Effects of Farmland Heterogeneity
on Bat Species Richness and Activity
in Agricultural Eastern Ontario

by

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Abstract

The effects of semi-natural habitat amount in agricultural landscapes on bat species richness and activity levels are well documented, however the way crops are arranged (configurational heterogeneity) or their diversity (compositional heterogeneity) may also influence bat communities. Smaller field sizes should increase both the accessibility and quality of foraging habitat. Increased diversity of crop types may benefit bats by creating more diverse, abundant, and temporally stable communities of prey insects. We conducted acoustic surveys in agricultural landscapes in Eastern Ontario to test predictions that bat species richness and activity should increase with increasing compositional and configurational heterogeneity of crops. Field size appeared to have mixed effects on bat activity levels across species while total bat activity and activity of several species (*Lasiurus noctivagans*, *L. cinereus*, *Myotis septentrionalis*, and *Eptesicus fuscus*) was higher in landscapes with higher diversity of crops. We hypothesize this is because diverse crops create more temporally stable prey communities.

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1. Introduction

Agriculture constitutes approximately 40% of land cover worldwide (Foley et al. 2005) and hence represents significant potential habitat for species that are able to survive in and use agricultural areas or the semi-natural habitats associated with them (Benton et al. 2003, Tschardt et al. 2005). These areas can support native plants (e.g. Boutin et al. 2008), insects (e.g. Wickramasinghe and Harris 2004, Marini et al. 2009) and other invertebrates (e.g. Sunderland and Samu 2000, Boschi and Baur 2007, Leslie et al. 2012), mammals (e.g. Michel et al. 2006, Pocock and Jettnings 2008, Boughey et al. 2011), birds (e.g. Chamberlain et al. 2000, Harvey et al. 2006, Garfinkel and Johnson 2015), fish (e.g. Colvin et al. 2009, Chester and Robson 2013), reptiles (e.g. Klug et al. 2010, Rotem et al. 2013) and amphibians (e.g. Attademo et al. 2005, Chester and Robson 2013). Some native species may use only semi-natural habitat within agricultural areas, while others may use crops or a mixture of crops and semi-natural area as habitat.

Farming practices within agricultural areas may influence a landscape's ability to support higher abundances or diversity of different taxa (Björklund et al. 1999, Wickramasinghe et al. 2003, Fuller et al. 2005, Fahrig et al. 2015). Within Canada, approximately 30.2% (19.6 million hectares) of total farm area is recognized as semi-natural habitat (i.e. woodlands, wetlands, and natural pastures), and a further 54.5% (35.4 million hectares) of total farm area is cropland (i.e. field crops, hay, vegetables, sod, fruit, berries and nuts) (Jeswiet et al. 2015). As demands on food production increase, conversion of non-cropped areas to crops, and intensive farming practices such as simplified crop rotation, and use of pesticides, fertilizers and herbicides, are likely to increase (Benton et al. 2003). The wide extent of farmland means that any change in its

ability to support native wildlife could produce substantial effects on biodiversity (Fahrig et al. 2011)

Increasing the amount of semi-natural cover within agricultural systems can be beneficial to native biodiversity. Semi-natural habitat within agriculture can include small forest patches, native grasslands used for pasture, ponds and other aquatic habitats, and wooded vegetation along streams, roads, or field boundaries (Bennett et al. 2006). These types of habitat can support diverse and stable ecological communities (Devictor and Jiguet 2007), can act as sources for sink populations in the surrounding landscape (Holland and Fahrig 2000, Sunderland and Samu 2000), and can provide crucial resources for species requiring multiple habitat types (Fahrig et al. 2011). Higher amounts of semi-natural habitat within agricultural areas are associated with increased diversity across a range of taxa including; birds (Trzcinski et al. 1999, Billeter et al. 2008), small mammals (Nupp and Swihart 2000), bats (Duchamp et al. 2004, Gorresen and Willig 2004, Ethier and Fahrig 2011), amphibians (Vallan 2000), and arthropods (Aviron et al. 2005, Billeter et al. 2008).

However, ways of enhancing agricultural biodiversity without reducing the area of production are important conservation tools to discover. The influence of the structure of cropped vegetation on biodiversity within agricultural landscapes has not been studied extensively, or for many taxa (Fahrig et al. 2011), although it may have a large role to play in the ecology of many species which use agricultural landscapes (Benton et al. 2003). In areas where demand for agriculture is high, or farming practices are becoming more intensive it is crucial to know how to conserve native biodiversity when natural habitat is converted to farmland. It can be difficult to get farmers to adopt policies which

remove productive crops in favour of creating semi-natural habitat that does not directly increase agricultural productivity (Burton et al. 2008). In light of this, investigating ways of increasing the carrying capacity of native wildlife in crop-producing areas is important for creating agricultural guidelines, and can complement policies aimed at preserving semi-natural habitat within agricultural areas.

One potential way to enhance biodiversity without taking land out of production is to alter the structure of crop cover within agricultural landscapes, while maintaining the same amount of crop cover. Species richness tends to respond to agricultural changes at a landscape, not local, scale (Hendrickx et al. 2007), and ecological services occur at a landscape scale (Tscharntke et al. 2005), so investigating ways of enhancing agricultural biodiversity without reducing the area of production at this scale is important for guiding management policy. The structure of a landscape is determined by the land cover types it contains, and their spatial configuration and composition. Configuration refers to how cover types within a landscape are arranged, while composition refers to the relative makeup of those cover types. For native species, different crops can represent different resources, corridors or barriers for movement, so their configuration and/or composition may affect species presence or abundance within an agricultural landscape (Fahrig et al. 2011).

Landscapes can be more or less heterogenous in their configuration or composition. Figure 1 and 2 illustrate how configurational heterogeneity can vary independently of compositional heterogeneity, and vice versa. More interspersed cover types, and higher edge density increase the configurational heterogeneity of a landscape (Lovett et al. 2004). Configurational heterogeneity may affect proximity of

different resources to each other (e.g. tall crops that can be used as cover from predators next to shorter crops that provide foraging opportunities) and/or the ability of an organism to move between semi-natural habitat fragments (e.g. wide square shaped fields may be riskier to cross while strip farming can provide shorter corridors between fields). A higher number of cover types, or more evenness of cover type proportions increases a landscape's compositional heterogeneity. Compositional heterogeneity may affect the variety of resources available and may contribute to habitat complementation (Dunning et al. 1992) for some species (Benton et al. 2003) (e.g. hay fields provide breeding grounds, row crops provide seeds for granivorous birds).

Configurational and compositional heterogeneity can be highly correlated, especially within agricultural systems, for example landscapes with smaller fields tend to have a greater number of types of crops. The relative roles of these two landscape metrics in determining biodiversity in agricultural ecosystems are not well explored (Fahrig et al. 2011). An additional challenge in studying the effects of heterogeneity of crop cover is that agricultural landscapes with more heterogenous cropped area also tend to have a larger proportion of semi-natural habitat, which may account for any positive effects of crop heterogeneity. It is necessary to disentangle the effects on biodiversity of agricultural configurational and compositional heterogeneity from each other, and from the well documented positive effects of semi-natural habitat amount to understand how to structure farmland to promote biodiversity.

Bat populations are particularly important to agriculture in North America as they contribute potentially massive amounts of pest insect removal in farmlands (Boyles et al. 2011). The feeding niche of nocturnal aerial insectivores is only occupied by bats, small

owls, and caprimulgiform birds (Humphrey 1975) and so bats are a critical link in the agricultural wildlife food web. Bats are likely responsible for suppressing pest populations (Kunz et al. 2011, Boyles et al. 2013), as a single colony can remove millions of pests annually (e.g. cucumber beetles, stinkbugs, leafhoppers, and corn earworm moths) (Whitaker 1995). Eastern Ontario is home to 8 species of bats, (*Myotis lucifugus*, *M. septentrionalis*, *M. leibii*, *Lasiurus borealis*, *L. cinereus*, *Eptesicus fuscus*, *Perimyotis subflavus*, and *Lasionycteris noctivagans*), all of which are nocturnal insectivores, and with the exception of *M. leibii*, all are commonly found in agricultural landscapes (van Zyll de Jong 1985). While some species may prefer certain types of prey, all are known to feed opportunistically on many insect taxa (van Zyll de Jong 1985, Agosta et al. 2003, Clare et al. 2009, 2011). As bats provide an ecological service to farmers, and represent a unique group of threatened mammals within Canada (Boyles et al. 2011), understanding how agricultural landscape structure influences bat diversity and abundance could be useful for integrative land management practices.

Previous studies have focused on the relationship between bat diversity and abundance and forest amount and fragmentation in agricultural landscapes. In general, agricultural landscapes with more forest appear to have higher bat diversity and abundance (Gehrt and Chelvig 2004, Duchamp and Swihart 2008). Landscapes with moderate amounts of forest may have higher, or comparable species richness to contiguously forested landscapes as these areas support generalists as well as species which prefer forest and open areas (Gorresen and Willig 2004). There is also growing evidence that increased interspersed forest and crops within agricultural landscapes may benefit bat communities (Estrada and Coates-Estrada 2002, Gorresen and Willig

2004, Bernard and Fenton 2007, Ethier and Fahrig 2011). This may be due to habitat complementation (Dunning et al. 1992) between roosting habitat (forest) and foraging habitat (agricultural fields) (Ethier and Fahrig 2011).

The way crops are arranged (configurational heterogeneity) or their diversity (compositional heterogeneity) may also affect bats' ability to use agricultural landscapes. A larger number of crop-crop interfaces created by smaller field sizes, or more complex field shapes should increase both the accessibility and quality of foraging habitat, resulting in higher bat activity levels. Bats prefer to forage and commute along linear landscape elements (Limpens et al. 1989, Verboom and Huitema 1997, Boughey et al. 2011, Lentini et al. 2012, Frey-Ehrenbold et al. 2013), which may function as navigational references, sources of insect prey, shelter from wind and/or protection from predators (Verboom and Huitema 1997). We predict that decreasing the mean field size would increase the diversity and abundance of bat species in an agricultural landscape.

The diversity of crop types in a landscape may also impact bat communities by supporting more diverse and abundant communities of prey insects. Some insect species use one or more crops as part of their life cycle (e.g. for food, breeding areas, or as cover) and a greater variety of crops will likely support a greater variety of these insects within an agricultural landscape. Agricultural landscapes with more diverse crops may also provide a more temporally stable foraging habitat for generalist bat species as different insects are active at different times of night (Rydell et al. 2013), and population cycles of pests may stagger food availability seasonally. We predicted that increasing the Shannon-Wiener diversity index of agricultural cover would increase the diversity and abundance of bats in an agricultural landscape.

We tested the above predictions that bat species richness and activity should increase with increasing configurational and compositional heterogeneity of crops in agricultural eastern Ontario, using 3km x 3km agricultural landscapes. We chose mean field size of crops as an index of configurational heterogeneity, and Shannon-diversity of crops as an index of compositional heterogeneity and used a landscape selection procedure which minimized correlation between these two variables. We then conducted acoustic surveys for bat species richness and activity (as a proxy for abundance). We also trapped insects overnight to investigate if landscape heterogeneity effects on bats were related to landscape heterogeneity effects on their insect prey. Finally, we combined our results with previous research on forest structure and bat diversity and abundance to draw inferences about the kinds of agricultural landscapes that favour diverse, active bat assemblages.

2. Methods

2.1 Study Region and Landscape Selection

This study was conducted in rural Eastern Ontario, near Ottawa, Canada (Figure 3). Approximately 50% of the 15 500 km² study area is covered by crop or pasture (Statistics Canada 2006) interspersed with fragments of mixed and deciduous forest (Thompson 2000).

Pasher et al. (2013) performed landscape selection as part of a larger project (Fahrig et al. 2015), using a moving window analysis on satellite imagery (Landsat-5 images, 30 m x 30 m pixel, from the 2007 growing season) to select a set of sample landscapes that met the following criteria. Each potential landscape was 3 km x 3 km in size, with 40-90% agricultural cover. From these a set of landscapes was selected such that there was a minimum of 3.5 km between landscape centres; no spatial autocorrelation between landscapes and their mean field size or Shannon Diversity of agriculture; and minimal correlation between mean field size and the Shannon Diversity of agriculture (Pasher et al. 2013).

We conducted acoustic surveys for bats at a random selection of 46 of the 93 landscapes selected for the larger project (Fahrig et al. 2015).

2.2 Landscape Predictor Variables

In 2012 aerial photography of all the landscapes was commissioned to obtain accurate measurements of the landscape variables during the field season in which bats

were surveyed. Pasher et al. (2013) used these photos to create detailed land cover maps of each landscape at 40 cm resolution, at 3 spatial extents - 1x1 km, 2x2 km, and 3x3 km (e.g. Figure 4). Field crews validated the maps by visiting each landscape. Separate crop or pasture fields were delineated based on visible field boundaries, a change in crop type, or both. Therefore, areas of the same crop type that were separated by a non-crop field boundary were considered separate fields, and areas of different crop types that were not separated by a non-crop boundary were also considered separate fields. From these detailed land cover maps, we calculated for each landscape, at each spatial extent (1, 2, and 3 km), three landscape variables: mean size of all agricultural fields in the landscape (configurational heterogeneity), Shannon Diversity of agricultural types within the farmland portion of the landscape (compositional heterogeneity) and proportion of the landscape covered by crops or pasture (proportion agriculture) (Pasher et al. 2013). We included proportion of agriculture to control for potential effects of overall agricultural cover on bat species richness and activity.

2.3 Bat Response Variables

2.3.1 Acoustic Surveys

We conducted acoustic surveys for echolocation calls to measure bat species richness and activity. In each landscape, two points were selected for bat acoustic surveys. To select these points we began by finding 6 potential points within the 46 central 1km x 1km landscapes using ArcGIS10 (ESRI Inc. 2011). Potential points were at least 200 m apart along field boundaries at least 50 m long, with at least 25 m of continuous boundary extending in opposite directions from the point. Points were also at

least 50 m from any non-agricultural land use, and were at least 100 m from a road, significant water feature, or building. We then visited the landscapes and eliminated any potential points that no longer met these criteria, as land use had sometimes changed since the 2007 spatial data used for landscape selection. From the remaining potential points we randomly selected 2 as our acoustic survey points for that landscape.

We conducted acoustic surveys from May 23rd to August 1st, 2012, the period when migratory species are present and nightly temperatures are high enough to support active foraging (Fenton 1992). We surveyed each landscape once over the course of the season, unless we experienced equipment failure, in which case we returned to the landscape later in the season. We generally surveyed two different landscapes per night, rotating through landscapes such that we avoided any possible correlation between survey date and landscape variables. If night-time temperature was expected to drop below 10°C, or heavy precipitation was anticipated, we did not conduct surveys as these conditions are expected to reduce bat activity (Erkert 1982).

At each surveying point, we mounted an AR 125 Ultrasonic Receiver (Binary Acoustic Technology) on a tripod at a height of one metre, and connected it to a laptop running SPECT'R recording software (Binary Acoustic Technology). We protected receivers with rain-guards, and directed them 45 degrees towards a plexiglass sheet which reflected sound, equivalent to directing them 45 degrees towards the sky. We directed receivers parallel to the field boundary, and away from the nearest non-agricultural feature to minimize sound obstruction by trees or other landscape features, and thus maximize detectability (Fenton 1992, Kunz and Parsons 2009). We placed laptops in plastic bins to protect them.

We set laptops to begin recording at sunset (ranged from ~20:30 to 21:00 during the study) for 3 hours. This is one of the peak foraging times for bats, and thus was likely to maximize encounter rates (Walsh et al. 2004). We programmed SPECT'R to record automatically for 20 seconds if a sound 10+ decibels above background noise and 15-120 kHz in frequency was detected. The recording ceased any time the sound stopped for 1 second or more. We selected these values to correspond to echolocation call attributes of local species (van Zyll de Jong 1985, Menzel et al. 2003).

2.3.2 Bat Call Classification

Bat calls consist of a rapid series of “chirps” emitted in quick succession; the entire sequence of chirps is referred to as a “call” or “pass”. Calls are typically divided into two categories: “search-phase calls” and “feeding buzzes” (Kalko et al. 2001). During a search-phase call a bat is searching for potential prey and the interval between chirps is between 50 and 100 milliseconds (Griffin et al. 1960). Once a bat has acquired a target it will emit a feeding buzz which has a smaller interval (<10 milliseconds), and varies depending on the target and context of pursuit (Griffin et al. 1960, Kalko et al. 2001). Analysis of the acoustic characteristics of search phase calls enables identification of many bat species (Fenton and Bell 1981) when other methods (e.g. physical capture, DNA analysis) are impractical, and allows determination of species presence and relative activity levels across sites (Walsh et al. 2004).

To identify the species of a call, we analyzed the acoustic parameters of the recorded chirps using a quadratic discriminate function analysis model (QDFA) created in Minitab 15 (2000) by Kevin Ethier (Ethier 2010). Discriminant Function Analysis (and

its quadratic variant) is used to determine which variable combinations distinguish between already defined categories if enough known references from all categories are available. The measurements of these variables from unknown observations can then be entered into the model to determine its likely categorical classification. Ethier (2010)'s QDFA compares the acoustic parameters of unknown search phase chirps to a library of validated reference calls (Russo and Jones 2002), and provides a posterior probability (0-100%) of the chirp belonging to each of the potential species in the model. Ethier (2010) created the QDFA using full-spectrum reference calls of local species from the Fenton Laboratory (Hooton and Adams, unpublished, University of Western Ontario). The recordings were of free-flying individuals recorded in various locations around Ontario including: *P. subflavus* (n = 33), *M. septentrionalis* (n = 21), *M. lucifugus* (n = 68), *L. noctivagans* (n = 28), *E. fuscus* (n = 51), *L. borealis* (n = 29), and *L. cinereus* (n = 39) (Ethier 2010). The acoustic characteristics used in the QDFA are chirp duration, interpulse interval, maximum frequency, minimum frequency, bandwidth, dominant frequency, characteristic frequency, slope, and curvature. The QDFA had an overall correct classification rate of 88.8% (239 of 269 reference calls correctly classified) (Ethier 2010). For each species expected in our study area, correct classification rates were: *P. subflavus* 87.9%; *M. septentrionalis* 95.2%; *M. lucifugus* 79.4%; *L. noctivagans* 92.9%; *E. fuscus* 90.2%; *L. borealis* 93.1%; and *L. cinereus* 94.9% (Ethier 2010).

We retained only recordings with 2 or more search-phase chirps to ensure the sound was part of a bat call and not due to other noise present in the landscape (Thomas 1988). We also visualized all recordings using SCAN'R and checked visually for irregularities. The search-phase chirp with the highest signal-to-noise ratio from each call

was selected for identification to species (Parsons and Jones 2000). For each chirp the QDFA identified the most likely species along with a probability of correct classification. If a chirp's probability of correct identification was $\geq 95\%$ this species was assigned to the call. For chirps with probabilities of correct identification 50-95%, we classified the remaining chirps in the call using the QDFA. If there were at least twice as many chirps assigned to one species relative to any others, we assigned the call to that species. We categorized as “unidentified” any calls where the chirp with the highest signal-to-noise ratio had a probability of correct identification of $<50\%$ and/or did not have at least 2 times as many chirps belonging to one species compared to any other species were categorized as “Unidentified” (~6% of calls).

2.4 Insect Trapping and Weather Monitoring

We estimated activity of flying insects at each acoustic recording point during the night of recording as an index of relative food availability for that night. We sampled flying insects using custom made cylindrical sticky traps. Each trap consisted of a sheet of 33 cm x 29.5 cm white paper secured around a PVC pipe mounted on an extendable pole 2m high (Barclay 1985). The cylindrical shape prevents wind directionality from biasing sampling (Kunz 1988). We secured traps with 3 guy ropes staked into the ground, and then painted the paper with Tangletrap, a non-attractive paste to which flying insects adhere upon collision. We positioned traps along field boundaries 10 m behind the acoustic receiver (Figure 5).

Upon collection the following morning, other field crews wrapped cling film around the sticky portion of the trap to secure trapped insects for later inspection. We

counted all insects, and divided them into size categories based on body length (<10 mm, 10 mm or larger, and 15 mm or larger) (Threlfall et al. 2012) and identified them to Order (Dipterans, Lepidoterans, Coleopterans, Hymenopterans, or Other).

At each landscape we chose the surveying point with the least obstruction to wind and erected a weather station (Ambient Weather WS-2080 Wireless Home Weather Stations) next to the insect trap, 10 m from the receiver. We programmed weather stations to record precipitation, temperature, and wind speed every 15 minutes during recording nights. Moonlight has been linked to changes in microhabitat use by insectivorous bats (Hecker and Brigham 1999), so we also recorded the percentage of moon illumination and the number of minutes the moon was above the horizon during surveying from local weather networks for each night. The product of these is an index of the moon illumination for the surveying period each night, however we were unable to account for cloud cover at individual landscapes.

2.5 Statistical Analysis

2.5.1 Bat Response Variables

For each bat acoustic survey point we calculated the number of species identified at that point (Species Richness), the total number of bat calls including unidentified calls (Total Activity), and the number of calls identified for each species (Species Activity). As all bat response variables except species richness showed evidence of overdispersion we used a negative binomial distribution in all models of total bat activity and species activity. We used zero-inflated models for the activity levels of all but the most

commonly recorded species (*E. fuscus*, and *L. cinereus*), as other species were not recorded at a large number points.

2.5.2 Selection of Confounding Variables for Inclusion in Landscape Models

We excluded average rain and average wind during surveying from consideration since we observed little variation in these variables over the course of the study, likely because we specifically avoided surveying on nights when heavy precipitation or strong winds were anticipated. We examined the remaining potential confounding variables (date, average temperature, and moon illumination) for normality, using Shapiro-Wilk's tests.

To determine which confounding variables should be included in models of mean field size and Shannon Diversity of agriculture (below), we created generalized linear mixed models relating each bat response variable (species richness, total activity, and each species' activity) to all combinations of potential confounding variables (date, average temperature, and moon illumination) with landscape included as a random effect to control for repeated measures on the same landscape. We then ranked the models by AICc scores and included null models in this comparison (Burnham and Anderson 2003). If the null model was not in the top models ($\Delta \text{AICc} < 2$), all potential confounding variables in the top models for a bat response were included in the models for that bat response in the analyses of landscape effects on Species Richness, Total Activity, and activity of each species (below).

2.5.3 Modelling Landscape Effects

We evaluated the effects of the landscape predictor variables using generalized linear mixed models. We examined all landscape variables (mean field size, Shannon Diversity of agriculture, and proportion agriculture at 1, 2, and 3km extents) for normality, using Shapiro-Wilk's tests. We log-transformed mean field size to normalize the data. We then standardized the landscape variables to estimate their relative effects (Smith et al. 2009, Grueber et al. 2011). For each bat response variable 3 models were created, one for each spatial scale (1, 2, 3km). Each model contained all 3 landscape variables (log mean field size, Shannon Diversity of agriculture, proportion agriculture) at that scale plus potential confounding variables as indicated by the AICc selection, and landscape as a random effect. We also specified a zero-inflation parameter for *L. noctivagans*, *M. septentrionalis*, *M. lucifugus*, *L. borealis*, and *P. subflavus* as they were not encountered at a high number of points.

2.5.4 Insect Analysis

To investigate the role insects might play in any observed effects of mean field size and Shannon Diversity of agriculture on bats, we first determined which sizes or Orders of insects had the strongest positive relationship with bat richness, total bat activity, and activity of each species. We created the following categories of insect abundance: total insects, insects 10+ mm in length, and insects 15+ mm in length. We also analyzed abundance of each Order (Dipterans, Lepidopterans, Coleopterans, Hymenopterans, or Other) regardless of body length. We examined abundance of all categories of insects for normality, using Shapiro-Wilk's tests, and log-transformed them to normalize the data. We then examined Pearson correlations between each bat response

variable (Species Richness, Total Activity, and activity of each species) and each category of insect. We then selected the category of insects which had the strongest positive correlation with bat Species Richness, Total Activity, and activity of each species, and examined correlations between this category and the landscape predictors (Log Mean Field Size, and Shannon Diversity of agriculture) at the 1, 2, and 3 km scales. We compared these correlations with the relationships observed between bat activity and richness and mean field size and Shannon Diversity of agriculture, to see if there was support for the idea that mean field size and Shannon Diversity of agriculture influenced bats through their influence on bat's prey.

To investigate whether landscapes with higher compositional heterogeneity provided more stable foraging resources for bats we divided landscapes into a group with “high” Shannon Diversity of agriculture (above the mean) or “low” Shannon Diversity of agriculture (below the mean). For each group we then calculated the coefficients of variation for total insects, and insect categories which were most strongly correlated with bat responses, and compared them.

We conducted all analyses in R version 3.1.2 using the MuMIn, MASS, and glmmADMB packages.

3. Results

We recorded 2,865 echolocation calls, of which 2,689 (93.9%) were identified. The number of echolocation calls per survey point ranged from 0-214, with a mean of 26.28. Each of the 7 expected species were found in at least 13 of the 46 landscapes surveyed. Hoary bats (*L. cinereus*) were found in all of the landscapes, and made up the

majority (53.4%) of calls recorded. Species richness for each point ranged from 0-7, with a mean of 2.85.

We focused on the 3 km scale as it encompasses the average commuting distance between foraging and roosting habitat for all local bat species (Brigham 1991, Campbell et al. 1996, Menzel et al. 2003, Sparks et al. 2005, Elmore et al. 2005, Broders et al. 2006) and was the scale at which we observed the strongest bat responses to our landscape predictor variables. We also explored these relationships at the 1, and 2 km scales, and the results were generally similar, but weaker (Appendix A).

The strength of correlations (absolute r-values) between landscape predictor variables and potential confounding variables ranged between 0.0229 and 0.2574 (Table 1). The strongest correlation was between average temperature and Shannon Diversity of agriculture ($r = 0.2574$). Log of Mean Field Size and Shannon Diversity of agriculture were negatively correlated ($r = -0.5625$, Table 1). The Proportion of Agriculture in a landscape was strongly correlated with the log of mean field size ($r = 0.7789$), and more weakly with Shannon Diversity of agriculture ($r = -0.2925$) (Table 1).

3.1 Effects of Landscape Predictors

The activity levels of 3 species of bat showed significant ($p < 0.05$) or near significant ($p < 0.10$) responses to log of mean field size. *L. borealis* and *M. lucifugus* activity levels both responded negatively to increasing field sizes, and *L. noctivagans* responded positively to increasing field sizes (Figure 6). We did not detect a significant effect of log mean field size on bat species richness or total bat activity.

The total activity level of bats, and of four species of bats showed a positive response to Shannon Diversity of agriculture. *L. noctivagans*, and *E. fuscus* both showed significant positive responses to Shannon Diversity of agriculture (Figure 7). Total bat activity, and activity of *L. cinereus*, and activity of *M. septentrionalis* showed near significant ($p < 0.10$) responses to Shannon Diversity of agriculture (Figure 7). We did not detect a significant effect of Shannon Diversity of agriculture on bat species richness.

The activity levels of 4 species of bat showed significant ($p < 0.05$) responses to proportion of agricultural cover. Both *Myotis* species and *L. borealis* responded positively to increasing amounts of agriculture and *L. noctivagans* responded negatively to increasing amounts of agriculture sizes (Figure 8). We did not detect a significant effect of proportion of agriculture on bat species richness or total bat activity.

3.2 Selection of Confounding Variables for Inclusion in Landscape Models

No combination of the potential confounding variables (date, average temperature, or moon illumination) was found to be an improvement over the null model (which included only landscape identity to account for repeated measures on landscapes) for any bat response (Table 2). Therefore no potential confounding variables were included in models of bat responses to landscape predictor variables.

3.3 Insect Analysis

We trapped 2 650 insects over 109 trap nights. Dipterans made up approximately 57.5% of the caught insects, followed by Coleopterans (16.7%), Hymenopterans (5.0%) and Lepidopterans (3.4%). The remaining insects were not classifiable into one of these categories (e.g. Hemiptera). The vast majority of insects caught were under 10 mm long (96.2%).

Of the insect categories we examined, the log of the number of moths had the strongest positive correlation with most bat response variables (Table 3). Exceptions to this were the activity levels of *L. noctivagans*, and *P. subflavus* which were more correlated with the number of insects 10+ mm long, and the activity levels of *M. lucifugus*, and *E. fuscus* which were more strongly correlated with the log of the number of beetles. Overall however, relationships between insects and bat responses were generally weak or negligible (absolute value of Pearson's $r < 0.30$) All insect categories investigated had weak or negligible negative correlations with log of mean field size, and weak or negligible positive correlations with Shannon Diversity of agriculture (Table 4). The coefficients of variation of insect counts in various categories in landscapes with low Shannon Diversity of agriculture were all slightly higher than those in landscapes with high Shannon Diversity of agriculture (Table 5).

4. Discussion

We predicted that configurational heterogeneity would have a positive relationship with bat species richness and activity within a landscape (i.e. a negative relationship with the log of the mean field size) as a larger number of field boundaries within an agricultural landscape should increase its quality and accessibility for bats. This

was, however, not well supported. Although reduced mean field sizes appeared to have a positive effect on the activity levels of two bat species (*M. lucifugus*, *L. borealis*), it also appeared to have a negative effect on *L. noctivagans*, and we did not detect a significant effect on bat species richness, total activity, or the activity levels of 4 other species.

These results are surprising because previous research indicates that bats are highly sensitive to the loss of field boundaries (Pocock and Jennings 2008), which can act as flight corridors, foraging habitat, and protection from wind or predators (Verboom and Huitema 1997). Insect abundance has also been shown to be higher along hedgerows than in fields (Gruebler et al. 2008), therefore we expected more field boundaries to provide higher quality foraging habitat.

It is possible that we did not detect more positive effects of reduced mean field size on bat activity because while bats may be more active along linear features, they will still forage in open areas within agriculture (Frey-Ehrenbold et al. 2013). Even at the lowest levels of configurational heterogeneity present in our study, there may still have been sufficient commuting and foraging corridors to allow these highly mobile species access to the agricultural landscape from their roosting habitat. While all local species are documented as most active along edges (Jantzen and Fenton 2013), this may not result in landscape scale effects of mean field size for all species. Indeed, for *L. noctivagans*, we observed a positive effect of mean field size.

We predicted that compositional heterogeneity would be positively related to bat species richness and activity, as different types of crops might support different insect communities representing more temporally stable foraging habitat. We found strong

support for a generally positive response of bat activity to increasing Shannon Diversity of agriculture: it had a significant positive effect on total bat activity, and the activity of four species of bats, and had positive standardized coefficients for another 2 bat responses.. This relationship was strongest at the 3 km scale (Figure 7), but appeared fairly consistent across the other scales examined (Appendix A).

We suspect that this pattern is being driven by the relationship between prey insects and the diversity of crops, especially over time. Bats are known to track the abundances of specific prey insects (McCracken et al. 2012, Krauel et al. 2014) and may exploit certain crops during periods of high pest activity, and forage in other habitats during periods of low pest activity (Maine 2014). Landscapes with more diverse crops have peaks of insect prey at different times, and thus remain viable foraging areas despite time of growing season. The bat species in this region do not tend to heavily specialize on any specific taxa of insect (Anthony and Kunz 1977, van Zyll de Jong 1985, Menzel et al. 2003, Harvey et al. 2011) and so are able to prey upon a large number of species within agricultural landscapes. These flexible diets means that local bat species would be able to forage in landscapes with diverse communities of prey insects resulting from diverse crops.

We did find that all insect categories we investigated had weak or negligible positive correlations with Shannon Diversity of agriculture (Table 4). Although weak, the positive relationship between moths, beetles, and 10+ mm insects with Shannon Diversity of agricultural cover may support the argument that the positive relationships between total bat activity levels, activity levels of *L. noctivagans*, *M. septentrionalis*, *L. cinereus*,

and *E. fuscus*, and Shannon Diversity of agriculture are due in part to the relationship between insects and Shannon Diversity of agriculture.

Similarly we found that landscapes with higher Shannon Diversity of agriculture had lower coefficients of variation for insect abundances. For insects 10mm+ long and moths, especially, there was approximately 25-30% more variation in counts within landscapes with above average Shannon Diversity of agricultural cover. This supports the idea that these landscapes may be less predictable foraging habitats for bats.

Correlations between semi-natural habitat, such as forests, and Shannon Diversity of agriculture did not likely influence our results, however crop type may play a role. There were apparent positive correlations between forest amount and bat species richness and some species activity levels within our study landscapes (Appendix C), but Shannon Diversity of agriculture did not appear to be correlated with forest amount ($r = 0.1684$, $p > 0.05$). However, it should be noted that reduced crop diversity and conversion of forest cover to agricultural cover are both common agricultural intensification practices (Tscharrntke et al. 2005) and so crop diversity and forest cover may be correlated in typical agricultural systems. Shannon Diversity of agriculture and proportion of a landscape covered with pasture or hay were also positively correlated ($r = 0.4018$, $p < 0.05$, and $r = 0.4514$, $p < 0.05$ respectively) and these cover types have been associated with higher microbat activity in Australian agricultural systems (Lentini et al. 2012).

We included the proportion of agricultural cover in landscape models of bat responses to control for any potential effects. Although the landscape selection procedure attempted to constrain the range of proportion of agricultural cover (Pasher et al 2013), a

wide range of values for proportion of agricultural cover were present in our study landscapes (0.4-0.9 at 3km). We observed a positive effect of proportion of agriculture on the activity levels of 3 species (*M. septentrionalis*, *M. lucifugus*, and *L. borealis*) and a negative effect on the activity of *L. noctivagans*. This was surprising given that proportion of agriculture was highly correlated with mean field size, and mean field size appeared to have opposite effects on these species' activity levels. It is possible that agricultural cover represented better foraging habitat than the non-cropped landcover within our study landscapes, or alternatively that in landscapes with a greater proportion of agricultural cover, foraging activity was less likely to be concentrated around forested edges (Jantzen and Fenton 2013) where we specifically avoided surveying.

Acoustic studies of bats often require compromises between the number of sites which can be surveyed, and the precision of data that can be obtained from each site (Fischer et al. 2009). Sampling in more locations per landscape, and/or more times per landscape across the season would also allow a more direct investigation into how the relationship between insect communities and Shannon Diversity of agriculture affects bat species richness and bat activity. Due to logistical constraints, however, we were unable to survey most landscapes repeatedly throughout the growing season, and were only able to survey at 2 points per landscape. This meant we were unable to specifically test our hypothesized mechanism responsible for the relationship observed between bat activity levels and Shannon Diversity of agriculture. That stated, we observed a consistent link between Shannon Diversity of agriculture and the activity levels of most bat species studied.

Our results add to the current understanding of how agricultural landscape structure influences bat communities in that we tested the effects of the heterogeneity of cropped land, not the heterogeneity of semi-natural habitat. Lentini et al (2012) examine the influences of different types of crops on bat communities in Australia, however we are aware of no similar studies in North American agriculture. There has been some research into the effects of organic vs. conventional farming methods on bats (Wickramasinghe et al. 2003, Fuller et al. 2005, Davy et al. 2007) and their prey (Wickramasinghe and Harris 2004); however, these have shown inconsistent effects and do not generally take landscape heterogeneity into account. Similarly, most agri-environmental schemes which compensate farmers for adopting certain farming practices, do not take landscape heterogeneity into account at a scale meaningful for bats (Fuentes-Montemayor et al. 2011).

4.1 Implications

Our findings can be used to inform farm management decisions by farmers and agricultural policy makers, especially considering the potential increase in pest removal services provided by bats. The scale at which we found the strongest effect of Shannon Diversity of agriculture was 3 km, which means that even single large farms, or small groups of neighboring farms (e.g. neighbouring farms run by family members) in this region can effectively make these management decisions. In Figure 9 we give an example of a typical landscape from the lowest and highest quartiles of Shannon Diversity of agriculture observed in our study, as well as the mean of bat responses for these two quartiles of landscapes in our study. For several bat species, landscapes with higher

Shannon Diversity of agriculture appear to have on average approximately 1 more species, almost twice as much total bat activity, and from 1.5 – 20 times more activity of individual species.

Diversified crops are associated with lower densities of pest insects (Tonhasca and Byrne 1994), and so increasing the compositional heterogeneity of agricultural landscapes may reduce pest densities in additional ways beyond increasing bat activity levels. As well, the pest removal services of birds appear to be additive to those of bats (Williams-Guillén et al. 2008), so by combining our recommendations with bird management guidelines it may be possible to maximize pest removal services from both these taxa. When generalist predators, such as bats in this region, have a consistent supply of food, they can be more effective in suppressing outbreaks of pest species, as they can maintain higher populations even when specific pest numbers are lower (Symondson et al. 2002). By increasing the diversity of crops within agricultural landscapes, farmers can help promote bat activity, and related pest removal.

Given our results, and other studies on bat activity patterns in agriculture, we suggest bat activity in agricultural landscapes can be promoted through planting diverse crop types including pasture and hay, and maintaining or creating interspersed forest fragments, vegetated field margins, and scattered trees (e.g. Figure 10). We demonstrate that Shannon Diversity of agricultural cover is positively associated with the activity levels of several local bat species, as well as total bat activity, and while North American studies are lacking Lentini et al. (2012) have shown that pasture is a key cover type in promoting bat activity in Australian agroecosystems. Forest is necessary to provide roosting habitat, and forest-field edges are areas of high bat activity (Jantzen and Fenton

2013). The activity levels of several local bats are also higher in landscapes with increased fragmentation (but not loss) of forest habitat (Ethier and Fahrig 2011) and bats may select roosts near forest edges to reduce commuting costs (O’Keefe et al. 2009). Although we did not find a strong positive effect of reduced mean field size on bat activity, there are multiple other studies which suggest that field margins provide multiple benefits to bats (Limpens et al. 1989, Verboom and Huitema 1997, Boughey et al. 2011, Lentini et al. 2012, Frey-Ehrenbold et al. 2013). Similarly, Fisher et al (2010), and Lentini et al. (2012) both find that scattered trees within agricultural landscapes have a disproportionately positive effect on bat activity, even in low numbers. Applying these guidelines to agricultural landscapes is perhaps most important in intensively farmed areas, to mitigate high intensity management and improve pest regulation (Weilbull and Ostman 2003, Tscharntke et al. 2005, Bianchi et al. 2006).

4.2 Conclusions

Based on our findings we recommend that farmers or agricultural organizations seeking to increase bat activity on farms without removing land from production focus on increasing the diversity of crops at 3km or larger scales. Overall bat activity (especially of certain species) is higher in landscapes with higher diversity of agricultural crop cover. We hypothesize this is likely because diverse crops, including hay and pasture, create more temporally stable insect food resources.

Tables

Table 1: Pearson correlations between potential confounding variables on bat species richness, total activity, and activity levels of individual species and landscape variables at 3km scale in agricultural study landscapes in Eastern Ontario

	Average Temperature	Moon Illumination	Log MFS (3km)	SHDI (3km)	Proportion Agriculture (3km)
Date	-0.0196	0.1245	-0.0229	0.1138	0.0792
Average Temperature		-0.3071	-0.1369	0.2574	-0.0434
Moon Illumination			0.1917	-0.1583	0.1651
Log MFS (3km)				-0.5625	0.7789
SHDI (3km)					-0.2925

Table 2: Top models of all combinations of potential confounding variables of bat responses ranked by AICc. Null models included only landscape identity as a random effect term to account for repeated measures on landscapes.

Response	Model	df	logLik	AICc	delta	weight
Species Richness						
	Null	2	-179.128	362.4	0	0.4
	Average Temperature	3	-179.045	364.4	1.97	0.149
Total Activity						
	Null	3	-402.23	810.7	0	0.312
	Average Temperature	4	-401.751	812	1.22	0.169
	Moon Illumination	4	-401.911	812.3	1.54	0.144
	Date	4	-402.02	812.5	1.76	0.129
<i>L. noctivagans</i>						
	Average Temperature	5	-79.243	169.2	0	0.251
	Moon	5	-79.65	170	0.81	0.168
	Moon + Average Temperature	6	-78.522	170	0.84	0.165
	Null	4	-80.963	170.4	1.21	0.138
	Date + Average Temperature	6	-78.964	170.9	1.72	0.106
	Date + Moon Illumination + Average Temperature	7	-78.316	171.9	2.77	0.063
<i>M. septentrionalis</i>						
	Null	4	-57.818	124.1	0	0.428
	Moon Illumination	5	-57.743	126.2	2.08	0.151
<i>M. lucifugus</i>						
	Null	3	-141.62	289.5	0	0.262
	Moon	4	-140.529	289.5	0	0.262
	Date + Moon Illumination	5	-140.251	291.2	1.68	0.113
	Average Temperature	4	-141.486	291.4	1.91	0.101
	Date	4	-141.498	291.4	1.94	0.1

L. cinereus

Null	3	-347.139	700.5	0	0.345
Date	4	-346.795	702	1.49	0.163
Moon Illumination	4	-346.846	702.1	1.6	0.155

L. borealis

Null	4	-96.254	201	0	0.285
Average Temperature	5	-95.296	201.3	0.32	0.243
Moon Illumination	5	-95.888	202.5	1.5	0.134

E. fuscus

Null	3	-257.093	520.5	0	0.286
Average Temperature	4	-256.075	520.6	0.15	0.266
Moon Illumination	4	-256.996	522.4	1.99	0.106

P. subflavus

Moon Illumination	5	-76.984	164.6	0	0.262
Date + Moon Illumination	6	-76.27	165.5	0.86	0.171
Null	4	-78.561	165.6	0.92	0.165
Date	5	-77.578	165.8	1.19	0.145
Moon Illumination + Average Temperature	6	-76.891	166.7	2.1	0.092

Table 3: Pearson correlations of bat responses and abundances of different size and taxonomic categories of insects trapped during acoustic surveys for bats in agricultural landscapes in Eastern Ontario

Bat Response	Log Beetles	Log Moths	Log Flies	Log Insects 10+ mm	Log Insects 15+mm	Log Total Insects
Species Richness	-0.0287	0.2206	-0.2006	0.1011	0.137	-0.0632
Total Activity	0.1598	0.2061	-0.0392	-0.0009	0.1139	-0.0574
<i>L. noctivagans</i>	-0.0533	0.0138	-0.0071	0.0398	0.0175	-0.0139
<i>M. septentrionalis</i>	0.0273	0.0748	-0.1235	-0.0177	0.0352	-0.0321
<i>M. lucifugus</i>	0.2028	0.1029	-0.0344	-0.0009	0.1195	0.0924
<i>L. cinereus</i>	0.1416	0.2554	-0.0135	0.0139	0.1114	-0.1274
<i>L. borealis</i>	0.0466	0.0677	-0.0939	-0.051	-0.0121	-0.1067
<i>E. fuscus</i>	0.1353	0.0827	-0.0465	-0.0288	0.0828	0.0257
<i>P. subflavus</i>	-0.1273	0.0021	-0.2121	0.0031	-0.0113	-0.0461

Table 4: Pearson correlations between landscape predictor variables in agricultural Eastern Ontario study landscapes and the abundance of insects from size and taxonomic categories of insects most highly correlated with bat species richness and activity responses during acoustic surveys.

Landscape Predictor	Log Beetles	Log Insects 10+ mm	Log Moths
Log MFS (3km)	-0.0889	-0.0893	-0.1713
SHDI (3km)	0.0887	0.2289	0.2192
PCTAG (3km)	-0.0446	-0.0446	-0.0348

Table 5: Coefficients of variation of insect totals for total insects, as well as size and taxonomic categories of insects most highly correlated with bat species richness and activity responses during acoustic surveys

	Total Insects	Insects 10mm+	Total Moths	Total Beetle
Low SHDI 3km	86.71	144.02	200.02	151.57
High SHDI 3km	83.76	115.09	153.18	150.06

Figures

Figure 1: Increasing configurational heterogeneity independent of compositional heterogeneity – each shade of grey represents a different crop type. The landscape on the right has higher configurational heterogeneity, but both landscapes have the same amount of each crop type (same compositional heterogeneity).

Figure 2: Increasing compositional heterogeneity independent of configurational heterogeneity – each shade of grey represents a different crop type. The landscape on the right has higher compositional heterogeneity, but both have the same 4 field layout (same configurational heterogeneity).

Figure 3: Location of study landscapes within agricultural Eastern Ontario.

Mean field size (LogMFS) and Shannon Diversity of agriculture (SHDI) existed on a continuous scale but were categorized as “High” or “Low” to allow rotation of sampling effort to avoid correlation of these categories with date. Landscapes here are represented at the 1 km x 1 km scale.

Figure 4: Example of agricultural study landscape with different land uses mapped at 3 spatial extents (inner square = 1 km x 1 km, middle square = 2 km x 2 km, outer square = 3km x 3km).

Figure 5: Diagram of layout of sampling equipment at each acoustic survey point, including bat recording station, and weather station/insect trap set up along field boundaries.

Figure 6: Standardized coefficients of Log Mean Field Size at 3 km in generalized mixed models of bat responses to landscape predictor variables (error bars show 95% confidence intervals, * indicates a p-value of <0.05, † indicates p-value of <0.10)

Figure 7: Standardized coefficients of Shannon Diversity of agriculture at 3 km in generalized mixed models of bat responses to landscape predictor variables (error bars show 95% confidence intervals, * indicates a p-value of <0.05, † indicates p-value of <0.10)

Figure 8: Standardized coefficients of Proportion of Agricultural Cover at 3 km in generalized mixed models of bat responses to landscape predictor variables (error bars show 95% confidence intervals, * indicates a p-value of <0.05, † indicates p-value of <0.10)

	Mean in Lowest Quartile of SHDI 3km	Mean in Highest Quartile of SHDI 3km
SHDI 3km	1.05	1.59
Species Richness	2.37	3.36
Total Activity	19.63	37.14
<i>L. noctivagans</i>	0.74	0.68
<i>M. septentrionalis</i>	0.26	0.54
<i>M. lucifugus</i>	0.15	3.04
<i>L. cinereus</i>	11.52	19.39
<i>L. borealis</i>	0.44	0.43
<i>E. fuscus</i>	4.19	11.04
<i>P. subflavus</i>	0.30	0.46

Figure 9: Examples of agricultural cover in typical landscape in the lowest quartile of Shannon Diversity of agriculture (left) and the highest quartile of Shannon Diversity of Agriculture (right), and means of bat responses observed in landscapes within these quartiles

Figure 10: Example of theoretical agricultural landscape which promotes bat activity. Agricultural land use is indicated by grey or cross hatching, while natural and semi-natural land use is indicated in green. Different shades of grey represent different crop types, with horizontal hatching representing hay, while diagonal hatching represents pasture. Forest fragments are indicated by rounded green areas, and at least one is adjacent to each field. Individual scattered trees are indicated by green triangles. Field margins have semi-natural vegetation such as grass, shrubs, and brush.

Appendices

Appendix A Standardized coefficients of landscape variables at 1, 2, and 3km scales in GLMM models of bat responses

A.1 Standardized coefficients of Log Mean Field Size at 1, 2, and 3 km scales in generalized mixed models

of bat responses to landscape predictor variables (error bars show 95% confidence intervals, * indicates a p-value of <0.05, † indicates p-value of <0.10)

A.2 Standardized coefficients of Shannon Diversity of Agriculture at 1, 2, and 3 km scales in generalized mixed models of bat responses to landscape predictor variables (error bars show 95% confidence intervals, * indicates a p-value of <0.05, † indicates p-value of <0.10)

A.3 Standardized coefficients of Proportion of Agricultural Cover at 1, 2, and 3 km scales in generalized

mixed models of bat responses to landscape predictor variables (error bars show 95% confidence intervals, * indicates a p-value of <0.05, † indicates p-value of <0.10)

Appendix B **Correlations between bat responses and landscape variables**

B.1 Correlations between Bat Responses and Log of Mean Field Size at 3 km in study landscapes in Eastern Ontario

B.2 Correlations between Bat Responses and Shannon Diversity of Agriculture at 3 km in study landscapes in Eastern Ontario

B.3 Correlations between Bat Responses and Proportion of Agriculture at 3 km in study landscapes in Eastern

Ontario

Appendix C Pearson correlations between percentage forest cover at 3 km scale and bat response variables recorded in acoustic surveys in agricultural Eastern Ontario study landscapes

Response	Forest (3km)
Species Richness	0.2465
Total Activity	0.264
<i>L. noctivagans</i>	0.11
<i>M. septentrionalis</i>	-0.0354
<i>M. lucifugus</i>	0.1517
<i>L. cinereus</i>	0.2388
<i>L. borealis</i>	0.2943
<i>E. fuscus</i>	0.2081
<i>P. subflavus</i>	0.2222

Appendix D **Raw Data – Bat Responses: Species richness, total number of calls, and calls per species recorded at each surveying point on a given night**

Landscape		Point	Julian Date	Total Activity	UnID	<i>L. noctivagans</i>	<i>M. septentrionalis</i>	<i>M. lucifugus</i>	<i>L. cinereus</i>	<i>L. borealis</i>	<i>E. fuscus</i>	<i>P. subflavus</i>	Species Richness
HH11	HH11.1		170	6	1	0	0	0	5	0	0	0	1
HH11	HH11.2		170	5	3	1	0	0	1	0	0	0	2
HH18	HH18.1		162	15	0	0	0	0	11	0	4	0	2
HH18	HH18.1		198	15	0	0	0	0	13	0	2	0	2
HH18	HH18.2		198	2	0	0	0	0	1	0	1	0	2
HH19	HH19.1		169	6	1	0	0	0	5	0	0	0	1
HH19	HH19.1		206	4	1	0	0	0	3	0	0	0	1
HH19	HH19.5		169	33	1	0	0	1	6	0	25	0	3
HH19	HH19.5		206	37	0	0	0	1	4	0	31	1	4
HH2	HH2.3		151	4	2	1	0	0	1	0	0	0	2
HH2	HH2.2		151	40	1	1	2	2	11	1	21	1	7
HH208	HH208.4		197	19	7	0	0	0	12	0	0	0	1
HH208	HH208.2		197	18	0	0	0	0	15	1	2	0	3
HH22	HH22.3		156	1	0	0	0	0	0	0	1	0	1
HH22	HH22.3		192	8	0	0	0	0	7	0	1	0	2
HH22	HH22.2		192	26	2	0	0	1	20	3	0	0	3
HH24	HH24.1		190	0	0	0	0	0	0	0	0	0	0
HH24	HH24.3		190	0	0	0	0	0	0	0	0	0	0
HH24	HH24.2		144	15	0	0	0	1	12	0	1	1	4
HH26	HH26.1		180	2	0	0	0	0	2	0	0	0	1
HH26	HH26.3		149	2	0	0	0	0	2	0	0	0	1
HH26	HH26.3		180	17	0	0	0	1	16	0	0	0	2
HH26	HH26.1		149	23	2	1	0	1	14	0	4	1	5
HH27	HH27.1		163	82	1	1	0	4	42	0	34	0	4
HH27	HH27.3		163	34	1	0	0	0	26	1	6	0	3
HH29	HH29.2		211	7	0	0	0	0	3	0	2	2	3
HH29	HH29.4		211	14	0	0	0	0	10	1	0	3	3
HH3	HH3.3		171	10	1	0	0	0	9	0	0	0	1
HH3	HH3.4		171	30	0	0	0	0	27	1	1	1	4
HH5	HH5.2		181	4	1	0	0	0	1	0	2	0	2
HH5	HH5.4		181	10	1	0	0	0	8	0	1	0	2
HH5	HH5.2		158	50	0	5	3	3	13	4	19	3	7

HH6	HH6.1	193	4	0	0	0	0	4	0	0	0	1
HH6	HH6.2	193	8	0	0	0	0	5	0	2	1	3
HH6	HH6.1	157	18	1	0	0	1	13	1	1	1	5
HH7	HH7.1	145	7	0	0	0	0	3	0	4	0	2
HH7	HH7.3	199	32	18	1	0	0	5	0	8	0	3
HH7	HH7.1	199	7	3	2	1	0	1	0	0	0	3
HH7	HH7.3	145	27	2	1	1	1	3	3	14	2	7
HH8	HH8.1	179	13	2	0	0	0	8	0	3	0	2
HH8	HH8.4	179	32	1	1	1	0	16	0	13	0	4
HH9	HH9.4	172	5	0	0	0	0	5	0	0	0	1
HH9	HH9.3	198	5	0	0	0	0	5	0	0	0	1
HH9	HH9.3	172	32	1	0	1	0	16	0	14	0	3
HH9	HH9.4	198	214	2	5	1	0	148	4	54	0	5
HL207	HL207.2	186	102	1	1	4	13	52	8	19	4	7
HL215	HL215.2	165	16	0	0	0	0	14	0	2	0	2
HL215	HL215.3	214	17	2	0	0	0	14	0	1	0	2
HL215	HL215.2	214	33	3	0	0	0	27	1	2	0	3
HL31	HL31.4	201	33	17	3	0	0	8	0	5	0	3
HL31	HL31.5	201	39	0	0	0	1	33	3	1	1	5
HL35	HL35.4	187	41	9	2	0	0	1	0	29	0	3
HL36	HL36.4	207	2	0	0	0	0	2	0	0	0	1
HL36	HL36.1	150	8	2	0	0	1	2	0	3	0	3
HL36	HL36.4	150	18	4	0	0	0	6	4	4	0	3
HL36	HL36.3	207	13	2	0	1	3	3	1	2	1	6
HL39	HL39.1	201	116	1	0	0	0	111	1	3	0	3
HL40	HL40.2	165	4	0	0	0	0	4	0	0	0	1
HL40	HL40.7	214	6	0	0	0	0	6	0	0	0	1
HL40	HL40.1	214	38	0	0	1	1	29	1	4	2	6
HL44	HL44.4	206	44	1	2	0	2	31	0	6	2	5
HL59	HL59.4	163	211	2	2	0	1	120	0	86	0	4
HL59	HL59.1	163	40	2	0	0	1	27	3	7	0	4
LH216	LH216.4	159	3	1	1	0	0	1	0	0	0	2
LH216	LH216.2	159	29	2	0	0	0	24	0	2	1	3
LH68	LH68.3mo d	212	3	0	0	0	0	2	0	1	0	2
LH68	LH68.4	212	80	1	0	0	1	15	2	61	0	4
LH72	LH72.6	194	16	1	0	1	1	6	0	7	0	4
LH72	LH72.8	194	7	0	0	1	0	3	0	2	1	4
LH73	LH73.2	149	34	1	0	0	0	24	0	9	0	2
LH73	LH73.2	200	3	0	0	0	0	2	0	1	0	2
LH73	LH73.3	200	8	0	0	0	0	7	0	1	0	2
LH74	LH74.4	200	91	2	1	1	6	27	0	53	1	6
LH82	LH82.2	173	3	0	0	0	0	3	0	0	0	1

LH82	LH82.4	173	16	0	0	0	0	10	0	6	0	2
LH87	LH87.1	185	9	0	0	0	1	3	0	5	0	3
LH87	LH87.3	185	13	0	0	0	0	11	1	1	0	3
LL102	LL102.2	190	13	0	0	0	0	13	0	0	0	1
LL102	LL102.4	190	9	0	0	0	0	8	0	1	0	2
LL105	LL105.2	156	6	0	0	0	0	6	0	0	0	1
LL105	LL105.1	156	5	0	0	0	1	3	1	0	0	3
LL118	LL118.2	181	37	1	2	0	0	26	4	3	1	5
LL118	LL118.3	181	67	3	1	1	0	55	1	4	2	6
LL20	LL20.1	180	3	0	0	0	0	3	0	0	0	1
LL20	LL20.1	208	8	0	0	0	0	8	0	0	0	1
LL20	LL20.3	208	1	0	0	0	0	1	0	0	0	1
LL202	LL202.1	194	2	0	0	0	0	1	0	1	0	2
LL202	LL202.2	204	60	5	1	0	3	33	0	17	1	5
LL202	LL202.1	204	60	2	1	0	4	33	0	18	2	5
LL203	LL203.2	158	15	6	2	0	0	4	0	3	0	3
LL203	LL203.5alt	158	5	2	0	0	1	2	0	0	0	2
LL204	LL204.4	145	1	0	0	0	0	1	0	0	0	1
LL204	LL204.4	186	48	16	10	0	0	15	0	7	0	3
LL211	LL211.6	172	18	1	0	0	0	5	0	12	0	2
LL211	LL211.3	172	18	8	2	0	1	2	0	5	0	4
LL217	LL217.2	191	32	1	2	0	0	14	0	15	0	3
LL217	LL217.3	159	101	5	0	4	27	31	1	33	0	5
LL217	LL217.2	178	58	1	2	0	2	34	3	16	0	5
LL217	LL217.3	191	3	0	0	0	0	2	0	0	1	2
LL217	LL217.3	178	199	9	6	7	36	39	0	99	3	6
LL75	LL75.2	160	7	0	0	0	0	6	1	0	0	2
LL75	LL75.4	160	7	0	0	1	2	0	1	2	1	5
LL79	LL79.4	166	0	0	0	0	0	0	0	0	0	0
LL79	LL79.1	166	8	0	0	3	1	1	1	2	0	5
LL80	LL80.2	157	4	3	0	0	0	1	0	0	0	1
LL80	LL80.4	157	8	0	0	0	0	6	1	1	0	3
LL91	LL91.6	169	12	1	0	0	0	9	1	1	0	3
LL93	LL93.1	162	1	1	0	0	0	0	0	0	0	0
LL93	LL93.4	162	10	1	0	0	0	8	1	0	0	2

Appendix E **Raw Data – Insect totals and potential confounding variables at
surveying points on a given night**

Point	Julian Date	Moon Minutes	Moth Total	Beetle Total	Fly Total	Hym Total	Insects Total	Insects 0-5mm	Insects 5-10mm	Insects 10-15mm	Insects 15+mm,,	Temp Avg	Wind Avg	Rain Avg
HH11.1	170	0	0	3	9	0	14	5	0	0	0	16.24	1.03	4.37
HH11.2	170	0	3	0	10	0	17	3	1	3	0	16.24	1.03	4.37
HH18.1	162	0	0	6	23	0	59	6	1	0	0			
HH18.1	198	0	0	10	11	0	22	7	3	0	1	24.71	4.91	0.00
HH18.2	198	0	0	5	16	2	24	6	0	1	1	24.71	4.91	0.00
HH19.1	169	0	0	1	35	0	37	0	0	1	0	21.87	6.77	0.00
HH19.1	206	4819.1	0	8	84	3	97	10	1	2	0	18.90	0.00	5.14
HH19.5	169	0	0	6	28	4	42	10	3	0	1	21.87	4.53	0.00
HH19.5	206	4819.1	2	4	29	0	37	3	3	1	0	18.90	0.00	5.14
HH2.3	151	13284										18.90	0.00	5.14
HH2.2	151	13284										18.90	0.00	5.14
HH208.4	197	0										21.49	0.00	6.30
HH208.2	197	0	1	9	86	3	101	13	2	0	0	21.49	0.00	6.30
		15184.												
HH22.3	156	8	0	1	6	0	7	1	0	0	0			
HH22.3	192	0	0	1	2	1	5	3	0	0	0	21.49	0.00	6.30
HH22.2	192	0	2	9	12	0	31	16	1	1	0	21.49	0.00	6.30
HH24.1	190	2046.6	0	5	35	7	49	14	0	0	0	27.81	6.94	0.00
HH24.3	190	2046.6	0	6	22	2	34	7	5	0	0	27.81	6.94	0.00
HH24.2	144	994	1	8	12	2	30	15	2	0	1	23.31	0.00	0.00
HH26.1	180	12762	0	12	20	9	44	23	1	0	0	21.64	0.00	0.00
HH26.3	149	12762	0	1	15	3	27	8	0	1	0	21.64	0.00	0.00
HH26.3	180	12762	0	40	22	1	66	40	2	1	1	20.68	0.00	0.00
HH26.1	149	9252	0	2	22	2	30	8	0	0	0	23.31	0.00	0.00
HH27.1	163	0	0	10	28	3	59	29	2	0	0	22.70	0.51	0.00
HH27.3	163	0	0	4	35	6	81	39	2	0	0	22.70	0.51	0.00
HH29.2	211	15858	0	7	11	0	22	9	1	1	0	21.81	1.19	0.00
HH29.4	211	15858	0	2	4	3	11	6	0	1	0	21.81	1.19	0.00
HH3.3	171	0										15.87	0.31	0.00
HH3.4	171	0	1	1	3	1	9	5	1	0	0	15.87	0.31	0.00

HH5.2	181	14634	0	2	34	0	42	8	0	0	0	17.77	0.00	0.00
HH5.4	181	14634	1	3	2	0	8	4	2	0	0	17.77	0.00	0.00
HH5.2	158	4950.4	0	0	9	0	10	0	0	1	0			
HH6.1	193	0	0	0	12	0	13	1	0	0	0	11.87	0.00	0.00
HH6.2	193	0	0	4	27	0	33	6	0	0	0	11.87	0.00	0.00
HH6.1	157	9612.7	3	5	31	0	39	4	2	2	0	16.14	0.87	0.00
HH7.1	145	2270.4	0	1	33	6	42	9	0	0	0	15.24	0.16	0.00
HH7.3	199	0												
HH7.1	199	0												
HH7.3	145	2270.4	0	0	0	0	0	0	0	0	0	15.24	0.16	0.00
HH8.1	179	10728	2	1	72	0	75	2	0	2	0	15.84	5.59	0.00
HH8.4	179	10728	4	0	10	1	15	3	0	2	0	15.84	5.59	0.00
HH9.4	172	63.7	3	8	12	1	24	3	8	1	0	24.37	8.12	0.00
HH9.3	198	0	1	3	13	1	18	1	4	1	0	22.14	3.33	0.00
HH9.3	172	63.7	4	0	10	1	15	3	0	2	0	22.14	3.33	0.00
HH9.4	198	0	2	4	11	1	18	2	4	1	1	24.37	8.12	0.00
		14043.												
HL207.2	186	6	0	3	7	2	15	7	1	0	0	17.37	0.00	0.86
HL215.2	165	17766	0	1	9	0	12	1	1	1	0	18.09	0.36	0.00
HL215.3	214	17766	6	2	8	0	16	4	2	0	4	15.77	0.00	0.00
HL215.2	214	0	2	4	7	0	14	5	1	1	0	15.77	0.00	0.00
HL31.4	201	1.5										19.81	0.63	1.93
HL31.5	201	1.5	5	1	4	1	11	3	6	2	1	20.20	0.00	0.00
		10368.												
HL35.4	187	3										19.81	0.63	1.93
HL36.4	207	8118	2	1	14	3	20	2	4	2	0	10.17	0.16	0.00
HL36.1	150	11304	6	2	5	0	13	4	2	2	1	20.20	0.00	0.00
HL36.4	150	11304	1	7	24	0	32	1	16	0	0	18.70	0.00	0.00
HL36.3	207	8118	1	0	1	0	2	1	0	0	0	13.79	0.00	0.00
HL39.1	201	1.5	7	3	20	3	33	7	14	0	0	18.70	0.00	0.00
HL40.2	165	0	1	5	7	0	13	1	6	1	0	15.10	0.00	0.00
HL40.7	214	17766	0	3	3	0	11	6	2	0	0	25.06	5.63	0.00
HL40.1	214	17766	5	1	4	0	10	4	1	0	1	25.06	5.63	0.00
						1								
HL44.4	206	4819.1	0	4	20	5	46	23	3	0	0	20.37	0.00	10.67
HL59.4	163	0	0	11	7	5	30	22	1	0	0	20.37	0.00	10.67
HL59.1	163	0	1	48	15	0	67	12	40	0	0	20.37	0.00	10.67
LH216.4	159	0										22.27	4.04	0.00
LH216.2	159	1419.2	0	5	5	2	18	12	1	0	0	22.27	4.04	0.00
LH68.3mo d	212	17046	0	0	0	0	0	0	0	0	0	15.37	0.36	0.00
LH68.4	212	17046	1	1	10	0	13	2	1	0	0	15.37	0.36	0.00
LH72.6	194	0	2	2	6	0	12	3	3	0	0	15.39	1.07	5.36
LH72.8	194	0	0	1	2	0	6	0	0	0	1	15.39	1.07	5.36
LH73.2	149	9252	0	0	3	0	6	0	0	0	0	15.81	0.36	6.17

LH73.2	200	0	0	0	9	0	10	1	0	0	0	15.00	0.67	0.00
LH73.3	200	0	0	1	10	0	12	1	0	0	1	15.00	0.67	0.00
LH74.4	200	0	0	2	0	0	3	2	0	0	1	15.33	3.03	0.00
LH82.2	173	386.4	0	0	2	0	3	1	0	0	0			
LH82.4	173	386.4	0	11	15	0	27	7	2	2	3			
LH87.1	185	17892	0	16	89	0	105	13	2	1	0	20.56	4.71	3.13
LH87.3	185	17892	1	3	6	0	27	18	1	0	2	20.56	4.71	3.13
LL102.2	190	2046.6	2	4	6	0	13	3	3	1	0	20.97	4.00	0.00
LL102.4	190	2046.6	0	5	6	0	11	3	1	0	1	20.97	4.00	0.00
		15184.										13.1		
LL105.2	156	8	0	3	5	2	11	5	1	0	0	10.22	5	0.00
		15184.										13.1		
LL105.1	156	8	0	7	14	0	22	7	0	1	0	10.22	5	0.00
LL118.2	181	14634	0	2	3	0	8	4	0	0	1	12.84	0.00	13.11
LL118.3	181	14634	0	0	13	2	20	6	0	1	0	12.84	0.00	13.11
LL20.1	180	12762	0	0	5	0	5	0	0	0	0	23.16	6.36	3.84
LL20.1	208	10260	0	0	3	0	4	1	0	0	0	12.20	0.16	0.00
LL20.3	208	10260	0	8	18	0	26	8	0	0	0	12.20	0.16	0.00
LL202.1	194	0	1	7	6	0	15	7	2	0	0	21.26	2.94	0.00
LL202.2	204	1261.5	3	1	4	0	10	3	2	1	0	23.16	6.36	3.84
LL202.1	204	1261.5	3	3	16	1	28	7	3	0	2	23.16	6.36	3.84
LL203.2	158	4950.4	0	1	13	0	15	2	0	0	0	23.43	3.53	0.00
LL203.5alt	158	2856	1	2	7	0	11	3	0	0	1	23.43	3.53	0.00
		14043.												
LL204.4	145	6	0	5	4	0	9	4	0	1	0	16.44	0.16	0.00
LL204.4	186	2270.4												
LL211.6	172	63.7	0	2	10	0	16	4	0	1	1	22.96	6.79	0.00
LL211.3	172	63.7	0	2	35	0	40	0	2	3	0	22.96	6.79	0.00
LL217.2	191	8622	2	2	14	6	32	16	1	0	1	22.91	1.14	0.47
LL217.3	159	1419.2	2	24	9	1	38	7	20	0	2	12.00	0.99	0.00
LL217.2	178	132.6	0	4	11	3	31	18	2	0	0	26.08	2.27	33.51
LL217.3	191	8622	0	0	2	0	3	1	0	0	0	22.91	1.14	0.47
LL217.3	178	132.6	1	6	13	1	23	4	6	0	0	26.08	2.27	33.51
LL75.2	160	0	0	4	6	2	19	10	3	0	0	21.26	0.36	0.00
LL75.4	160	0	1	5	4	1	16	9	4	2	0	21.26	0.36	0.00
LL79.4	166	0	0	4	22	0	52	4	0	0	0	15.00	5.96	1.63
LL79.1	166	0	0	4	8	3	32	6	3	0	0	15.00	5.96	1.63
LL80.2	157	9612.7	0	0	17	0	17	0	0	0	0	12.30	0.51	0.00
						1								
LL80.4	157	9612.7	0	2	33	7	82	48	1	0	0	12.30	0.51	0.00
LL91.6	169	0	0	5	20	6	67	15	1	0	0	15.06		13.93
LL93.1	162	0										12.30	0.51	0.00
						1								
LL93.4	162	0	0	0	28	2	80	52	0	0	0	12.30	0.51	0.00

Appendix F **Raw Data – Study landscapes: Location, Log of mean field size, proportion agricultural cover, Shannon Diversity of agriculture, and proportion forest cover**

Landscape	Center Point UTM Zone 18T (Northing, Easting)	LogMFS 1km	LogMFS 2km	LogMFS 3km	PCTAG 1km	PCTAG 2km	PCTAG 3km	SHDI 1km	SHDI 2km	SHDI 3km	Forest 1km	Forest 2km	Forest 3km
HH11	5009832.0696, 488333.4720	4.523	4.721	4.764	0.666	0.737	0.793	0.995	1.111	1.228	0	0.007	0.005
HH18	5003675.4656, 475107.3701	4.809	4.821	4.795	0.838	0.761	0.782	1.04	1.276	1.387	0.088	0.03	0.044
HH19	5009882.8149, 467946.5324	4.737	4.732	4.722	0.709	0.688	0.691	1.26	1.257	1.405	0.052	0.116	0.097
HH2	4990228.4823, 470439.9725	4.588	4.569	4.568	0.736	0.677	0.625	1.244	1.563	1.624	0.095	0.058	0.04
HH208	4976829.6297, 467382.8993	4.791	4.861	4.787	0.928	0.89	0.789	0.723	0.935	1.115	0	0.026	0.102
HH22	5031823.9146, 470476.7552	4.717	4.576	4.608	0.937	0.809	0.77	0.874	1.405	1.356	0	0.023	0.068
HH24	4994932.1790, 457278.0681	4.577	4.676	4.67	0.831	0.771	0.733	1.066	1.179	1.314	0.036	0.121	0.151
HH26	5004284.1193, 482333.5322	4.378	4.645	4.782	0.621	0.706	0.713	1.172	0.996	0.955	0.201	0.132	0.134
HH27	4998421.2130, 459573.8776	4.967	4.635	4.65	0.835	0.722	0.654	0.551	1.396	1.555	0.116	0.153	0.215
HH29	4982244.9063, 467731.9985	4.9	4.912	4.882	0.875	0.817	0.788	0.578	1.086	1.13	0	0.018	0.048
HH3	5016571.8448, 462984.2220	4.864	4.687	4.698	0.804	0.56	0.538	0.274	0.887	1.317	0.139	0.226	0.193
HH5	4979168.2671, 473516.2255	4.933	4.887	4.884	0.942	0.849	0.825	0.563	0.974	1.266	0	0.073	0.074
HH6	5008474.0765, 483517.0039	4.662	4.585	4.714	0.872	0.702	0.718	1.058	1.372	1.232	0.051	0.096	0.104
HH7	5010051.2186, 433890.7714	4.674	4.795	4.725	0.708	0.748	0.684	0.822	0.953	1.056	0.056	0.052	0.074
HH8	5022529.0491, 505368.5493	4.641	4.72	4.804	0.787	0.709	0.715	0.894	1.306	1.371	0.003	0.056	0.048
HH9	5004491.1019, 487046.2994	5.008	5.022	4.968	0.917	0.816	0.795	0.719	0.99	1.093	0.005	0.006	0.019
HL207	4985718.3203, 471026.5420	4.498	4.721	4.795	0.913	0.921	0.873	0.812	1.014	1.211	0	0	0.005
HL215	5020344.6511, 501316.1707	4.633	4.714	4.829	0.903	0.868	0.885	1.235	1.485	1.5	0	0.003	0.007
HL31	4985489.6337, 463309.6311	4.304	4.496	4.621	0.645	0.642	0.683	1.184	1.409	1.268	0.135	0.154	0.144

HL35	4997517.9591, 497754.8918	4.714	4.642	4.679	0.829	0.636	0.637	0.424	0.955	1.174	0.062	0.247	0.227
HL36	5003163.3341, 478847.4310	4.11	4.351	4.541	0.605	0.667	0.714	1.458	1.5	1.423	0.173	0.137	0.133
HL39	4970806.3585, 476130.8404	4.394	4.497	4.536	0.693	0.676	0.679	1.456	1.69	1.553	0.078	0.185	0.183
HL40	5014450.8618, 484299.7690	4.59	4.518	4.584	0.739	0.487	0.511	0.971	1.588	1.566	0.045	0.234	0.23
HL44	5013991.4040, 466244.5001	4.627	4.646	4.66	0.677	0.675	0.624	1.75	1.739	1.604	0.234	0.159	0.196
HL59	4992540.9543, 439652.7659	4.752	4.779	4.711	0.847	0.706	0.628	1.075	1.199	1.324	0.051	0.088	0.145
LH216	5027790.2991, 513496.5654	5.104	4.847	4.862	0.89	0.808	0.793	1.057	1.174	1.351	0.085	0.089	0.106
LH68	4993285.1031, 480768.7873	4.551	4.717	4.744	0.782	0.703	0.683	1.026	1.253	1.291	0.234	0.159	0.196
LH72	4981836.7118, 439320.7956	4.586	4.533	4.555	0.656	0.64	0.506	0.859	1.253	1.392	0	0.04	0.186
LH73	4998429.4011, 474403.5486	5.023	5.141	4.971	0.949	0.864	0.81	0.885	1.049	1.155	0	0.018	0.074
LH74	4974046.4787, 471119.8557	4.885	4.758	4.765	0.921	0.802	0.764	0.954	1.163	1.249	0	0.051	0.081
LH82	4995188.3787, 467227.7627	4.706	4.672	4.714	0.712	0.598	0.649	1.046	1.513	1.665	0.022	0.033	0.077
LH87	5010629.9988, 446666.2300	4.654	4.87	4.917	0.856	0.889	0.853	1.322	1.508	1.499	0	0.01	0.042
LL102	4970176.9070, 471599.8094	4.441	4.543	4.521	0.497	0.48	0.394	0.579	1.033	1.288	0.155	0.205	0.233
LL105	5015179.3932, 476199.8999	4.505	4.61	4.648	0.64	0.631	0.548	0.693	0.91	1.152	0.043	0.053	0.136

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