxa comprise a large portion of the overall biodiversity. Landscape factors could also drive differences in grazing effects between arid and mesic habitats. Many pollinator species are adapted to nest in conditions with exposed bare ground, crevices, sandy soils and with a significant litter and wood component. Such ground cover characteristics may be more common in semi-arid rangelands. In addition, higher overall soil moisture content and precipitation inputs in very-humid rangelands might contribute to more readily compacted soil (El-Swaify et al., 1985) with potentially deleterious effects on ground-nesting pollinators (e.g. Xie et al., 2013).

We also report that bee life histories are important when considering grazing-mediated impacts on pollinator assemblages. Grazing was more likely to negatively impact the abundance and species richness of butterflies and social bees (i.e. *Bombus* spp.) than solitary bee taxa, for which there was no evidence of declining richness under grazing. However, effect sizes were relatively similar across pollinator types. This finding may partially explain the contrasting results of grazing effects between semi-arid and very-humid systems (Figure 2): in semi-arid habitats, bee taxa with a solitary life history are more species rich than social bee taxa (Michener, 2007).

Recent studies suggest that cattle grazing has varying impacts on pollinators in semi-arid ecosystems, but these effects are not necessarily driven by effects of cattle on forb communities and instead may be associated with impacts on cover and soil properties. For instance, Thapa-Magar et al. (2020) found evidence for a seasonal reduction in functional dispersion of native bee communities in mid-grass prairie sites of eastern Colorado (USA) grazed by cattle, but concluded that these shifts were due to effects on bee nesting habitats rather than foraging resources. Kimoto et al. (2012), reported similar results for bumblebee (*Bombus* spp.) communities in a semi-arid prairie system in Oregon (USA), and showed that cattle presence caused soil compaction and a reduction in herbaceous litter. In contrast, tests of cattle-mediated effects on bee communities in arid Mediterranean habitats reported null effects on wild bee abundance and richness, despite impacts on forb communities and bee foraging preferences (Shapira et al., 2019). These collective findings and our own meta-analysis indicate that cattle grazing impacts on bee biodiversity are likely habitat mediated rather than food mediated, which may suggest an overall limited role of evolutionary history of grazing in predicting bee community responses to livestock disturbances.

Livestock grazing effects on pollinator communities are complex and estimation of a single parameter (grazing pressure described as qualitative categories of low, moderate and high) may not be sufficient for describing ecological outcomes. Use of other variables including stocking rates would help to standardize grazing intensity estimates across studies. Currently most of the available studies describing grazing effects on pollinator communities do not report this variable, indicating a need for greater standardization across studies. In addition, incorporation of stocking rates alone may not be informative without some estimate of primary productivity (e.g. plant biomass production per unit area); for example, similar stocking rates may result in differential grazing pressures when compared between high- and low-productivity sites. This nuance could potentially explain the finding of no effects of heavy grazing pressure on pollinator richness across an aridity gradient (Figure 2). Physiographic factors including light intensity (as predicted by aspect), elevation and temperature and heat load index could also interact with primary productivity to mediate effects of stocking rates and alter relative grazing pressure across landscapes. Therefore, incorporating a more complex set of interacting predictors could help to inform further studies investigating grazing effects on pollinator communities. In addition to standardization of grazing pressure estimates, experimental designs that consider appropriate reference conditions are needed to understand effects of livestock grazing on pollinator communities. For example, in systems that evolved with grazing by large herbivores, removal of livestock grazing does not necessarily represent an appropriate ecological reference condition.

5 | IMPLICATIONS AND CONCLUSIONS

The interactions we outline here are likely to have consequences for conservation efforts and the maintenance of ecosystem services, and it is probable that cattle and other large livestock affect pollinator assemblages primarily via impacts on nesting resources rather than foraging resources. These effects should be considered in grazing management practices. Solitary bees are potentially more tolerant of livestock impacts than social bees, but the mechanisms underlying this pattern remain undescribed. In addition, further empirical work is needed to develop a clearer understanding of how different livestock species (e.g. cattle, sheep, bison, goats, etc.) affect pollinator communities, as very few direct comparative studies are available for making conclusions. However, it seems clear that increasing grazing intensity beyond low or moderate intensities has generally negative effects on pollinator abundance and species richness across a global collection of studies, and these effects are more pronounced in mesic habitats than arid habitats. Although evolutionary history of ungulate grazing is difficult to ascribe with certainty, this is a useful concept for identifying which ecoregions and rangelands may be more likely to suffer negative consequences from pastoral practices and can help to prioritize conservation efforts.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

All authors collaborated in the conception of the research question. TSD acquired the funding for the project. KTM performed the systematic review and codified the papers in collaboration with MFG. KTM analysed the data and wrote the first draft of the manuscript. All authors contributed to editing and revising the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rv15dv496 (Thapa-Magar et al., 2022).

PEER REVIEW

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