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Pest suppression by bats and management strategies to favour it: a global review

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ABSTRACT

Fighting insect pests is a major challenge for agriculture worldwide, and biological control and integrated pest management constitute well-recognised, cost-effective ways to prevent and overcome this problem. Bats are important arthropod predators globally and, in recent decades, an increasing number of studies have focused on the role of bats as natural enemies of agricultural pests. This review assesses the state of knowledge of the ecosystem services provided by bats as pest consumers at a global level and provides recommendations that may favour the efficiency of pest predation by bats. Through a systematic review, we assess evidence for predation, the top-down effect of bats on crops and the economic value of ecosystem services these mammals provide, describing the different methodological approaches used in a total of 66 reviewed articles and 18 agroecosystem types. We also provide a list of detailed conservation measures and management recommendations found in the scientific literature that may favour the delivery of this important ecosystem service, including actions aimed at restoring bat populations in agroecosystems. The most frequent recommendations include increasing habitat heterogeneity, providing additional roosts, and implementing laws to protect bats and reduce agrochemical use. However, very little evidence is available on the direct consequences of these practices on bat insectivory in farmland. Additionally, through a second in-depth systematic review of scientific articles focused on bat diet and, as part of the ongoing European Cost Action project CA18107, we provide a complete list of 2308 documented interactions between bat species and their respective insect pest prey. These pertain to 81 bat species belonging to 36 different genera preying upon 760 insect pests from 14 orders in agroecosystems and other habitats such as forest or urban areas. The data set is publicly available and updatable.

I. INTRODUCTION

One of the major challenges for agriculture, both locally and globally, is the prevalence of herbivorous insect pests (Oerke, 2006; Savary *et al*., 2019). Although standardised information on crop losses is difficult to compile, global crop losses due to herbivorous arthropod pests has been estimated at 25–50%, reaching much higher values in several regions, such as in sorghum plantations in Kenya (88% yield loss) and rice fields in the Philippines (66% yield loss), in both cases due to moth species of the genus *Chilo* (Pimentel *et al*., 1978; Myers *et al*., 2017; Savary *et al*., 2019). To overcome this problem, conventional agriculture adopts pesticides despite their well-known adverse consequences such as alteration of ecosystem dynamics, the development of toxicity resistance by pests, and human health risks (Carvalho, 2006). In contrast, organic farming has developed chemical-free management systems to deal with pests (Zehnder *et al*., 2007). Among the multiple strategies applied in organic farming, the use of the pest control services provided by natural predators of insects such as bats and birds has become increasingly popular (Puig-Montserrat *et al*., 2015; Olmos-Moya *et al*., 2022).

Chiroptera is the second most biodiverse group of mammals with >1460 species worldwide (Burgin *et al*., 2018; Simmons & Cirranello, 2022). Most bat species are insectivores, consuming up to 70–84% of their body mass in insects each night (Kurta *et al*., 1989; Kalka & Kalko, 2006; Kunz *et al*., 2011), and sometimes >100% (Kunz & Stern, 1995). Bats use different hunting strategies depending on their foraging guilds, some species specialising on flying insects (aerial-hawking bats) and others seizing prey directly from the foliage or ground (gleaning bats). Several authors have reported the vital ecosystem services provided by bats as insect pest suppressors, which are beneficial for both ecosystems and farmers (e.g. Leelapaibul, Bumrungsri & Pattanavibool, 2005; Cleveland *et al*., 2006; Kunz *et al*., 2011; Puig-Montserrat *et al*., 2015; Kemp *et al*., 2019; Linden *et al*., 2019). Efforts have been made to quantify the importance of these ecosystem services, despite the difficulty of valuing them. For instance, Boyles *et al*. (2011) valued the pest suppression services provided by bats at $22.6 billion/year in cotton fields in the USA; Wanger *et al*. (2014) estimated that bats prevent losses of more than $1.2 million each year in the rice fields of Thailand, and Taylor *et al*. (2018) calculated that annual costs of around $613/ha in the macadamia orchards of South Africa are avoided due to the presence of bats.

Integrated pest management (IPM) is an ecosystem-based strategy increasingly adopted to prevent and fight agricultural pests (Stenberg, 2017). It consists of using multiple techniques to regulate pests cost effectively, encouraging biological control, pesticide reduction, and sustainable practices to reduce ecological and human health impacts (Kogan, 1998; Dent, 2000; Ehler, 2006; Stenberg, 2017). IPM is based on different interacting management elements that create either synergistic or antagonistic effects when applied simultaneously in farmlands (Stenberg, 2017). Use of IPM practices attempts to restrict damage levels due to pests below a certain economic threshold, reducing the need for pesticides and thus protecting the environment (Vreysen & Hendrichs, 2007; Alwang, Norton & Larochelle, 2019). However, evaluating the efficiency of any conservation interventions is essential to understand what works and what does not (see Sutherland *et al*., 2013).

Despite the potential benefits of bats as natural enemies of insect pests in agriculture, there remains a lack of information on their provision of ecosystem services and for evidence-based conservation strategies, as well as appropriate recommendations, guidelines, and protocols to help farmers adopt sustainable practices (Adams & Sandbrook, 2013). There is also a considerable knowledge gap regarding the diet of most insectivorous bat species, limiting our understanding of which species prey upon a given pest and the magnitude of pest suppression they provide (Boyles *et al*., 2013). The complexity of identifying prey at the species level in bat faeces using traditional methods (i.e. visual inspection) has hampered progress for decades, but recent improvements in molecular technologies now offer potential for a more precise picture of bat–pest interactions. Quantifying their ecosystem services, however, remains challenging due to a lack of suitable methods to extrapolate the true abundance of prey from such genetic analyses, the difficulty of detecting predatory bats from acoustic surveys, and due to the inherent complexity of designing experiments to assess pest suppression/control by aerial vertebrates such as bats.

This study provides an assessment of the state of knowledge about the role of bats as pest suppressors at a global level, summarises the available evidence, and provides recommendations on how to enhance the efficiency of bat pest suppression in agriculture. We present a review of the ecosystem services provided by insectivorous bats in different agroecosystems, and specifically: (*i*) examine the crop types covered, the pest species detected, and the bat species involved; (*ii*) assess whether the reviewed studies provided evidence for predation of insect pests, demonstrated a top-down effect of bat predation on crops, and economically quantified the benefits of bats to agriculture; (*iii*) summarise conservation measures, actions, and agricultural recommendations documented in the scientific literature to favour bat foraging as a form of natural pest suppression; (*iv*) from a second review focused on bat diet, provide a complete list of known interactions between bat species and pest insect species worldwide which we make publicly available in an online open repository.

II. MATERIALS AND METHODS

(1) Bats as insect pest suppressors in agroecosystems

We conducted a first literature search (LS1) in ISI *Web of Science* of indexed articles and book chapters in English, using the following terms in the TOPIC field (searching both the title and the abstract): ‘agricultur*’, ‘pest’, ‘insect*’ and ‘bat*’ or ‘bats’. The search was performed by C.

T.-C. in October 2022 obtaining 173 references, of which only 66 of were considered for the review after checking the whole text (see online Supporting information, Fig. S1). We only included articles directly studying and assessing the effect of bats as pest controllers, either as direct predators of one or several pests (providing or not evidence of predation), evaluating their effect as top predators or quantifying economically their suppressive effect. We excluded any work that only mentioned the potential of bats as insect pest suppressors as an indirect topic of their research. For each of the included studies (see Table S1), we extracted information following a semi-structured questionnaire: (*i*) the year and country where the study was performed; (*ii*) the agroecosystem type studied; (*iii*) the insect pest species detected and the bat species on which the study was focused; (*iv*) whether predation of bats upon pest species was demonstrated; (*v*) whether the study demonstrated a top-down effect of bats on that agroecosystem; (*vi*) whether the benefits of bat ecosystem services were quantified economically, and what methods were used to estimate the economic value of bats as pest suppressors; and (*vii*) the conservation and management strategies proposed in the articles and their potential application.

(2) Bat–insect pest interactions

We compiled a comprehensive list of agricultural insect pests occurring in temperate and tropical regions. Since no more recent public documents or published lists were available, we extracted the main agricultural insect pests cited in Hill (1983, 1987). Note that species might be considered pests in certain regions while not in others, meaning that this comprehensive list will need careful review by entomologists and local or regional experts for use in agricultural management.

We assembled a first list of 1236 insect pest species or genera extracted from Hill (1987, 1983). We then conducted a second literature search (LS2) in the ISI *Web of Science* using the R package *wosr*. We searched for any indexed document containing the following terms in the topic field: 'pest species name' AND 'bat*', where 'pest species name' refers to each of the 1236 species in Table S2. After the first check of the articles found, we added 562 new pest species to the first list, which were not included in Hill (1987, 1983) but were studied in the papers found. The updated list consisting of 1798 insect pest species then was used to perform the same literature search with the R package *wosr*. In addition, we also performed three literature searches including the following terms: (*i*) 'bat' or 'bats', 'diet*', and 'insect*'; (*ii*) 'bat' or 'bats', 'predat*', and 'insect*'; (*iii*) 'bat' or 'bats', 'diet*', and 'arthropod*'. We identified a total of 3620 articles, of which only 366 were assessed for eligibility. Of the latter, we finally retained only those that identified bat prey at the genus or species level ($N = 95$) (see Fig. S2).

For each article, the following information was extracted: year, country, habitat type, diet assessment methods, bat species, and pest species consumed. For the variable 'habitat type' we considered five categories: agricultural (dominated by agricultural lands), forested (dominated by woodlands and forests), urban (landscape dominated by urban areas), others (when the habitat described in the study did not match the above categories; e.g. desert, grasslands), not specified (when the authors mentioned the study area or the specific place without describing the habitat in which it is found). The variable 'diet assessment methods' considered the methods applied by authors in order to study the diet of bats: 'acoustics and insect remains' (when authors combined acoustic recordings and analysis of insect remains discarded by hunting bats), 'acoustics and visual' (when authors combined acoustic recordings and visual observations), 'insect remains' (when authors used insect remains discarded by bats), 'DNA faeces' (when authors studied DNA extracted from faeces), 'DNA stomach' (when authors studied DNA extracted from stomach contents), 'faeces dissection' (when authors dissected faecal samples to study insect remains).

Predator and prey information was organised into two data sets. In the first data set, we recorded each bat species with the insect pest species it consumed, and the method used to confirm predation (see Table S3). In the latter, for each pest species known to be preyed upon by bats, we recorded the crop types they affected (see Table S4). Crop types were classified into several categories for analysis: cereals (e.g. wheat, maize, corn, rice, barley, sorghum); forest (e.g. beech, oak, poplar, willow); fruit crops (e.g. apple, pear, apricot, strawberry, cranberry); grasses (e.g. sugarcane, turfs, pastures); legumes (e.g. pea, bean, alfalfa, soybean); ornamental (e.g. garden species); other (cotton, tea, tobacco, hop, flax, rubber tree, hemp, peppermint, jute, rapeseed, kenaf, ashwagandha, mushrooms, honeybees); stored products (e.g. stored cereals, stored tobacco, dried fruits); and vegetables (e.g. tomato, lettuce, spinach, potato, onion).

To present our findings graphically, we created food webs using the function *plotweb* of the R package *bipartite*, to show the interactions between different bat genera and insect pest orders consumed by them. We finally assessed the distribution of these insect pest orders according to the different crop types affected and the different habitats surveyed. All analyses were carried out with R software version 4.0.3 (R Core Team, 2022).

We performed all systematic reviews following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (O'Dea *et al*., 2021).

III. RESULTS

(1) Bats as insect pest suppressors in agroecosystems

We retrieved 66 articles in LS1 published from 1995 to 2022 (Fig. S1), with the publishing rate for these articles showing a clear positive trend with time (Fig. S3). The studies were conducted in 25 countries, primarily in North America (USA and Mexico; 27 articles, 40.9%), Europe (especially southern Europe; 11 articles, 16.7%), and southeast Asia (Thailand, Malaysia, Indonesia, and the Philippines; seven articles, 10.6%) (Fig. 1). Almost no studies were found for north and central Asia (only one published article for India). We found clear knowledge gaps for the African continent, where seven studies assessing the role of bats as pest suppressors have been carried out: five in South Africa, and one each in Madagascar and Senegal. A similar focus on only a few regions was found for Central and South America and the Caribbean islands: the ecosystem services of bats as pest suppressors have been assessed only in Brazil (three articles), Costa Rica (two articles), Chile (one article) and Peru (one article).

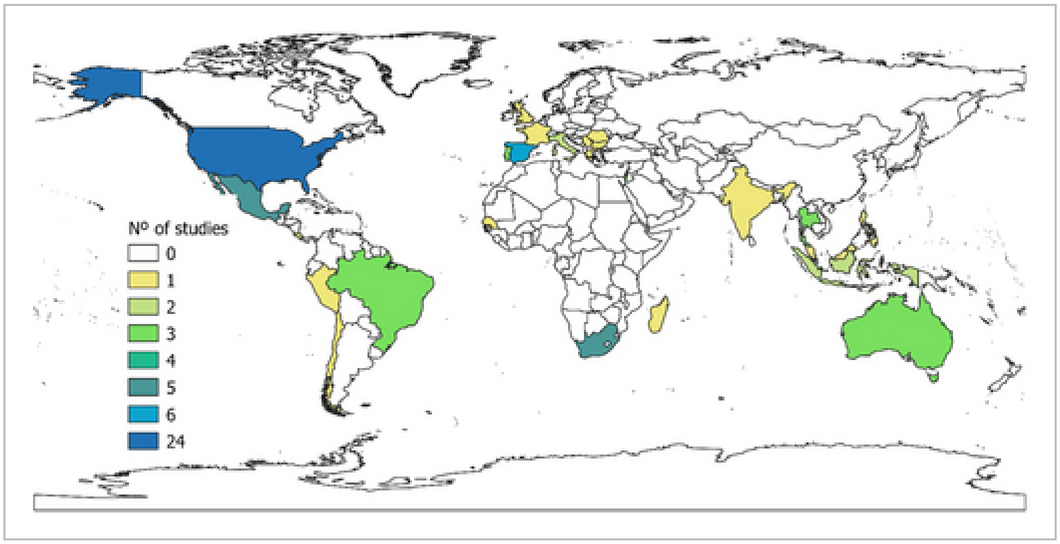

Fig. 1

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Geographic distribution of studies assessing the ecosystem services provided by bats as suppressors of agricultural insect pests.

Of a total of 18 agroecosystem types surveyed, cotton was the most studied (22.7%), followed by rice (13.6%), coffee (7.6%), corn (7.6%), fruit trees (7.6%), macadamia (7.6%), and vineyards (7.6%) (Table 1). A considerable proportion of articles (16.7%) did not specify the crop types cultivated in the study area.

Table 1. Agroecosystem types studied in the 66 articles located by our first literature search (LS1). Some articles considered more than one agroecosystem, and hence the total percentage does not sum to 100.

Agroecosystem	Number of articles	References
Cotton	15 (22.7%)	Cleveland *et al*. (2006); Federico *et al*. (2008); Boyles *et al*. (2011); Lopez-Hoffman *et al*. (2014, 2017); Wiederholt *et al*. (2015, 2017); Davidai *et al*. (2015); Medellin *et al*. (2017); Krauel *et al*. (2018); Cohen *et al*. (2020); Kolkert *et al*. (2020*a*,*b*, 2021); Korine *et al*. (2020)
Not specified	11 (16.7%)	Whitaker (1995); Agosta & Morton (2003); McCraken *et al*. (2012); Valentin *et al*. (2016); Aizpurua *et al*. (2018); Kahnonitch *et al*. (2018); Olimpi & Philpott (2018); Hughes *et al*. (2021); Mata *et al*. (2021); Ancilloto *et al*. (2022); O'Rourke *et al*. (2022)
Rice	9 (13.6%)	Leelapaibul *et al*. (2005); Wanger *et al*. (2014); Puig-Montserrat *et al*. (2015, 2020); Srilopan *et al*. (2018); Kemp *et al*. (2019); Sedlock *et al*. (2019); Montauban *et al*. (2021); Bhalla *et al*. (2023)
Coffee	5 (7.6%)	Williams-Guillen *et al*. (2008); Karp *et al*. (2013); Karp & Daily (2014); Librán-Embid *et al*. (2017); Schmitt *et al*. (2021)
Corn	5 (7.6%)	Maine & Boyles (2015); Davidai *et al*. (2015); Krauel *et al*. (2018); Harms *et al*. (2020); Whitby *et al*. (2020)
Macadamia	5 (7.6%)	Taylor *et al*. (2017, 2018); Weier *et al*. (2018, 2019); Linden *et al*. (2019)
Vineyard	5 (7.6%)	Baroja *et al*. (2019); Polyakov *et al*. (2019); Rodríguez-San Pedro *et al*. (2020); Charbonnier *et al*. (2021); Baroja *et al*. (2021)

(a) *Predation, top-down effect, and economic value assessment*

The 66 reviewed articles reported that 102 bat species preyed upon a total of 208 pest species (Table **S1**). Only half of the studies (33 articles) demonstrated that bats feed on these agricultural pests, while the remaining articles, although declaring a focus on bats as pest consumers, did not provide evidence for predation. Methods used to confirm predation included molecular techniques (DNA barcoding and metabarcoding) to analyse bat diets (28/33 articles, 84.8%) or visual identification of insect parts from faeces using stereo or digital microscopy (4/33 articles, 12.1%). Only 13 out of the 66 articles (19.7%) provided evidence for a top-down effect of bats on harvest or yield, in all cases by comparing the damage recorded in crops from which the bats had been experimentally excluded with control plots that were fully accessible. Economic quantification of the ecosystem services delivered by bats was provided by only 18 (27.3%) of the 66 studies, for several regions of the world and for different crop types. Seventeen of these studies contained an explicit calculation of the economic benefits provided by bats as pest suppressors, or sufficient information to perform this calculation (Table 2).

Table 2. Articles assessing the economic value of the ecosystem services provided by bats as agricultural insect pest suppressors organised by country and type of crop. Where valuations were made in the original study in other currencies these have been converted to US $. Method: ACM, avoided cost model; BT, benefit transfer model; EE, exclosure experiment. Bt, genetically modified pest-resistant variety.

Country	Agroecosystem	US $/ha/year		Total amount (US $/year)	Method	Reference
USA	Cotton	$183.11* [$29.90–$426.26]*		$741,000 [$121,000–$1,725,000]	ACM	Cleveland *et al*. (2006)
USA	Cotton	*Conventional cotton* Pesticide use: $86 Non-pesticide use: $683	*Bt cotton* Pesticide use: $46 Non-pesticide use: $214	$688,000 (conventional cotton)	ACM	Federico *et al*. (2008)
USA	Cotton	$182.90* [$29.66–$427.58]*		$22.9 billion [$3.7 billion–$53 billion]	BT	Boyles *et al*. (2011)
USA	Cotton	$34.05* $66.65 (1990)–$13.58 (2008)*		$12.24 million [$23.96 million (1990)–$4.88 (2008)	ACM	López-Hoffman *et al*. (2014)
USA and	Cotton	–		$11.67 million	ACM	Wiederholt

* Calculated using values found in the article. ** Values calculated at a global level.

The most common method used to calculate the economic value of ecosystem services provided by bats was an avoided cost model (62.7%, $N = 11$), which estimates avoided costs related to reduced crop damage and/or pesticide use; only four articles (23.5%) used exclusion experiments to calculate economic benefits, and two articles (11.8%) applied a benefit transfer model, which uses the same calculations as the avoided cost model but with published data from other studies.

(b) *Integrated pest management – guidelines to enhance bat activity in agroecosystems*

We classified the suggestions provided in the consulted literature into seven different groups (Table 3, Fig. 2).

Table 3. Recommendation measures to enhance bat activity in agroecosystems taken from the reviewed articles. AS indicates the number of articles supporting each measure. Since more than one action was often recommended in a single article, the sum of the percentages is >100.

	Action focus	Measures proposed	AS	%
1	Landscape heterogeneity	Increasing landscape heterogeneity to improve arthropod diversity and bat activity (e.g. hedgerows, patches of natural vegetation, higher diversity of cover types, connectivity with natural areas)	24	36.3
2	Legislation	Improving appropriate conservation legislation and protection measures (e.g. monitoring programs, protection of bat roosts, cave protection initiatives, control of artificial light, habitat conservation, reducing mortality from wind farms)	21	31.8
3	Roost availability	Installing artificial bat roosts (e.g. bat boxes) to attract bats	19	28.8
4	Agrochemical use	Improving pesticide management (e.g. reduction of chemical pesticide use, scheduling use with regard to bat activity patterns, promotion of organic farming)	13	19.7
5	Water sources	Increasing proximity of water sources or the use of safe water troughs	6	9.1
6	Education	Supporting education initiatives to inform landowners and the wider public about the benefits and economic value of ecosystem services provided by bats in agroecosystems	5	7.6
7	Bat lures	Broadcasting feeding buzzes or social calls to attract bats to agroecosystems	1	1.5

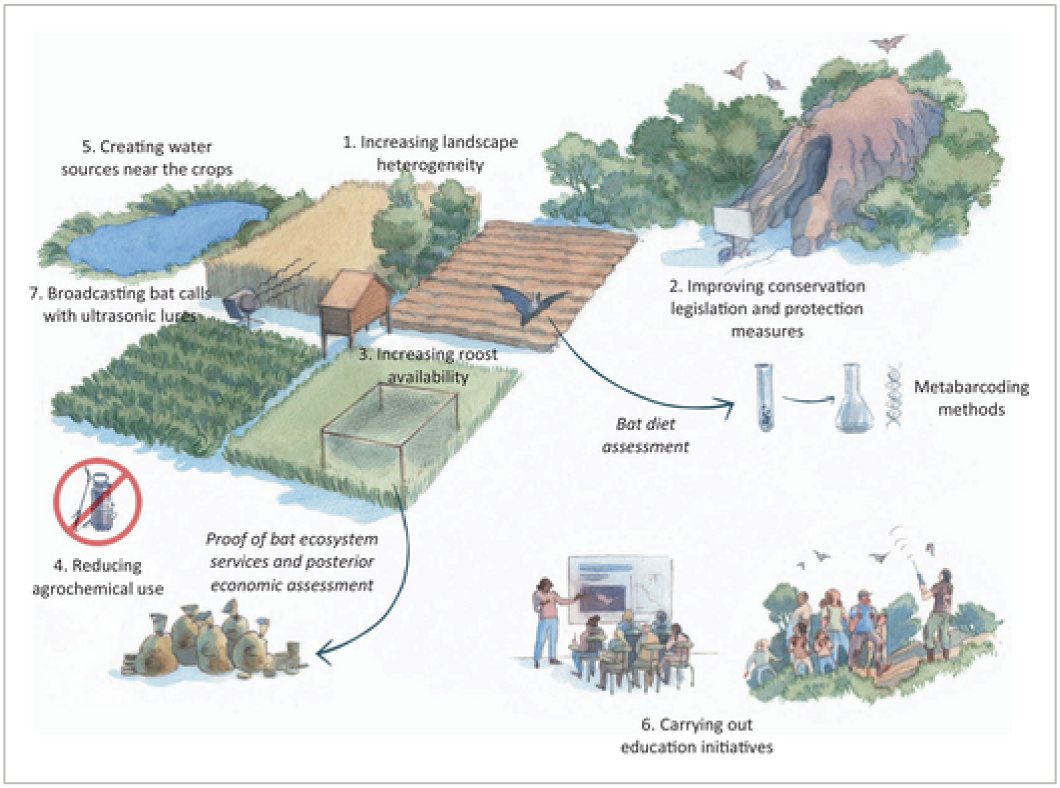

Fig. 2

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Recommendation measures provided in the scientific literature to enhance the efficiency of ecosystem services provided by bats as pest suppressors. To highlight their importance in future research, bat diet assessment, searching for proof of bat ecosystem services, and economic assessment of pest suppression have also been included.

(2) Bat–insect pest interactions

We found 95 papers in the second literature search (LS2) that documented prey identity at the species or genus level (Fig. S2). We provide a complete list of 2308 recorded interactions between bat predator species and insect prey worldwide in Table S3.

In total, 81 bat species belonging to 36 genera and six families were listed as consumers of insect pests (Tables 4 and S5). A total of 694 species and 66 genera of agricultural pests belonging to 14 different orders were detected as bat prey (see Table S3, https://doi.org/10.5281/zenodo.7821119). The bat genera reported most often to eat agricultural insect pests were *Myotis* (31.2%), *Rhinolophus* (17.3%), *Eptesicus* (13.2%), and *Pipistrellus* (10.5%), with *Plecotus*, *Tadarida*, *Miniopterus*, *Lasiurus*, *Barbastella*, *Nycticeius*, and *Antrozous* reported in fewer studies (<5% each). Table 4 shows the number of agricultural pests consumed by each bat species, with *Myotis lucifugus* consuming the highest number of pest species (201 species; 26.4% of all pests detected). Different studies identified the consumed pest species through one or a combination of techniques including: DNA extraction from faeces (69.8%), visual identification from faeces dissection (18.3%), acoustics (8.4%), visual observations (5.4%), insect remains found on the ground (5.4%) or DNA extraction from stomach contents (2.2%). The largest proportion of pest species was from the order Lepidoptera (59.2%), members of which were consumed by almost all bat genera, followed by Coleoptera (13.9%), Diptera (11.1%), Hemiptera (10.7%), and Orthoptera (2.2%) (Fig. 3). The prey species belonging to these orders are pests of economically important crops such as fruits, vegetables, and cereals (Fig. S4).

Table 4. Bat species, IUCN conservation status and the number of agricultural insect pest species they were reported to consume. Data are only shown for bat species reported to consume more than 10 insect pest species; see Table S5 for the full list. IUCN categories: DD, Data Deficient; EN, Endangered; LC, Least Concern; NT, Near Threatened; VU, Vulnerable.

Bat species	IUCN category	Number of pest species consumed
Myotis lucifugus	EN	201
Eptesicus fuscus	LC	180
Myotis escalerai	LC	139
Rhinolophus hipposideros	LC	113
Myotis crypticus	DD	111
Pipistrellus pipistrellus	LC	102
Rhinolophus euryale	NT	97
Pipistrellus kuhlii	LC	78
Eptesicus serotinus	LC	67
Miniopterus schreibersii	VU	62
Myotis daubentonii	LC	56
Plecotus auritus	LC	54
Rhinolophus ferrumequinum	LC	49
Tadarida teniotis	LC	47
Plecotus austriacus	NT	39

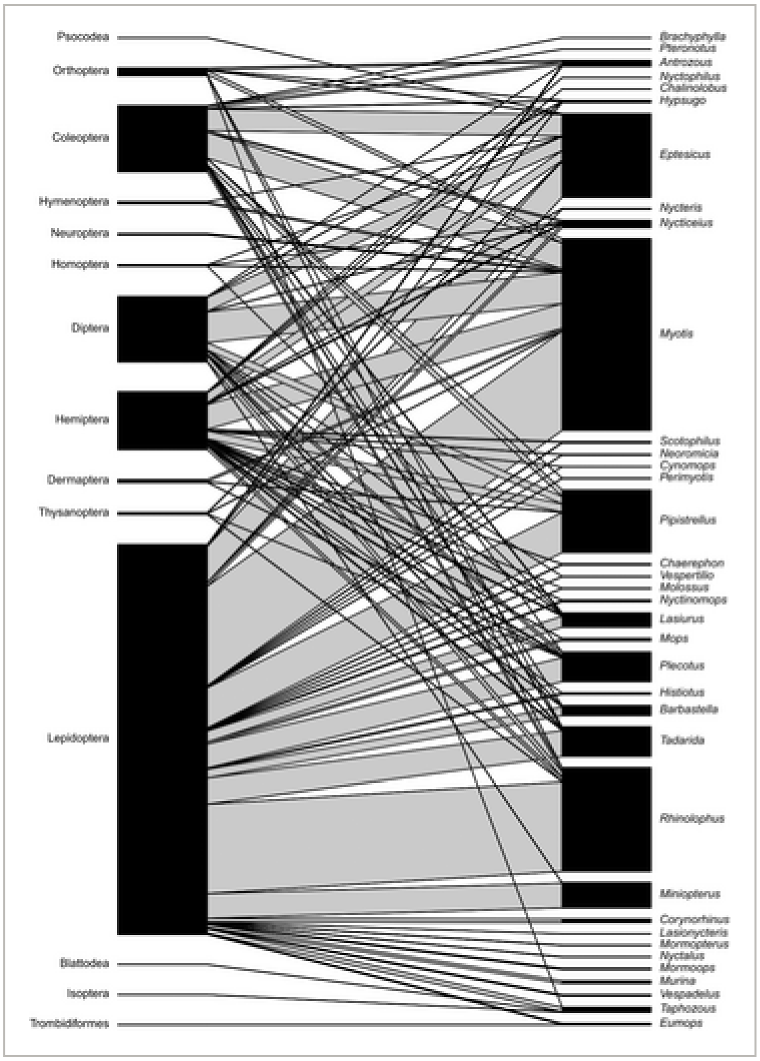

Fig. 3

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Food web illustrating the proportions of pest insect taxa (left) consumed by different bat genera (right).

We also assessed whether the type of habitat (agricultural, forested, urban, others, not specified) in which the studies were carried out affected the pest types detected in bat diets. As shown in Fig. 4, the proportions of different types of pests categorised by the crop they attack are similar across the different surveyed habitats.

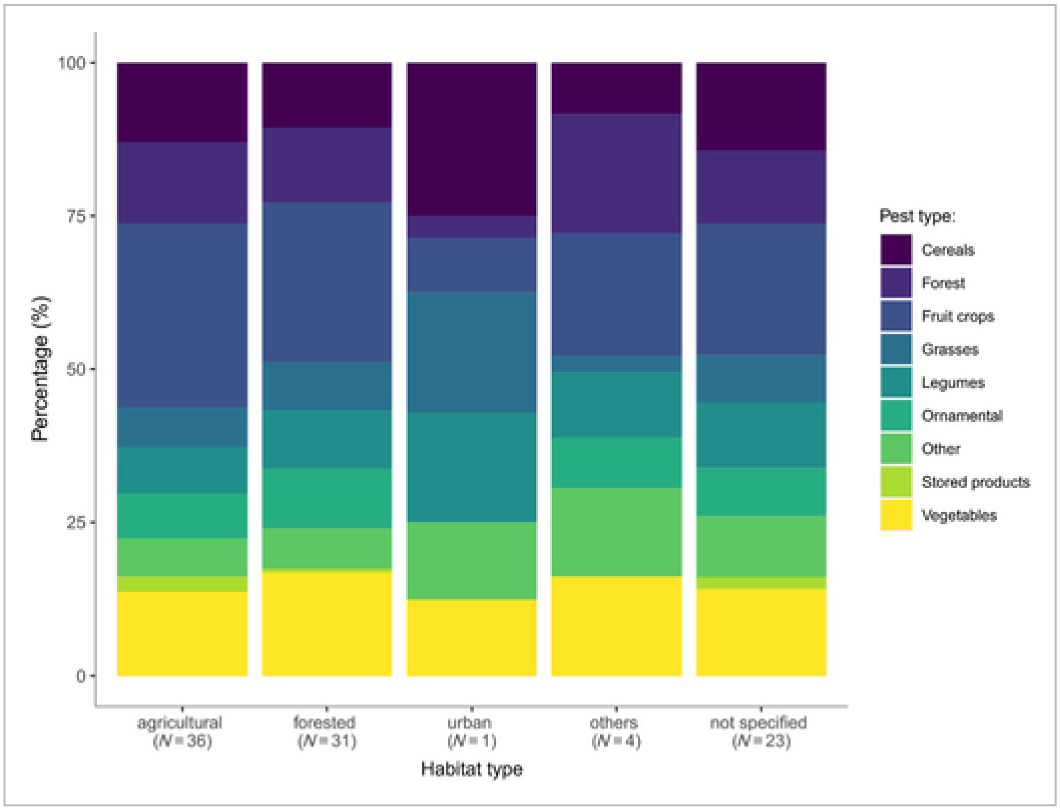

Fig. 4

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The proportion of pest species types (categorised by the crop type they attack) detected in the diet of bats in the different habitats surveyed in the articles reviewed in the second literature search (LS2). Data are expressed as a percentage of pest species types.

IV. DISCUSSION

(1) Bats as insect pest suppressors in agroecosystems

We detected a bias in the geographical distribution of the studies we examined, identifying knowledge gaps and priority areas for future research in the Global South, particularly in Africa, Central and South America and parts of Asia, where the use of pesticides is currently increasing (Oerke, 2006; Kunstadter, 2007; Schreinemachers & Tipraqsa, 2012; Bon *et al*., 2014; Snyder *et al*., 2015; Schreinemachers *et al*., 2015; Sharma *et al*., 2019). There may be other studies conducted in these areas that were not accessible to our search (e.g. published as local reports or in non-indexed formats, or in languages other than English). Many of these areas with scarce or no research on biological pest suppression provided by bats are also those with higher percentages of smallholder farmers dependent on subsistence agriculture (e.g. sub-Saharan Africa and central Asia; Altieri & Koohafkan, 2008; FAO, 2014; Rapsomanikis, 2015), and where yield losses caused by pests tend to be more severe due to relatively inaccessible crop protection methods (Oerke & Dehne, 1997, 2004; Oerke, 2006; Świetlik, 2018). Our results highlight an urgent need to invest research efforts in these regions to enhance food security and rural welfare. There is a clear positive trend in the number of articles published in recent years, identifying this as a topic of increasing interest for the scientific community.

Although half of the studies proved that bats preyed upon pest species, very little evidence exists for a top-down effect of bats directly on crops and few studies directly quantify their economic benefits. We provide a compilation of 2308 recorded interactions between bats and insect pests (Table S3, https://doi.org/10.5281/zenodo.7821119) to stimulate future work on these interactions.

A wide diversity of crop types has been surveyed in studies assessing the role of bats as insect pest suppressors. Some of the best-studied crop types – cotton, rice, coffee, and corn – are important in terms of food security and/or represent essential economic incomes in developing countries (Shiferaw *et al*., 2011; Muthayya *et al*., 2014; Khan *et al*., 2020; FAO, 2022). The ecosystem services provided by bats as pest consumers have not yet been studied in some important crops such as wheat, a cereal representing 18.3% of the global human caloric intake (Savary *et al*., 2019). It is also important to note that some crops studied have poor representation in the reviewed articles (e.g. alfalfa, sorghum, sugarcane; Table 1) or have only been studied in particular regions (e.g. rice, where nine studies are available but only from Spain, Thailand, the Philippines, India and Madagascar). The average annual rice intake worldwide is 54 kg per person, and represents almost 20% of the daily calorie intake. This value is much higher in regions such as Asia, the major rice producer worldwide, where rice contributes >50% of calorie intake and annual consumption exceeds 100 kg per person (Maclean, Hardy & Hettel, 2013). This cereal is seen as essential to overcome food insecurity in several African countries such as Madagascar, Sierra Leone, Guinea, Guinea-Bissau, and Senegal. Rice cultivation also is increasing in Latin American and Caribbean countries (Maclean *et al*., 2013). In these regions there are limited strategies to reduce harvest losses due to pests (Oerke & Dehne, 1997; Oerke, 2006; Świetlik, 2018). Thus, understanding the pest-suppression benefits provided by bats within these regions is a next essential step.

(a) *Predation, top-down effect, and economic value assessment*

Most studies used DNA metabarcoding to identify predation by bats on agricultural pests. This is the most sensitive and accurate method available to assess bat diet, although it is also the most expensive. A few studies used visual identification of insect parts from faeces, but this approach is limited by poor taxonomic resolution (Russo, Bosso & Ancillotto, 2018); identifying the undigested parts of insects to species or even genus level is a challenge. A new technique for predation studies was developed by Denan *et al*. (2020), who created artificial caterpillars from non-toxic plasticine and deployed them on vegetation surfaces. They could identify different predator groups by the marks left on the caterpillars. Although they could not identify predators to a detailed taxonomic level, their results suggested bat predation of potential insect pests in several crop types.

Several studies assessed directly the top-down effects of bats on crops. In these studies, exclosures were generally deployed in different crop types to prevent access by bats and, in some cases, also by birds and primates. Linden *et al*. (2019) detected a 27% decrease in total yield (kg/ha) in coffee plantations in South Africa when bats were excluded. Maine & Boyles (2015) reported 56% higher ear infestation in excluded corn plots in the USA. In Chile, Rodríguez-San Pedro *et al*. (2020) demonstrated that bats prevented a 7% loss of total production in vineyards. Assessing the magnitude of the ecosystem services that bats provide as pest suppressors through exclosures is crucial to understand their true benefit to agriculture. This approach also allows assessment of the economic impact of bats on a crop by comparing the yield obtained in areas patrolled by bats with areas where bats were excluded (Maas, Clough & Tscharntke, 2013; Maine & Boyles, 2015; Linden *et al*., 2019; Rodríguez-San Pedro *et al*., 2020). Although bat exclosures are the most appropriate method to measure bat ecosystem services in the field, several disadvantages hinder their application to specific crops or insect species, including: their relatively small sizes compared to the crop area and the insects' flight height; their inability to exclude predation by bats flying near the exclosure; high costs of materials (especially in crops where it is not possible to isolate individual plants) and time (it requires continuous monitoring and maintenance); and potential influences of the exclusion nets on insect behaviour. Recently, Maas *et al*. (2019) reviewed studies in which bird and bat exclosures were used to assess pest control in agricultural lands across 14 countries and 12 different crops. The authors provided a list of guidelines to improve the performance and validity of this type of research, including common pitfalls associated with experimental design, duration, material choice, and experimental conditions.

Several articles estimated the economic benefits of bats related to pest suppression. For example, Boyles *et al*. (2011) valued at $22.9 billion/year the ecosystem services provided by *Tadarida brasiliensis* in the cotton fields of the USA. This estimate considered not only the prevention of crop damage caused by the corn earworm (*Helicoverpa zea*) but also the economic savings related to pesticide applications. The estimated value was even higher for cotton fields in Australia, where the bat *Chalinolobus gouldii* is responsible for saving up to $63 million each year as a natural controller of the cotton bollworm (*Helicoverpa armigera*) (Kolkert *et al*., 2021). Wanger *et al*. (2014) estimated the economic value of bat ecosystem services for rice production at more than $1.2 million/year. More recently, Linden *et al*. (2019) estimated the impacts of bats in macadamia orchards of South Africa to be worth $2421.61/ha/year, with these benefits related to both yield and nut quality. Evaluating the economic importance of bats in agroecosystems might represent a valuable and efficient way to connect farmers with bat biology and conservation.

Most studies used an avoided cost model to estimate the economic value of bats. The costs avoided when foraging bats are present include lower crop damage (due to smaller pest populations) and/or reductions in costs related to the less-frequent use of pesticides. This model does require assumptions to be made, but the model is easy to apply to different crops or regions. By contrast, benefit transfer approaches may provide less-accurate results since this method involves applying ecosystem service values that have been estimated at one location to a new location (Wilson & Hoehn, 2006; Medellin, Wiederholt & Lopez-Hoffman, 2017). Interestingly, we found that fewer articles assessed the effect of top-down bat activity on the harvest (19.7%) compared with those that quantified the pest control services provided by these animals (27.3%). This may reflect the difficulties inherent in direct assessment of bat pest suppression on crops compared with making theoretical estimates of the economic value of their ecosystem services. Economically quantifying the pest control services provided requires assumptions to be made, and there are probably many sources of biases and site-to-site variation. For example, the trade-offs between services and disservices also need to be properly assessed to understand the true magnitude of the ecosystem services bats provide and to establish clear guidelines to enhance these (see, e.g. Vansynghel *et al*., 2022), but this layer of complexity has often been disregarded to date.

Confirmation of bat predation of insect pests, providing evidence for bat ecosystem services and their economic evaluation represents a promising approach to persuade farmers to embrace sustainable practices and to raise awareness about the importance of bats for their crops.

(b) *Integrated pest management – guidelines to enhance bat activity in agroecosystems*

Most authors of the reviewed articles proposed recommendations and management measures to favour bat communities in agroecosystems and increase the benefits these mammals provide (Fig. 2, Table 1). However, we found almost no information regarding the effectiveness of the suggested measures. This serious knowledge gap needs to be addressed to recommend bats as part of IPM practices.

(i) Landscape heterogeneity

The most popular recommendation in the reviewed articles was to increase landscape heterogeneity (36.3%). An increase in heterogeneity and structural complexity in agroecosystems generally translates into increased biodiversity (Benton, Vickery & Wilson, 2003; Graham *et al*., 2018). A more complex landscape provides more niches allowing higher arthropod diversity, in turn favouring predators such as bats through higher food resource availability (Benton *et al*., 2003; Graham *et al*., 2018). During recent decades, rapid agricultural intensification has led to homogenisation of farmland landscape structure, argued to be the leading cause of diversity declines in these environments (Gardner, 1996; Krebs *et al*., 1999; Benton *et al*., 2003). Promoting heterogeneity by creating and maintaining hedgerows, leaving patches of natural vegetation, planting a higher diversity of cover types, and/or enabling good connectivity of croplands with natural areas will favour arthropod populations and increase foraging habitat for bats (Costa *et al*., 2020). Landscape-level heterogeneity in agroecosystems can increase biological pest control not only due to enhanced bat activity (Graham *et al*., 2018; Monck-Whipp *et al*., 2018; Froidevaux *et al*., 2019) but also due to larger populations of natural enemies of agricultural pests (Redlich, Martin & Steffan-Dewenter, 2018). Many studies provide evidence for the success of these practices (Frey-Ehrenbold *et al*., 2013; Heim *et al*., 2015; Kalda, Kalda & Liira, 2015; Froidevaux, Louboutin & Jones, 2017; Froidevaux *et al*., 2019; Kahnonitch, Lubin & Korine, 2018; Lacoeuilhe *et al*., 2018; Rodríguez-San Pedro *et al*., 2018, 2019). Froidevaux *et al*. (2019) detected positive effects on bat populations following a reduction in hedgerow trimming frequency. In the vineyards of Chile, bat activity and diversity were higher in agricultural landscapes with more complex structural configurations (Rodríguez-San Pedro *et al*., 2019). Smaller and irregular patches, as well as higher edge density, favoured the presence of both bats and insects. Several studies highlight the importance of hedgerows and forested patches in agroecosystems since bats commonly use them as corridors and they can act as shelters for arthropods, thus these structures represent valuable foraging habitats for insectivorous bats (Heim *et al*., 2015; Rodríguez-San Pedro *et al*., 2018, 2019).

(ii) Legislation

Nearly one third of the studies argued for improved conservation legislation and measures to protect bat population stability in agroecosystems as well as in other habitats. Implementing effective and well-designed monitoring programs represents a significant challenge that must be met to fill knowledge gaps regarding the status of bat populations and to detect potential threats in different ecosystems (Kingston, 2010; Jung *et al*., 2014; Frick, Kingston & Flanders, 2020). Conservation of natural habitats and roost protection initiatives are also essential to ensure the viability of bat communities. This is particularly important for cave-dwelling species, some of which are also important pest suppressors (Aizpurua *et al*., 2018; Kemp *et al*., 2019). These underground habitats are susceptible to perturbations and are increasingly under pressure from human recreational activities, vandalism, guano mining, pollution, and other factors (Medellin *et al*., 2017). The disturbance and disappearance of large colonies can impact bat populations, and the protection and regulation of caves and mines is likely to be fundamental to keeping these populations stable (O'Shea *et al*., 2016; Medellin *et al*., 2017). Several countries, such as the USA and Australia, have already applied laws to protect these underground ecosystems and manage tourism appropriately. Medellín (2003) reported evidence of bat population recovery after restoration of a cave environment in Mexico. Other authors highlight the importance of reducing bat mortality at wind farms (Kunz *et al*., 2007; Arnett & Baerwald, 2013) or integrating light pollution into conservation action plans to maintain biodiversity in anthropogenic habitats (Azam *et al*., 2016).

(iii) Roost availability

Installation of artificial roots such as bat boxes was the next most common strategy (28.8%). Intensive logging practices and agricultural expansion are significant drivers of habitat loss, directly threatening tree-dwelling species of bats (López-Baucells *et al*., 2017). Such artificial roosts can be a good alternative for some bat species in areas with low availability of natural roosts such as agroecosystems (Flaquer, Torre & Ruiz-Jarillo, 2006; Long, Kiser & Kiser, 2006). New roost opportunities in these habitats may attract bats, increasing the ecosystem services they provide (Flaquer *et al*., 2006; Long *et al*., 2006; Boyles *et al*., 2013). Puig-Montserrat *et al*. (2015) detected a significant decline in damage due to the stripped rice borer moth *Chilo suppressalis* in the Ebro Delta (Spain) after the installation of bat boxes and their subsequent occupation by 3500 soprano pipistrelles (*Pipistrellus pygmaeus*). The authors estimated that 9–16 bats/ha were needed to reduce rice borer moth levels below the aerial treatment threshold and 42–67 bats/ha to suppress any need for treatment. Brown, Braun de Torrez & McCracken (2015) reported high proportions of insect pests in bat faeces collected from artificial roosts distributed in pecan orchards in the southern USA. Weier *et al*. (2019) also installed artificial roosts in macadamia orchards in South Africa that were occupied by several species. In Australia, bats and other small vertebrates occupied nesting boxes in farm forestry plantations more frequently than boxes installed in intact forests (Smith & Agnew, 2002). This was probably due to the scarcer natural roost availability in plantations than in the natural forest. Where they are adopted by bats, artificial roosts can enable increases in bat densities in agricultural areas. However, although the use of artificial roosts is popular in regions such as Europe or North America, this practice is still in its infancy in Asian and African countries, and its impact on a variety of agricultural environments and crops has not been tested.

(iv) Agrochemical use

One in five articles highlighted the importance of the correct use of agrochemicals. Pesticide use is one of the primary drivers of the mass insect extinction worldwide, threatening insect predators such as bats (Sánchez-Bayo & Wyckhuys, 2019). The European Food Security Agency has recently highlighted the need for a bat-focused pesticide risk assessment (Hernández-Jerez *et al*., 2019). Many studies argue that chemical spraying affects bats adversely by reducing their prey resources (Park, 2015; Williams-Guillén *et al*., 2016; Kahnonitch *et al*., 2018). For example, Korine *et al*. (2020) detected a reduction in bat activity after the application of pesticides and these effects lasted for several nights. High levels of biodiversity (e.g. bat richness and activity) are directly related to lower-intensity agricultural practices, which could enhance the efficiency of pest suppression they provide (Park, 2015; Williams-Guillén *et al*., 2016; Kahnonitch *et al*., 2018). Bats often exhibit fidelity to foraging sites with predictable resource availability (Kapfer *et al*., 2008; Hillen, Kiefer & Veith, 2009; Perry, 2011), a condition that agroecosystems exposed to repeated chemical spraying are not likely to fulfil due to their fluctuating availability of insects. However, we only found two studies describing direct poisoning of bats due to the consumption of insects, flowers or fruits exposed to agrochemicals or roost pollution (Bayat *et al*., 2014; O'Shea *et al*., 2016).

(v) Water sources

Many studies have reported a positive influence of water sources on the abundance of bats due to higher concentrations of prey and provision of a drinking resource (Stahlschmidt *et al*., 2012; Sirami, Jacobs & Cumming, 2013; Cruz *et al*., 2016; Froidevaux *et al*., 2017). In this review, 9.1% of studies emphasised the importance of increasing water availability (Russo & Jones, 2003; Stahlschmidt *et al*., 2012; Sirami *et al*., 2013; Kahnonitch *et al*., 2018). In arid or semiarid ecosystems where natural water sources are scarce during some periods of the year, artificial sources may be the only perennial water available during dry periods (Tuttle, Chambers & Theimer, 2006; Korine *et al*., 2015). In Germany, Stahlschmidt *et al*. (2012) showed that both bat activity and insect abundance were significantly higher in vineyards with ponds than in those without them. Sirami *et al*. (2013) supported this finding in a study in Western Cape (South Africa), where farm dams played an essential role for all bat species. In both cases, well-managed artificial water sources in agricultural areas contributed to the availability of insect prey, attracting bats and consequently favouring the ecosystem services provided by them (Stahlschmidt *et al*., 2012; Sirami *et al*., 2013).

(vi) Education

Integration of social strategies into conservation plans has increased in recent years (Robinson, 2006; Ban *et al*., 2013; Guerrero & Wilson, 2017). Of the articles reviewed, five proposed education initiatives to enhance and promote bat conservation in agriculture. Suggestions included the implementation of educational activities, citizen science projects, public communication, and other outreach projects to involve local communities in the conservation of wildlife, enhancing their connection with nature (Dietz & Stern, 2002; Braus, 2009; Ardoin & Heimlich, 2013). This is particularly important for bats given their historical negative perceptions (Kingston, 2016). Misconceptions or exaggerated and misinformed news about disease outbreaks have led to an erroneous view of bats worldwide (Hoffmaster, Vonk & Mies, 2016; López-Baucells, Rocha & Fernández-Llamazares, 2018; Rocha *et al*., 2021*a*; Rocha, López-Baucells & Fernández-Llamazares, 2021*b*). Educating policymakers, farmers and local communities about the benefits of insectivorous bats in agriculture and quantifying the value of the ecosystem services they provide as pest suppressors will be an indispensable tool for promoting more sustainable practices in agroecosystems as well as for mitigating human–bat conflict and enhancing the conservation of bat populations (Deshpande & Kelkar, 2015; Aizpurua *et al*., 2018; Linden *et al*., 2019). In urban areas, where intense pressure on wildlife exists, informing people about the benefits of bats as natural controllers of agricultural pests but also as predators of human disease vectors (e.g. those carrying malaria, filariasis, encephalitis, yellow fever, dengue) can also help to promote the use of bats as biological controllers. For example, Hoffmaster *et al*. (2016) reported that educational programs changed participants' perceptions about bats and their willingness to protect these mammals. However, it remains essential to understand how farmers in different cultures perceive bats to be able to offer biocultural approaches to bat conservation (Deshpande & Kelkar, 2015; Forth, 2021; Laverty *et al*., 2021; Low *et al*., 2021; Rocha *et al*., 2021*a*,*b*; Shapiro *et al*., 2021).

(vii) Bat lures

One publication suggested the use of bat lures to enhance bat activity. Several studies have reported the effectiveness of bat lures that broadcast conspecific calls in attracting bat species (Gillam, 2007; Arnold & Wilkinson, 2011; Carter *et al*., 2015). Indeed, this strategy is used to capture bats in mist nets, especially rare or difficult-to-catch species (Hill & Greenaway, 2005; Loeb & Britzke, 2010; Lintott *et al*., 2013; Braun De Torrez *et al*., 2017). Braun de Torrez *et al*. (2019) proposed this technique to attract bats to agroecosystems since many species associate conspecific feeding buzzes with high-quality foraging areas (Gillam, 2007; Dechmann *et al*., 2010; Wright, Wilkinson & Moss, 2011), but further evidence regarding the impact of this recommendation is needed.

(2) Bat–insect pest interactions

In all, 81 bat species belonging to 36 bat genera and eight bat families were listed as consumers of 760 insect pests, in 2308 different bat–insect interactions. Several bat species classified as Vulnerable, Near Threatened, or Endangered by the IUCN were agricultural pest consumers. Our results suggest that bats might represent important providers of ecosystem services as pest suppressors worldwide. The insect pest taxa consumed most often by bats belong to Lepidoptera, Coleoptera and Hemiptera. Major pests of crops including fruit (e.g. grapevine, apple, strawberry), vegetables (e.g. lettuce, potato, tomato), cereals (e.g. maize, corn, rice) and other economically important products such as cotton, tea and tobacco belong to these insect orders. Many other insect pests are consumed by these bat species, and many other bat species are probably predators of agricultural pests.

The similar proportions of pests found in bat faeces from different study habitats underscore the remarkable mobility of most bat species, the uneven distribution of their roosts across landscapes, and their ability to cover long distances during nocturnal flights. While it is crucial to protect insectivorous bats in agricultural areas, other habitats such as caves, forests, rivers, lakes, and urban areas, as well as heterogeneous landscape mosaics are also critical for the survival of these beneficial arthropod predators.

V. CONCLUSIONS

(1) Investigation of the role of bats as pest suppressors has been increasing in recent years. However, studies have not taken place uniformly throughout different regions. Very little research has focused on regions such as the African continent, Central and South America, and most parts of Asia; in these areas food security is highly dependent on subsistence agriculture, and the use of agrochemicals is currently increasing.

(2) We recommend that future research directly assesses the top-down effects of bats on crops as well as their economic benefits as pest suppressors. Providing evidence for bat predation and their ecosystem services represents a promising way to encourage farmers to apply sustainable and eco-friendly strategies to fight pests as well as to raise awareness about the importance of bats in agroecosystems.

(3) We reviewed conservation recommendations suggested in the literature to promote foraging bats in agroecosystems and to increase their effectiveness in suppressing pests. Actions such as increasing habitat heterogeneity, installing artificial bat roosts, and strict management of pesticide use could attract foraging bats to farmland. Such actions should be combined with conservation legislation and protection measures appropriate to the agricultural market in each region. A transdisciplinary social and ecological approach with broad collaborations between scientists and practitioners should be employed as a more inclusive and integrative way to implement scientific research with land use policy (Maas, Ocampo-Ariza & Whelan, 2021).

(4) We provide a publicly available and updatable list of 2308 registrations of bat–insect pest interactions reported to date (https://doi.org/10.5281/zenodo.7821119).

(5) This review aims to provide a practical assessment of current knowledge for researchers and farmers concerning the pest control services provided by bats to agriculture and how to improve IPM.

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Open Research

DATA AVAILABILITY STATEMENT

The data set documenting bat–pest insect interactions is available in the Zenodo open-access repository (https://doi.org/10.5281/zenodo.7821119).

Supporting Information

Filename	Description
brv12967-sup-0001-Figures.docx Word 2007 document , 944.7 KB	**Fig. S1.** PRISMA flow diagram illustrating the systematic review process for studies assessing bats as insect pest suppressors in agroecosystems. **Fig. S2.** PRISMA flow diagram illustrating the systematic review process for studies reporting evidence of bat predation of insect pests. **Fig. S3.** Publication year of the 66 articles focused on bats as natural pest controllers identified in the first literature search (LS1). **Fig. S4.** Food web illustrating the relationships between insect pest orders consumed by bats and the crops that those pests damage.
brv12967-sup-0002-TableS1.xlsx Excel 2007 spreadsheet , 24.5 KB	**Table S1.** Articles located by the first literature search (LS1) and the main information extracted.
brv12967-sup-0003-TableS2.xlsx Excel 2007 spreadsheet , 50.5 KB	**Table S2.** List of agricultural insect pests used in the second literature search (LS2).
brv12967-sup-0004-TableS3.xlsx Excel 2007 spreadsheet , 110.1 KB	**Table S3.** Bat–pest insect interactions identified in the second literature search (LS2)
brv12967-sup-0005-TableS4.xlsx Excel 2007 spreadsheet , 62.2 KB	**Table S4.** Pest species preyed upon by bats and the crop types affected by them.
brv12967-sup-0006-TableS5.xlsx Excel 2007 spreadsheet , 13.9 KB	**Table S5.** Bat species, IUCN conservation status and the number of agricultural insect pests they consumed.

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