Journal of Insect Conservation (2022) 26:359–374
https://doi.org/10.1007/s10841-022-00373-8

REVIEW PAPER

Can cattle grazing benefit grassland butterflies?

Samantha K. Bussan[1]

Received: 28 July 2021 / Accepted: 12 January 2022 / Published online: 31 January 2022

Abstract

Grassland insects face some of the most severe declines in species diversity and total abundance, in part due to agriculture. Livestock grazing is the largest agricultural land use and can have both positive and negative effects on insect communities and populations. A global synthesis is needed to guide butterfly conservation and provide recommendations for scientists, managers, and other stakeholders seeking to use grazing as a tool for butterfly conservation. Here I review 115 studies that evaluate how cattle grazing affects butterfly communities and species. I discuss how various aspects of cattle grazing affect butterfly community and species responses. Thirty-five studies concluded cattle grazing has positive effects on butterflies, while 20 concluded cattle grazing has negative effects. Thirty-six were inconclusive or found no effect of grazing. Conclusions depended heavily on the management chosen as well as environmental and evolutionary factors. Eighty-five studies (74%) were located in Europe, providing a useful framework for the rest of the world, but also creating opportunities for further research.

Implications for practice Low to moderate grazing intensity is the most beneficial grazing management strategy for butterflies. There is also potential for rotational grazing to provide benefits, but more research is needed. It is important to have variation in grazing management and other disturbance types in the landscape (mowing, prescribed fire, etc.) to accommodate differing habitat needs of butterfly species. Cattle grazing has potential as a land-sharing opportunity to promote grassland butterfly diversity in agroecosystems.

Keywords Cattle grazing · Butterflies · Conservation · Agriculture · Habitat · Land-sharing

Introduction

Insect species are in decline worldwide (Hallmann et al. 2017, Wagner 2020), with grassland insects facing some of the most severe declines in species diversity and total abundance (Kuussaari et al. 2007; Seibold et al. 2019). Scientists attribute this decline to a combination of climate change, land use change, habitat loss and degradation, and agricultural intensification (Wagner 2020). Agricultural land use, particularly livestock grazing, is often considered one of the largest threats to grassland habitats (e.g. Noss 1994; Cross 2020). Livestock and feed for livestock occupy approximately 30% of habitable land worldwide (UN Food and Agriculture Administration, 2012).

Studies indicate both positive and negative effects of livestock grazing on ecosystems. Grazing influences grassland systems through herbivory, trampling, water pollution, soil compaction, and erosion (Fleischner 1994). This causes reduced plant and animal diversity, local extirpation of sensitive species, invasion of nonnative species, vegetation community compositional shifts, and vegetation structure alteration (Fleischner 1994; Manley et al. 1997). Conversely, many studies indicate that grazing can be used to restore or maintain native grassland communities and species (Kruess and Tscharntke 2002a, b; Pöyry et al. 2004; Wang et al. 2007; Zakkak et al. 2014; Delaney et al. 2016). Most grasslands need disturbance to maintain ecosystem structure and function or they will succeed to shrubland or forest. Many grasslands were grazed historically by megafaunal herbivores (Galetti et al. 2018); therefore, livestock may fill the niche when large herbivores are extirpated or extinct (Hall and Bunce 2019). Livestock can prevent woody plant encroachment through trampling and foraging (Balmer and Erhardt 2000). As most

✉ Samantha K. Bussan
samantha.bussan@wsu.edu

[1] Washington State University Vancouver, 14204 NE Salmon Creek Avenue, Vancouver, WA 98686, USA

domestic large herbivores preferentially consume grass, they can reduce competition from native and nonnative grasses, maintain lower vegetation heights, and increase the proportion of forbs, benefitting many grassland insects (Wallis De Vries et al. 2007; Skaer et al. 2013; Shapira et al. 2020).

Grazing effects on insects in grassland ecosystems create a unique opportunity to examine land-sharing approaches to agriculture. First formally proposed by Green et al. (2005), land-sharing, also known as wildlife-friendly farming, is low-intensity agriculture that may include strategies such as the retention of patches of natural habitat or semi-natural habitats within farmland. Land-sharing often necessitates payments to farmers for reducing production to maintain natural or semi-natural habitat on farms or rangeland. Livestock grazing can incorporate land-sharing since it does not necessarily require destruction of the original grassland ecosystem (Barry and Huntsinger 2021). This does not hold true if forest or other ecosystems are destroyed to accommodate livestock (McIntyre and Hobbs 1999).

Understanding how specific insect taxa respond to grazing may help managers better account for conservation needs of insects in agricultural land. Lepidopterans, mainly butterflies, are well-studied compared to most other orders of insects, are good indicators of ecosystem health due to their unique habitat requirements and are relatively easy to survey as adults (Kerr 2000).

Livestock grazing is a contentious issue within the conservation community, with many activists, politicians, and some scientists decrying its potential negative effects (e.g. Fleischner 1994; Cross 2020). Conversely, conservation managers increasingly seek to use grazing as a tool for conservation, while farmers are increasingly under pressure to provide conservation benefits and ecosystem services with their grazing operations. While there have been previous literature reviews on the effects of cattle grazing on insects (e.g. Swengel 2001; van Klink et al. 2015, Bubová et al. 2015), all included relatively few studies focused on butterflies or grazing specifically, were limited in their geographic and ecological scope, or did not include a detailed evaluation of the effects of different types of grazing management on butterflies. A global synthesis of butterflies and grazing management strategies is necessary to guide next steps for conservation of at-risk species and communities and provide insight for scientists, conservation managers, producers, and policy makers seeking to use grazing as a tool for butterfly conservation. This review seeks to fill this gap and to evaluate the current knowledge of how different grazing practices affect butterfly communities and species, understand how to use grazing as a land-sharing approach to conserving butterflies in agricultural land, and make recommendations for next steps for research and conservation.

Methods

Following the methods of Pullin and Stewart (2006), I conducted a systematic search of the literature using *Web of Science* with all combinations of search terms related to butterflies ("butterfl*," "lepidopter*," "insect*," "arthropod*," or "invertebrate*") paired with search terms related to grazing ("graz*," "cattle," "cow*," or "livestock"). While some search combinations resulted in studies broader in scope (e.g. "insect*" and "graz*"), I limited the studies in this review to those specifically related in some aspect to butterflies and cattle grazing in grasslands. I focused on cattle because the majority of the available literature evaluates cattle grazing rather than other types of domestic livestock. I excluded studies related solely to grazing by other herbivores (e.g. sheep or bison) but included studies that compared cattle grazing to grazing by other herbivores. Similarly, I excluded studies related solely to non-butterfly taxa, but included studies that evaluated butterfly responses to grazing in addition to other taxa.

For each study, I recorded general study characteristics, including the year(s) data were gathered for the study and the type of study (experimental, observational, or modeling), and study location. I recorded what type of data were collected for butterflies (species richness, abundance, diversity, species composition, presence/absence, species traits, occurrence or occupancy, movement/behavior, vital rates (rates of survival and fecundity), larval/egg abundance) and whether butterfly communities or specific species or families were studied. I also recorded what type of data were collected for grazing (intensity, grazing system, type of grazer, grazing as a type of disturbance, simple presence, or livestock productivity/socioeconomics). I classified the conclusions of the study related to grazing management or intensity (where appropriate), conclusions related to overall effect of grazing (where appropriate), and purpose of grazing (for profit, restoration/conservation, or both). See Supplementary Information Table 1 for individual study citations, information, and classifications.

Grazing intensity is usually defined as the number of livestock units (LU) per hectare, though other units were reported as well (Supplementary Information Table 2). Some studies used different though related terms for grazing intensity, including stocking rate, grazing pressure, or grazing density. Extensive and intensive grazing were frequently used to describe grazing intensity as well. Extensive grazing referred to low intensity, free range grazing over large tracts of land and intensive grazing referred to high intensity grazing in smaller pastures. Rotational grazing is a grazing system in which livestock are moved between pastures or paddocks to allow for periods of rest for the plant community (Blanchet et al. 2000). Continuous grazing is a system in which livestock have unrestricted access to the full pasture throughout the season (Blanchet et al. 2000).

Where possible based on the study design, I classified the overall combined effect of grazing on the target butterfly response(s) as "positive," "negative," "inconclusive," or "no effect" (Supplementary Information Table 1). I made this classification if the study compared butterfly responses under grazing management to butterfly responses under no grazing management, though the ungrazed grassland could be managed in other ways (e.g. fire, mowing, etc.). I recorded the quantitative results of the target butterfly response types (species richness, total abundance, movement rates, etc.) under grazing and no grazing. Then I compared the results across response types and weighted them by the authors' interpretation of their results and conclusions and by their interpretation of the most important response types. For studies focused on butterfly communities, sensitive or specialist species received greater weight than common species. Some studies were very clear in their conclusions, but some had to be inferred. I classified the overall effect as "positive" if most of the target butterfly responses were benefitted by grazing as compared to no grazing. I classified the overall effect as "inconclusive" if the target responses were split evenly between positive and negative effects and "negative" if most of the target butterfly responses were adversely impacted by grazing in comparison to no grazing. I classified the overall effect as "no effect" if grazing did not influence the target butterfly responses. See Supplementary Information Table 1 for the complete butterfly response results and overall effect classifications and justifications.

I classified the purpose of grazing as "for profit" if the goal of the grazing in the study was mainly to make a livelihood for the rancher or farmer and involved actively grazed lands. Here I do not refer to large-scale industrial farms, feedlots, or Concentrated Animal Feeding Operations (CAFOs) as there were none in any of the studies in this review. I classified the grazing purpose as "restoration/conservation" if the main goal was to restore or maintain the plant communities or to create habitat for butterflies. I classified the purpose as "both" if the study made mention of both goals, even if one or the other was not actively analyzed. If the goal of the grazing was unclear based on the explanation in the study, I classified the goal as "unclear" (Supplementary Information Table 1).

Results

The selected search terms returned 115 relevant studies. I included only primary research with two exceptions. The primary research studies included experimental (n = 32), observational (n = 73) and modeling (n = 8) studies. I included two reviews or summaries of long-term research programs (Thomas et al. 2009; Woodcock et al. 2012), as these studies provide an efficient synthesis of long-term programs. On average, the studies were conducted for 3–4 years, although they ranged from a single season to 37 years of data.

Butterfly responses

The review resulted in 53 studies focused on single butterfly species responses to grazing and 62 focused on butterfly community responses to grazing (Fig. 1).

Within the studies focused on single species responses, butterfly abundance or density (n = 28) and occupancy (n = 28) were the most common response variables measured. The standard Pollard Walk method (Pollard 1977) was the most common method of data collection (n = 19). Five studies evaluated movement, dispersal, and/or behavior and seven collected demographic or vital rate data (Fig. 1).

Within the studies focused on butterfly community responses to grazing, most studies included some combination of measures of species richness (n = 56), abundance or density (n = 47), diversity (n = 15), or community composition (n = 27) (Fig. 1). Studies focused on community responses tended to be less varied in the types of butterfly responses measured than studies focused on single species responses (Fig. 1). The standard Pollard walk (Pollard 1977) was the most common (n = 46) method of obtaining butterfly community data.

Grazing influence on butterflies

There were many different grazing attributes measured including grazing intensity, grazing system, and type of grazer (Fig. 1). Grazing was also considered as a tool for conservation management and type of disturbance or one of many variables influencing "Habitat quality" (Fig. 1). Most studies collected data on more than one attribute. The type of grazing management and the framing of the question played strong roles in the outcome, or overall effect of the grazing on butterfly responses.

Overall effect of grazing

The overall effect of grazing was largely positive (Fig. 2a), though there were differences between overall effects on communities and overall effects on species (Fig. 2b). Out of the 91 studies in which I was able to make this determination, 35 were positive, 20 were negative, 18 were inconclusive, and 18 found no effect of grazing (Fig. 2a).

Butterfly community responses were spread nearly evenly between positive, inconclusive, negative, and no effect

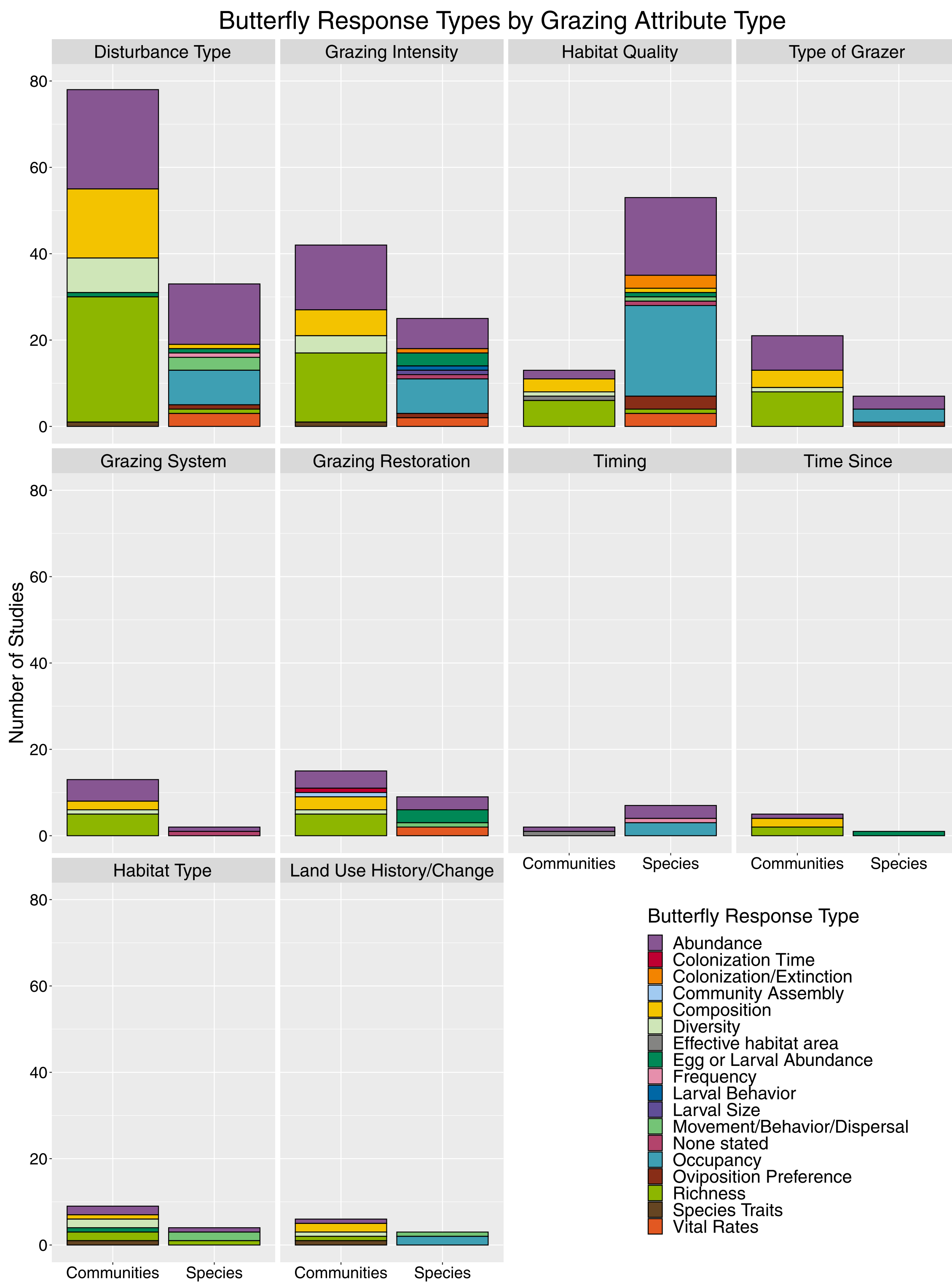

Fig. 1 Number of studies examining butterfly response types for both communities and species by grazing attribute type within the published literature. Many studies examined more than one grazing attribute and more than one butterfly response type

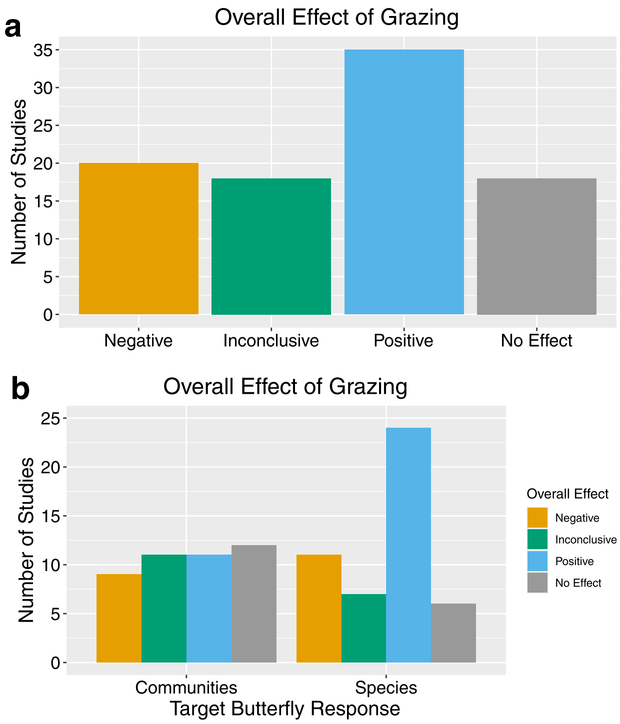

Fig. 2 **a** The number of studies that found the overall effects of grazing to be negative, inconclusive, positive, or no effect (n = 91). **b** The number of studies reporting overall effects of grazing separated by butterfly communities (n = 43) and single species (n = 48)

(Fig. 2b). Single species responses were more likely to be positive and are likely driving the overall effect of grazing towards positive effects (Fig. 2a, b).

Table 1 The number of studies comparing other disturbance types to cattle grazing

Disturbance type	Number of studies	Percentage
Mowing	27	56.3
Fire	12	25.00
Ungrazed/abandoned	19	39.58
Cropping	4	8.33
Other	11	22.92

Many compared multiple types of disturbance, so the "number of studies" column sums to greater than the number of studies comparing disturbance types. Ungrazed/abandoned refers to a lack of grazing represented in the study as "ungrazed" without other management mentioned. Abandoned refers specifically to pastures that were formerly grazed but are now fallow. The "percentage" column was calculated based on the number of studies comparing disturbance types (n = 48)

Grazing effectiveness relative to other management actions

Forty-eight studies tested grazing as a tool for conservation management (hereafter disturbance type to distinguish between other types of grazing management). These studies compared grazing to other types of conservation strategies that promote disturbance to maintain the grassland or against ungrazed or abandoned pastures. Mowing for hay was the most common disturbance type that was compared to grazing, followed by fire and abandoned or ungrazed land (Table 1). Many studies compared more than one type of management to grazing.

The 15 studies comparing the effects of grazing and mowing on butterfly communities tended to have inconclusive or no effect (Fig. 3). The 11 studies comparing the effects of grazing and mowing on single butterfly species found mostly inconclusive or positive effects. No single species studies found negative effects of mowing (Fig. 3).

The six studies comparing the effects of grazing and fire on butterfly communities observed inconclusive effects (Fig. 3). The five studies evaluating single butterfly species were split nearly evenly between the categories (Fig. 3).

Grazing intensity

Thirty-one studies compared different grazing intensities. There were a variety of metrics used to measure grazing intensity and some used more than one. Fifteen studies reported grazing intensity directly, while the other 14 used other metrics such as vegetation height as a proxy for grazing intensity. Sixteen studies compared a gradient of grazing intensities, eight compared two levels of grazing intensity and six compared three.

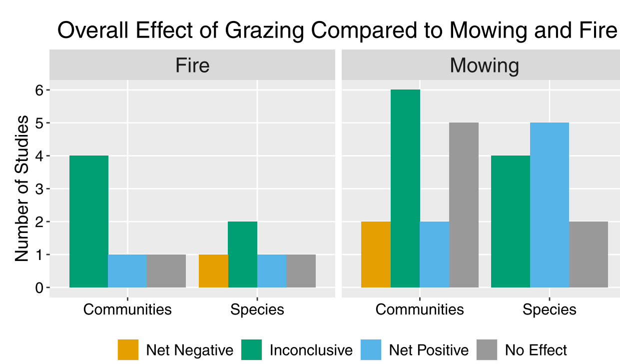

Fig. 3 The number of studies reporting overall effects of grazing in comparison to mowing by target butterfly response (n = 26) and the number of studies reporting overall effects of grazing in comparison to fire by target butterfly response (n = 11)

Table 2 The number of studies that recommended each grazing intensity level

Most beneficial grazing intensity	Number of studies
Zero intensity (no grazing at all)	0
No-low intensity	4
Low intensity	13
Low-intermediate intensity	3
Moderate intensity	4
High intensity	2
No effect	2

Most studies recommended low grazing intensity as most beneficial to butterfly communities and species (n = 13; Table 2). The exact definition of "low," "intermediate," or "high" intensity varied depending on the study and the associated grassland ecotype (Supplementary Information Table 2). Two studies recommended high grazing intensity, but both recommended that the high intensity be late in the season or only happen every two–three years.

Grazing system

Out of 115 studies in this review, seven studies compared different grazing systems. Five of these compared rotational grazing to continuous grazing. Out of the five studies that compared rotational and continuous grazing, three found positive effects of rotational grazing in comparison to continuous grazing on butterfly communities, and one found no effect. There was only one study that observed a positive effect of continuous grazing instead of rotational grazing, specifically on the host plant of the target butterfly species. The other two studies that compared grazing systems compared pastures registered under European Agri-Environment Schemes (AES; see Discussion) to non-AES pastures and reported beneficial effects of AES programs.

Type of grazer

Twelve studies compared types of grazers, whether comparing breeds or types of cattle (n = 3), types of domestic livestock (e.g. cattle to sheep or horses, n = 7), or domestic cattle against wild grazers (n = 3). No studies found an effect of cattle breed on butterfly communities or species, though one found an effect of cattle type (lactating dairy cows vs non-lactating heifers). Two studies found sheep to be more detrimental to butterflies than cattle, one found cattle to be more detrimental than mixed sheep/horse grazing, and two found no effect of livestock type. Two studies observed positive effects of mixed sheep and cattle grazing systems on butterfly species richness. Two of the three studies comparing wild grazers to cattle found wild grazers to be more beneficial for butterflies, though cattle were still more beneficial than no grazing.

Habitat quality

Thirty-six studies framed grazing as one of many factors affecting habitat quality, which was then used to understand butterfly species distribution, occupancy, or habitat preference (for studies focused on single butterfly species responses) or community composition (for studies focused on butterfly community responses).

Other study characteristics

Livestock productivity and socioeconomics

Very few studies considered livestock productivity or the socioeconomic side of conserving butterflies on farms or on grazing land. Six studies measured livestock productivity or animal performance under different grazing systems or intensities. Two studies measured the effect of the grazing treatment on nutrition value for livestock. One study compared the economic cost of implementing certain management types.

Location

Out of the 115 studies, 85 were located in Europe and 22 were located in North America (Fig. 4). Other global regions covered included Africa (n = 6) and Asia (n = 2). No studies were in Central America, South America, or Southeast Asia/South Pacific, including Australia (Fig. 4).

Of the European studies, western (n = 53) and northern (n = 18) Europe were most well-studied. Comparatively few studies were in Mediterranean grasslands, such as Spain (n = 2) or Greece (n = 3).

North America, in contrast to Europe, had less extensive literature that covered fewer years. Most North American studies took place in current or former prairies of the Midwest (n = 13). There was only one study located in Canada and two in Mexico.

There were six studies located in Africa, spread throughout the continent, including South Africa (n = 2) and Burkina Faso (n = 2). There were two studies located in Asia.

Purpose of grazing

There were a total of 38 studies in which I classified the purpose of grazing as "for profit," 18 studies in which the purpose of grazing was "restoration/conservation," and 48 in which the purpose of grazing was classified as "both." There were 11 studies whose grazing purpose was unclear. There were

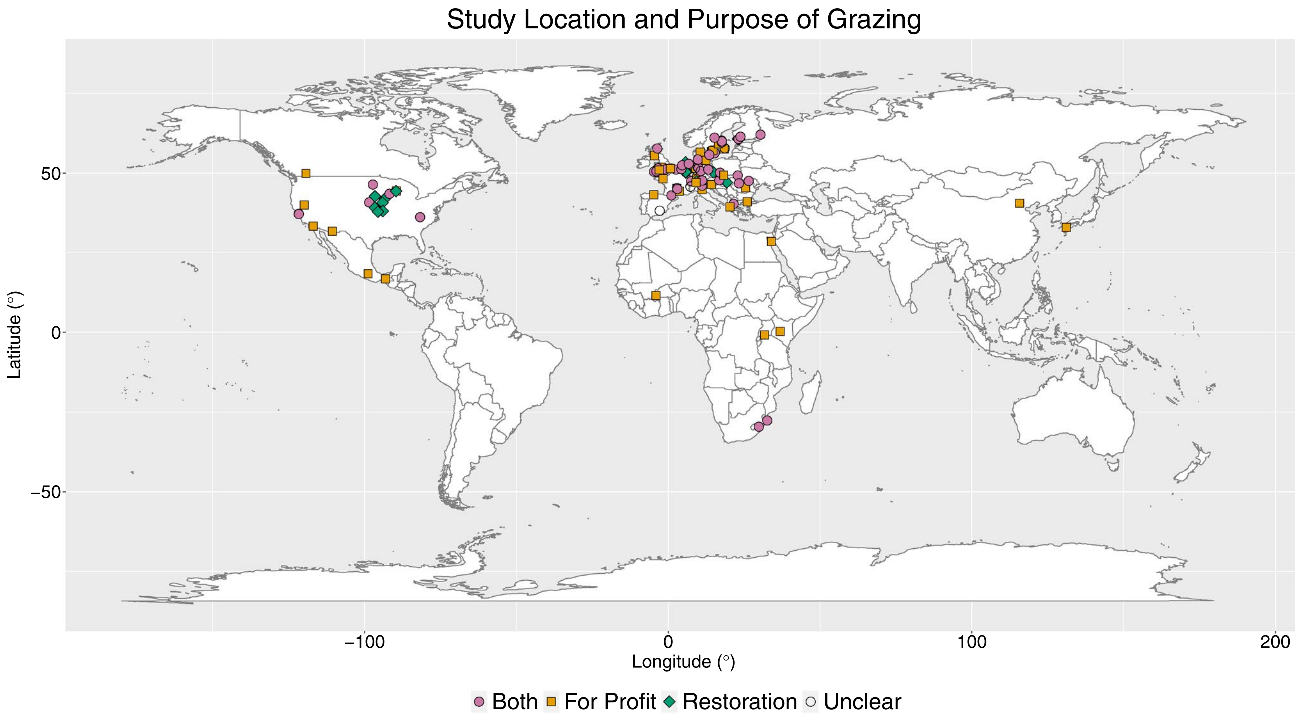

Fig. 4 A map showing study locations worldwide and the associated purpose of grazing. Each dot represents one study. For studies which took place in multiple locations, states, or countries, one location was randomly chosen to represent the study in this map. The color and shape of the dot represents the purpose of grazing in the study

Table 3 The number of studies in each category of purpose of grazing separated by continents

Purpose of Grazing	Continent				Total
	Africa	Asia	Europe	North America	
For profit	5	2	25	8	40
Restoration	0	0	8	9	17
Both	2	0	42	5	49
Unclear	0	0	9	1	10
Total	7	2	84	23	

strong locational differences in the purpose of grazing within the literature (Fig. 4; Table 3). Europe had the greatest focus on satisfying both economic and conservation goals.

Discussion

When cattle grazing is used to support single butterfly species conservation, the effects are often positive, while the effects of grazing on butterfly communities are context-dependent. Grazing can be used as a tool for conservation and a source of disturbance within the grassland ecosystem; grazing is often contrasted with mowing and prescribed fire. Grazing intensity, grazing system, type of grazer, land use history, and the purpose or goal of the management all contribute to differences in the effect of grazing on butterflies. While the effect of grazing is well-documented in Europe, studies are limited in other parts of the world, even in regions where cattle grazing is a primary land use (e.g. western North America). In addition, European and African studies were more likely to employ land-sharing approaches to grazing than other locations.

Overall effect of grazing

In both single species- and community-focused studies, grazing was more likely have positive effects on butterflies when it included low-moderate intensity or extensive grazing (e.g. Elligsen et al. 1997; De Groot et al. 2009; van Klink et al. 2016; Johansson et al. 2017). High-intensity or for-profit grazing was more likely to result in negative effects, especially when compared to conservation-focused disturbance types (e.g. prescribed fire) (Swengel 1998; Cole et al. 2015; Kormann et al. 2019). Additionally, grazing in mesic grasslands was more likely to have positive effects than grazing in dry grasslands (e.g. Hoyle and James 2005; Akite 2008; Johansson et al. 2017). The outcome of grazing on butterfly communities varied depending on how the authors weighted coarse community metrics (richness, abundance, etc.) over community composition or sensitive species responses in their conclusions.

Grazing effectiveness relative to other management actions

Relative to mowing, grazing had inconclusive effects on butterfly communities and generally positive effects on single species (Fig. 3). Cattle grazing can benefit butterflies in comparison to mowing because grazing creates more fine-scale structural heterogeneity and warmer microclimates throughout the season (WallisDeVries and Raemakers 2001; D'Aniello et al. 2011; Pérez-Sánchez et al. 2020). Mowing has detrimental effects on immobile butterfly larvae if the cut is too early in the growing season or there are too many in a season (Konvicka et al. 2008). Interestingly, mowing combined with late season grazing could control competitively dominant grasses and create higher structural heterogeneity, thus increasing butterfly diversity (Mazalová et al. 2015). However, grazing cattle may reduce nectar flower abundance more than mowing (Saarinen and Jantunen 2005).

There is little consensus in the literature on the effects of grazing relative to prescribed fire on butterflies (Fig. 3). A combination of grazing and fire (pyric herbivory; Fuhlendorf and Engle 2001) caused butterfly and plant communities to increase in similarity to their reference site more than grazing or fire alone (Delaney et al. 2016). Community response metrics such as richness, abundance, and diversity showed variable responses to grazing and fire treatments (Vogel et al. 2007). In contrast, Debinski et al. (2011) concluded land use history was more important to butterfly diversity than the current grazing and fire management (see Land Use History below). Sensitive prairie specialists such as *Speyeria idalia* may be more abundant in low intensity grazing than fire treatments if litter cover is maintained (Vogel et al. 2007; Caven et al. 2017).

Grazing intensity

Low grazing intensity is the most beneficial for butterfly species and community metrics. Low to moderate intensity creates greater spatial and structural heterogeneity in the plant community on a fine scale, which increases the number of niches available, in turn increasing butterfly richness and diversity (Pöyry et al. 2004, 2006; Wallis De Vries et al. 2007; WallisDeVries et al. 2016). High grazing intensity increases the risk of negative grazing effects such as disruption of trophic interactions between larvae and their host plants (Kruess and Tscharntke 2002b), invasion of nonnative plant species, vegetation community compositional shifts, and vegetation structure alteration (Fleischner 1994; Manley et al. 1997). The absolute measurement of grazing intensity associated with "low," "intermediate," or "high" intensity varied by system and the study's definition of grazing intensity level, potentially confounding direct intensity comparisons (Supplementary Information Table 2).

Comparatively higher levels of grazing intensity tend to favor thermophilic and early successional butterfly species due to the reduction in vegetation height within the plant community (WallisDeVries et al. 2016). In many semi-natural grassland systems, the loss of grazing or reduction in intensity has caused the decline of thermophilic butterfly species (e.g. Thomas et al. 2009).

Environmental moisture and evolutionary grazing history affect plant diversity relationships with grazing intensity (Milchunas et al. 1988); it is possible that similar relationships affect butterfly diversity responses to grazing intensity. Six studies detected decreasing butterfly diversity with increasing grazing intensity; four of these were associated with wet or dry grasslands. In contrast, four studies observed the highest diversity at intermediate levels of grazing intensity (i.e. a unimodal relationship). All four studies observing a unimodal relationship were associated with mesic grasslands (Pöyry et al. 2004, 2006; Dumont et al. 2009; Jerrentrup et al. 2014). Pöyry et al. (2006) attributed this relationship to the intermediate disturbance hypothesis (IDH; Grime 1973; Connell 1978).

Grazing systems

Rotational grazing, though often recommended as a strategy to promote butterfly diversity through increasing structural heterogeneity (e.g. Balmer and Erhardt 2000; Pöyry et al. 2004; WallisDeVries et al. 2016), is not well-studied within the literature. Of the five studies that compared rotational and continuous grazing, three concluded that rotational grazing is more beneficial for butterflies (Farruggia et al. 2012; Kruse et al. 2016; Ravetto Enri et al. 2017), suggesting that rotational grazing may benefit butterflies over continuous grazing, but this cannot be concluded with the limited information available. This relationship is further complicated by grazing intensity differences within and between studies. Farruggia et al. (2012) observed rotationally grazed plots to have higher total butterfly abundance and richness, as well as higher vegetation heights and flower cover at the high stocking rate (1.6 LU/ha), but little difference between rotational grazing and continuous grazing at the lenient stocking rate (1.15 LU/ha). Furthermore, other studies which observed either no effect of grazing system (Bendel et al. 2018), marginal effects of grazing system (Kruse et al. 2016), or a positive effect of continuous grazing over rotational grazing (Goodenough and Sharp 2016) were operating at much lower grazing intensities (approximately 0.5 LU/ha–0.75 LU/ha). Unfortunately, Goodenough and Sharp (2016) did not include a direct analysis of the focal butterfly and only included the response of the host plant (see Gaps and concerns for further discussion).

Type of grazer

The type of grazer may influence grazing outcomes due to behavioral differences and nutritional needs of the herbivores. Sheep, as forb feeders, may reduce plant species richness and therefore reduce butterfly species richness (Öckinger et al. 2006). In contrast, sheep grazing combined with cattle grazing can improve livestock productivity and promote higher butterfly abundance and diversity than sheep alone since cattle are less selective grass grazers and thus reduce invasive, competitively dominant grasses (Fraser et al. 2014).

In African grasslands, native wild grazers promoted a higher diversity of butterflies than domestic livestock, but domestic livestock promoted more butterfly diversity than no grazing at all (Pryke et al. 2016). The differences between cattle and wild herbivore nutritional needs can also benefit butterfly species; cattle grazing was more beneficial to butterflies in the *Colotis* genus than wild herbivore grazing since cattle maintained the grassland but did not consume *Colotis'* host plant *Cadaba farinosa* (Wilkerson et al. 2013).

Natural and land use history

Grazing outcomes on butterfly species are mediated by natural history and land use (management) history. Many grasslands evolved in concert with megafaunal ungulate herbivores, many of which were extirpated or reduced in the late-Pleistocene, early Holocene, and in some cases by recent settler-colonial human activity (Johnson 2009; Galetti et al. 2018; Barnard 2020). Grazer removal from grassland ecosystems caused massive cascading effects (Johnson 2009). Cattle may serve to fill the ungulate herbivore niche in disturbance-dependent grasslands when wild herbivores have been extirpated (Hall and Bunce 2019; Konvička et al. 2021), as seen in European semi-natural grasslands (see Regional trends below).

Land use history strongly affects butterfly community response to grazing. This history refers to history of management within a site or the grazing intensity history. Land use legacies may be more influential predictors of butterfly community diversity and abundance in prairie restorations than current grazing management (Debinski et al. 2011; Moranz et al. 2012).

In semi-natural grasslands of Europe and Asia, maintaining the traditional land use and grazing intensity maintains community diversity and benefits species adapted to those conditions (Murata and Matsuura 2013; Schwarz and Fartmann 2021). Introducing grazing to a site that was historically mowed, or removing grazing or mowing from a landscape where they were previously present will drastically reduce butterfly community diversity and extirpate species (Nilsson et al. 2008, Mazalová et al. 2015). Murata and Matsuura (2013) observed more *Shijimiaeoides divinus asonis* larvae and their obligate host ants at the "customary" grazing intensity that had been used by Japanese farmers for thousands of years. A reduction or loss of grazing resulted in reduced populations of both.

Regional trends

The literature on grazing and butterfly species and communities was most extensive in Europe in part because historical amateur naturalists' observations are accessible to researchers. For example, Nilsson et al. (2008) compared butterfly censuses from 1904 to 1913 to their own surveys conducted in 2001–2005 to show the impact that pasture abandonment had on butterfly populations in Sweden. Dolek and Geyer (1997) reported grazing records for their sites existing since the fifteenth century. Similar data are lacking in other parts of the world.

Europe's history of free range low intensity livestock and megafaunal herbivore grazing created a shifting mosaic of semi-natural grasslands regulated by grazing that varied greatly in space and time (Balmer and Erhardt 2000; Nilsson et al. 2008; WallisDeVries et al. 2016). Since the 1950s, agricultural intensification has caused the abandonment and subsequent succession of many former pastures, which has in turn caused the decline of many plant and animal species endemic to semi-natural grasslands (Pöyry et al. 2004; Wallis De Vries et al. 2007). Agri-environment schemes were created by the European Union (Science for Environment Policy 2017) to combat habitat loss caused by agricultural intensification.

While no European studies in this review explicitly referenced land-sharing approaches to managing grazing for butterfly diversity, AES programs are inherently a land-sharing approach as they attempt to accommodate conservation needs within actively grazed lands and compensate farmers for potential lost productivity (Science for Environment Policy 2017). AES pastures are generally beneficial for butterfly richness and abundance over non-AES pastures (Brereton et al. 2008; MacDonald et al. 2012). However, many studies cautioned that even when overall diversity is benefitted by AES programs, no one grazing system, grazing intensity, disturbance type, or other management prescription benefitted all butterfly species and called for more heterogeneity in management on local, regional, and landscape scales to accommodate the differing habitat needs of multiple species (e.g. Pöyry et al. 2006, 2009; Sjödin et al. 2008; Fiedler et al. 2017).

North America, in contrast to Europe, had less extensive literature. There was a heavy emphasis on contrasting responses of butterfly communities and species to prescribed fire and grazing (see Grazing effectiveness relative to other management actions above). Only three North American studies (Delaney et al. 2016; Caven et al. 2017; Bendel et al. 2018) compared butterfly responses to grazing at different intensity levels and all three were more focused on contrasting grazing and fire management strategies, restoration status, or grazing system respectively than grazing intensity. Within the scope of the limited data, studies suggest similar responses by North American butterflies to European butterflies. Low to moderate grazing intensity may help maintain the ecosystem and control invasive grasses while minimizing the negative potential effects on butterfly diversity (Delaney et al. 2016).

North American literature did not emphasize land-sharing approaches to agriculture through the satisfaction of both economic and conservation goals. The United States does have programs similar to European AES that offer various types of conservation grazing easements to compensate producers for engaging in conservation activities (USDA Natural Resources Conservation Service 2021). However, there is little focus in the literature on evaluating the potential benefits of conservation grazing easements for butterflies.

Similar to European and North American literature, livestock grazing in Africa can benefit butterflies by maintaining the ecosystem, especially in the absence of wild herbivores. However, there was a large risk of overgrazing in arid or semi-arid ecosystems (e.g. Gardiner et al. 2005). Akite (2008) and Hoyle and James (2005) observed increasing grazing intensity to have detrimental effects on butterfly species richness and the persistence of *Pseudophilotes sinaicus* respectively.

Two studies within the African literature evaluated the ability of land-sharing approaches called ecological networks (ENs) to conserve butterfly diversity (Pryke et al. 2016; Joubert-van der Merwe et al. 2019). ENs are a series of interconnected reserves and conservation corridors allowing movement in landscapes fragmented by human activity (Samways and Pryke 2016). Both Pryke et al. (2016) and Joubert-van der Merwe et al. (2019) found ENs to benefit butterfly communities, though Joubert-van der Merwe et al. (2019) emphasized the need to manage ENs with moderate patch-burn grazing to promote spatial and temporal heterogeneity on multiple scales.

Butterflies of semi-natural grasslands in Asia had similar responses to other parts of the world. Both Asian studies found that their target butterflies, *Euphydryas aurinia* and *Melitaea phoebe* (Wang et al. 2007) and *S.d. asonis*, (Murata and Matsuura 2013) were benefitted in occupancy and abundance by moderate grazing. Wang et al. (2007) hypothesized that moderate grazing produces more open space than low intensity grazing, but maintains a higher vegetation height, structural diversity, and food plant density than high intensity grazing.

Purpose of grazing

In the European and African literature, there is much more of an emphasis on satisfying both economic and conservation goals (Fig. 4; Table 3). It is likely that the larger percentage of studies classified as "both" in Europe is due to the AES program discussed above and the focus on evaluating the management prescriptions laid out by the program. In contrast, there is much less focus within the North American literature on satisfying both goals with livestock grazing. The literature on cattle grazing effects on butterflies in North America, specifically the United States, should incorporate a land-sharing framework into butterfly conservation research and management on grazed land.

Gaps and concerns

There are some gaps in the types of questions the literature asks about butterfly responses to grazing. For studies evaluating single species responses to grazing, very few collected movement or demographic data to analyze species responses in detail. Most (n = 47; Fig. 1) studies simply compared species abundance or occupancy under different disturbance types, grazing systems, intensities, or other grazing attributes. These studies make the implicit assumption that higher occupancy or abundance indicates higher habitat preference and therefore habitat quality. This is problematic because abundance, habitat preference, and habitat quality are not always linked (Van Horne 1983; Bock and Jones 2004). Studies comparing vital rate or demographic data obtain a more accurate measure of the habitat quality and associated management (Mouquet et al. 2005; Thomas et al. 2009, Schultz et al. 2019). Studies using movement and behavior data obtain a more detailed understanding of butterfly habitat preference from the perspective of the focal species (Ouin et al. 2004, Schtickzelle et al. 2007, Schultz et al. 2019, Ehl et al. 2019).

For studies evaluating butterfly community responses, there was a tendency to report coarse measures such as species richness or diversity without including community composition analysis or other details of individual species responses. Only 27 studies analyzed community composition, though all also reported some combination of measures of species richness, abundance, and diversity. Richness, abundance, and diversity measures without community composition analysis obscure individual species responses and make interpretation of the results more difficult. Individual species may be negatively affected by a management decision or habitat characteristic even when overall species richness, abundance, or diversity is high (e.g. Pöyry et al. 2005).

The range of grazing practices evaluated does not encapsulate the range of grazing practices in use. Only five studies compared the effects of rotational and continuous grazing on butterfly species or communities, though rotational grazing was frequently recommended as a source of heterogeneity in the system by other studies who did not analyze grazing systems. Thus, more research would reveal if rotational grazing is indeed beneficial for butterflies and clarify the potential interaction between grazing system and grazing intensity indicated by Farruggia et al. (2012), as well as clarify how often cattle should be rotated.

In addition, few studies evaluated multiple levels of grazing intensities directly. Direct measurements of grazing intensity will clarify the potential relationship between grassland type and grazing intensity effects on butterfly species diversity and better provide management recommendations for grazing intensities. Furthermore, though the absolute grazing intensities that maximize butterfly diversity are well-studied in European grasslands, there is little understanding of the effects of grazing intensity on other grasslands throughout the world, hindering conservation and management decision- and policy-making.

A major gap in the literature is a lack of quantitative measurements of the effects of habitat heterogeneity in management and disturbance on butterflies. It is expected that greater amounts of in-patch and large scale heterogeneity will increase resources and thus habitat quality for butterflies (Dennis et al. 2006). Only two studies in this review explicitly quantified the effects of heterogeneity in management on multiple scales (Söderström et al. 2001; Sjödin et al. 2008), yet many studies recommended variation in management on fine, local, regional, and landscape scales (e.g. Eichel and Fartmann 2008; Fiedler et al. 2017; Bonari et al. 2017). No one disturbance type, grazing intensity level, or type of grazer benefitted all butterfly species in any study. In a fragmented landscape, butterflies may be able to fulfill multiple needs in different habitats (e.g. resting in grazed habitat, nectaring in road lanes, etc.) (Ouin et al. 2004).

Farmers and ranchers make their livelihoods through their grazing operations and are increasingly expected to provide conservation benefits while doing so. Only nine out of 115 studies in this review included any evaluation of the effects of the recommended grazing strategy on animal performance, farmer costs, or sociological perceptions on the part of the farming community. It would be beneficial to understand the effect of recommended butterfly-friendly grazing strategies on farmers' livelihoods and how to encourage adoption of potentially unpopular options such as low grazing intensity or labor intensive strategies such as rotational grazing.

There were common issues in study design or reporting across the reviewed literature. First, grazing intensity, system, and/or timing was often not reported, which would provide context for the results. Thirty-eight studies compared butterfly species or communities on grazed and ungrazed land without reporting the grazing intensity or any other attribute. This tendency was strong in the studies whose focus was on understanding butterfly habitat preferences or species distribution, where grazing was one of many variables within a larger model (Fig. 1, "Habitat quality").

There were frequent issues with poor study design and lack of replication. Replication across sites and years is key to producing a better understanding of grazing effects. Two studies analyzed only host plant responses to grazing, and yet made conclusions regarding the target butterfly. Insects do not respond to disturbance in the same way as plant communities (Kruess and Tscharntke 2002a), highlighting the importance of using caution when making management recommendations for butterfly conservation if the effects of grazing on the butterfly species or community itself were not examined.

Implications for conservation

Cattle grazing has high potential to advance butterfly conservation in agricultural lands through land-sharing approaches. Though more studies observed positive effects of grazing on butterfly species than negative, the effects on butterfly communities were context-dependent. The effects of cattle grazing on butterflies vary greatly depending on individual species biology and habitat requirements, whether there is an evolutionary history of grazing, the type of grassland system, and the grazing system and intensity chosen by the farmer or manager. Current research indicates low to moderate grazing intensity is most beneficial to butterflies. Grazing may be used as a tool for conservation in disturbance-dependent systems, though other disturbances such as mowing should be maintained in the landscape.

Knowledge of European butterflies and their conservation needs enables better understanding of how to manage grazing as a tool to promote butterfly diversity in the agricultural landscape. Similar knowledge in other parts of the world would improve conservation success in agricultural lands. In addition, the land-sharing approaches to grazing management in Europe and Africa (i.e. AES programs and Ecological Networks, respectively) have potential to provide habitat for butterflies outside of conservation reserves.

Current understanding of grazing effects on butterflies is limited by the use of coarse metrics (i.e. richness, abundance, diversity) without including mechanistic measures that are better able to account for butterfly species needs in agricultural land (i.e. movement, demography, community composition). Future studies should quantify the effects of grazing systems, the most beneficial grazing intensities across multiple grassland ecotypes, and the levels of spatial and temporal heterogeneity needed on local, regional, and landscape scales to provide habitat for all species of butterflies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-022-00373-8.

Acknowledgements I thank Cheryl B. Schultz, Sarah Hamman, and Kelsey C. King for valuable discussions and helpful comments on earlier versions of this manuscript. Funding provided by WSU CEREO, USDA Western SARE, and CREOi was critical to the completion of this work.

Author contributions The author confirms sole responsibility for the following: review conception, literature review, interpretation of results, and manuscript preparation.

Funding This work was funded by Washington State University Center for Environmental Research, Education, and Outreach (CEREO), U.S. Department of Agriculture Western Sustainable Agriculture Research and Education (SARE), and Conservation, Research and Education Opportunities International (CREOi).

Data availability List of studies and relevant information will be made available.

Code availability Not applicable.

Declarations

Conflict of interest The author certifies that there are no financial or proprietary interests in any material discussed in this article.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Akite P (2008) Effects of anthropogenic disturbances on the diversity and composition of the butterfly fauna of sites in the Sango Bay and Iriiri areas, Uganda: implications for conservation. Afr J Ecol 46:3–13

Balmer O, Erhardt A (2000) Consequences of succession on extensively grazed grasslands for central european butterfly communities: rethinking conservation practices. Conserv Biol 14:746–757

Barnard JL (2020) The bison and the cow: food, empire, extinction. Am Q 72:377–401

Barry S, Huntsinger L (2021) Rangeland Land-Sharing, Livestock Grazing's Role in the Conservation of Imperiled Species. Sustainability 13:4466

Bartoňová A, Kolář V, Marešová J, Šašić M, Šlancarová J, Sucháček P, Konvička M (2017) Isolated Asian steppe element in the Balkans: habitats of *Proterebia afra* (Lepidoptera: Nymphalidae: Satyrinae) and associated butterfly communities. J Insect Conserv 21:559–571

Batáry P, Örvössy N, Kőrösi A, Nagy M, Peregovits L (2007) Microhabitat preferences of *Maculinea teleius* (Lepidoptera: Lycaenidae). Eur J Entomol 104:731–736

Beck JJ, Hernández DL, Pasari JR, Zavaleta ES (2015) Grazing maintains native plant diversity and promotes community stability in an annual grassland. Ecol Appl 25:1259–1270

Bendel CR, Hovick TJ, Limb RF, Harmon JP (2018) Variation in grazing management practices supports diverse butterfly communities across grassland working landscapes. J Insect Conserv 22:99–111

Berg Å, Ahrné K, Öckinger E, Svensson R, Wissman J (2013) Butterflies in semi-natural pastures and power-line corridors—effects of flower richness, management, and structural vegetation characteristics. Insect Conserv Divers 6:639–657

Blanchet K, Moechnig H, DeJong-Hughes J (2000) Grazing systems planning guide. University of Minnesota Extension Service, US

Bock CE, Jones ZF (2004) Avian habitat evaluation: should counting birds count? Front Ecol Environ 2:403–410

Bonari G, Fajmon K, Malenovský I, Zelený D, Holuša J, Jongepierová I, Kočárek P, Konvička O, Uřičář J, Chytrý M (2017) Management of semi-natural grasslands benefiting both plant and insect diversity: the importance of heterogeneity and tradition. Agric Ecosyst Environ 246:243–252

Bonte D, Maes D (2008) Trampling affects the distribution of specialised coastal dune arthropods. Basic Appl Ecol 9:726–734

Börschig C, Klein A-M, von Wehrden H, Krauss J (2013) Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. Basic Appl Ecol 14:547–554

Brereton TM, Warren MS, Roy DB, Stewart K (2008) The changing status of the Chalkhill blue butterfly *Polyommatus coridon* in the UK: the impacts of conservation policies and environmental factors. J Insect Conserv 12:629–638

Bubová T, Vrabec V, Kulma M, Nowicki P (2015) Land management impacts on European butterflies of conservation concern: a review. J Insect Conserv 19:805–821

Caven AJ, King KC, Wiese JD, Brinley Buckley EM (2017) A descriptive analysis of regal fritillary (*Speyeria idalia*) habitat utilizing biological monitoring data along the big bend of the Platte River, NE. J Insect Conserv 21:183–205

Clausen HD, Holbeck HB, Reddersen J (2001) Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. Biol Cons 98:167–178

Cole LJ, Brocklehurst S, Robertson D, Harrison W, McCracken DI (2015) Riparian buffer strips: their role in the conservation of insect pollinators in intensive grassland systems. Agric Ecosyst Environ 211:207–220

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Cozzi G, Müller CB, Krauss J (2008) How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? Landscape Ecol 23:269–283

Cross DT (2020) Farming animals reduces biodiversity and threatens our health. Sustainability Times. Accessed 20 Nov 2021

D'Aniello B, Stanislao I, Bonelli S, Balletto E (2011) Haying and grazing effects on the butterfly communities of two Mediterranean-area grasslands. Biodivers Conserv 20:1731–1744

De Groot M, Rebeusek F, Grobelnik V, Govedic M, Salamun A, Verovnik R (2009) Distribution modelling as an approach to the conservation of a threatened alpine endemic butterfly (Lepidoptera: Satyridae). European Journal of Entomology 106:77–84

De Kort H, Prunier JG, Tessier M, Turlure C, Baguette M, Stevens VM (2018) Interacting grassland species under threat of multiple global change drivers. J Biogeogr 45:2133–2145

Debinski DM, Moranz RA, Delaney JT, Miller JR, Engle DM, Winkler LB, McGranahan DA, Barney RJ, Trager JC, Stephenson AL, Gillespie MK (2011) A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. Ecosphere 2:art131

Delaney JT, Moranz RA, Debinski DM, Engle DM, Miller JR (2016) Exotic-dominated grasslands show signs of recovery with cattle grazing and fire. Plos One 11:e0165758

Dennis RLH, Shreeve TG, Van Dyck H (2006) Habitats and resources: the need for a resource-based definition to conserve butterflies. Biodivers Conserv 15:1943–1966

Dierks A, Fischer K (2009) Habitat requirements and niche selection of *Maculinea nausithous* and *M. teleius* (Lepidoptera: Lycaenidae) within a large sympatric metapopulation. Biodivers Conserv 18:3663–3676

Dolek M, Geyer A (1997) Influence of management on butterflies of rare grassland ecosystems in Germany. J Insect Conserv 1:125–130

Dover JW, Rescia A, Fungariño S, Fairburn J, Carey P, Lunt P, Arnot C, Dennis RLH, Dover CJ (2011) Land-use, environment, and their impact on butterfly populations in a mountainous pastoral landscape: species richness and family-level abundance. J Insect Conserv 15:523–538

Dumont B, Farruggia A, Garel JP, Bachelard P, Boitier E, Frain M (2009) How does grazing intensity influence the diversity of plants and insects in a species-rich upland grassland on basalt soils? Grass Forage Sci 64:92–105

Ehl S, Böhm N, Wörner M, Rákosy L, Schmitt T (2019) Dispersal and adaptation strategies of the high mountain butterfly Boloria pales in the Romanian Carpathians. Front Zool 16:1

Eichel S, Fartmann T (2008) Management of calcareous grasslands for Nickerl's fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation, and patch area. J Insect Conserv 12:677–688

Elligsen H, Beinlich B, Plachter H (1997) Effects of large-scale cattle grazing on populations of *Coenonympha glycerion* and *Lasiommata megera* (Lepidoptera: Satyridae). J Insect Conserv 1:13–23

Elmer A, Lane J, Summerville KS, Lown L (2012) Does low-density grazing affect butterfly (Lepidoptera) colonization of a previously flooded tallgrass prairie reconstruction? Great Lakes Entomologist 45:1–10

Elwell SL, Griswold T, Elle E (2016) Habitat type plays a greater role than livestock grazing in structuring shrubsteppe plant–pollinator communities. J Insect Conserv 20:515–525

Farruggia A, Dumont B, Scohier A, Leroy T, Pradel P, Garel JP (2012) An alternative rotational stocking management designed to favour butterflies in permanent grasslands. Grass Forage Sci 67:136–149

Fartmann T (2006) Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (*Hamearis lucina*) in calcareous grasslands in central Germany. Ann Zool Fenn 43:335–347

Fiedler K, Wrbka T, Dullinger S (2017) Pluralism in grassland management promotes butterfly diversity in a large Central European conservation area. J Insect Conserv 21:277–285

Fleischner TL (1994) Ecological costs of livestock grazing in western north america. Conserv Biol 8:629–644

Fourcade Y, Öckinger E (2017) Host plant density and patch isolation drive occupancy and abundance at a butterfly's northern range margin. Ecol Evol 7:331–345

Franzén M, Nilsson SG (2008) How can we preserve and restore species richness of pollinating insects on agricultural land? Ecography 31:698–708

Fraser MD, Moorby JM, Vale JE, Evans DM (2014) Mixed grazing systems benefit both upland biodiversity and livestock production. Plos One 9:e89054

Fuhlendorf SD, Engle DM (2001) Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51:625

Galetti M, Moleón M, Jordano P, Pires MM, Guimarães PR, Pape T, Nichols E, Hansen D, Olesen JM, Munk M, de Mattos JS, Schweiger AH, Owen-Smith N, Johnson CN, Marquis RJ, Svenning J-C (2018) Ecological and evolutionary legacy of megafauna extinctions. Biol Rev Camb Philos Soc 93:845–862

Gardiner AJ, Ried RS, Kiema S (2005) Impact of land-use on butterflies in Southwestern Burkina Faso. Afr Entomol 13:201–212

Goffart P, Schtickzelle N, Turlure C (2010) Conservation and management of the habitats of two relict butterflies in the Belgian Ardenne: *Proclossiana eunomia* and Lycaena helle. In: Habel JC, Assmann T (eds) Relict species. Springer, Berlin, pp 357–370

Goodenough AE, Sharp MH (2016) Managing calcareous grassland for the declining Duke of Burgundy *Hamearis lucina* butterfly: effects of grazing management on Primula host plants. J Insect Conserv 20:1087–1098

Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. Science 307:550–555

Grill A, Cleary DFR (2003) Diversity patterns in butterfly communities of the Greek nature reserve Dadia. Biol Cons 114:427–436

Grime JP (1973) Control of species density in herbaceous vegetation. J Environ Manage 1:151–167

Hall SJG, Bunce RGH (2019) The use of cattle Bos taurus for restoring and maintaining holarctic landscapes: conclusions from a long-term study (1946–2017) in northern England. Ecol Evol 9:5859–5869

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLOS ONE 12(10):e0185809. https://doi.org/10.1371/journal.pone.0185809

Hodgson JA, Kunin WE, Thomas CD, Benton TG, Gabriel D (2010) Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. Ecol Lett 13:1358–1367

Hoyle M, James M (2005) Global warming, human population pressure, and viability of the world's smallest butterfly. Conserv Biol 19:1113–1124

Jerrentrup JS, Wrage-Mönnig N, Röver K-U, Isselstein J (2014) Grazing intensity affects insect diversity via sward structure and heterogeneity in a long-term experiment. J Appl Ecol 51:968–977

Jerrentrup JS, Klimek S, Marchiori E, Bittante G, Ramanzin M, Sturaro E, Marini L (2016) Impact of dairy farming on butterfly diversity in Alpine summer pastures. Agric Ecosyst Environ 232:38–45

Johansson V, Knape J, Franzén M (2017) Population dynamics and future persistence of the clouded Apollo butterfly in southern Scandinavia: The importance of low intensity grazing and creation of habitat patches. Biol Cons 206:120–131

Johansson V, Kindvall O, Askling J, Franzén M (2019) Intense grazing of calcareous grasslands has negative consequences for the threatened marsh fritillary butterfly. Biol Conserv 239:108280

Johansson V, Kindvall O, Askling J, Franzén M (2020) Extreme weather affects colonization–extinction dynamics and the persistence of a threatened butterfly. J Appl Ecol 57:1068–1077

Johnson CN (2009) Ecological consequences of late quaternary extinctions of megafauna. Proc Biol Sci 276:2509–2519

Johst K, Drechsler M, Mewes M, Sturm A, Wätzold F (2015) A novel modeling approach to evaluate the ecological effects of timing

and location of grassland conservation measures. Biol Conserv 182:44–52
Joubert-van der Merwe L, Pryke JS, Samways MJ (2019) Well-managed grassland heterogeneity promotes butterfly conservation in a corridor network. J Environ Manage 238:382–395
Juan-Baeza I, Martínez-Garza C, Del-Val E (2015) Recovering more than tree cover: herbivores and herbivory in a restored tropical dry forest. Plos One 10:e0128583
Kati V, Zografou K, Tzirkalli E, Chitos T, Willemse L (2012) Butterfly and grasshopper diversity patterns in humid Mediterranean grasslands: the roles of disturbance and environmental factors. J Insect Conserv 16:807–818
Kerr JT, Sugar A, Packer L (2000) Indicator Taxa Rapid Biodiversity Assessment and Nestedness in an Endangered Ecosystem. Conserv Biol 14(6):1726–34
Konvicka M, Benes J, Cizek O, Kopecek F, Konvicka O, Vitaz L (2008) How too much care kills species: grassland reserves, agri-environmental schemes and extinction of *Colias myrmidone* (Lepidoptera: Pieridae) from its former stronghold. J Insect Conserv 12:519–525
Konvička M, Ričl D, Vodičková V, Beneš J, Jirků M (2021) Restoring a butterfly hot spot by large ungulates refaunation: the case of the Milovice military training range, Czech Republic. BMC Ecol Evol 21:73
Kormann UG, Scherber C, Tscharntke T, Batáry P, Rösch V (2019) Connectedness of habitat fragments boosts conservation benefits for butterflies, but only in landscapes with little cropland. Landsc Ecol 34:1045–1056
Krauss J, Steffan-Dewenter I, Tscharntke T (2004) Landscape occupancy and local population size depends on host plant distribution in the butterfly *Cupido minimus*. Biol Cons 120:355–361
Kruess A, Tscharntke T (2002a) Contrasting responses of plant and insect diversity to variation in grazing intensity. Biol Conserv 106:293–302
Kruess A, Tscharntke T (2002b) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. Conserv Biol 16:1570–1580
Kruse M, Stein-Bachinger K, Gottwald F, Schmidt E, Heinken T (2016) Influence of grassland management on the biodiversity of plants and butterflies on organic suckler cow farms. Tuexenis 36:97–119
Kuussaari M, Heliölä J, Pöyry J, Saarinen K (2007) Contrasting trends of butterfly species preferring semi-natural grasslands, field margins and forest edges in northern Europe. J Insect Conserv 11:351–366
León-Cortés JL, Pérez-Espinoza F, Marín L, Molina-Martínez A (2004) Complex habitat requirements and conservation needs of the only extant Baroniinae swallowtail butterfly. Animal Conserv 7:241–250
Lewis OT, Hurford C (1997) Assessing the status of the marsh fritillary butterfly (*Eurodryas aurinia*): an example from Glamorgan, UK. J Insect Conserv 1:159–166
Loos J, Vizauer T-C, Kastal A, Davies M, Hedrich H, Dolek M (2020) A highly endangered species on the edge: distribution, habitat use and outlook for *Colias myrmidone* in newly established Natura 2000 areas in Romania. Environ, Dev Sustain 22:1–16
MacDonald MA, Cobbold G, Mathews F, Denny MJH, Walker LK, Grice PV, Anderson GQA (2012) Effects of agri-environment management for cirl buntings on other biodiversity. Biodivers Conserv 21:1477–1492
Manley WA, Hart RH, Samuel MJ, Smith MA, Waggoner JW, Manley JT (1997) Vegetation, cattle, and economic responses to grazing strategies and pressures. J Range Manag 50:638
Marschalek DA, Faulkner DK, Deutschman DH (2017) Livestock grazing shapes the vegetation structure and subsequent habitat use by the endangered skipper *Pyrgus ruralis lagunae* (Lepidoptera: Hesperiidae). Environ Entomol 46:445–453
Mazalova M, Sipos J, Rada S, Kasak J, Sarapatka B, Kuras T (2015) Responses of grassland arthropods to various biodiversity-friendly management practices: Is there a compromise? Eur J Entomol 112:734–746
McCullough K, Albanese G, Haukos DA, Ricketts AM, Stratton S (2019) Management regime and habitat response influence abundance of regal fritillary (*Speyeria idalia*) in tallgrass prairie. Ecosphere. https://doi.org/10.1002/ecs2.2845
McIntyre S, Hobbs R (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conserv Biol 13:1282–1292
Milberg P, Bergman K-O, Cronvall E, Eriksson ÅI, Glimskär A, Islamovic A, Jonason D, Löfqvist Z, Westerberg L (2016) Flower abundance and vegetation height as predictors for nectar-feeding insect occurrence in Swedish semi-natural grasslands. Agric Ecosyst Environ 230:47–54
Milchunas DG, Sala OE, Lauenroth WK (1988) A generalized model of the effects of grazing by large herbivores on grassland community structure. Am Nat 132:87–106
Moranz RA, Debinski DM, McGranahan DA, Engle DM, Miller JR (2012) Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. Biodivers Conserv 21:2719–2746
Moranz RA, Fuhlendorf SD, Engle DM (2014) Making sense of a prairie butterfly paradox: the effects of grazing, time since fire, and sampling period on regal fritillary abundance. Biol Conserv 173:32–41
Moschetti M, Besnard A, Couturier T, Fonderflick J (2020) Grazing intensity negatively affects the maintenance of *Gentiana pneumonanthe* and the survival of *Phengaris alcon* egg-laying. J Insect Conserv 24:343–351
Mouquet N, Belrose V, Thomas JA, Elmes GW, Clarke RT, Hochberg ME (2005) Conserving community modules: a case study of the endangered lycaenid butterfly *Maculinea alcon*. Ecology 86:3160–3173
Munguira ML, Barea-Azcón JM, Castro-Cobo S, García-Barros E, Miteva S, Olivares J, Romo H (2017) Ecology and recovery plans for the four Spanish endangered endemic butterfly species. J Insect Conserv 21:423–437
Murata K, Matsuura A (2013) Effect of grazing intensity on the interaction between *Shijimiaeoides divinus asonis* (Matsumura, 1929) and its attendant ants. Entomol Sci. https://doi.org/10.1111/ens.12026
Nilsson SG, Franzén M, Jönsson E (2008) Long-term land-use changes and extinction of specialised butterflies. Insect Conserv Divers. https://doi.org/10.1111/j.1752-4598.2008.00027.x
Noss RF (1994) Cows and conservation biology. Conserv Biol 8:613–616
Öckinger E, Eriksson AK, Smith HG (2006) Effects of grassland abandonment, restoration and management on butterflies and vascular plants. Biol Cons 133:291–300
Ogden S, Haukos DA, Olson K, Lemmon J, Alexander J, Gatson GA, Fick WH (2019) Grassland bird and butterfly responses to sericea lespedeza control via late-season grazing pressure. Am Midl Nat 181:147
Ouin A, Aviron S, Dover J, Burel F (2004) Complementation/supplementation of resources for butterflies in agricultural landscapes. Agric Ecosyst Environ 103:473–479
Pérez-Sánchez AJ, Schibalski A, Schröder B, Klimek S, Dauber J (2020) Disentangling the effects of host resources, local, and landscape variables on the occurrence pattern of the dusky large blue butterfly (*Phengaris nausithous*) in upland grasslands. J Insect Conserv 24:327–341

Pollard E (1977) A method for assessing changes in the abundance of butterflies. Biol Conserv 12(2) 115–134. https://doi.org/10.1016/0006-3207(77)90065-9

Potts SG, Woodcock BA, Roberts SPM, Tscheulin T, Pilgrim ES, Brown VK, Tallowin JR (2009) Enhancing pollinator biodiversity in intensive grasslands. J Appl Ecol 46:369–379

Pöyry J, Lindgren S, Salminen J, Kuussaari M (2004) Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. Ecol Appl 14:1656–1670

Pöyry J, Lindgren S, Salminen J, Kuussaari M (2005) Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. Biol Conserv 122:465–478

Pöyry J, Luoto M, Paukkunen J, Pykälä J, Raatikainen K, Kuussaari M (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. Oikos 115:401–412

Pöyry J, Paukkunen J, Heliölä J, Kuussaari M (2009) Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. Oecologia 160:577–587

Pryke JS, Roets F, Samways MJ (2016) Wild herbivore grazing enhances insect diversity over livestock grazing in an African grassland system. Plos One 11:e0164198

Pullin AS, Stewart GB (2006) Guidelines for systematic review in conservation and environmental management. Conserv Biol 20:1647–1656

Ravetto Enri S, Probo M, Farruggia A, Lanore L, Blanchetete A, Dumont B (2017) A biodiversity-friendly rotational grazing system enhancing flower-visiting insect assemblages while maintaining animal and grassland productivity. Agric Ecosyst Environ 241:1–10

Saarinen K, Jantunen J (2005) Grassland butterfly fauna under traditional animal husbandry: contrasts in diversity in mown meadows and grazed pastures. Biodivers Conserv 14:3201–3213

Samways MJ, Pryke JS (2016) Large-scale ecological networks do work in an ecologically complex biodiversity hotspot. Ambio 45:161–172

Sanford MP (2011) Improving conservation and management of the imperiled carson valley silverpot butterfly *Speyeria nokomis carsonensis* (Lepidoptera: Nymphalidae) based on rapid assessments of distribution, habitat, and threats. J Insect Conserv 15:715–725

Schtickzelle N, Baguette M (2004) Metapopulation viability analysis of the bog fritillary butterfly using RAMAS/GIS. Oikos 104:277–290

Schtickzelle N, Turlure C, Baguette M (2007) Grazing management impacts on the viability of the threatened bog fritillary butterfly *Proclossiana eunomia*. Biol Conserv 136:651–660

Schultz CB, Haddad NM, Henry EH, Crone EE (2019) Movement and Demography of At-Risk Butterflies: Building Blocks for Conservation. Annu Rev Entomol 64:167–184

Schwarz C, Fartmann T (2021) Conservation of a strongly declining butterfly species depends on traditionally managed grasslands. J Insect Conserv 25:255–271

Science for Environment Policy (2017) Agri-environment schemes: impacts on the agricultural environment. European Commission DG Environment, Science Communication Unit

Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, Ammer C, Bauhus J, Fischer M, Habel JC, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze E-D, Vogt J, Wöllauer S, Weisser WW (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574:671–674

Shapira T, Henkin Z, Dag A, Mandelik Y (2020) Rangeland sharing by cattle and bees: moderate grazing does not impair bee communities and resource availability. Ecol Appl 30:e02066

Sjödin NE, Bengtsson J, Ekbom B (2008) The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. J Appl Ecol 45:763–772

Skaer MJ, Graydon DJ, Cushman JH (2013) Community-level consequences of cattle grazing for an invaded grassland: variable responses of native and exotic vegetation. J Veg Sci 24:332–343

Smee M, Smyth W, Tunmore M, Ffrench-Constant R, Hodgson D (2011) Butterflies on the brink: habitat requirements for declining populations of the marsh fritillary (*Euphydryas aurinia*) in SW England. J Insect Conserv 15:153–163

Smith LM, Cherry R (2014) Effects of management techniques on grassland butterfly species composition and community structure. Am Midl Nat 172:227–235

Söderström B, Svensson B, Vessby K, Glimskär A (2001) Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodivers Conserv 10:1839–1863

Spitzer L, Benes J, Dandova J, Jaskova V, Konvicka M (2009) The large blue butterfly, *Phengaris* [Maculinea] arion, as a conservation umbrella on a landscape scale: the case of the Czech Carpathians. Ecol Ind 9:1056–1063

Stuhldreher G, Fartmann T (2014) When habitat management can be a bad thing: effects of habitat quality, isolation and climate on a declining grassland butterfly. J Insect Conserv 18:965–979

Swengel AB (1998) Effects of management on butterfly abundance in tallgrass prairie and pine barrens. Biol Cons 83:77–89

Swengel A (2001) A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodivers Conserv 10:1141–1169

Swengel AB, Swengel SR (2001a) A ten-year study to monitor populations of the regal fritillary, *Speyeria idalia*, (Lepidoptera: Nymphalidae) in Wisconsin, U.S.A. Gt Lakes Entomol 34:97–115

Swengel A, Swengel S (2001b) Effects of prairie and barrens management on butterfly faunal composition. Biodivers Conserv 10:1757–1785

Szentirmai I, Mesterházy A, Varga I, Schubert Z, Sándor LC, Ábrahám L, Kőrösi Á (2014) Habitat use and population biology of the Danube clouded yellow butterfly *Colias myrmidone* (Lepidoptera: Pieridae) in Romania. J Insect Conserv 18:417–425

Thomas JA, Simcox DJ, Clarke RT (2009) Successful conservation of a threatened Maculinea butterfly. Science 325:80–83

United Nations Food and Agriculture Administration (2012) LIVESTOCK AND LANDSCAPE. https://www.fao.org/3/ar591e/ar591e.pdf. Accessed 15 Jun 2021

USDA Natural Resources Conservation Service (2021) Easements|NRCS. https://www.nrcs.usda.gov/wps/portal/nrcs/main/national/programs/easements/. Accessed 27 Jul 2021

Van Horne B (1983) Density as a misleading indicator of habitat quality. J Wildl Manag 47:893–901

van Klink R, van der Plas F, van Noordwijk CGET, WallisDeVries MF, Olff H (2015) Effects of large herbivores on grassland arthropod diversity. Biol Rev 90:347–366

van Klink R, Nolte S, Mandema FS, Lagendijk DDG, WallisDeVries MF, Bakker JP, Esselink P, Smit C (2016) Effects of grazing management on biodiversity across trophic levels–the importance of livestock species and stocking density in salt marshes. Agric Ecosyst Environ 235:329–339

Vessby K, Söderström B, Glimskär A, Svensson B (2002) Species-richness correlations of six different taxa in swedish seminatural grasslands. Conserv Biol 16:430–439

Vogel JA, Debinski DM, Koford RR, Miller JR (2007) Butterfly responses to prairie restoration through fire and grazing. Biol Conserv 140:78–90

Wagner DL (2020) Insect declines in the anthropocene. Annu Rev Entomol 65:457–480

Wallis De Vries MF, Parkinson AE, Dulphy JP, Sayer M, Diana E (2007) Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity. Grass Forage Sci 62:185–197

WallisDeVries M (2004) A quantitative conservation approach for the endangered butterfly *Maculinea alcon*. Conserv Biol 18:489–499

WallisDeVries MF, Raemakers I (2001) Does extensive grazing benefit butterflies in coastal dunes? Restor Ecol 9:179–188

WallisDeVries MF, Noordijk J, Colijn EO, Smit JT, Veling K (2016) Contrasting responses of insect communities to grazing intensity in lowland heathlands. Agric Ecosyst Environ 234:72–80

Wang Y, Chen J, Liu W, Xu R (2007) Effect of cultivating croplands and grazing in aridgrassland habitats on the conservation of melitaeinebutterflies in a mountainous area in Northern China. Sci China, Ser C: Life Sci 50:40–46

Wätzold F, Drechsler M, Johst K, Mewes M, Sturm A (2016) A novel, spatiotemporally explicit ecological-economic modeling procedure for the design of cost-effective agri-environment schemes to conserve biodiversity. Am J Agric Econ 98:489–512

Weiss SB (1999) Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conserv Biol 13:1476–1486

Weking S, Hermann G, Fartmann T (2013) Effects of mire type, land use and climate on a strongly declining wetland butterfly. J Insect Conserv 17:1081–1091

Westin A, Lennartsson T, Björklund J-O (2018) The historical ecology approach in species conservation–identifying suitable habitat management for the endangered clouded Apollo butterfly (*Parnassius mnemosyne* L.) in Sweden. AIMS Environ Sci 5:244–272

Wettstein W, Schmid B (1999) Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J Appl Ecol 36:363–373

Wilkerson ML, Roche LM, Young TP (2013) Indirect effects of domestic and wild herbivores on butterflies in an African savanna. Ecol Evol 3:3672–3682

Woodcock BA, Potts SG, Tscheulin T, Pilgrim E, Ramsey AJ, Harrison-Cripps J, Brown VK, Tallowin JR (2009) Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. J Appl Ecol 46:920–929

Woodcock BA, Bullock JM, Mortimer SR, Brereton T, Redhead JW, Thomas JA, Pywell RF (2012) Identifying time lags in the restoration of grassland butterfly communities: a multi-site assessment. Biol Conserv 155:50–58

Woodcock BA, Savage J, Bullock JM, Nowakowski M, Orr R, Tallowin JRB, Pywell RF (2014) Enhancing floral resources for pollinators in productive agricultural grasslands. Biol Conserv 171:44–51

Zakkak S, Chatzaki M, Karamalis N, Kati V (2014) Spiders in the context of agricultural land abandonment in Greek Mountains: species responses, community structure and the need to preserve traditional agricultural landscapes. J Insect Conserv 18:599–611