Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators

Kirsty Park

Biological and Environmental Sciences
University of Stirling
Stirling,
Scotland, UK
FK9 4LA
Email: k.j.park@stir.ac.uk
Tel. + 44 (0) 1786 821811

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ABSTRACT

Agriculture is a dominant land use worldwide with approximately 40% of the land's surface used for farming. In many countries, particularly parts of Europe, this figure is substantially higher and most agricultural land is under intensive practices aimed at maximising the production of food. The intensification and expansion of modern agricultural practices led to the biological simplification of the farmed environment, which has resulted in declines in farmland biodiversity during the last century. As with other taxa, many bat species have suffered severe population declines during the 20th century, with agriculture believed to be one of the main drivers reducing roost availability and foraging habitat. Lower intensity farming methods, and the creation or management of habitat features on farmland could potentially mitigate some of these negative impacts but the effects of this on bats, in comparison to other taxa, have received relatively little attention. Here, I review evidence on the impacts of efforts to increase biodiversity in agricultural landscapes on bat populations, and explore whether responses of bats to agricultural activities are similar to those of other taxa, a necessary requirement if they are to be used as bioindicator species.

The review revealed that there are relatively few studies with which to assess the effects of management interventions on bats in agricultural landscapes, and these are restricted to only a few countries. Nevertheless, there is evidence that bats benefit from lower intensity agricultural systems, specifically organic farming and shaded agroforestry: these systems tend to be associated with higher bat abundance, species richness and diversity, and are more heavily utilised by foraging bats. Whilst very few studies have explicitly tested the utility of bats as bioindicators in agricultural landscapes, overall, the response of bats to lower intensity agricultural systems also reflect responses by other taxa. These studies have been largely restricted to temperate regions, however. The review highlights several major gaps in our knowledge of bats in agricultural landscapes and where future research could be usefully directed including: 1) a broader geographical range of studies examining both the efficacy, and the underlying mechanisms through which lower intensity agricultural systems may benefit bats; 2) the potential for lower intensity systems in key crops such as oil-palm; 3) studies of the demographic effects of conservation management on bats; 4) in order to assess the potential of bats as bioindicators, studies quantifying the response of both bats and other taxa to environmental change in a wider range of biomes and regions are needed.

Keywords: Chiroptera, agriculture, conservation, bioindicator species

INTRODUCTION

In the past ten thousand years, as *Homo sapiens* switched from a largely nomadic subsistence way of life to settlements and farming, the demands of the rapidly growing population have driven the expansion of world's terrestrial surface used for agricultural production to 40 % (Ramankutty et al. 2008). However, it wasn't until the end of the Second World War in 1945 that the "industrialisation" of agriculture started to gain in acceleration, with increasing mechanisation, the development of a wide range of chemical applications to control weeds and insect pests, and a far higher degree of specialisation on individual farms. Such trends were exported to many developing countries where agriculture had shifted from wholly susbsistence production to land used for the export market following European colonialism in the 17th and 18th centuries (Perfecto and Vandermeer 2008).

The practical effects of such changes from diverse low-intensity agriculture to intensive monocultures greatly improved yields from crops and livestock, but drastically reduced native habitat cover, leading to an impoverished agricultural matrix, and exposure of many wildlife species to toxic levels of pesticides. The implications of such changes for wildlife started to be recognised in the 1960s and was brought to the public's attention with publications such as Rachel Carson's Silent Spring (1962). In the last few decades compelling evidence of the disastrous effects of an increasingly intensive agricultural industry on biodiversity worldwide has accumulated (e.g. Pain and Pienkowski 1996; Krebs et al. 1999; Tilman 1999). The mechanism by which agricultural activities impinge on wildlife are varied and differ according to taxa, but are primarily related to the loss of resources required for food and shelter, and the effects, both direct and indirect, of chemical applications. The overall reduction in suitable habitat also means that the remnants are fragmented and increasing isolated, reducing landscape connectivity and making populations vulnerable to local extinctions.

The recognition of the biodiversity impacts arising from agricultural activities has led, in many countries, to an increased interest in more sustainable farming methods, such as organic farming, agri-environment schemes and agroforestry. The amount of land farmed organically, a low intensity system using crop rotation, compost, and biological pest control, has expanded greatly, increasing by 135% in the decade 2001-2011 (Paull 2011), and in 2012 stood at 37.5 million hectares, although this is still only 1% of total agricultural land worldwide (FiBL-IFOAM Survey 2014). Agri-environment schemes (AES) have been introduced in Europe, North America and Australia, with similar programmes in other countries as an attempt to reverse biodiversity declines by the adoption of less intensive, environmentally-sensitive agricultural practices (e.g. extensive grazing, reductions in chemical inputs and maintenance of landscape features; EEA, 2005). Whilst schemes in Europe and the United States (Conservation Reserve Programme) include financial incentives to encourage farmer uptake, the Australian Landcare Programme is a largely unsubsidised, community-based approach (Abensperg-Traun et al. 2004). Approximately 25% of all agriculture land in the 15 longest-standing

EU countries is under some form of AES management (EU 2005), and in some countries this figure is considerably higher (e.g. 45% in the UK: DEFRA, 2008). Agroforestry, the inclusion of woody perennials within farming systems (e.g. for coffee and cacao) is a traditional land use for subsistence farmers throughout much of the world and, depending on the system, has a high potential for biodiversity conservation (Perfecto and Vandermeer 2008). Global estimates are difficult to calculate as the percentage tree cover varies greatly; however Zomer et al. (2009) estimated 17% of worldwide agricultural land involves agroforesty with > 30% tree cover, rising to 46% with > 10% tree cover.

Nevertheless, with the expansion of crops such as oil palm that employ intensive management and, based on current consumption patterns, forecasts of a 100-110% increase in global crop demands by 2050 (Tilman et al. 2011), large areas of land continue to be converted for intensive agriculture. Quantifying biodiversity responses to different management regimes is crucial if we are to examine the effects of current agricultural systems and for providing an evidence-base with which to improve future agricultural policy for nature conservation.

Bats and agriculture

It has been estimated that 16% of the world's 1150 bat species are under threat from extinction with the main driving forces being the loss of roosting and foraging habitats (IUCN Mammal Red List 2008; Mickleburgh et al. 2002), primarily from agricultural intensification and urbanisation. At the same time there is increasing evidence of the economic value of bats for agricultural production, at least in some systems. Across species, bats have a diverse array of diets; whilst approximately 70% of all bats are predominately insectivorous, nectivorous and frugivorous species are known to be important pollinators and seed dispersers for a large number of wild and cultivated plants (e.g. Fleming et al. 1994; Kunz et al. 2011). The potential role of bats in controlling insect pests in agricultural systems has long been suggested but it is only in the last few years that the necessary experiments to quantify this have been conducted, with marked effects of bats on insect herbivores (Williams-Guillén et al. 2008; Boyles et al. 2011), culminating in substantially increased crop yields due to bat predation (Maas et al. 2013).

Intensification of agricultural practices can potentially impact upon bats through reductions in prey availability, reduced survival through loss of suitable roost sites, loss or degradation of foraging areas and exposure to toxic compounds used in agrochemicals (Stebbings 1988; Defra 2005). In Europe, North America and Australia where habitat selection studies are commonly conducted using radiotracking or acoustic detectors, research has consistently indicated avoidance of intensive agricultural habitats (e.g. improved grassland, arable crops) and selection of native woodland or remnants of semi-natural habitat within agricultural landscapes (e.g. Walsh et al. 1996; Vaughan et al.

1997; Henderson and Broders 2008; Fischer et al. 2010a,b; Fuentes-Montemayor et al. 2013; Womack et al. 2013). Similarly, trapping studies in the tropics have shown reductions in abundance and species richness as previously forested land is converted to pasture and crop monocultures (e.g. Estrada et al. 1993; Harvey and González Villalobos 2007; Castro-Luna and Galindo- González 2012). It has been suggested that the perception that bats may be at lower risk of extinction due to their ability to fly has led to their being overlooked in tropical biodiversity assessments and fragmentation research (Struebig et al. 2008). However, as Struebig et al. 2008 argue, there are many aspects of bat ecology, including strong site fidelity and slow rate of reproduction, that are likely to make them very susceptible to habitat loss and fragmentation, particularly for tree and foliage roosting species.

Responses to changes in the extent and configuration of native vegetation varies considerably between bat species, corresponding to their foraging guilds (based on echolocation calls and wing morphology) and roosting behaviour which influence habitat selection (Jung et al. 2012; Fuentes-Montemayor et al. 2013), and I refer to the differential response of bats according to guild characterstics throughout this review. For example, some bats are highly manoeuvrable and are able to forage in dense cluttered environments; others predominately forage along woodland edges, whilst fast flyers with high aspect ratio wings and wing loading typically fly in open habitats or above vegetation (Altringham 2011).

Bats as bioindicators?

Concern over the loss of ecosystem services, such as pollination and insect pest control, has heighted awareness of how reliant humans are upon high quality, functioning ecosystems and the use of bioindicators (biological processes, species, or communities) has been suggested as one way of assessing changes in environmental quality over time as a result of anthropogenic impacts (e.g. Carignan and Villard 2002; Holt and Miller 2010). The potential role for bats as bioindicator species has been highlighted by Jones et al. (2009) and this special edition of *Mammalian Biology* is the result of an exploration of these ideas. Jones et al. (2009) outline a range of characteristics that may make bats suitable bioindicator species, including their position at high trophic levels, widespread distribution and relative taxonomic stability. In order to be suitable as a bioindicator however, it is also critical that their responses to anthropogenic disturbance, such as habitat loss, and attempts at mitigating against habitat loss, reflects those of other species.

Aims of the review

The aims of this review are to evaluate the impacts of efforts to increase biodiversity in agricultural landscapes on bat populations, and explore whether responses of bats to agricultural activities correlate with those of other taxa (i.e. their potential as bioindicator species). Specifically I shall address the following questions:

1. What evidence is there that lower intensity agricultural systems (e.g. organic farming, agroforestry) are beneficial for bats relative to high intensity systems?
2. What habitat features in agricultural landscapes, and at what scale, can be used to mitigate negative effects of agriculture on bat populations?
3. Is there evidence from these studies that bats are useful indicator species for other taxa?

A recent synopsis on conservation interventions for bats, including those on farmland, provides a useful summary of studies relating to questions 1 and 2 above (Berthinussen et al. 2014). Here, my intention is to explore the various approaches to these questions in different geographical regions, and look to highlight gaps in our knowledge, and where future research efforts would be usefully directed. In assessing the suitability of bats as bioindicator species, I shall focus specifically on the association, or lack of, between the responses of bats to agricultural activities and those of other species.

METHODS

Criteria for inclusion

Agriculture can be defined as the practice of cultivation by humans for food, fibre, fuels and raw materials, and on this basis would also include forestry plantations (Spedding 1988). Since there has been a recent review on the effects of silviculture on bats (Lacki et al. in press), I have excluded forestry for timber production from studies reviewed here. In order to evaluate the value of lower intensity agricultural systems for bats, I restricted my focus to studies where metrics for bat responses (e.g. species richness, diversity metrics, abundance, activity) have been quantified for at least two different levels/types of agricultural system (e.g. organic farming versus its conventional equivalent). Chemical applications are a fundamental aspect of modern agriculture and some are known to impact on bat populations (e.g. Jeffries 1972). However, other than indirectly through agricultural systems that reduce or prohibit certain fertilisers or pesticides, this is outside the scope of the current review and is dealt with by another paper in this special edition (Korine in review).

Literature reviewing

In order to source publications (up to May 2014) that assessed responses of bats in relation to levels of agricultural intensity (question 1), the following combinations of keywords were used as a Web of Science search: bat OR bats and any one of the following: agricultur*, farm*, organic, agri-environment, agroforestry, conservation reserve programme, landcare scheme (the U.S. and Australian programmes respectively). To ensure that I had not missed studies that omitted these terms I also included specific names of some agricultural systems or crops including biofuel*, cotton, oil palm, sugar, soy. In addition, I included grey literature where there was sufficient information to allow evaluation. In this review all but one study is published as a peer reviewed paper with one UK government report, available online, also sourced. Many of these studies also measured the responses of other taxa as part of the same study; these were used to evaluate the extent to which the response of bats to variation in agricultural intensity compares with those of other taxa (question 3).

In addition to recognised agricultural systems (e.g. organic farming) that may benefit biodiversity, efforts to improve the quality of agricultural landscapes may also involve the creation or maintenance of natural or created habitat features; therefore studies evaluating bat utilisation of such habitat features were incorporated into the literature search in order to address question 2. These studies were were identified as part of the reviewing for questions 1 and 3 and references cited therein.

RESULTS AND DISCUSSION

1. What evidence is there that lower intensity agricultural systems are beneficial for bats relative to high intensity systems?

A total of 14 studies were found that quantified bat responses within agricultural landscapes that differed in their level of management intensity (Table 1): five European studies provided an assessment for organic methods of farming; three European studies (including one which also assessed organic farming so is double counted here), evaluated the effects of agri-environment schemes (AES); and seven studies in the Neotropics have examined the response of bats to different agroforestry regimes, primarily coffee, but two incorporating other crops such as banana, cacao, plantain, citrus and allspice (Table 1). Across these studies, seven also assessed the responses of other taxa including, invertebrates (n=6), plants (n=3) and birds (n=2) which were used for comparing with bat-management associations. All the European studies exclusively used acoustic detectors and therefore the response metrics for these studies are primarily levels of foraging activity using number of bat passes. Whilst some of these studies make a distinction between bat activity and foraging activity (i.e. bat passes containing distinctive feeding buzzes), here I use total bat passes as a proxy for foraging activity. Numerous studies have found a strong correlation between the two measures (e.g. Park and Cristinacce 2006), and there are often too few feeding buzzes recorded to allow statistical analysis. Since many bats can be identified by their echolocation calls, information was provided on species presence/absence and also activity measures for particular species, species richness and other diversity indices (e.g. Shannon’s H index, evenness, dominance). Some bat calls, however, are very similar making it hard to distinguish between species so authors either grouped together bats with similar calls (e.g. the genus *Myotis*), or used discriminant analyses with call libraries of known species to assign a level of probability to passes (e.g. Davy et al. 2007).

Overall, lower intensity agricultural systems had higher levels of bat activity, higher species richness and diversity scores (Table 1). Four studies on organic farming, focussing on arable, pastural or mixed farming were from the U.K; three of these showed a higher number of bat species on organic farms than their conventional counterparts and higher levels of activity by at least some species (Wickramsinghe et al. 2003; Fuller et al. 2005; Macdonald et al. 2012a). Fuller et al. 2005 also found lower dominance scores indicating higher diversity on organic farms. The fourth, Pocock and Jennings (2008) was primarily designed to uncover the mechanism(s) through which organic arable farming may benefit bats which precludes a simple comparison between farming types. Interestingly, this study showed no effects of agrochemical inputs, or from the use of hay rather than silage, but suggested that most bats were highly sensitive to boundary loss (e.g. hedgerows, field margins) and that these features may be more important than other management practices such as use of agrochemicals. In one study in Greece, foraging activity of bats (all species) was approximately 25% greater in organic vs non-organic olive groves (Davy et al. 2007), although the non-organic orchards in this study were relatively low intensity (one chemical application per year), which may explain why the differences were relatively modest (and not statistically significant).

The effect of agri-environment schemes on bats has been addressed by only three studies, all in the U.K. In a replicated paired study, activity of *Pipistrellus pygmaeus* and *P. pipistrellus* was 38% and 50% lower (respectively) on AES farms than their conventional counterparts (Fuentes-Montemayor et al. 2011a). When examined at habitat level (four habitats within each farm type were examined), bat activity of both species was lower at AES managed hedgerows, water margins and species-rich grasslands, but higher at AES field margins. However at this scale the differences were not significant which the authors attribute to over-dispersion in the data and a consequent loss of statistical power. None of the six bat species surveyed under AES management by MacDonald et al. (2012a) demonstrated any differences in activity when compared to conventional farms, other than those that were also under organic management (see above). In a study to assess whether there were any additional biodiversity benefits through AES designed for cirl buntings *Emberiza cirlus*, MacDonald et al. (2012b), found bat activity on AES farms was 2.6x higher than on conventional farms, although this difference was not significant.

In contrast to the European studies above, all but one of the studies on agroforestry in the tropics included native forest as one of their comparator habitats. Agricultural landscapes have been a dominant feature in some parts of Europe for over 2000 years (Williamson 1986) so choosing control habitats with which to compare agricultural practices in such areas would not be feasible. Nevertheless, having a “original” habitat control, where possible, provides a measure of the relative benefits of any particular agricultural system. There are a wide diversity of agroforestry practices for the production of different crops which involve varying levels of management, vegetation types and structural complexity; most of the studies reviewed here were for coffee production and were based in Mexico and Colombia. In Mexico five main production systems have been described for coffee increasing in management intensity (Moguel and Toledo 1999), and similar features are also commonly found in other coffee producing countries: rustic and traditional polyculture, which use a diversity of native trees for shading (Table 1: low intensity); commercial polyculture which has fewer strata in the vegetation and may involve the use of chemicals (Table 1: medium intensity); shaded monocultures, using a single canopy species and unshaded monocultures with no canopy and high levels of chemical applications (Table 1: high intensity). Where possible I have modified the term used by authors to fit within this system, as a way of easing comparisons between studies.

All the studies comparing the effect of agroforestry intensity on bats used trapping to estimate abundance and species diversity and one additionally used acoustic surveys (Table 1). Overall, species richness and Shannon's diversity index decreased from natural forest to coffee produced using increasingly intensive management (Table 1). In several studies bat abundance was actually higher in the low-input traditional polyculture than forest fragments but then declined with intensive methods such as shade monoculture (Williams-Guillen and Perfecto 2010) or unshaded production (Estrada and Coates-Estrada 2001). Focussing specfically on insectivorous bats, Williams-Guillen and Perfecto (2011) found contrasting patterns between open-space foragers and forest-bats. Whilst abundance and activity of forest bats were similar in the forest and low-medium intensity coffee plantations, it dropped sharply in high intensity plantations. The activity of open-space foragers, however, was highest in the high intensity plantations. Unusually, Estrada et al. 2006 found that bat abundance was higher in coffee systems across a range of production intensities, in comparison to forest fragments with the exception of shade monoculture; however, the sample size for this study was only one site per treatment. Species richness and abundance were considerably higher in traditional (low intensity) than commercial polyculture (medium intensity), which was similar to pasture, a common alternative land use in Mexico (Castro-Luna and Galindo-Gonzalez 2012). Numa et al. (2005) highlight the importance of the surrounding landscape for making such comparisons; they found little difference in phyllostomid species richness between forest, shaded coffee and high intensity unshaded coffee in landscapes with high levels of forest cover. In contrast, in landscapes with low forest cover species richness was highest in forest fragments, followed by shaded coffee with fewest species in unshaded coffee areas. This landscape effect is further supported by comparisons of shade agroforestry to forest fragments in Brazil; in areas with a large proportion of forest remaining, bat and bird diversity was higher in shade plantations compared to nearby forest. However, in areas dominated by shade plantations, diversity was considerably higher in forest fragments than plantations (Faria et al. 2006).

2. What habitat features in agricultural landscapes, and at what scale, can be used to mitigate negative effects of agriculture on bat populations?

Whilst there are relatively few studies that have explicitly tested the effects of different agricultural management intensities on bats, there are many more that provide valuable information regarding the types of mitigation that may improve the habitat quality for bats (see also Berthinussen et al. 2014).

These can be broadly grouped into i) connective elements; ii) scattered trees and woodland patches; iii) water features, and are discussed in turn below.

i) Connective elements

Studies have repeatedly noted a close affinity of many bats to landscape elements, usually, but not exclusively, consisting of vegetation or water which likely relates to their use for foraging, as shelterbelts and/or protection from predation (e.g. Limpens and Kapteyn 1991; Verboom and Huitema 1997; Lentini et al. 2012). It has also been suggested that they are used as navigation aids (Verboom and Huitema 1997), and as such bats with shorter-range echolocation calls might be expected to be more susceptible to habitat fragmentation than those with long-range calls. Frey-Ehrenbold et al. (2013) examined the influence of landscape connectivity across the Swiss Central Plateau between bats with short (e.g. *Plecotus spp.*), medium (e.g. *Pipistrellus* spp.) and long-range (e.g. *Nyctalus* spp.) echolocation calls. Activity was between 1.4 - 2.8 x higher around landscape elements versus open areas for all bats but the difference was most marked for those with short-range echolocation calls. They also found that the shape of elements (i.e. whether it was linear or patchy) was less important than percentage cover in the landscape and how well connected these were. Connective elements, such as hedgerows are a traditional feature of many agricultural landscapes but the expansion and intensification of agriculture in Europe over the past 50 years has led to a substantial decline in their extent and condition (e.g. between 1984-1990, hedgerow loss was estimated at 23% across the UK; Barr and Gillespie 2000). There is a strong association between bat activity levels and the presence of hedgerows and treelines indicating the high potential of these features to improve the quality of the agricultural matrix (Downs and Racey, 2006; Linton et al. in press; Boughey et al. 2011a). This association varies between species, however, with a strong response from *Pipistrellus* spp. but little effect on *Eptesicus serotinus* and *Nyctalus noctula* (Boughey et al. 2011a). There is also evidence that the presence of trees within hedgerows is associated with higher activity levels for some species (Linton et al. in press; Boughey et al. 2011a). A positive correlation between feeding buzzes and hedgerow height, which were taller on organic farms, was proposed as one reason for higher bat activity on organic farms in England, UK (Wickramsinghe et al. 2003). Hedgerow width, however, has not been shown to have an effect of levels of foraging activity (Boughey et al. 2011a).

"Live fences" are a common feature across large parts of South and Central America, used to delineate boundaries and enclose livestock or crops; these consist of fences established using large cuttings from trees to which strings of wire are attached (Estrada and Coates-Estrada 2001; Harvey et al. 2005). Estrada and Coates-Estrada (2001) compared the bat community at one live fence with three replicates of linear forest fragments in Mexico. Whilst bats were commonly trapped adjacent to the live fence, there was lower species richness and abundance than at forest fragments, and the authors suggested that live fences lack sufficient cover and tree species diversity (although it should be noted that there were potential confounding issues with the live fence also being more isolated from large areas of natural forest than two of three of the forest fragments). Harvey et al. (2005) surveyed bats, dung beetles, butterflies and birds at live fences in Costa Rica and Nicaragua; species richness of all taxa increased with the density of live fences in the landscape, and the capture rate of bats compared favourably to those in forested habitats. In a follow up study, comparing live fences to a range of other habitats, bat abundance at live fences was second only to that of riparian corridors, and considerably higher than secondary forest or pasture habitats; species richness was also marginally higher (Harvey et al. 2006). In agricultural regions of Australia "stock routes", roadside corridors of remnant vegetation, are a common example of connective elements. In one study bat activity was double that of adjacent open fields although there was no difference in species richness or the number of feeding buzzes (Lentini et al. 2012). The authors suggested that bats would benefit from agri-environment schemes that incorporated the use of connective elements, scattered trees, and lower intensity land uses such as unimproved pasture (Lentini et al. 2012).

ii) Scattered trees and woodland patches

Scattered trees and small woodland patches are a feature of agricultural landscapes around the world, and numerous studies have indicated their value for biodiversity, including bats (e.g. Henderson and Broders 2008; Fischer et al. 2010a,b; Fuentes-Montemayor et al. 2011a). Declines of farmland trees have been reported in North America, Central America, and parts of southern Europe, partly due to clearance for cropland and also because of ecological and anthropogenic processes leading to heighted mortality and low recruitment (Fischer et al. 2010a). The effect of such losses in Australia has been predicted to lead to declines in birds and bats of up to 50% by 2100 (Fischer et al. 2010a).

Several countries have introduced financial aid for woodland creation and management in agricultural areas (e.g. woodland grant schemes in EU; revegetation programmes in Australia). The resultant woodland patches are often very small (Fuentes-Montemayor et al. unpublished data) but could potentially help in enlarging existing patches, improve connectivity and increase the permeability of the agricultural matrix. Even fairly low tree densities can result in marked biodiversity benefits, but the relationship between tree density and metrics related to bat abundance differs between studies. Lumsden and Bennett (2005) found that relative abundance, as assessed by trapping, showed a linear increase with increasing tree density, whilst the highest activity of bats was at intermediate tree densities. Fischer et al. (2010b), however, found that the marginal value of trees was highest for both birds and bats when tree cover was at its lowest: compared to treeless sites the presence of 3-5 trees within a 2 ha site was associated with a tripling of bat species richness, and an 100-fold increase in activity. After this point, the marginal effect of additional trees on birds and bats diminished rapidly (Fischer et al. 2010b). A comparison of roosts and random non-roost locations in the U.K. showed that *P. pipistrellus, P. pygmaeus, Rhinolophus hipposideros, E. serotinus* and *Myotis nattereri* were more likely to be found in landscapes with higher proportions of woodland, and that the greatest effect was seen as woodland cover rose from 0 to 20% (Boughey et al. 2011b). Roosts were found closer to broadleaved woodland than expected by chance but importantly, the size of the woodland was not important indicating that even small woodland patches can contribute to improvements in agricultural landscapes (Boughey et al. 2011b).

The benefits of woodland creation schemes for bats are likely to take a long time to be realised, but there has been little work on the effect of the age of woodlands on their utilisation by bats. On-going research in the UK suggests that even sites planted with deciduous trees 30-40 years ago have much lower bat activity than older sites (Fuentes-Montemayor et al. unpublished data). Similarly, eucalypts are routinely used in Australia as part of revegetation programmes to stem land degradation and biodiversity loss (Law and Chidel 2006; Australian State of the Environment Committee 2001). An assessment of the benefits of these schemes for bats found that, with the exception of larger (> 10 ha), older (> 10 years) plantings, bat species richness and activity was similar to treeless paddocks and considerably lower than that in native remnants. Similar results, also from Australia, were found by Hobbs et al. 2003 but here the plantations were all very young (4-6 years old). Both studies stress the importance of retaining old native remnants given the low use of young plantations, although there is the potential for realising greater biodiversity benefits from plantations once they have matured which, for eucalypts as fast growing trees, will be earlier than many European deciduous species. There is considerable variation in the responses of different bat species to the extent and character of woodland within agricultural landscapes that reflects their foraging guild; for example, Australian farmland sites with low tree cover were dominated by large, fast flyers, and sites with dense tree cover by smaller, highly manoeuvrable species (Hanspach et al. 2012). They also respond differently to characteristics such as tree density and understorey cover indicating that management of woodland should take into account the needs of the bats present and encourage habitat heterogeneity to fulfil the requirements of different species (Law and Chidel 2006; Medina et al. 2007; Murphy et al. 2012; Fuentes-Montemayor et al. 2013).

iii) Water features

Wetlands are an essential element in the landscape for a wide range of ecosystem services, as well as supporting wildlife populations. High densities of invertebrates associated with water bodies attract large numbers of bats and numerous studies have noted the importance of riparian habitat for foraging and, in more arid environments, for drinking (e.g. Adams and Hayes 2008; Salsamendi et al. 2012). Worldwide, it is estimated that 50% of wetlands have been lost for conversion to agricultural land or industrial and urban areas (Verhoeven and Setter 2010). Some effort is now being made to create and manage wetland areas through agri-environment schemes although few studies have examined the effects of these on bats (but see Fuentes-Montemayor et al. 2011a). However, several studies have examined the use of artificial wetlands by bats, created for a variety of purposes including irrigation and to reduce erosion and which may also mitigate against some of the effects of agricultural intensification on bats. Comparisons of water infrastructures with other habitats indicate that foraging activity is highest over and adjacent to water bodies (Lison and Calvo 2011; Stahlschmidt et al. 2012; Sirami et al. 2013), although it is not possible from these studies to assess how these compare with bat activity at natural wetland features. The characteristics of newly created water bodies are important; Sirami et al. (2013) found activity increased with wetland size in South Africa, whilst Lison and Calvo (2011) suggested that the lack of rarer species detected at irrigation ponds in Spain was probably due to the absence of suitable riparian vegetation.

3. Is there evidence from studies on the effects of lower intensity agricultural systems that bats are useful indicator species for other taxa?

Other than studies on bats in Neotropical forests (see conclusions) there has been little formal quantitative assessment of whether the response of bats to environmental change co-incides with those of other taxa. Nevertheless, numerous studies have measured the responses of other taxa, in addition to bats, to comparisons between high and low intensity agriculture so are included here (Table 2). The bulk of these were conducted in Europe and consist of invertebrate responses conducted as part of the same study as bats, with the remainder small numbers of responses from birds, other mammals and plants.

Whilst Table 2 provides only a crude assessment of how bat responses compare to those of other taxa it does indicate that overall, bats responded in a similar way to other taxa where lower intensity farming consisted of organic farming and agroforestry. The main exception to this was the comparison with carabid beetles (Fuller et al. 2005); in this study bat abundance, species richness and diversity (dominance score) all showed favourable responses to organic farming whilst carabid beetle responses varied according to the metric being used as well as spatial and temporal factors. The picture for agri-environment schemes was more equivocal. There were more instances where bats and other taxa differed in their response to agri-environment measures, but the strength of the sign for association was usually lower than for organic and agroforestry systems. This arises as the response measures for both groups were, in the few studies that compared multiple taxa, similar between agri-environment and conventional farms. The main exception to this pattern was a study where moth abundance was substantially higher at agri-environment scheme farms, but bat activity was considerably higher at conventional farms (Fuentes-Montemayor et al. 2011a,b).

A key study missing from Table 2 is that of Pocock and Jennings (2008); this study examined responses of 30 species or other taxonomic groupings, including four species/groups of bat, to three key features of agricultural intensification (use of agrochemicals, the switch from hay to silage, and loss of boundaries both in cereal crops and grass fields). Rather than include the very high number of comparisons that inclusion in Table 2 would necessitate, a summary of responses for broader taxonomic groupings is provided in the text. Whilst this study was primarily designed to test the sensitivity of taxa to agricultural intensification, it also allows an assessment of how bat responses compare to those of shrews and three orders of insect (Coleoptera, Diptera and Lepidoptera). None of the bats (*P. pygmaeus*, *P. pipistrellus*, *Nyctalus/Eptesicus* spp., *Myotis* spp.) responded to the use of agrochemicals in common with 17 of the 22 other species/groups for which there were sufficient data. Similarly, none of the bats responded to the switch from hay to silage, in common with 15 of the 22 other species/groups for which there were sufficient data. In contrast, all bat groups with the exception of *Nyctalus/Eptesicus* spp. responded negatively to boundary loss as did just over 50% (13/24) of the other species/groups in cereal crops, and over 60% (13/21) in grass fields. So, whilst the conclusions of the study highlight caution in the choice of indicator species regarding their sensitivity to intensification measures, there is at least some evidence that many bats respond in similar ways to quite different taxa. The lack of response from *Nyctalus* and *Eptesicus* species is not unexpected as they are fast flyers who are most active over open habitats and water bodies so may be less dependent on boundaries and other linear features in comparison to other species (Vaughan et al. 1997; Boughey et al. 2011a). The authors conclude that the sensitivity of the taxa examined to changes in agricultural practices was highly variable, and that none could be used alone as indicators of agricultural intensification.

CONCLUSIONS

It is widely acknowledged that conservation initiatives to improve biodiversity on agricultural land have had mixed success, with widely varying responses between taxa and regions (e.g. Hole et al. 2005; Kleijn et al. 2011). A conceptual model developed by Tscharntke et al. (2005) predicts maximum gains from conservation initiatives in relatively simple agricultural landscapes (low diversity, 1–20% non-crop habitat), although these will diminish in completely cleared habitats (< 1% non-crop habitat), and this is broadly in-line with some of the findings reviewed here (e.g. marginal effects of scattered trees, Fischer et al. 2010b; infuence of woodcover cover on location of bat roosts, Boughey et al. 2011b). However, Kleijn et al. (2011) argue that where the aim of management is to maximise biodiversity conservation, the focus should be on land which is already extensively managed and complex as it will be easier to protect degradation of this than to restore areas where biodiversity has already been diminished. Either approach would require a more specific targeting of resources than is currently employed in many countries.

Overall, the paucity of studies and their geographical restriction have limited the ability of this review both to assess the effects of management interventions on bats in agricultural landscapes, and their utility as bioindicators. Nevertheless, there is evidence that bats benefit from lower intensity agricultural systems, specifically organic farming and shaded agroforestry: these systems tend to be associated with higher bat abundance, species richness and diversity, and are more heavily utilised by foraging bats. The picture for the efficacy of agri-environment schemes is equivocal however, with only one study from the four sourced showing any trend, albeit non-significant, towards higher bat activity at farms employing with these schemes (Macdonald et al. 2012b), and one study finding significantly higher activity at conventional farms (Fuentes-Montemayor et al. 2011a). It is not currently clear why these agri-environment schemes do not appear to be benefitting foraging bats but it is possible in some cases the implementation of management and the relatively small scale over which it operates are not sufficient to exert a positive response (Whittingham 2007). In addition, studies designed to assess such effects need to consider whether there may be other differences in management which have not been examined (e.g. some AES involve grazing restrictions which may reduce amounts of organic matter and consequently invertebrate populations), or whether their sample of non-AES farmers, who may be more likely to refuse access, is representative.

There was a surprising lack of studies investigating the value of lower intensity or alternative agricultural systems outside of Europe, Central and South America, and the majority of studies came from the UK and Mexico. The top three countries with the most organic agricultural land are Australia (12 m ha), Argentina (3.6 m ha) and the United States (2.2 m ha) but I was unable to find any published studies on the influence of organic farming on bats from these areas. Similarly, there are large knowledge gaps for the several key systems including food crops such as oil palm, soybean, rice and materials, for example, cotton and biofuels. Oil-palm production is currently the greatest threat to biodiversity in Southeast Asia with 1.7-3.0 million hectares of forest cleared in Indonesia between 1990-2005 (Wilcove and Koh 2010; FAO 2010). An initiative to develop a more sustainable agricultural system for palm oil (Roundtable on Sustainable Palm Oil 2013) has been launched involving reduced use of pesticides and fires, and a focus on conserving “high conservation value” habitats, but currently this represents a very small fraction of total production. In a landscape being converted to oil palm production, Struebig et al. (2008) assessed the conservation value of forest fragments to Palaeotropic bats. Whilst showing that there was a strong association between fragment size and the abundance and various diversity metrics for bats, they suggested that small fragments could nevertheless contribute substantially to landscape-level bat diversity, and facilitate the movements of some species across landscapes managed for oil palms. Further research on the efficacy, or otherwise of efforts towards sustainability for crops such as these is urgently needed.

No studies were sourced on possible effects of aquaculture on bats. Effluent from fish farms can damage the ecosystem nearby and unconsumed feed and faecal matter can result in large accumulations of organic matter in the sediment (Kırkağaç et al. 2009). This could potentially impact upon bats through changes in the prey community or through drinking water.

The mechanism through which organic farming benefits wildlife, for the majority of species is not known and potentially could be driven by one of several factors e.g. reduced use of agrochemicals, greater use of rotational practices, taller hedgerows etc (Wickramsinghe et al. 2003). Whilst these are all important features they are not exclusive to organic farming (Hole et al. 2005) and, given the very low percentage of land currently under organic management, our lack of understanding over key drivers which could improve farmland biodiversity is likely hampering efforts to scale-up such benefits. It has been suggested that most of the benefits of organic farming in temperate regions are delivered through overall higher habitat heterogeneity on organic farms rather than any specific prescriptions (Krebs et al. 1999; Benton et al. 2003). Consequently, policy frameworks and farmland management that focus on increasing heterogeneity at multiple spatial scales are likely to be of most benefit for nature conservation in agricultural landscapes. Unfortunately, in many parts of the world the required policy frameworks still do relatively little to stem biodiversity loss; the recently announced EU Common Agricultural Policy reforms, for example, are largely perceived by conservationists as a wasted opportunity and likely to lead to further habitat loss (e.g. RSPB 2013).

In line with research on other taxa, the vast majority of studies in this review focussed on metrics of bat abundance and diversity, although in some cases there was also an assessment of rare species or those particularly sensitive to changes in land use. Using differences in species richness or abundance to infer effects of conservation action, however can be problematic due to a range of ecological phenomena including source-sink dynamics, spill over effects and extinction debts (Klein et al. 2011). Information on demographic variables such as sex ratio, breeding productivity and survival would enable much greater insight into the effects of anthropogenic disturbance, and the effectiveness of attempts to mitigate this. Collection of demographic data on wild bat populations is extremely difficult but information on the age and sex of bats captured as part of trapping programmes would enable an assessment of whether only males were using particular areas or if breeding females were present as well. Males may be able to utilise a wider range of conditions as they have lower energy demands than reproductive females and studies on habitat selection have uncovered marked differences between sexes (e.g. Barclay 1991; Altringham and Senior 2005; Saldaña-Vázquez et al. 2013; Lintott et al. in review). Equally, information on population structure and diversity from genetic material have revealed that considerably larger areas of undisturbed habitat are needed for conserving genetic diversity than for species diversity (Struebig et al. 2011), but this information is generally lacking.

There are several characteristics required for species to be useful bioindicators (McGeogh 1998). This review has examined just one of these; whether responses of bats to lower intensity agricultural systems reflect responses by other taxa. The studies reviewed here indicate that overall, bats responded in a similar way to other taxa and this may be because organic farming and agroforestry appear to deliver broad beneficial effects for a wide range of species, whilst the studies assessing bat responses to agri-environment schemes found relatively modest, if any, positive effects.

Research in Neotropical forests, primarily on species in the family Phyllostomidae, has previously suggested that the response of bat assemblages to habitat disturbance is not shared by other taxa, which typically are more heavily affected (Pineda et al. 2005; Barlow et al. 2007). Subsequent work in both the Neotropics and Palaeotropics has suggested that partitioning analyses based on foraging or roosting strategies, rather than at the assemblage level, may result in an improved ability to detect responses to land-use changes (Castro-Luna 2007; Struebig et al. 2008). Studies in a wider range of biomes and regions are now needed to assess whether bat responses mirror those of other species (see also Struebig et al. 2008).

In summary, the relatively limited number of studies reviewed here indicates that bats can benefit from some lower intensity agricultural systems and by the inclusion of features, particularly those consisting of woody and aquatic elements to improve habitat quality and connectivity. In relation to the utility of bats as bioindicators, a qualitative assessment suggests that the responses of bats to agricultural change is largely mirrored by those of other taxa. However, the review has revealed large knowledge gaps where future research would be usefully directed:

1. A broader geographical range of studies is needed: evidence on the efficacy of organic systems and agri-environment schemes for bats is limited to Europe, and agroforestry studies have taken place exclusively in Central and South America.
2. As has been previously noted for other taxa (Hole et al. 2005), the underlying mechanism(s) through which bats benefit from organic farming is not clear, and studies to elucidate key drivers are required.
3. Research on the efficacy, or otherwise, of efforts to improve the sustainability of intensively managed crops such as oil palms in areas of high biodiversity is lacking and urgently needed.
4. Studies of the demographic effects of conservation management on bats in agricultural landscapes are urgently needed to aid our interpretation of their impact at the population level.
5. Currently, it is not clear to what extent bats in general, and which species/groups of bats in particular, are useful as bioindicators. Studies quantifying the response of bats and other taxa to environmental change in a wider range of biomes and regions are needed.

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