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REVIEW

Experimental field exclosure of birds and bats in agricultural systems — Methodological insights, potential improvements, and cost-benefit trade-offs

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Abstract

Experimental exclosure of birds and bats constitutes a powerful tool to study the impacts of wildlife on pests and crop yields in agricultural systems. Though widely utilized, exclosure experiments are not standardized across studies. Indeed, key differences surrounding the design, materials, and protocols for implementing field-based exclosure experiments of flying vertebrates increase heterogeneity across studies, and limit our understanding of biodiversity-friendly land use management. We reviewed the available literature on studies in which bird and bat exclosures were applied to study pest control in agricultural settings, and isolated 30 studies from both tropical and temperate land use systems, involving 12 crop types across 14 countries. Focusing on exclosure effects on crop yield, we analyzed effect detectability for a subset of suitable data. We then analyzed

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the potential of exclosure methods and possible extensions to improve our understanding of complex food webs and ecosystem services affecting the productivity of agricultural systems. While preferences exist in materials (e.g., nylon nets and bamboo frames), experimental exclosure studies of birds and bats differed greatly in their respective design, related costs, and effort — limiting the generalization and transferability of results at larger spatial scales. Most studies were based on experiments conducted in the United States and the Neotropics, mainly in coffee and cacao farms. A lack of preliminary or long-term data with repeated measurements makes it impossible to apply power analysis in most studies. Common constraints include, among other things, the choice of material and experimental duration, as well as the consideration of local versus landscape factors. We discuss such limitations, related common pitfalls, and options for optimization to inform improved planning, design, and execution of exclosure studies. By doing so, we aim to promote more comparable and transferable approaches in future field research on biodiversity-mediated ecosystem services.

Keywords: Ecosystem services; Pest control; Predator exclusion

Introduction

Field experiments can yield key insights into complex food webs, and promote a better understanding of how trophic and environmental interactions shape ecosystem processes in the Anthropocene. In agricultural systems, field experiments are increasingly used to determine how maintaining or enhancing farmland biodiversity can affect delivery of desired ecosystem services and crop yields (e.g., Classen et al. 2014; Kross, Kelsey, McColl, & Townsend 2016). For example, field experiments in tropical coffee and cacao plantations have demonstrated that native birds and bats can strongly regulate pest abundances and increase the quantity and quality of crop yields (e.g., Karp et al. 2013; Maas, Clough, & Tscharntke 2013; Maas et al. 2016). These experiments demonstrate the potential for ecological intensification to serve as an alternative to high-input, intensive farming (e.g., Jezeer, Verweij, Santos, & Boot 2017) — but persistent knowledge gaps and methodological challenges limit progress.

Quantifying the impact of biodiversity-driven ecosystem services on agricultural productivity requires implementing well-designed experimental studies in the field, as well as a deep understanding of service provider species. With respect to pest control, prior studies have shown that native birds and bats are particularly effective at regulating pest densities and crop yields. However, effects may vary across systems depending on local management, landscape context, complex multitrophic interactions, and functional trade-offs (e.g., Martin, Reineking, Seo, & Steffan-Dewenter 2013; Classen et al. 2014; Maas et al. 2016; Gras et al. 2016; Martínez-Salinas et al. 2016). Although such relationships are increasingly well understood at local scales, contrasting results at larger spatial scales (Karp et al. 2018) still limit the targeted implementation of biodiversity-friendly land use management. Another limiting factor challenging many research projects is the efficient design of such field studies, which can be time-consuming and costly, especially when large-scale experimental studies are planned and applied for the first time.

Field exclosure experiments allow researchers to differentiate between the group-specific and combined effects of birds and bats on arthropod communities, crop yields, and farm revenues (e.g., Karp et al. 2013; Maas et al. 2013). In their most basic form, exclosure experiments constitute a form of size selection: focal plants are enveloped with mesh nets that prevent access of foraging birds and bats but allow access by arthropods (Fig. 1), thereby simulating the absence of flying vertebrates from the studied crop. To quantify the relative contribution of birds and bats to pest control, group-specific exclosures can be activated at different times of the day to preferentially exclude diurnal birds versus nocturnal bats. The combined contribution of birds and bats to pest-control can be assessed with permanent 24 h-exclosures.

While the very basic implementation of field-based exclosures has generally been consistent across studies, many nuances exist in the design and execution of exclosure studies that lead to key differences in research methodology. For example, while exclosure experiments are generally suitable for use in most agricultural systems and climatic zones, there are notable differences in the suitability and availability of materials, as well as in the consideration of possible experimental, environmental, or sampling effects. Accordingly, individual studies vary considerably in associated costs and efforts. Future studies could thus be optimized not only in terms of their comparability and transferability, but also in their effectiveness and the quality of data output.

Here, we describe and discuss advantages and disadvantages of different methods used in bird and bat exclosure studies across twelve different agricultural systems in 14 countries, to provide detailed methodological insights and recommendations on potential improvements of experimental designs tested under field conditions. We discuss several options to optimize (1) study design, (2) material choice, and (3) the overall applicability of bird and bat exclosure experiments to promote increased efficacy and transferability of future studies.

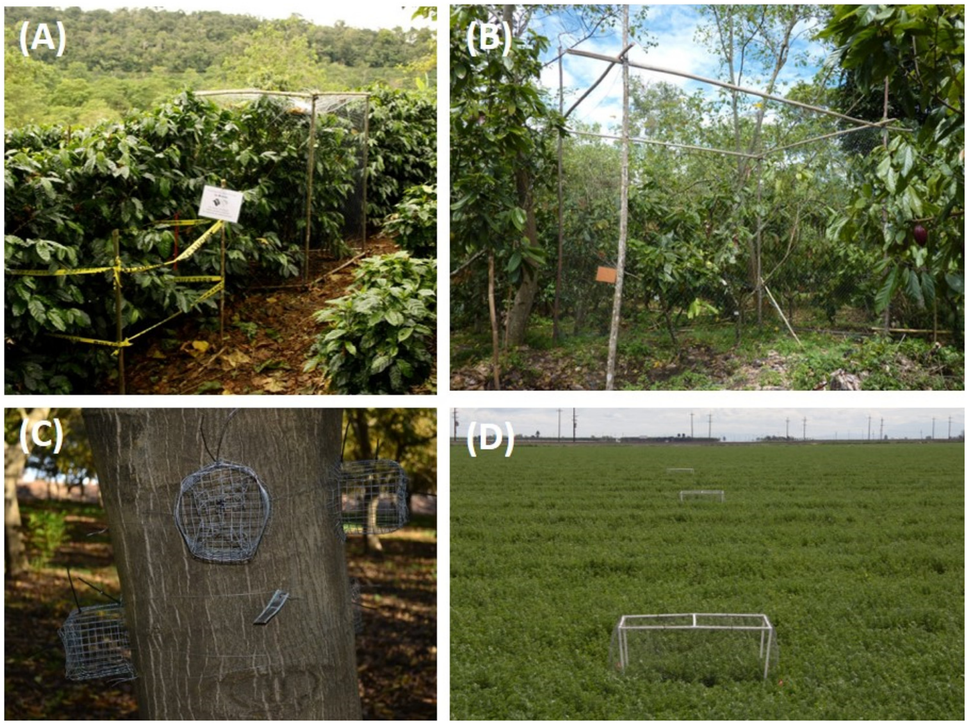

Fig. 1. Experimental exclosures of birds and bats in (A) coffee plantations in Costa Rica, © Daniel Karp; (B) cacao plantations in Indonesia, © Bea Maas; (C) walnut orchards in the United States © Sacha Heath; and (D) alfalfa fields in the United States © Sara Kross.

Methods

Literature review and data compilation from prior exclosure studies

We reviewed the available scientific literature from the past twelve years and contacted authors of bird and bat exclosure studies to extract published and unpublished information on exclosure experiments in agricultural systems. To review the existing body of literature, we used Google Scholar and entered the following key words: "bird*" AND "bat*" AND "exclusion" OR "exclosure" AND "agricultur*" OR "agroforest*" OR "farm*." We excluded the term "wind farm" to minimize the number of such studies for our search. The results were sorted according to relevance: we only included studies providing direct information and results on experimental bird and bat field exclosures (excluding reviews; conference abstracts and project reports) that were published between 2005 and 2017 (Table A1). This literature review yielded 18 suitable exclosure studies whose first authors were directly consulted in order to obtain unpublished information on materials; cost; time and sampling effort of their respective studies. To increase the number of considered studies; these authors were asked to propose additional studies not appearing in our literature search for this methodological comparison; adding 12 more studies to our list (Table A1).

Through this combined approach of literature review and author feedback, we reviewed a total of 125 potentially suitable studies and identified 30 of which sufficient information on material, cost, time and sampling effort was provided by authors (n = 18) or extracted from publications (n = 12). We used uniform calculations, units, and methods (Table A2) in order to compare sampling design and measured effect sizes of all studies. For example, material costs were converted to US dollar, and invested time and personnel effort were calculated per sampling site for each considered study to allow for comparison between them. The costs shown are limited to the installation costs for exclosures as transport costs were not available for most studies. For the studies that measured the effects of bird and bat exclosures on arthropod communities and/or yield in their respective crop systems, we also used a uniform calculation method (Table A2) to compare effect sizes between studies. In order to assess differences in study design and material choice, the collected data (see Tables A1 and A3) were summarized (Table 1) and discussed within the group of authors of this manuscript, to identify common pitfalls and options for optimization.

Power analysis on effect detectability

One of the most obvious constraints in experimental exclosure studies is the number of independent sampling units needed to detect effects of bird and/or bird exclosures (here: number of study sites and number of yield measurements). Studies using experimental field exclosures of birds and bats focus not only on their interaction with other taxa, environ-

Table 1. Overview of selected bird and bat exclosure studies (n = 30), showing the origin of each study (tropical/trop. vs. temperate/temp. realm and country), the period of data collection (study period), the applied exclosure approach (24 h = permament exclosures of birds and bats; SC = both group-specific and combined exclosures of birds and bats; * indicates studies that excluded other taxa such as ants or pollinators) and the studied crop type (+ and − indicate if pesticides were applied/+ or not/−). The total number of study sites, farms, or fields (sites), and the number of bird/bat exclosure treatments and controls per study site (Treatm./site) is shown, as well as the mean or total number of plants included in each exclosure treatment (Plants/treatm.; partial plant exclusion was denoted with <1). Further, details on materials are reported (Mesh size in mm; net and frame material), as well as the mean volume of each exclosure (length × width × height in m) and the mean costs (in US$), working hours (h) and number of workers (mean values) needed to install exclosures per study site. Empty cells indicate studies for which respective information were not available or recorded. Additional information on the listed studies are provided in Tables A1 and A2.

ID	Realm	Country	Study period	Excl. type	Crop type	Sites (n)	Treatm./ site	Plants/ treatm.	Mesh (mm)	Net material	Frame material	Mean cage size (m^3)	Mean material costs/ site (US$)	Mean working hours/ site	Mean workers/ site
1	Trop	Jamaica	2005–2006	24 h	Coffee −	30	2	1	58	Nylon	Wood	15	27	2.4	4
2	Trop	Jamaica	2005–2006	24 h	Coffee −	30	16	1	58	Nylon	Wood	15	27	2.4	4
3	Trop	Jamaica	2005–2006	24 h	Coffee −	8	2	3	58	Nylon	Wood	54	100	7.5	2
4	Trop	Mexico	2007–2008	SC	Coffee −	22	4	1	19	Nylon	Wood	2	60	88.0	2
5	Trop	Costa Rica	2010–2011	SC	Coffee −	9	4	4	38	Nylon	Bamboo	12	40	8.0	5
6	Trop	Costa Rica	2010–2011	24 h	Coffee +	30	2	1	38	Nylon	Bamboo	2	5	1.0	5
7	Trop	Tanzania	2011–2012	SC*	Coffee +/−	12	2	1	30	Plastic	Wood	8	48	23	5
8	Trop	Costa Rica	2013	24 h	Coffee +	10	2	1	20	Plastic	Bamboo	4.50	48	1.6	2
9	Trop	Indonesia	2010–2011	SC	Cacao −	15	4	2	20	Nylon	Bamboo	210	40	10.7	4
10	Trop	Indonesia	2011–2012	SC*	Cacao −	15	8	2	35	Nylon	Bamboo	210	39	10.7	4
11	Trop	Brazil	2011–2012	SC	Cacao −	6	16	1	40	Nylon	Ropes		863	32	2
12	Trop	Indonesia	2013–2015	24 h*	Oil palm −	6	4	4	25	Nylon	Metal	1280	800	840	5
13	Trop	South Africa	2015–2016	SC	Macadam. −	12	4	2	20	Nylon	Wood	250	400	10.0	3
14	Trop	Brazil	2014–2015	24 h	Coffee +/−	8	8	4	25	Nylon	Bamboo	14.40	40	8	4
15	Temp	USA	2014–2015	24 h	Alfalfa +	32	4	380	22.5	Nylon & steel	Pipe	1.69	39	1.0	2
16	Temp	USA	2010	24 h	Cottonw. −	28	2	1	25	Nylon	Pipe	12	54	3.4	3
17	Temp	USA	2012	24 h	Kale −	7	8	5	25	Nylon	Pipe	1.13	100	2.9	3
18	Temp	USA	2013–2014	24 h	Walnut +	20	100	1	6.35	Steel	Wire	0.0017	25	5.0	2
19	Trop	Mexico	2000	24 h	Coffee −	4	12 or 20	9.60	50	Nylon		150			
20	Trop	Mexico	2000	24 h	Coffee −	42	2	1.87	35	Nylon		150			
21	Trop	USA (PR)	2000	24 h	Coffee	3	2	12		Nylon	Pipe				
22	Trop	Costa Rica	2009–2010	24 h	Coffee	6	6	3	21	Nylon	Metal				
23	Trop	Panama	2004	24 h	Cacao −	2	20	1	30	Nylon	Ropes				
24	Trop	Malaysia	2007	24 h	Oil palm −	8	2	1	25	Steel	Wire	1.20			
25	Trop	Kenya	2011–2012	24 h	Kale	2	18	1	25	Steel	Wire	0.11			
26	Temp	USA	2005	24 h	Hops −	1	10	1		Plastic	Pipe	2.88			
27	Temp	USA	2010	24 h	Rice	4	2		11.27	Nylon	Pipe	578			
28	Temp	South Korea	2010	24 h	Cabbage −	18	2	4	15	Steel		0.02			
29	Temp	Australia	2014–2015	24 h	Apples −	6	20	<1	15	Plastic					
30	Temp	Australia	2014	24 h	Apples +/−	6	20	<1	15	Plastic					

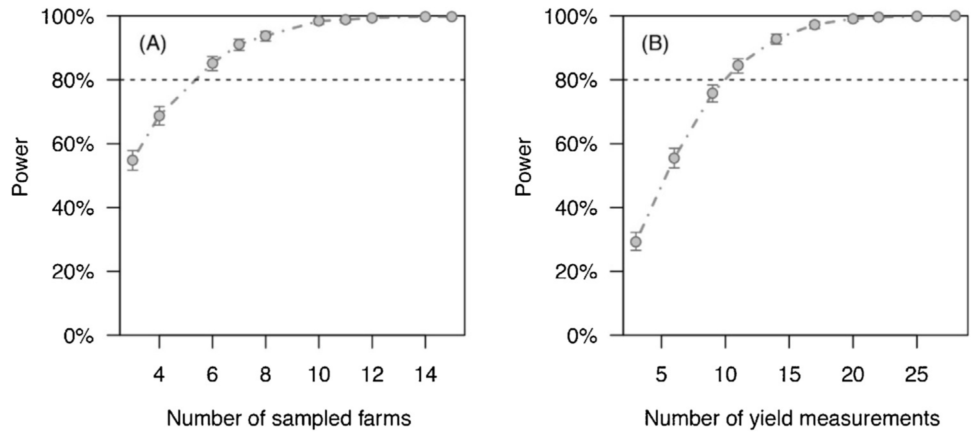

Fig. 2. Power (±95 CI) to detect treatment effects of bird and bat exclosure (control, birds excluded, bats excluded, both excluded) on differences in cacao yield in Indonesian smallholder farms with increasing (A) number of sampled farms and (B) yield measurements per treatment (taken at all study trees and farms). Data from Maas et al. (2013), for detailed estimates see Tables A3 and A4.

mental or landscape factors, but also increasingly seek to investigate potential effects on crop yield quantity and quality. Since such findings are both ecologically and economically relevant, they appeal to a wide audience of stakeholders — which is why we decided to focus on yield effects in more detail, using additional analyses of available data.

A power analysis provides information on the statistical power given at different levels of sampling effort (e.g., number of repeated measurements) per sampling unit. Such results can be used to optimize the study design in field experiments. Traditionally, 80% power is considered adequate to allow for rejecting the null hypothesis and avoiding a Type II error that can result from too low sampling intensity (Green & MacLeod 2016).

Power analyses require availability of repeated measurements of a target variable taken at regular intervals. From our set of 18 feedback studies, six studies provided potentially useful data and were analyzed using this approach (see Table 1: studies with ID 4, 8, 9, 11, 15 and 16), but only one study ultimately proved suitable and revealed results due to sufficient amount and frequency of collected data (Maas et al. 2013; ID 9). The respective study design comprised 15 cacao plantations. At each farm, four exclosure treatments were set up (i.e., control, group-specific and permanent/combined bird and bat exclosures). Yield measurements of cacao trees were taken at intervals of 10–14 days between July 2010 and July 2011, with a total of 28 measurements for each study tree in each farm and exclosure treatment (see Maas et al. 2013).

We ran two analyses varying in (a) the number of sampled farms and (b) the number of measurements per treatment (function ‘powerCurve’ in R-package ‘simr’ version 1.0.2, Green and MacLeod 2016). For the analyses, we first set up a linear mixed-effect model whereby cacao yield (sqrt-transformed) was modelled in response to exclosure treatments, with number of farms (n = 15) and repeated independent measurements over time (n = 28) as random effects. Using the ‘powerCurve’-function, we then created artificial subsets of the data corresponding to a reduced sampling effort (i.e., lower number of study sites or yield measurements) and remodelled the treatment effects, up until the point when the statistical power became insufficient (Fig. 2; Tables A3 and A4).

Results

Survey of bird and bat exclosure studies

We collected data from 30 group-specific or combined bird and bat exclosure studies conducted across 12 different agricultural systems in 14 countries (Table 1). Studies from both temperate and tropical areas were considered in the literature review. However, the number of studies from Neotropical countries (n = 15) notably exceeds the number of Paleotropical studies (n = 6), corresponding with previously published reviews on the effects of bird and bat exclosures in tropical areas (Maas et al. 2016). The majority of selected studies were conducted in the United States of America (n = 7), and countries within the Neotropical realm such as Costa Rica (n = 4), Jamaica (n = 3), Mexico (n = 3), Brazil (n = 2) and Panama (n = 1). The Paleotropical realm is represented by studies from Indonesia (n = 3), Australia (n = 2), as well as South Africa, Tanzania, Kenya, South Korea, and Malaysian Borneo (n = 1).

Studies that were conducted over a one-year period were performed equally in temperate and tropical areas (n = 6), while two-year studies were mostly conducted in tropical areas (15 out of 18 studies), and only one study was conducted over a three-year period. Sampling effort and methodology were highly heterogeneous between studies and included, for example, repeated sampling, visual observation, fogging, or a combination of these methods for different arthropod groups. Therefore, these data were not considered for study comparison and are summarized in the supplementary information (Table A2). The systematic comparison of sampling effort requires repeated measurements, which was only fulfilled by one study (see results on effect detectability below). The majority of investigated studies used permanent 24-h exclosures, excluding both birds and bats (n = 23), while a smaller proportion of studies used permanent and group-specific bird and bat exclosures in combination (n = 7). Group-specific exclosures require a distinction between diurnal and nocturnal activities, resulting in an informal added value of the studies, but also in additional methodological challenges compared to permanent/combined exclosures that we discuss here. Most studies investigated effects of either group-specific or combined bird and bat predation services in coffee (n = 13) and cacao (n = 4), while a smaller number of studies focused on apple orchards, oil palm, and kale (n = 2), or other crops such as rice, cabbage, hops, alfalfa, cottonwood, macadamia or walnut orchards (n = 1 each). Major differences existed in the total number of study sites (i.e., experimental farms, fields, or replicates within a single farm; n = 1–42), as well as the number of experimental treatments within a single site (bird/bat exclosures and controls; n = 2–8), and the number of studied plant individuals (i.e., focal crop; n = 1–380). Variation was also found for mesh sizes of exclosure nets, which ranged from 6.35 × 6.35 to 58 × 58 mm between studies, though most of the studies used mesh sizes larger than 20 × 20 mm (n = 23).

Differences in the use of or costs for materials were not clearly related to the study area, the number of treatments, sites, or plants per cage (Table 1). The majority of studies used nylon nets for the exclosures (n = 21) versus plastic (n = 5) or steel (n = 4) mesh. Bamboo, wood, or PVC pipes were mostly used as frame materials (n = 6, respectively); while fewer studies applied wire (n = 3), metal bars, or ropes (n = 2, respectively) to construct the frames. In five studies, the frame material was not reported. Birds and bats were excluded from both single plant parts or branches, and whole plants. Thus, the size of exclosures varied greatly depending on these factors, ranging from 0.0017 to 1280 m^3.

Considerable differences existed in related individual costs (ranging from US$5 to US$863 per study site) and time efforts (ranging from 1 to 840 h) needed for installation of experiments per site (Table 1). Excluding the only three-year study in our set, in which an extraordinary amount of time and effort was invested to install exclosures around oil palms (840 h per study site), the installation of exclosure treatments took ~7.5 h on average per study site, regardless of other factors. On average, 3–4 workers were needed to install the exclosure treatments in the reported studies (n = 8), while systems with smaller study plants needed only 2 assistants for installing the cages (n = 6) and larger crops (e.g., oil palm and coffee) needed up to 5 workers for this work (n = 4).

In addition, effects of bird and bat exclosures on arthropod abundances and crop yield were calculated for the 18 studies for which direct feedback from authors existed. For this, a uniform calculation method was used (Table A2) to allow comparison of those studies. Due to the incompleteness and heterogeneity of these results, and because they are discussed in the respective publications, this information is presented in the Appendix. Table A2 also shows differences between studies in the consideration of local and landscape effects. All studies used an open control treatment (no manipulation of birds and bats) in addition to the different exclosure treatments (Table A2), either using open controls (n = 26), or faux controls that were surrounded by a frame but not covered by netting material (n = 4). Additionally, some studies controlled for the effect of ants and other invertebrates, lizards, small mammals or pollinators, either by preventing access in all treatments and the control, or by adding separate additional exclosure treatments to the exclosures of birds and bats (Table A2). These data, however, should be compared and interpreted with caution due to the fundamental differences between the studied regions and agricultural systems (e.g., details discussed in the respective publications; also see Maas et al. 2016) as well as the applied experimental and sampling methods.

Effect detectability

We performed a power analysis using the data set of Maas et al. (2013), considering effects of study design (number of sampled farms) and sampling effort (number of repeated yield measurement per exclosure treatment). Our simulation of a decreased sampling effort revealed that a statistical power of 80% can be achieved at much reduced sample effort (Fig. 2). Accordingly, the analysis revealed that a sampling effort of approximately 6 farms and 10 yield measurements during the 1-year census (instead of the 15 farms and 28 measurements of the original design) would have been adequate (Fig. 2; Tables A3 and A4).

Discussion

More than forty years ago, Solomon, Glen, Kendall, and Milsom (1976) covered apple logs with wire netting to exclude birds, and investigate the effects of avian predation on moth larvae, thereby demonstrating the importance of arthropod suppression in agricultural systems. Today, the experimental exclosure of predators has developed into a major tool in ecological research allowing the investigation of predator effects and interactions with other taxa (e.g., Karp et al. 2013; Classen et al. 2014; Kross et al. 2016; Maas et al. 2016). However, while standard concepts of land use and biodiversity conservation have been changing and much discussed during the last few decades, methodological approaches of field manipulation experiments to quantify ecosystem services, such as biological control, remained surprisingly unchanged.

Our comparison of bird and bat exclosure studies in agricultural systems demonstrates a number of similarities and differences among studies in the application of this method. Due to the heterogeneity of existing studies and considerable differences in applied methods (e.g., study location, duration, choice of materials, sampling effort and units), we found that the available body of literature is not yet suitable to perform a meta-analysis. It is sufficiently diverse, however, to discuss common pitfalls that emerged among the selected set of studies, and to provide multiple options for optimizing cost-benefit trade-offs, material choice, and applicability of results related to overall study design of future bird and bat exclosure studies.

Study design and implementation

To improve the planning and efficiency of bird and bat field exclosure experiments, several factors should be considered in the study design and implementation. Study area and system are related to fundamental differences in expected costs for an exclosure experiment, because materials, rents or transport costs are variable among regions, and required sizes of exclosures depend on the studied system. Nonetheless, some options exist regarding the choice of study sites, the number of replicates, and the required duration of different methods (i.e., daily maintained group-specific exclosures versus permanent/combined exclosures), that can help to reduce costs and maximize benefits in the application of this approach.

Experimental sites should be chosen to be as homogenous (i.e., in altitude, rainfall, temperature, soil type/moisture) as possible in order to maximize their comparability. If, for example, local or landscape management effects are to be investigated as additional factors, a sufficient number of comparable replicates need to be established in systems showing determinable land use intensification gradients. Further, it is advisable to select sites that encompass the most extreme contrasts for comparison (e.g., sites with particularly high or low values in shade management, forest proximity, or altitude).

Both environmental and land use management factors can influence the occurrence and interactions of predators and herbivores, and should therefore be taken into account in the study design. For example, climatic factors might be of importance for crop productivity and arthropod composition/diversity, and possible seasonal fluctuations should be taken into account. Crop management activities such as pesticide application might also have important effects on the studied species communities. Here, farmer records or other expert data on chemical applications should be considered in the study design, and integrated in data analysis; or land owners could be asked to exclude the experimental plants from their management practices to avoid unwanted interference with the experiments.

In general, preliminary studies can greatly contribute to cost considerations, more targeted study design and implementation, because they provide valuable information about which factors, materials, methodological approaches, or sampling efforts should be considered for a certain study area or question.

While expenditure on exclosure maintenance could not be included in our analyses due to high variability, this may add substantial costs to the study. Particularly, night or day-time only exclosures (bat or bird) require changing net positions twice per day (in early morning and in the evening). In these cases, number of sites will highly influence study cost, as more sites will demand more assistants or transport effort between sites. For example, assuming the same cost per exclosure across studies, a study with 4 sites (e.g., farms) and 15 exclosures per site will have higher costs per site than a study with 15 sites (e.g., farms) and 4 exclosures per site. Increasing the number of samples per site can be an option, at the cost of losing independent replicates.

Study system

The focal crop (tree, shrub, or forage) was the most obvious characteristic related to costs and effort applied per site. Small plants (e.g., alfalfa, vegetables) can be enclosed in smaller cages, which are cheaper and demand little effort to be installed. In addition, studies with small plants allow for the assessment of exclosure impacts on a greater number of individual plants. For instance, the study encompassing alfalfa comprised 380 individuals within a single treatment, while the assessments on the remaining crops were limited to only parts of individual plants (branches) or up to 12 experimental plants per treatment in a study on coffee (Table 1). The comparison of existing studies shows that scientific evidence related to vertebrate exclosures, quantified impact on crop productivity, and resulting implications for ecological management of bird- and bat-mediated ecosystem services are highly limited for many regions and systems (especially in the Paleotropics), highlighting the need for further research in such areas. It also shows that the consideration of pesticide effects is highly inconsistent between studies, which should receive more attention due to the direct possible effects on arthropod communities and interactions.

Depending on the heterogeneity of the study area and the system, different numbers of replicates will be needed to cover relevant management effects at local and landscape level, but at least three sites per predictor variable (e.g., for each studied level of local shade or landscape effect such as forest proximity) are recommended to obtain robust results. It should be taken into account that a structurally complex and diverse surrounding landscape may compensate for locally high intensive management (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies 2005; Karp et al. 2013).

Study duration and sampling effort

The duration of the exclosure studies has an impact on the validity and generalizability of obtained results. Careful consideration should be given to whether study duration includes important phenological events in the system such as, the occurrence and impact of harvest peaks, changes in seasonal abundances of predators, or the occurrence of rare species.

The required sample size and effort for both group-specific and permanent/combined exclosures, as well as adequate durations of exclosure experiments, can be determined through power analyses, as shown here for a suitable data set with continuous measurements (Fig. 2). While we do not suggest that the results of this single study from Indonesian cacao should be applied to other study systems, the example demonstrates a valuable approach to estimating expected sampling effort in future exclosure studies, which should help optimize design. This approach requires both a continuous and regular series of measurements from preliminary or comparable studies. However, based on the design and results of all other studies presented here (Tables 1 and A2), we suggest that, on average, 8 study sites (e.g., 8 separate farms) and 10 repeated measurements (across space or time) should be sufficient to measure effects of bird and bat exclosures on common arthropod species and crop productivity. Required sampling effort will also depend on whether the effects of rare species groups, or local versus landscape factors, are to be estimated.

While the direct effects of common pest species abundance and related suppression of dis-services (increased pest infestation or herbivory rates) might be detectable in relatively short time periods, crop yield often responds with a time-lag to shifts in pest predation, arthropod abundances, and related mesopredator effects. Thus, the design of exclosure experiments requires detailed knowledge of the study species' life cycle at different levels of the food web, to identify the most suitable period and duration for exclosure experiments. For example, coffee berry borer (*Hypothenemus hampei*) infestation patterns depend on coffee berry availability, and unripe berries are attacked when insufficient mature berries are available at the beginning of the season, or when frequent harvesting is practiced (Damon 2000). For exclosure studies, such life cycle and management effects of studied species and systems must be taken into account to avoid biased results and to provide both exclosures and controls with the same probability of colonization/infestation at the beginning of the experiment. To account for seasonal variation in species abundances and interactions related to crop productivity, at least one whole crop growing season should be covered by the experiment.

Furthermore, thorough knowledge on the biology of the species of interest, including potential predators, will allow researchers to determine appropriate experimental durations. For instance, short-term studies might not account for seasonal variations affecting predator availability. Seasonal fluctuations in ecosystem services, such as those caused by the presence or absence of migratory birds (Van Bael et al. 2008), can either be addressed in long-term or seasonally replicated short-term experiments. However, long-term studies provide the opportunity to further analyse complementarity effects such as fluctuations in the provision of pest control services when migratory populations are either present or absent (e.g., Karp et al. 2013; Martínez-Salinas et al. 2016).

The effects of rare arthropods and pests, which may still substantially contribute to crop damage, are likely to be detected only with extended sampling. For example, many species of grasshoppers, crickets, or dragonflies are relevant for crop damage or as food resource for birds and bats in most agricultural systems, but require longer observation periods to be recorded in sufficient numbers, or to detect vertebrate exclosure effects. In a study on Indonesian cacao, six monthly observations were needed to statistically identify such effects on larger or less abundant arthropod groups (e.g., Maas et al. 2013).

Ultimately, the determination of reasonable timing, duration and sampling effort based on target species life cycles and observed statistical trends can be useful for more efficient experimental design, but can also serve as a tool for land users (such as farmers) to improve crop harvesting and pest management schedules.

Group-specific or permanent bird and bat exclosures?

Evaluating both the individual and combined impact of birds and bats on arthropod populations and crop productivity can reveal interesting insights on their contribution to ecosystem services and multitrophic interactions (Maas et al. 2016). However, group-specific exclosures that differentiate between diurnal and nocturnal predators will always be associated with higher costs and time effort than permanent exclosures, because they require daily maintenance (i.e., daily opening and closing of exclosures), and increase the amount of replicates, treatments, and personnel needed to perform the experiment. From the 30 studies we compare here, only 7 used daily maintained group-specific exclosures, while the other 23 studies used permanent 24-h exclosures. A way to save costs in the study of individual bird or bat effects may be the establishment of daily maintained group-specific exclosures for shorter periods of time, after which they are continued as permanent exclosures. Such an approach could be applied, for example, if the detection of species-specific predation or pollination effects takes less time than the assessment of yield or other plant-level responses; or to detect combined long-term effects on arthropod communities and crop yield in addition to individual bird or bat contribution. It could further be used to simulate the effects of phenological mismatches between migratory insectivores and crop-pests as a result of climate change.

Choice of materials

On average, the material used to install exclosures in the 18 feedback studies cost US$153 per study site, with individual studies costing as low as US$5 (in coffee) and others investing up to US$863 (in cacao) per study site. Here, we only compare costs needed for the installation of exclosures at the respective study sites, because information on other costs, such as transportation costs, were not available for most studies. We found that the choice of netting or framing material was closely related to study costs, but also to a number of avoidable pitfalls that should be considered.

Netting material

Nylon mesh was by far the most frequently used netting material, and appeared to be related to lower installation costs than other materials, but also varied greatly in mesh size (from 6.35 × 6.35 to 58 × 58 mm). Choosing the right mesh size, however, is critical. The choice of mesh size should be carefully considered and based on the size of the organisms to be allowed and excluded. Morphometric measurements of birds and bats are widely available in the literature (e.g., for birds, publicly available banding databases with these measurements can be accessed for many species). While nets of larger mesh size may be cheaper, they will not restrict smaller predators from accessing the focal plant. Exceedingly small mesh sizes (<20 mm) may also not be desired if they restrict large arthropods (e.g., pests, predatory insects, or pollinators) from entering cages. Furthermore, unsuitable mesh sizes and loose suspensions can lead to unintended and harmful catches of birds, bats, or other animals.

Most of the presented studies used mesh sizes of 20 mm or larger. Discussion of ‘safe mesh sizes’ among authors revealed that above all, a tight suspension and firm tension of exclosure nets should be ensured to avoid unintentional capture of vertebrates, and that a significant reduction of birds and bats within the exclosures (i.e., >90% reduced occurrence) should be sought rather than risking potential harm or damage through trapping of species. For example, in the two-year study in Indonesian cocoa that used the above described approach (Maas et al. 2013), only four individual birds were ever observed within the exclosures, and only four birds and two bats were accidentally caught in the netting, but could be released quickly thanks to regular observations and well-trained staff. Thus, we recommend planning additional time effort and costs for regular check-ups of installed exclosures.

In addition to mesh size, the colour and thickness of netting materials can have an unintentional effect on environmental conditions within the exclosures (e.g., shading, temperature, humidity and wind circulation), especially when exposed to direct sunlight, which may affect arthropod communities. For instance, temperature may affect coffee berry borer breeding success (Damon 2000) and thus infestation rates. Thus, monitoring temperatures within exclosures is recommended to assess such potential effects. Further, darker colours might be more easily recognized and therefore avoided by birds and bats than, for example, transparent nets.

If treatments include group-specific bird and bat exclosures, they must be easy and quick to open and close daily. Screws, nails and hooks should be avoided as the net gets easily entangled. Pulleys and adjustable rope systems appear more adequate, especially in larger exclosures surrounding tree crops such as cacao (e.g., Maas et al. 2013), also because they simplify the re-tensioning of the nets. In addition, it should be considered that non-target animals such as monkeys, pigs or other farm animals in crop areas can potentially damage the net, so where these or other animals are common, working within fenced areas or leaving an open passage between exclosure net and ground is recommended. Finally, because several taxa other than birds, bats, or arthropods might also be excluded from or have access to consumable focal plant arthropods (e.g., terrestrial mammals, lizards), researchers should at minimum explicitly consider these possible contributions to predation rates and yield outcomes.

Another possible problem is theft of materials: netting materials may be used as fishing gear, for example, and might be considered quite valuable in some regions. If possible, cages should be monitored and frequently controlled to avoid major damage, theft, or injury to trapped animals. For ethical reasons, the re-use and recycling of the exclosure nets should be carefully considered and they should not be passed on carelessly (Costello et al. 2016). In general, we recommend building a prototype for exclosure cages and operating it for a couple of weeks, to test its practicability in the field. In particular, we recommend the selection of transparent nylon nets, with a mesh size of at least 20 mm (but not more than 55 mm), and using disposable or recyclable materials.

Framing material

The use of manufactured frame materials, such as PVC pipe, iron and ropes, increased study costs. On the other hand, cages built with wood and bamboo may decrease costs only in some cases, most likely when these materials are available and easy to transport in the study area. While rope, bamboo, and PVC pipes can be easily transported, wood and metal pole cages tend to be heavier, especially if cages are previously constructed rather than built in the field. On the other hand, though rope frames are very easy to transport, their use may not be possible in most crops, as it demands large trees as support (e.g., canopy trees in shaded agroforestry systems). Though the ‘ideal’ frame material will undoubtedly vary across systems, we recommend using ‘natural’ materials such as wood or bamboo that are readily available within the study system. These materials are cheaper, and at lower risk of being stolen relative to manufactured structures. If, however, exclosures are to be installed for a long period, manufactured materials (e.g., metal or PVC) may be a more cost effective option due to their durability. In case of a wooden frame, it is important to use hard and treated wood, to avoid damage by rain or termites. Materials such as bamboo may be painted with disperse paint on the lower end of the framing pole, which is fixed in the ground, to make it more durable. Regarding the height and size of the cages, plant growth should be taken into account, so that there is space provided between plant foliage and the exclosure until the end of the experiment, to avoid direct foraging of excluded vertebrates or damage to the crop from the exclosure.

To prevent bias between treatments and control sites, it is advisable to construct ‘faux controls’ consisting of an empty frame, as the cage structure of exclosures might attract organisms that could affect the experiments (e.g., birds, lizards, spiders, termites). Likewise, manufactured materials such as metal bars or PCV poles could be avoided by some species, and the use of natural materials such as bamboo or wood should be preferred in such cases, especially if they are more sustainable in terms of disposal or reuse in the respective study area.

General options for optimization

Quantification of ecosystem services using exclosure experiments can be approached from different perspectives. While farmers and stakeholders may be mainly interested in the economic value of the considered ecosystem service, conservationists are potentially interested in the efficiency of the service delivered by individual species or taxa. The design of exclosure experiments should meet the demands and behaviour of target groups (i.e., species delivering pest control services and pest species being controlled). For example, from a farmer's perspective, pest consumption by flying vertebrates may be of biggest concern, and separating the effects of individual taxa through group-specific exclosures might not be relevant. Therefore, permanent bird and bat exclosures are not only cheaper and less labor-intensive than group-specific exclosures, but also provide sufficient, robust information for predictive crop modelling, yield optimization, and to test landscape-wide environmental influences on crop development. On the other hand, understanding cause-effect relationships is key in basic research, and effective management of ecosystem services might require group or species-specific knowledge (Maas, Tscharntke, Saleh, Dwi Putra, & Clough 2015). Furthermore, the study of hitherto underrepresented taxa (e.g., bats and arthropods), study regions (e.g., Paleotropics) and interactions (e.g., multi-trophic interactions, impact on dis-services such as crop damage), provides a valuable contribution to fill existing knowledge gaps, as well as arguments relevant to the conservation of such species. Therefore, we conclude that highly controlled small-scale experiments should target both species-specific and interactive effects to disentangle effects of bats and birds on arthropods and plants.

Methodological differences among studies limit the validity and transferability of experimental exclosures in relation to targeted research questions. Future studies should pay more attention to comparability with other studies, allowing for comparisons of effect sizes at larger spatial scales, for example through meta-analyses. The example of this study shows that the extraction of comparable effect sizes required for systematic meta-analyses is often not possible or highly limited due to the significant heterogeneity between studies, the lack of information of population changes over time, or the small number of studies conducted beyond small local scales, which has been highlighted in previous studies (e.g., Bengtsson, Ahnström, & Weibull 2005; Chaplin-Kramer, O'Rourke, Blitzer, & Kremen 2011). The comparison of existing studies has shown here and before (Maas et al. 2016) that, for example, analyses of herbivory data or landscape level effects are highly limited (but see Karp et al. 2013), and can reveal contrasting results. Future studies should also account for the potential interactions between ecosystem services and management strategies: while shade cover is often considered (Table A2), variation in fertilization, irrigation, pesticide application, soil pH, and nitrogen availability can equally alter the quantity and quality of ecosystem services (Boreux, Kushalappa, Vaast, & Ghazoul, 2013). For example, the impact of herbivory on crop yield may strongly depend on environmental resource levels (Wise & Abrahamson, 2007). Similarly, effect sizes of exclosure treatments might decrease with increasing pesticide application or overall increase in crop agronomic management. Exclosure studies conducted along specifically selected land use intensity gradients can effectively disentangle such interacting factors and generalize our understanding of pest predation services in crops. To avoid common pitfalls, minimize the risk of unwanted costs or inefficient sampling, and maximize the benefits of exclosure studies, we recommend the consideration of such persistent knowledge gaps and the conduction of preliminary studies in the design and application of exclosure experiments, especially in regions where information on occurring species, their life cycles, and the impact of environmental conditions are limited.

With the advancing development of new technologies, there are also additional possibilities for more efficient design of exclosure experiments. In recent years, results from experimental field studies, the availability of long-term data sets, and innovative modeling approaches have contributed significantly to our understanding of multiple ecosystem services and underlying complex trophic interactions in tropical agroforestry systems (e.g., Classen et al. 2014; Maas et al. 2016). DNA barcoding of vertebrate faeces and stable isotope analyses across food chains, combined with regular monitoring of vertebrate, mesopredator, and herbivore compositions, provides a powerful approach to investigate complex trophic cascades and food-web interactions that greatly impact vertebrate exclosure effects (Martin et al. 2013). For example, with diet metabarcoding (based on the analyses of manageable numbers of vertebrate faecal samples and selected prey items) the diets of hundreds of animals can be determined simultaneously to estimate diversity, composition, and frequency of occurring prey items (Pompanon et al. 2012). These methods can significantly improve our ecological knowledge of bird and bat mediated ecosystem services in agricultural systems (e.g., Mata et al. 2018; Crisol-Martínez, Moreno-Moyano, Wormington, Brown, & Stanley 2016).

Conscientious project management and supervision during the field season can help avoid common pitfalls and encourage improvements in exclosure studies. For example, because opening and closing of exclosures need to be performed very carefully to avoid the unintentional harming of animals, hiring inexperienced field assistants adds a potential risk. Employee skills and motivation can be addressed though in-depth communication, training, and regular check-ins. In addition, exclosure studies in agricultural landscapes, but also in other ecosystems, are often conducted in close collaboration with local communities, stakeholders, and experts, who can provide valuable input to develop a deeper understanding of the studied system (Huntington, Gearheard, Mahoney, & Salomon 2011). In particular, studies in agricultural systems will greatly benefit from close cooperation and regular knowledge exchange with local farmers (Maas et al. 2018), who can provide crucial information on management practices, harvest cycles, perceptions towards biodiversity, and regional land use issues, which can promote the applicability of results from exclosure studies in agricultural systems (Maas et al. 2018).

Conclusions and implications for future research

The experimental exclosure of birds and bats from agricultural systems can provide valuable insights into ecosystem services, but their potential outcome is often limited by common pitfalls related to study design, duration, and material choice, or co-varying experimental conditions (e.g., local versus landscape effects). While some pitfalls appear to be avoidable, as discussed here, other costs and efforts related to experimental exclosures should be carefully assessed in order to maximize benefits.

In order to improve the feasibility, efficiency, and validity of future exclosure studies, we provide multiple options for improvement to be considered during study design. We also recommend estimating required sampling effort based on pilot studies, power analyses and expert knowledge. The consideration of cost-benefit trade-offs and open questions discussed here will improve experimental optimization, and facilitate the comparability and transferability of future exclosure studies on bird-and bat-mediated ecosystem services.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.12.002.

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