Chapter 6
Bats in the Anthropogenic Matrix: Challenges and Opportunities for the Conservation of Chiroptera and Their Ecosystem Services in Agricultural Landscapes

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Abstract Intensification in land-use and farming practices has had largely negative effects on bats, leading to population declines and concomitant losses of ecosystem services. Current trends in land-use change suggest that agricultural areas will further expand, while production systems may either experience further intensification (particularly in developing nations) or become more environmentally friendly (especially in Europe). In this chapter, we review the existing literature

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on how agricultural management affects the bat assemblages and the behavior of individual bat species, as well as the literature on provision of ecosystem services by bats (pest insect suppression and pollination) in agricultural systems. Bats show highly variable responses to habitat conversion, with no significant change in species richness or measures of activity or abundance. In contrast, intensification within agricultural systems (i.e., increased agrochemical inputs, reduction of natural structuring elements such as hedges, woods, and marshes) had more consistently negative effects on abundance and species richness. Agroforestry systems appear to mitigate negative consequences of habitat conversion and intensification, often having higher abundances and activity levels than natural areas. Across biomes, bats play key roles in limiting populations of arthropods by consuming various agricultural pests. In tropical areas, bats are key pollinators of several commercial fruit species. However, these substantial benefits may go unrecognized by farmers, who sometimes associate bats with ecosystem disservices such as crop raiding. Given the importance of bats for global food production, future agricultural management should focus on "wildlife-friendly" farming practices that allow more bats to exploit and persist in the anthropogenic matrix so as to enhance provision of ecosystem services. Pressing research topics include (1) a better understanding of how local-level versus landscape-level management practices interact to structure bat assemblages, (2) the effects of new pesticide classes and GM crops on bat populations, and (3) how increased documentation and valuation of the ecosystem services provided by bats could improve attitudes of producers toward their conservation.

6.1 Introduction

Agricultural areas cover approximately 40 % of our planet's terrestrial ecosystems (FAOSTAT 2011), with the 5 billion ha of land under farming and grazing now surpassing the extent of the world's forested areas (Robertson and Swinton 2005; Power 2010). Agricultural areas are expected to continue to expand with increasing human population growth and resultant resource use: Low- and middle-income countries will experience a 100 % increase in demand for agricultural products by 2050 (Defries et al. 2010; FAO 2011). In the face of increasing pressure on natural resources, the conservation of remaining natural areas is critical for the survival of multitudes of species. However, the ubiquity of agriculture means that farmland cannot be ignored in the context of landscape-level approaches to biodiversity conservation (Vandermeer and Perfecto 2007; Loos et al. 2014).

A growing body of research demonstrates that not only do some agricultural systems harbor high levels of biodiversity and provide a variety of ecosystem services (Tilman 1999; Foley et al. 2005; Tscharntke et al. 2005), but also that characteristics of these agricultural systems may have profound effects upon remaining natural areas (Perfecto and Vandermeer 2010). Agricultural matrices can vary drastically in their quality and permeability, impacting dispersal rates, and hence,

long-term population stability of organisms found in less disturbed areas (Ricketts 2001; Laurance 2008; Perfecto and Vandermeer 2010; Tscharntke et al. 2012). On a local scale, different agricultural management approaches often coexist. Some rely on varying chemical inputs (pesticides, fertilizer), or novel plant types (e.g., genetically modified crops incorporating genes for characteristics such as insecticide functions), resulting in environmental contamination, pollution, and dissemination of toxins that could negatively impact biodiversity across multiple spatial scales (Nelson et al. 2009; Power 2010). As a consequence, agricultural management has effects not only on biodiversity, but also on human health and economies.

In the tropics, the expansion of export-oriented agriculture results from population growth and shifts in consumption patterns of developing nations, and is carried out mostly to the detriment of old growth forests and extensively managed grasslands such as pastures (Defries et al. 2010; Lambin and Meyfroidt 2011). As a consequence, croplands are still expanding dramatically, and agricultural practices are likely to further intensify in the near future (more chemical and mechanical inputs, reliance on genetically modified plants with novel manufactured traits). Short-term increases in yield will come at the cost of reduced structural and taxonomic diversity within agricultural systems (Loos et al. 2014) and concomitant loss of crucial ecosystem services.

An additional factor affecting agriculture in the Anthropocene is climate change and the need to adapt cultures to novel environmental conditions: Many areas may become unsuitable for cultivation of their current dominant crops, while extreme weather events may result in reduced yields. Resulting declines in calorie availability, particularly in the developing world (Nelson et al. 2009), will increase the need for agricultural practices that meet both productivity and sustainability goals (Tilman et al. 2002; McShane et al. 2011; Tscharntke et al. 2012). These trends portend major shifts in land-use patterns (Lambin and Meyfroidt 2011) and hence biodiversity, with agricultural intensification, forest and tree roost loss anticipated to have particularly negative effects on bat species richness, abundance, and functional diversity (Fischer et al. 2009, 2010; Jones et al. 2009).

These emerging trends pose major threats to farmland bat assemblages and populations (Jones et al. 2009; Kunz et al. 2011) and could negatively impact human populations by altering the ecosystem services that bats provide. Thus, there is a critical need to assess how agricultural management affects bat populations, and how affected bat populations will in turn affect agricultural production. In this chapter, we review the effects of agricultural land use and management on bat assemblages and the behavior and ecology of individual bat species at field, farm, and landscape scales (Vickery and Arlettaz 2012). We also review the developing literature on ecosystem services—and disservices—provided by bats in agricultural areas. Finally, we synthesize this information to suggest key management recommendations necessary to maintain bat populations in agricultural landscapes and highlight critical knowledge gaps that must be resolved in order to conserve bat diversity and ecosystem functions in a planet increasingly dominated by food production.

6.2 Methods

We used the Web of Knowledge, Google Scholar, and PubMed search engines to locate publications with the keywords "bats" AND "agriculture," "agroforestry," "farm," and "farmland." Given the potential importance of bats in provisioning ecosystem services in agricultural areas, we also searched for "bats" AND "ecosystem services," "pollination," "pest consumption," "pest control," and "pest limitation." The majority of sources stemmed from peer-reviewed publications, although we also included Master's and Ph.D. theses and published reports if results from the study in question were not available as journal articles. We also inspected the bibliographies of relevant publications. Each co-author focused on a specific geographic area (RA, assisted by Olivier Roth: Europe; BM: Australia and tropical Asia; EO: temperate North America; PT: sub-Saharan Africa; KWG: tropical Americas). Our searches were limited to publications with English language text or summaries. We focused on agriculture and animal husbandry for the production of calories for human or animal consumption, excluding forestry systems dedicated to timber or fiber production (see Law et al., Chap. 4), studies in which fallows or abandoned fields were the only agricultural systems investigated, as well as investigations that focused on fragmentation without explicit consideration of the effect of agricultural matrix (see Meyer et al., Chap. 3).

We divided results from the literature search into two broad categories of investigations: (1) How agricultural practices affect bat assemblages, ecology, behavior, and/or physiology; and (2) how bats affect agriculture through the provision of ecosystem services such as pollination and pest suppression. Within the first category, most studies addressed effects of land conversion and agricultural management on bat assemblage structure, abundance, activity levels, and behavior. We further subdivided results to consider habitat conversion to agriculture and agricultural intensification. We define agricultural intensification as consisting of at least one of the following: decreased structural complexity of native vegetation (natural and seminatural elements structuring the landscapes such as woodland patches and hedges), increased application of agrochemicals (pesticides, fertilizer), increased crop plant density, increased mechanization, or increased reliance on GM plants. We reviewed results from searches to locate studies which contrasted aspects of bat assemblage structure, abundance, activity, ranging behavior, or diet in either natural and agricultural habitat, or different agricultural systems of contrasting management.

To better quantify the responses of bats to habitat conversion and agricultural intensification across multiple disparate studies, we conducted a meta-analysis. We emphasize that this meta-analysis is based on correlational studies, rather than from controlled experiments; because assignment of treatment locations is not randomized in the majority of these studies, confounding factors could result in spurious effect sizes (Egger et al. 1998). We thus view our meta-analysis as a tool for exploring trends across a diverse suite of studies, with limited conclusive power.

We reviewed studies for the inclusion of mean values for at least one response variable in both natural and agricultural areas, or two or more agricultural areas of differing intensification; 32 studies using mist netting, harp trapping, acoustic monitoring, or a combination of these methods included appropriate data. We classify the response variable metrics into two separate categories for analyses, measures of species richness and measures of relative activity or abundance (i.e., pass rates from acoustic monitoring or capture rates from mist netting). We also consider habitat conversion and intensification responses separately.

For each pairwise comparison (natural–agricultural, or agricultural–agricultural), we calculated the effect size as the log odds ratio of the mean value from the lower intensity system divided by the mean from the higher intensity system. Thus, a positive effect size indicates higher species richness or activity/abundance in natural versus agricultural areas or lower intensity versus higher intensity agriculture. We followed García-Morales et al. (2013) and considered mean effect sizes with 95 % confidence intervals that did not include 0 as indicative of a significant effect. In the case of studies comparing multiple natural or agricultural habitats or presenting means for multiple species or species groups (i.e., producing multiple pairwise comparisons for any given combination of metric and response type), we averaged the odds ratio to avoid pseudo replication. Due to the diverse nature of the studies and a lack of clarity about numbers of replicates in some studies, we did not weight studies by sample size or replicates. For our analysis, we thus considered each study as an equally weighted case for the final model. We conducted analyses in R Version 3.0.2 (R Development Core Team 2013) using the packages lme4 and lmerTest. This diverse set of studies includes different methods (e.g., acoustic monitoring versus mist netting) from different regions with ecologically and taxonomically characteristic bat assemblages. To account for some of this variation, we included study method and continent as random effects. Fixed factors included latitudinal zone (temperate, subtropical, and tropical) and whether or not the high-intensity system comprised an agroforestry system (including monocultural orchards).

We also located several studies on ecotoxicology and demography, focusing on the effects of pesticide and GMOs use on bats. A complete review of the effects of pesticides on bats is beyond the scope of this chapter, particularly since bats and contaminants have received recent reviews (O'Shea and Johnston 2009; Bayat et al. 2014). We therefore focus on studies that explicitly link bat agrochemical exposure to changes in bat populations. Similarly, although fertilizers comprise a large portion of the chemical inputs to agriculture, their impacts on bats are indirect.

In considering the benefits of bats for agricultural production (i.e., crop yield), we focus on the provision of two ecosystem services: agricultural pest limitation by insectivorous bats and pollination by tropical bats. We did not consider their role as seed dispersers since human management of farmland vegetation limits the effect and value of bat seed dispersal. Similarly, although bat pollination is key for the unmanaged reproduction of several economically important crops, such as

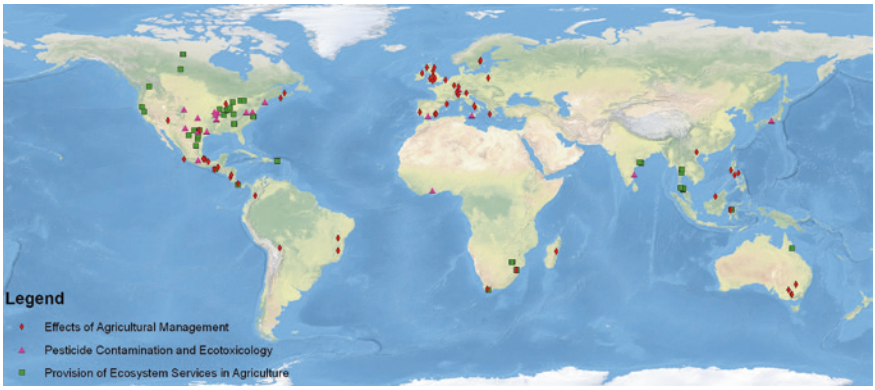

Fig. 6.1 Locations of studies on effects of habitat conversion or agricultural intensification (*red diamonds*) on bats, pesticide contamination (*pink triangles*) on bats, and ecosystem services (*green squares*) provided by bats in agriculture

bananas and agaves (Kunz et al. 2011), we did not consider these particular crops because they are mostly propagated vegetatively in such plantations. We instead focus on crops that are almost exclusively reliant on bat pollination under standard cultivation practices. Multiple investigations have characterized the diets of insectivorous bats at the order level, claiming potential consumption of pest insects. To more confidently assess consumption of insects damaging crops, we focused on studies in which known (species level identity) or probable (family level identity) agricultural pests were identified from feces of bats foraging in farms or areas dominated by agriculture. We exclude dietary studies that have sampled exclusively from natural habitats or do not describe the agricultural systems within which bats may have been foraging. We also briefly contrast these with ecosystem *disservices* of bats in agricultural areas. Bats are associated with costs to agriculturalists, particularly in the subtropics and tropics where frugivorous bats raid crops and sanguivorous bats attack domestic livestock. As with other sections, we focus on direct impacts on productive systems and do not consider the impacts of bat transmission of disease except where it directly impacts agriculture.

The majority of the nearly 140 investigations reviewed in this chapter have been conducted in temperate North America and Europe (Fig. 6.1). The bulk of studies documenting how habitat conversion or agricultural intensification affects bats has been conducted in Europe and the Neotropics (Fig. 6.1, Table 6.1). Within temperate zones, studies have focused mainly on annual cultivars and pasture, while research in tropical areas is dominated by studies on agroforestry systems, particularly coffee and cacao. Results on ecotoxicology of farmland bats come primarily from North America. Studies demonstrating the consumption of agricultural pests also derive primarily from North America, whereas studies of other ecosystem services provided by bats are limited to the tropics.

Table 6.1 Studies investigating the effects of agriculture on bat assemblage structure, ecology, or behavior across six continents

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
North America					
Braun de Torrez (2014)[a]	Temperate woodland savannah (mesquite-juniper)	Native and commercial pecan groves	General bat assemblage	≈ species richness, ↑ abundance, activity, habitat use	≈ species richness, abundance, activity, ↕ by species
Farrow and Broders (2011)	Boreal forest, temperate broadleaf forest	Mixed agricultural landscape	*Perimyotis subflavus*	↓ activity levels	
Gehrt and Chelsvig (2003)[a]	Temperate prairie, woodlands, and wetlands	"Intensive" agricultural landscape	General bat assemblage	↓ activity, habitat selection	
Henderson and Broders (2008)	Boreal forest, temperate broadleaf forest	Mixed agricultural landscape	*Myotis septentrionalis*	↓ mobility	
Rambaldini and Brigham (2011)[a]	Montane forest	Vineyards	*Antrozous pallidus*	↓ activity	
Tuttle et al. (2006)	Arid desert	Rangeland with troughs	*Myotis* spp., *Antrozous pallidus*		↓ drinking efficiency
Europe					
Arlettaz and Perrin (1995), Arlettaz (1996,1999), Arlettaz et al. (1997), 2001)	Temperate agricultural landscape within European Alps	Mixed farmland	*Myotis myotis, Myotis blythii*	↕ foraging habitat selection	↕ habitat use, ↓ dietary diversity
Bontadina et al. (2002)	Temperate agricultural landscape	Mixed farmland	*Rhinolophus hipposideros*	↓ foraging habitat selection	
Boughey et al. (2011)	Temperate agricultural landscape	Conventional farmland	*Pipistrellus* spp., *Nyctalus noctula*, *Eptesicus serotinus*		↕ activity
Davy et al. (2007)[a]	Mediterranean landscape	Olive groves	General bat assemblage	↓ activity	↓ activity

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Dietz et al. (2013)	Temperate agricultural landscape	Traditional farmlands (orchards, meadows, pastures)	*Rhinolophus ferrumequinum*, *Myotis emarginatus*	↑ habitat selection	↓ habitat selection
Downs and Racey (2006)	Temperate agricultural landscape	Mixed farmland with woodlands and hedges	*Pipistrellus* spp., *M. daubentonii*	↓ activity	↓ activity
Drescher (2004)	Temperate agricultural landscape	Apple orchards, vineyards, pastures	*Myotis myotis*	↑ foraging activity	↓ foraging activity
Ekman and de Jong (1996)[a]	Temperate agricultural landscape	Habitat islands within crop fields	*Myotis brandti*, *Eptesicus nilssoni*, *Plecotus auritus*, *Pipistrellus pipistrellus*	↓ activity, species occurrence	
Flaquer et al. (2008)	Mediterranean landscape	Olive groves, fruit orchards, rice	*Myotis emarginatus*	↑ foraging activity (olive groves)	↓ foraging activity (orchards, rice)
Frey-Ehrenbold et al. (2013)[a]	Temperate agricultural landscape	Seminatural to intensively managed farmland	General bat assemblage		↓ activity, species richness
Fuentes-Montemayor et al. (2011)	Temperate agricultural landscape	Conventional farmland and agri-environment scheme farmlands	*Pipistrellus* spp.		↑ activity
Fuller et al. (2005)[a]	Temperate agricultural/woodland landscape	Organic and non-organic cereals	General bat assemblage		↓ species density, activity
Jones and Morton (1992)	Temperate agricultural/woodland landscape	Hay/silage, grazing	*Rhinolophus ferrumequinum*		↓ activity
de Jong (1995)	Temperate agricultural landscape	Agriculture-dominated landscape	*Myotis* spp., *Pipistrellus pipistrellus*, *Plecotus auritus*	↓ activity	
Lesiński et al. (2013)	Temperate agricultural and woodlands	Annual crops (organic and conventional)	*Eptesicus serotinus*		↓ activity

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Lisón and Calvo (2011)[a]	Semiarid Mediterranean landscape	Rainfed olive/almond, irrigated peach/citrus	General bat assemblage	≈ activity	
Lisón and Calvo (2013)	Semiarid Mediterranean landscape	Rain fed crops/xerophytic vegetation	*Pipistrellus* spp.	↕ activity (varies by species)	
Lundy and Montgomery (2010)	Temperate agricultural landscape	Improved and unimproved pasture	General bat assemblage		↓ foraging activity
Obrist et al. (2011)[a]	Temperate agricultural landscape	Managed and abandoned chestnut orchards	General bat assemblage		↑ foraging activity
Pocock and Jennings (2007)[a]	Temperate agricultural landscape	Organic/conventional farmland; hay/silage fields	General bat assemblage		↓ activity (loss of linear features), ≈ activity (agrochemical use, silage)
Rainho (2007)	Semiarid Mediterranean landscape	Cereal crops and olive groves	General bat assemblage	↓ activity	↓ activity
Russ and Montgomery (2002)	Temperate agricultural landscape	Mixed farmland with woodlands, tree lines	General bat assemblage	↓ activity	↓ activity
Russo and Jones (2003)[a]	Mediterranean landscape	Traditional farmland habitats, chestnut woodland	General bat assemblage	≈ activity	
Russo et al. (2002)	Mediterranean landscape	Olive groves, traditional farmlands	*Rhinolophus euryale*	↑ home range composition, foraging time	
Stahlschmidt et al. (2012), Stahlschmidt and Brühl (2012)[a]	Temperate agricultural/woodland landscape	Apple orchard	General bat assemblage	↓ activity (*Pipistrelle*, *Eptesicus*), ≈ activity (*Myotis)*	

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Verboom and Huitema (1997)	Temperate agricultural landscape	Linear features in traditional farmland landscapes	*Pipistrellus pipistrellus*, *Eptesicus serotinus*		↓ activity
Walsh and Harris (1996a, b)	Temperate agricultural landscape	Mixed farmland	General bat assemblage	↓ activity	↓ activity
Wickramasinghe et al. (2003, 2004)	Temperate agricultural landscape	Organic and conventional farmland	General bat assemblage		↓ activity
Australia					
Fischer et al. (2010)	Temperate woodland/agricultural landscape	Low tree density livestock pasture	General bat assemblage		↓ activity
Hanspach et al. (2012)	Temperate woodland/agricultural landscape	Pasture with varying levels of tree cover	General bat assemblage	↕ activity, species richness (peaks at intermediate tree cover)	↓ activity, species richness
Lentini et al. (2012)[a]	Temperate woodland/agricultural landscape	Cereal, canola, and pasture-dominated landscape with and without linear features	Mollossidae; Vespertilionidae; Emballonuridae		↓ activity, ≈ species richness, feeding
Lumsden et al. (2002)	Temperate woodland/agricultural landscape	Fragmented human-dominated landscape	*Nyctophilus geoffroyi*, *Chalinolobus gouldii*	↕ roost locations	↓ roost locations
Lumsden and Bennett (2005)[a]	Temperate woodland/agricultural landscape	Pasture with varying densities of trees	General bat assemblage	↓ abundance, ↑ activity	↓ abundance, activity
Neotropics					
Avila-Cabadilla et al. (2009)	Tropical dry forest	Pasture	Phyllostomids	↓ abundance, species richness	
Castro-Luna and Galindo-González (2012)[a]	Tropical montane rainforest	Diverse and simplified shade coffee, pasture	Frugivorous phyllostomids		↓ abundance, species richness

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Estrada et al. (1993)	Lowland tropical rainforest	Shaded (coffee, cacao, mixed) and unshaded (citrus, allspice) plantations, pastures	Phyllostomids, non-phyllostomids sampled with mist nets	↓ species richness	↓ species richness
Estrada and Coates-Estrada (2001)	Lowland tropical rainforest	Shaded (coffee, cacao, mixed) and unshaded (citrus, allspice) plantation	General bat assemblage	↑ abundance, ↓ expected species richness	↓ abundance, expected species richness
Estrada and Coates-Estrada (2002)[a]	Lowland tropical rainforest	Coffee, cacao, citrus, banana, pasture	General bat assemblage	↑ abundance, ≈ species richness	
Estrada et al. (2004)[a]	Lowland tropical rainforest	Fencerows, citrus, pasture	Non-phyllostomids	≈ activity	↓ activity
Faria (2006)[a]	Brazilian Atlantic forest	Shade cacao in a forest dominant landscape	General bat assemblage	↑ abundance, species richness	
Faria et al. (2006)[a]	Brazilian Atlantic forest	Shade cacao in a cacao dominant matrix	General bat assemblage	≈ species richness	
Faria and Baumgarten (2007)[a]	Brazilian Atlantic forest	Shade cacao in two contrasting landscapes	General bat assemblage		↓ abundance, species richness
García Estrada et al. (2006, 2012)	Montane tropical rainforest	Shade coffee	Phyllostomids	≈ abundance, dietary diversity, ↓ species richness	≈ abundance, dietary diversity, species richness
Harvey et al. (2006)[a]	Tropical dry forest	High and low tree cover pasture	General bat assemblage	↓ abundance, species richness (frugivores, nectarivores)	↓ abundance, species richness (frugivores), ≈ abundance (nectarivores)
Harvey and González Villalobos (2007)[a]	Tropical humid forest, premontane wet forest	Cacao agroforest, banana agroforest, plantain monoculture	General bat assemblage	↕ abundance, species richness	↓ abundance, species richness

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Medellin et al. (2000)	Montane tropical rainforest	Cacao, oldfield, and corn	General bat assemblage	↑ abundance, ↓ species richness	↓ abundance, species richness
Medina et al. (2007)[a]	Tropical moist forest	High and low tree cover pasture	General bat assemblage	↓ abundance, species richness	↓ abundance, species richness
Numa et al. (2005)[a]	Tropical montane rainforest	Sun and shade coffee in contrasting landscapes	Phyllostomids	↑ abundance, ↓ estimated species richness	≈ estimated species richness (within landscape), ↓ estimated species richness (between landscapes)
Pineda et al. (2005)[a]	Tropical montane cloud forest	Shade coffee	General bat assemblage	↑ abundance, ≈ species richness	
Saldaña Vázquez et al. (2013)	Tropical montane rainforest	Shade coffee	*Sturnira ludovici*	↓ abundance, females	
Sosa et al. (2008)	Tropical montane rainforest	Shade coffee	General bat assemblage	≈ species richness	↓ abundance
Williams-Guillén and Perfecto (2010)[a]	Tropical montane rainforest	Shade coffee	Phyllostomids	↑ abundance, ≈ species richness	↓ abundance, ≈ species richness
Williams-Guillén and Perfecto (2011)[a]	Tropical montane rainforest	Shade coffee	Non-Phyllostomids	↓ activity (cluttered space foragers), ↑ abundance (open space foragers), ≈ species richness	↓ activity (cluttered space foragers), ↑ abundance (open space foragers), ≈ species richness
Vargas Espinoza et al. (2008)	Premontane tropical rainforest	Citrus orchards	General bat assemblage	≈ abundance, species richness	
Africa					
Noer et al. (2012)	Subtropical Savanna	Sugarcane	*Chaerephon pumilus*, *Mops condylurus*	↑ foraging time	

(continued)

Table 6.1 (continued)

Source	Biome/life zone	Agricultural system	Bat taxa assessed	Conversion response	Intensification response
Randrianandrianina et al. (2006)[a]	Tropical rainforest/ mixed use landscape	Smallholder gardens	General bat assemblage	↓ species richness, ↑ activity, foraging	
Sirami et al. (2013)[a]	Subtropical grassland, fynbos	Intensive wheat, vineyards, orchards	General bat assemblage	↓ abundance, ≈ species richness	↓ abundance, ≈ species richness
Taylor et al. (2013b)[a]	Subtropical Savanna	Macadamia	General bat assemblage	≈ activity (molossids), ↓ activity (vespertilionids)	
Asia					
Fukuda et al. (2009)[a]	Fragmented tropical rainforest	Orchards, palm oil	Hipposideridae, Vespertilionidae, Pteropodidae	↑ abundance, ↓ species richness	≈ abundance, ↓ species richness
Furey et al. (2010)[a]	Limestone karst, tropical rainforest	Landscapes dominated by rice paddies and degraded forest	Insectivorous bat assemblage		↓ abundance, ≈ species richness
Graf (2010)[a]	Montane tropical rainforest	Forest and shade cacao	General bat assemblage	↑ abundance, species richness	↓ species richness
Mildenstein et al. (2005)	Tropical moist forest	Fruit orchards and hardwood tree plantations	Pteropodidae bat assemblage	↓ habitat selection	
Sedlock et al. (2008)	Montane and premontane rainforest	Mosaic of pasture, root crops, orchards, and fallows	Insectivorous bat assemblage	↓ species accumulation	
Van Weerd and Snelder (2008)[a]	Tropical moist forest	Village homegarden polycultures, shrublands used for grazing	General bat assemblage	↑ abundance, species richness	↓ abundance, ≈ species richness

[a]Studies included in meta-analysis

"Conversion response" indicates effects of agriculture versus non-anthropogenic habitat; "intensification response" indicates effects of agricultural intensification (i.e., increased amount of agrochemicals, decreased structural complexity, infrastructure construction). "↓" indicates a negative effect on specified response variable; "↕" variable effects depending on species, ensemble, or habitat contrast; "≈" no marked effects observed; "↑" positive effect on response variable

6.3 Effects of Agricultural Intensity on Bat Assemblage Structure, Behavior, and Ecology

We found 70 studies addressing the effects of habitat conversion or management on the assemblage structure, behavior, or ecology of bats. Fifty-two studies assessed bats in both natural and agricultural areas. Twenty-two studies (42 %) demonstrated negative effects of habitat conversion, twelve (23 %) showed variable responses (e.g., only some species or ensembles declined, different agricultural systems were associated with different effects), twelve (23 %) showed increased richness, activity, or abundance in agricultural areas, and six (12 %) showed little or no difference between agricultural and natural areas. Forty-five studies addressed some aspect of agricultural intensification, with 38 of these (84 %) documenting a negative effect of intensification on bats, four showing variable or neutral (9 %) responses, while three studies (7 %) documented increases in bat richness, abundance, or activity in more intensive systems.

Response variables differ in response to habitat conversion and agricultural intensification (Fig. 6.2, Table 6.2), with measures of species richness showing no significant change between treatments. In contrast, measures of relative activity and abundance show stronger responses (Fig. 6.2). Agroforestry systems are more structurally similar to the original non-anthropogenic land uses, making them less intensive than annual crops dominated by one plant species or pasture systems lacking structural complexity. This relationship presumably explains why agricultural systems that incorporate trees and other large woody perennials on farms and throughout the agricultural landscape have little effect on bat activity and abundance (Fig. 6.2). Agroforestry systems appear to mitigate negative effects on bat assemblages in cases of both habitat conversion and agricultural intensification (Table 6.2).

Several studies have considered the effects of agricultural management at landscape scales versus focusing exclusively on farm-level management practices (Estrada et al. 1993; Ekman and de Jong 1996; Verboom and Huitema 1997; Numa et al. 2005; Faria et al. 2006, 2007; Faria and Baumgarten 2007; Fuentes-Montemayor et al. 2011; Boughey et al. 2011; Maas et al. 2013). Within agricultural areas, bat activity increases with proximity to natural areas (Estrada et al. 1993; Verboom and Huitema 1997; Boughey et al. 2011) and in less fragmented landscapes (Fuentes-Montemayor et al. 2011; Frey-Ehrenbold et al. 2013) or in landscapes with more natural elements such as hedgerows and woodlots (Verboom and Huitema 1997).

Agricultural areas also serve as matrix habitat connecting fragmented non-anthropogenic habitats. Although one study has suggested that landscapes dominated by crops and open fields have a stronger negative influence on bats than water (Ekman and de Jong 1996), a recent analysis of bat responses to isolation on islands versus in forest fragments embedded in agricultural matrix suggests that the anthropogenic matrix is more permeable than water matrix (Mendenhall et al.

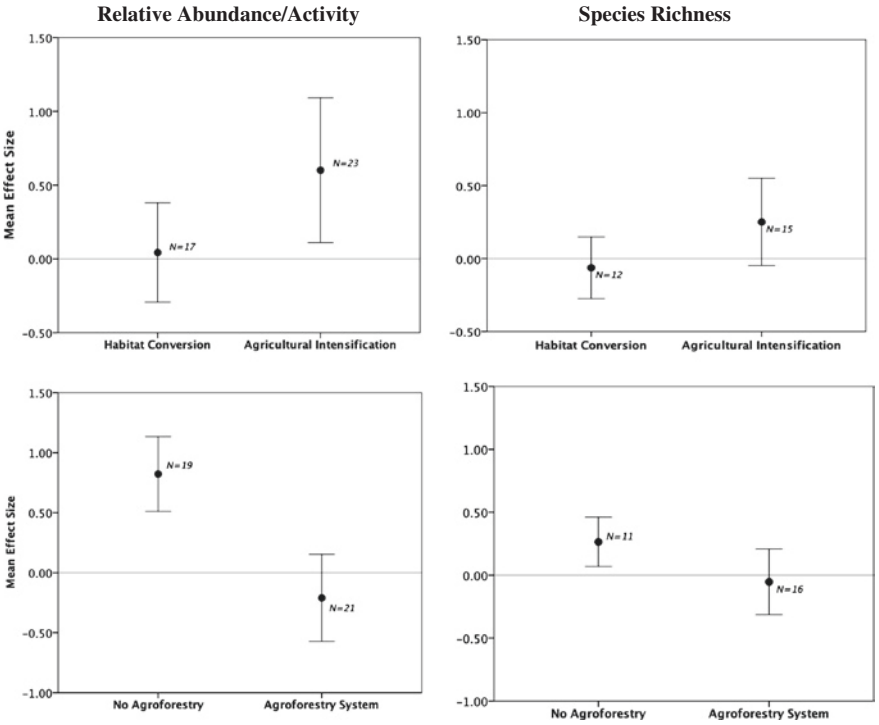

Fig. 6.2 Mean effect size (log odds ratio, circles) ±95 % CI of relative abundance and activity (*left*) and species richness (*right*) of habitat conversion versus agricultural intensification (*top row*), and of contrasts (both habitat conversion and agricultural intensification) with and without agroforestry systems (*bottom row*). Positive effect sizes indicate reductions in relative abundance and activity or species richness in response to habitat conversion and intensification

2014). Thus, agricultural intensification at the landscape level should make the matrix less permeable due to the reduction of natural resources and structural elements such as trees, affecting not only the persistence of bats in fragmented landscapes, but *also* the degree to which bat assemblages show a negative response to agriculture. A few investigations have confirmed such interactions between farm- and landscape-level intensification: Intensification in cacao matrices in Brazil (Faria et al. 2006, 2007; Faria and Baumgarten 2007) and coffee matrices in Colombia (Numa et al. 2005) resulted in reductions in the species richness and abundance of bats in diverse shade agroforests relative to forest fragments. In Europe, effects of landscape management on bat assemblage structure and ecology in temperate landscapes dedicated to the production of annual crops remain largely unexplored compared to the extensive information available at the field and farm scales.

Table 6.2 Effects of latitudinal zone and agroforestry systems on effect size (log odds ratio) for two response variable types under habitat conversion and agricultural intensification

Response variable	Land change type	Model	AIC	χ^2	*P*
Abundance/ activity	Habitat conversion	Effect size ~ (Method) + (Continent)	60.7		
		Effect size ~ Agroforestry + (Method) + (Continent)	**49.7**	**13.00**	**<0.001**
		Effect size ~ Latitude + (Method) + (Continent)	62.0	0.00	1.000
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	51.9	12.15	<0.001
	Intensification	Effect size ~ (Method) + (Continent)	52.4		
		Effect size ~ Agroforestry + (Method) + (Continent)	**49.2**	**5.22**	**0.022**
		Effect size ~ Latitude + (Method) + (Continent)	53.6	0.00	1.000
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	50.6	4.923	0.026
Species richness	Habitat conversion	**Effect size ~ (Method) + (Continent)**	**20.7**		
		Effect size ~ Agroforestry + (Method) + (Continent)	21.7	0.99	0.319
		Effect size ~ Latitude + (Method) + (Continent)	24.0	0.00	1.000
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	24.1	1.82	0.178
	Intensification	**Effect size ~ (Method) + (Continent)**	**22.9**		
		Effect size ~ Agroforestry + (Method) + (Continent)	24.4	0.54	0.460
		Effect size ~ Latitude + (Method) + (Continent)	26.3	0.06	0.806
		Effect size ~ Agroforestry + Latitude + (Method) + (Continent)	27.0	1.34	0.248

Parentheses indicate random effects, and *bold text* indicates best fitting model based on AIC value

6.4 Pesticide Impacts on Bat Populations

Agricultural intensification may remove potential habitat for bats and their prey; the effects of increased agrochemical inputs, such as increased exposure and changes in prey availability, may put resident bats under further pressure.

Bats may directly consume pesticides by feeding on fruits, flowers, and arthropods exposed to chemical application. Even bats foraging outside of agricultural areas can be exposed to pesticides via biomagnification as residues are incorporated into the tissues of organisms at higher trophic levels (Bayat et al. 2014).

Investigations of exposure of bats to pesticides and its effects on physiology and mortality first appeared in the 1970s, amid a wave of growing concern regarding the effects of organochlorine pesticides (e.g., DDT, DDE, dieldrin, lindane, endosulfan, aldrin) on ecosystems and observations of declining bat populations at high-profile sites such as the Carlsbad Caverns in New Mexico, USA (Clark 1988, 2001). In some cases, DDT and other organochlorines were even applied directly to bat roosts in efforts to exterminate "vermin" (Kunz et al. 1977), and declines in high-profile bat colonies were linked to organochlorine use (Clark et al. 1978; Clark 2001). Even sublethal exposure to pesticides can have negative consequences for bats, resulting in increased metabolic rates (Swanepoel et al. 1998), and ingestion of pesticide residues on arthropods may poses a potential reproductive risk to certain bat species (Stahlschmidt and Brühl 2012).

Organochlorine residues have been documented in bats in a wide variety of both agricultural and non-agricultural landscapes, although several studies have found increased contaminant loads in bats sampled near agricultural areas (Clark and Prouty 1976; White and Krynitsky 1986) or near sites of pesticide manufacture (O'Shea et al. 2001). In some cases, temporal changes in levels of different contaminants reflect shifts in local agricultural practice as farmers adopt new pesticide regimes (Miura et al. 1978; Clark et al. 1980). Organochlorines are notorious for their persistence in ecosystems, and a variety of studies demonstrate that bats continue to harbor these contaminants in their tissues 20–30 years after the use of these pesticides was banned in sampling areas (Clawson and Clark 1989; Guillén et al. 1994; Schmidt et al. 2000; Sasse 2005). In some cases, persistence may reflect the continued use of these pesticides in lower income nations, as may be the case for the migratory *Tadarida brasiliensis* (Thies and Thies 1997; Bennett and Thies 2007). Investigations in India (Senthilkumar et al. 2001) and Benin (Stechert et al. 2014) have detected levels or metabolites of organochlorines in bat samples indicative of continued recent use in these regions, especially to fight against malaria. Furthermore, pesticide standards vary between different countries, application often appears to occur non-selectively, and farmers with limited training (especially in developing countries, where agricultural expansion is greatest) are likely to be unaware of the multitude of negative nontargeted environmental impacts affecting human health and biodiversity (Tilman et al. 2001; Yadav 2010).

Despite the clear negative impacts of organochlorines on bats, the effects of agrochemical classes such as pyrethroids and neonicotinoids remain largely unknown (O'Shea and Johnston 2009; Quarles 2013; Bayat et al. 2014), although

recent research demonstrates a negative impact on birds (Hallmann et al. 2014). In North America, pesticide contamination has been implicated in bat mortality associated with the fungal pathogen causing white-nose syndrome (WNS), since pesticide load can lead to immunosuppression and endocrine disruption that could make bats more vulnerable to infection (Kannan et al. 2010). "Back of the envelope" calculations suggest declines in bat populations attributed to WNS could translate into an additional 1320 metric tons of insects escaping predation each year (Quarles 2013). The trickle-down impacts on agricultural production could be substantial, although quantitative evidence is lacking. The effects of GM crops incorporating insecticidal traits have been investigated largely in the context of the provisioning of predation services (Federico et al. 2008; Lopez-Hoffman et al. 2014; see next section); however, declines in pest numbers associated with the use of these crops could result in population declines of insectivorous bats (Lopez-Hoffman et al. 2014).

6.5 Ecosystem Services Provided by Bats in Agricultural Systems

6.5.1 Insectivorous Bats and Pest Limitation

Of the potential ecosystem services provided by bats, their role in consuming insect pests has received the most attention within agricultural systems. Insectivorous bats have a global distribution and have long been identified as key suppressors of arthropod pests in agricultural systems (Kunz et al. 2011). However, surprisingly little evidence exists quantifying the impact of their predation on arthropod populations, plant damage, or its economic value (Boyles et al. 2013; Maas et al. 2013). Several studies have characterized diets of insectivorous bats (reviewed by Kunz et al. 2011), and the recent development of DNA-based methods for dietary analysis provides an unprecedented amount of detail on the composition of bat diets and allows for the identification of individual pest species. Although few studies have documented direct impacts of bat predation on agricultural pests, an increasing body of evidence documents pest consumption, impacts on arthropods, and estimates of direct economic impacts.

We review 15 studies documenting the consumption of known or probable crop pests by insectivorous bats (Table 6.3). The diets of temperate North American insectivores have received particular attention. Many bat species consume lepidopterans, and studies in North America demonstrate bat predation on devastating pests such as corn earworm (*Helicoverpa zea*) and fall armyworm (*Spodoptera frugiperda*) moths (Lee and McCracken 2005; McCracken et al. 2012). Bat species across the world feed on folivorous beetles from a variety of damaging families

Table 6.3 Dietary investigations of insectivorous bat in agricultural areas documenting consumption of pest insect families or species

Study region	Source	Bat species	Crop	Pest insects consumed
Africa (South Africa)	Taylor et al. (2012, 2013a)	Various species	Macadamia nuts	• Hemiptera: *Nezara viridula*
Africa (Swaziland)	Bohmann et al. (2011)	*Chaerephon pumilus*, *Mops condylurus*	Sugarcane	• Hemiptera: Aphidadae, Lygaeidae, Pentatomidae • Lepidoptera: *Eldana saccharina*, *Mythimna phaea*
Asia (Thailand)	Leelapaibul et al. (2005)	*Chaerephon plicatus*	Rice	• Hemiptera: *Sogatella* sp.
Europe (Switzerland)	Arlettaz and Perrin (1995, 1997, 2001)	*Myotis myotis*, *M. blythii*	Agricultural landscape with orchards, pasture	• Coleoptera: *Melolontha* sp.
Latin America (Mexico)	Williams-Guillén (unpublished data)	Various species	Shade coffee	• Coleoptera: *Hypothenemus hampeii*, *Rhabdopterus jansoni* • Orthoptera: *Idiarthron subquadratum*
North America (Canada)	Clare et al. (2011)	*Myotis lucifugus*	Agricultural landscape	• Coleoptera: *Phyllophaga* spp., *Amphimallon majale*, *Phyllobius oblongus*; Curculionidae, Chrysomelidae • Diptera: *Delia antiqua* • Hemiptera: Aphididae • Lepidoptera: *Korscheltellus lupulina*
North America (Canada)	Rambaldini and Brigham (2011)	*Antrozous pallidus*	Grapes	• Coleoptera: Curculionidae, Tenebrionidae • Orthoptera: Acrididae
North America (USA)	Braun de Torrez (2014)	Various species	Pecan	• Lepidoptera: *Acrobasis nuxvorella*

(continued)

Table 6.3 (continued)

Study region	Source	Bat species	Crop	Pest insects consumed
North America (USA)	Lee and McCracken (2005)	*Tadarida brasiliensis*	Landscape with corn and cotton	• Coleoptera: Scarabaeidae • Hemiptera: Cercopidae, Delphacidae, Pentatomidae • Lepidoptera: *Spodoptera frugiperda, Helicoverpa zea*
North America (USA)	McCracken et al. (2012)	*Tadarida brasiliensis*	Corn, cotton	• Lepidoptera: *Helicoverpa zea*
North America (USA)	Storm and Whitaker (2008)	*Eptesicus fuscus*	Agricultural landscape	• Coleoptera: Curculionidae • Hemiptera: Cicadelidae
North America (USA)	Whitaker (1995)	*Eptesicus fuscus*	Agricultural landscape	• Coleoptera: Curculionidae, Scarabaeidae • Hemiptera: Cicadellidae, Pentatomidae

and species, particularly weevils, leaf beetles, and scarab beetles. Bats may also be underappreciated predators of hemipteran pests, with many studies demonstrating consumption of leafhoppers, froghoppers, spittle bugs, and stink bugs. We emphasize that direct consumption alone is not sufficient to prove that bats are limiting insect pests: Damaging insects may comprise a small proportion of the diet, and nearly every study summarized in Table 6.3 also demonstrated consumption of the predatory arthropods that comprise part of the assemblage of natural enemies. Such intraguild predation could counteract the pest-limiting effects of bat insectivory (Brashares et al. 2010), although herbivores generally comprise the majority of diet by volume in investigations using fecal pellet dissections (Kunz et al. 2011). That the relative abundance, diets, and movements of bats may track populations of agricultural pests (Lee and McCracken 2005; McCracken et al. 2012; Taylor et al. 2013b) suggests that many species are indeed preying heavily on herbivorous insects. This has been assessed in mouse-eared bats, *Myotis* spp., that track cyclic, massive local aggregations of cockchafers known since centuries for the damages they cause to fruit trees in Central Europe (Arlettaz 1996; Arlettaz et al. 2001).

During lactation, small bat species consume 75 % to over 100 % of their body weight each night (Kurta et al. 1989; Kunz et al. 1995, 2011), and a single maternity colony of 1 million Brazilian free-tailed bats is capable of consuming over 8 tons of insects per night (Kunz et al. 2011). These numbers suggest the staggering potential for bat predation to limit pest insect

populations and provide a valuable ecosystem service for agricultural production. Until recently, surprisingly little work had quantified the impact of bat predation on insect biomass (Maas et al. 2015). Exclosure studies have long been a mainstay for studying the impacts of bird predation; however, it was widely assumed that such methods would not be suitable to measure the impact of bat insectivory, due to the misconception that all insect eating bats take highly mobile, flying prey. However, bats capable of gleaning insect prey from substrates exist throughout the world, and their impacts could be monitored via exclosure studies and disentangled from those of birds. This approach has been used fruitfully in the past five years, demonstrating significant increases in arthropod density when bats are absent, in agroecosystems (Williams-Guillén et al. 2008; Maas et al. 2013), reforestation (Morrison and Lindell 2012), and natural forests (Kalka et al. 2008). In Mexican polycultural shade coffee, arthropod densities on coffee plants during the rainy season nearly doubled in the absence of bats, with marked increases in densities of hoppers, katydids, cockroaches, and beetles (Williams-Guillén et al. 2008). However, no effects on plant damage were observed in that study, perhaps as a result of the short duration of the study or release of spiders and other arthropod predators. In Indonesian shade cacao, excluding bats resulted in a 29 % increase in arthropod numbers (Maas et al. 2013). Although herbivory did not differ significantly between cacao plantations with different levels of shade or proximities to primary habitats within the landscape, exclosure of bats resulted in a significant decrease in yields, with the effects of bird and bat predation together valued at an astonishing US $730 per ha and year (bat predation was valued at US $520 per ha and year). However, the effects of bat predation on crop pests are not universal: An exclosure study in Costa Rican coffee found that excluding bats alone had virtually no effect on the density or damage caused to beans by the devastating coffee berry borer (Karp et al. 2013).

Exclosure studies are not suitable to measure the impact of high-flying insectivores, such as molossids. However, careful extrapolations taking into account bat feeding rates, population sizes, pest reproduction, and survivorship, and the costs of inputs allow for estimation of the economic impact of predation for other bats, particularly molossids forming large colonies. Cleveland et al. (2006) estimate that Mexican free-tailed bats (*T. brasiliensis*) feeding on the cotton bollworm moth in Texas provide pest limitation services worth roughly US $183 per ha and year to cotton growers. Extending these estimates to agricultural areas throughout the USA suggests that bat predation could have a value of nearly US $23 billion annually (Boyles et al. 2011). These benefits hold for both conventional and transgenic cotton (Federico et al. 2008), although the introduction of *Bt* cotton (a genetically modified organism whose tissues produce an insecticide derived from the bacterium *Bacillus thuringiensis*), coupled with reduced area in cotton cultivation, has led to a decline in the overall value of this pest limitation service (Lopez-Hoffman et al. 2014).

Valuation of bat-mediated pest suppression is limited for staple crops and for sites outside the southern USA. In northern Mexico, the impact of *T. brasiliensis* predation on avoided agricultural costs across a variety of staple and commodity crops was estimated at a far more modest $19 per ha and year (Gándara Fierro et al. 2006). In Thailand, the value of wrinkle-lipped bat (*Tadarida plicata*) predation on a major rice pest, the white-back planthopper (*Sogatella furcifera*), was estimated to have a monetary value of $1.2 million annually (Wanger et al. 2014). This estimate results in a seemingly paltry $0.13 per ha and year value considered against Thailand's 8.7 million ha (Redfern et al. 2012) of rice paddies, but in this case an economic approach obscures the true value of the service: This single bat species prevents the loss of nearly 2900 metric tons of rice per year, enough to feed Thailand's entire population of 66.8 million people for a week. Such investigations underscore the potentially grave consequences for human food security should global bat populations continue declining (Kunz et al. 2011).

6.5.2 Nectarivorous Bats and Pollination Services

Pollination services to crops by bats are poorly documented. Bats are key pollinators of wild *Agave* and *Musa* spp. (Kunz et al. 2011). Although these plants are propagated vegetatively under cultivation, bat pollination plays a critical role in sustaining genetic diversity in the wild relatives of these domestic species, a key aspect of maintaining future food security (Hopkins and Maxted 2011). Within the Americas, several bat pollinated cacti are commercially important fruit species (Kunz et al. 2011). Several species of the hemiepiphytic cactus *Hylocereus* (pitahaya, dragonfruit) endemic to the Neotropics are now cultivated worldwide. In Mexico, visitation of *Hylocereus undatus* fruits by bats resulted in significantly higher fruit set than did visitation by diurnal pollinators (Valiente-Banuet et al. 2007). Although *H. undatus* is self-compatible, other species such as *H. costaricensis* (an important fruit crop in southern Mesoamerica) apparently rely on pollination by bats and sphingid moths (Weiss et al. 1994; Le Bellec et al. 2006). Nectarivorous bats, particularly the cave nectar bat (*Eonycteris spelaea*) feed on the flowers of tree beans or petai (*Parkia* spp.) (Bumrungsri et al. 2008a, b, 2013) and durian (*Durio zibethinus*) (Bumrungsri et al. 2008b), pollinating these plants in the process. The economic value of this pollination has been estimated at over US $13 million annually in three provinces of Thailand (Petchmunee 2008).

6.6 The Issue of Ecosystem Disservices of Bats to Agricultural Production

Unfortunately, while the ecosystem services provided by bats are largely invisible, their disservices are obvious. In the Paleotropics, crop raiding by frugivorous pteropodids can cause substantial losses of commercial fruits (see Aziz et al., Chap. 12). For example, in Indian vineyards, *Cynopterus sphinx* damages up to 90 % of the crop along peripheries of plantations and may cause revenue losses of up to US $590 per ha and year (Srinivasulu and Srinivasulu 2002). In the Neotropics, sanguivorous vampire bats can cause substantial economic damage: Estimates for 1968 placed losses at $47.5 million USD for over 512,000 rabies-related cattle deaths in Latin America (Arellano-Sota 1988). Harassment by vampire bats can put cattle off their feed, resulting in annual weight losses estimated at roughly 40 kg/head and milk production loss of 261 L/head (Schmidt and Badger 1979). These estimates fail to take into account the effects of vampire bats on the medium and small domestic animals (e.g., chickens, pigs, goats) that provide critical sources of animal protein for millions of smallholder farmers across the region.

Not surprisingly, farmers with first-hand experiences of economic losses engendered by bats are more likely to have negative attitudes or report a willingness to destroy bat roosts (Reid 2013). Failure to explicitly address the negative impacts of some bat species likely reduces the efficacy of conservation messages; meanwhile, practical measures to reduce these disservices could benefit multiple bat species by reducing indiscriminate persecution. Different functional groups provide most of the ecosystem services (insectivores, nectarivores) and disservices (frugivores, sanguivores). However, local farmers may not distinguish between these groups. For example, farmers and agricultural technicians in Latin America often attempt to cull vampire bat populations by destroying bat roosts; unfortunately, the widespread belief that all bats are "*vampiros*" frequently results in the destruction of colonies of beneficial bat species (Mayen 2003; Aguiar et al. 2010). If local people perceive the ecosystem services of one bat group as offsetting the damages of another, then an ecosystem service approach could provide a framework for bat conservation more broadly. Unfortunately, the extent to which knowledge of ecosystem services changes attitudes toward bats in developing countries remains unknown.

6.7 Discussion

Our review suggests that in all biogeographic regions investigated, at least some bat species persist in and exploit agricultural areas. In many agricultural systems (e.g., tropical agroforestry or historical landscapes of Europe), bat assemblages

maintain richness and may even exceed abundances observed in unmanaged areas. Nevertheless, agricultural intensification has a generally negative effect on bats and thus presumably on the ecosystem services they provide. Our analysis did not address differences between bat taxa in their sensitivity to habitat change and intensification. However, evidence from speciose assemblages suggests that forest-adapted insectivorous species are particularly sensitive to habitat conversion (Medellin et al. 2000; Faria and Baumgarten 2007; Williams-Guillén and Perfecto 2010), implying that in some regions, this valuable ecosystem service could be particularly vulnerable to loss in the face of habitat loss.

Although few investigations have considered the scale of intensification, limited information suggests that less managed systems embedded in regions dominated by intensive agriculture may show depauperate bat faunas (Numa et al. 2005; Faria et al. 2007). Declines in bat populations in agricultural regions are concerning not only from the point of view of biodiversity conservation but also regarding human well-being and food security, especially in many tropical areas where smallholder farming systems are dominant. Ongoing losses of these generalist vertebrate predators could have major impacts on insect pest limitation for a wide variety of staple and commodity crops. However, the smallholder farmers in developing nations who most depend on the ecosystem services provided by bats (due to limited access to manufactured inputs or cultivation of bat pollinated crops) may have highly negative attitudes toward these mammals as a result of visible damages caused to crops and livestock (López del Toro et al. 2009; Reid 2013), whereas beneficial impacts on crop yield productivity and the value of biodiversity (i.e., increased ecosystem resilience) are often unknown or unappreciated (Williams-Guillén, unpublished data). These results suggest a pressing need to reassess common approaches to conservation and agricultural management in the Anthropocene.

6.7.1 Sparing, Sharing, and the Devaluation of Manufactured Capital

Given the anticipated need to nearly double global food production in the twenty-first century, a vigorous debate has emerged with respect to the most viable path to increase production without degrading ecosystem services or reducing biodiversity: land sparing, which posits that increased intensification and yields will reduce pressure to convert non-agricultural lands, versus land sharing, in which agricultural areas are less intensively farmed in order to increase associated biodiversity and habitat permeability (Fischer et al. 2008). Given the vagility and critical role of bats in agricultural production, land sharing approaches might be preferable with respect to the provision of bat-dependent ecosystem services. Many sensitive bat ensembles and species (e.g.,

many forest-adapted and insectivorous species, e.g., from Phyllostomidae or Vespertilionidae) will require well-structured farmland, i.e., cultivated landscapes including patches of natural and seminatural features for their long-term existence. However, not only do many bat species thrive in diverse agricultural landscapes, but also their loss could affect the provision of pest suppression and pollination services and result in reduced crop productivity. Given the many disadvantages of chemical control of pests, managing agricultural landscapes to maximize the abundance and diversity of bats and other natural enemies must form a key aspect of sustainable agricultural production. However, the design and management of such systems to maximize bat diversity, activity, and ecosystem services is largely unknown, although European conservationists are at the forefront with their strategies to promote biodiversity-friendly farming.

Chemical and mechanical inputs are not the only tools of agricultural intensification. Within recent decades, genetic modification of crops (e.g., *Bt* corn and cotton) has become increasingly prevalent (James 2011). In the short term, adoption of such varieties does reduce the need to rely on bats and other predators for pest limitation (Lopez-Hoffman et al. 2014), resulting in a "devaluation" of the natural capital provided by bats, and undermines arguments for bat conservation that are based exclusively on provision of ecosystem services. However, as is the case with pesticides, insects are rapidly evolving resistance to *Bt* crops across the world, resulting in a rapid devaluation of *manufactured* capital (Lopez-Hoffman et al. 2014). While the value of bats' natural capital may fluctuate, it likely devalues far less slowly: Bats and insects are engaged in an evolutionary arms race dating back millions of years (Conner and Corcoran 2012). Without bats to buffer the inevitable loss of efficacy of chemical inputs and GM crops, the technological advances that make agricultural intensification possible leave production vulnerable to potentially catastrophic failures to limit pest damage.

6.8 Research Priorities

6.8.1 Filling in Biogeographical Knowledge Gaps

Although the effects of habitat conversion and management have been well investigated in Europe and the Neotropics, the extent to which these processes may differ in other regions of the world remains unknown. We highlight a particular lack of knowledge from Africa and Asia; we did not find any studies from East Asia, although we suspect information exists in the Chinese language literature. Understanding the types and magnitudes of ecosystem services provided by bats in a variety of agricultural systems and regions is particularly important.

6.8.2 Linking Farm Management, Ecosystem Services, and Landscape-Level Processes

The effects of farm-level management on biodiversity and ecosystem services cannot be adequately considered without taking account of landscape-level processes (Tscharntke et al. 2005; Vickery and Arlettaz 2012). Nevertheless, the extent to which local- and landscape-level management interact to shape pest suppression or pollination services is largely uninvestigated. The effect of bats in limiting arthropod pests in agricultural areas is still poorly documented. However, the limited data that exist can demonstrate a vexing degree of divergence in results. For example, bats in Mexican shade coffee have substantial effects on herbivorous insects (Williams-Guillén et al. 2008), while bats in Costa Rican shade coffee had no significant effect on herbivores (Karp et al. 2013). In Indonesian cacao agroforestry systems, insectivorous bats strongly contribute to the suppression of many different pest insect groups and crop yield productivity across gradients of local shade-tree management and forest proximity within the agricultural landscape (Maas et al. 2013). In general, the study sites differ in landscape structure and land use, local farm history and management, habitat dynamics and conversion, intensity of farming practices, and vertebrate insectivore assemblage structure. Elucidating the factors of bat ecosystem service provision is key to managing agricultural areas to sustain bat populations and enhance food production (Maas et al. 2015).

6.8.3 Pest Suppression in the Face of Climate Change, Pesticides, and GM Crops

Not only will warming climates lead to shifts in the areas suitable for agricultural production, but it will also likely lead to range expansions of tropical pests, increases in pest numbers and damage, with a parallel risk of a drop in the efficacy of pest suppression by natural enemies that might be negatively affected by climate change (Thomson et al. 2010; Bebber et al. 2013). Such changes will make the ecosystem services provided by generalist predators like insectivorous bats more valuable than ever before. However, if agricultural adaptation to climate change relies on landscape-level intensification as a strategy, bats are likely to decline further, reducing their provision of pest suppression services. Despite the myriad negative effects of pesticides (i.e., affecting livelihoods, food security, environment, and health; reviewed by Yadav 2010), farmers across the world might turn to agrochemicals as a first response to increases in pest damage (Wilson and Tisdell 2001), with the Old World's rapid development of more environmentally friendly farming practices appearing as an exception in this general move. As reviewed in this chapter, older pesticide classes such as organochlorines

have particularly detrimental effects on bat populations. However, the degree to which newer pesticide classes affect bats is largely unknown. The neonicotinoids, once touted for their low toxicity, have now been linked to major declines in bees (Van der Sluijs et al. 2013) and more recently in several species of passerines as a result of insect resource depletion (Hallmann et al. 2014). The extent to which use of next-generation pesticides and GM crops is driving and interacting with bat declines and resultant increases in pest damage is a critical research area.

6.8.4 Quantifying Impact and Value Across Crops and Biomes

Additional valuation of bats' ecosystem services could provide both guidance for bat management priorities in agricultural areas and compelling rationales for conservation. However, valuation efforts have focused almost exclusively on commodity crops quantified along the single dimension of monetary value. Most of the world's smallholder farmers focus on staple crop cultivation and may not have the means to substitute the manufactured capital of pesticides and GM crops for bat predation. As Wanger et al. (2014) demonstrate, valuation based on dollars of damage prevented misses many of the criteria most important to subsistence farmers seeking food security. There is an urgent need to better understand the importance of bat ecosystem services across a variety of crop types, regions, and management approaches. Research also highlights the importance of better quantifying the fluctuations in bat service provision across years and seasons, in relation to population fluctuations, reproductive phenology, and agricultural management (Lopez-Hoffman et al. 2014; Wanger et al. 2014; Maas et al. 2015). This level of local, nuanced knowledge is key to managing pest suppression services in such a way that they are actively used as alternatives to agrochemical inputs and GM crops, and to contribute to more biodiversity-friendly and sustainable land-use practices (Tilman et al. 2002; Maas et al. 2015).

6.8.5 Changing Attitudes and Behaviors Toward Bats in the Developing World

Although the conservation of tropical biodiversity is highly beneficial to global society (Rands et al. 2010), ultimately it is the attitudes and beliefs of farmers and other rural populations that will determine its fate (Brechin et al. 2002; Tscharntke et al. 2012). Throughout the world, bats are subject to misconceptions and poor public perceptions (see Kingston and Barlow, this volume Chap. 17). However, exposure to environmental education can significantly

decrease negative attitudes toward bats (López del Toro et al. 2009; Prokop et al. 2009; Reid 2013). These results suggest that reducing bat disservices, conducting environmental education, and building local valuation of beneficial bats could work in concert to improve conservation outcomes. As much as there is a critical need to manage agricultural landscapes to conserve bats, there is a parallel need to understand the local drivers of attitudes toward bats and to develop culturally appropriate, evidence-based interventions that encourage farmers to sustainably manage bat populations and other biodiversity associated with ecosystem services and ecosystem resilience.

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