Medical and Veterinary Entomology (2016), doi: 10.1111/mve.12193

Mosquitoes of field and forest: the scale of habitat segregation in a diverse mosquito assemblage

M. H. REISKIND[1], R. H. GRIFFIN[2], M. S. JANAIRO[1] and K. A. HOPPERSTAD[1]

[1]Department of Entomology, North Carolina State University, Raleigh, NC, U.S.A. and [2]Department of Evolutionary Anthropology, Duke University, Durham, NC, U.S.A.

Abstract. Knowledge of the distribution of arthropod vectors across a landscape is important in determining the risk for vector-borne disease. This has been well explored for ticks, but not for mosquitoes, despite their importance in the transmission of a variety of pathogens. This study examined the importance of habitat, habitat edges, and the scale at which mosquito abundance and diversity vary in a rural landscape by trapping along transects from grassland areas into forest patches. Significant patterns of vector diversity and distinct mosquito assemblages across habitats were found. The scale of individual species' responses to habitat edges was often dramatic, with several species rarely straying even 10 m from the edge. The present results suggest blood-seeking mosquito species are faithful to certain habitats, which has consequences for patterns of vector diversity and risk for pathogen transmission. This implies that analysts of risk for pathogen transmission and foci of control, and developers of land management strategies should assess habitat at a finer scale than previously considered.

Key words. Disease ecology, habitat edges, landscape ecology, vector-borne pathogens.

Introduction

The natural nidality of a vector-borne disease refers to the coincidence of host, vector and pathogen in the landscape, each of which is necessary for disease transmission (Pavlovsky, 1966). In vector-borne disease systems the rate of pathogen transmission may vary with changes in host and vector diversity, abundance and distribution across a landscape, resulting in spatial heterogeneity in disease transmission. Therefore, understanding the geography of host and vector diversity and abundance is critical to predicting where disease transmission will occur. The scale at which these factors occur is also important as regional species lists may not capture local distributions of vectors or hosts, and a habitat-based approach may be more precise (Reisen, 2010). This would allow for the fine-scale prediction of risk associated with mosquito-borne disease and the provision of appropriate control that minimizes non-target impacts.

Vector incrimination, in which a single species is implicated as the most important vector for a given pathogen, has dominated the study of vector-borne disease transmission since the early 20th century (Bradley, 1994). However, many vector-borne pathosystems, such as those of Rift Valley fever virus, dog heartworm and human lymphatic filarial worms, may involve a variety of mosquito vectors (Turell *et al.*, 2008; Manguin *et al.*, 2010; Farajollahi *et al.*, 2011; Ledesma & Harrington, 2011). The issue of how biodiversity affects the transmission of disease has been well studied, but overwhelmingly from the perspective of how the diversity of hosts (not vectors) affects transmission (Keesing *et al.*, 2006; Ostfeld & Keesing, 2012). The diversity of vectors in a vector-borne pathosystem has received scant attention and any examinations have been primarily descriptive (Foley & Piovia-Scott, 2014). Both patterns of vector diversity and the distributions of particular species may be critical determinants of the spatial dynamics of vector-borne disease.

The importance of vector distributions has been demonstrated at a coarse scale. For example, European colonists established retreats in highland areas of the tropics to escape *Anopheles*-transmitted malaria (Harrison, 1978). At a fine scale, ectoparasite-transmitted pathogens, such as scrub typhus (*Orientia tsutsugamushi*), and tick-borne pathogens have been linked

Correspondence: Michael H. Reiskind, Campus Box 7613, Department of Entomology, NCSU, Raleigh, NC 27695-7613, U.S.A. Tel.: + 1 919-515-0719; Fax: + 1 919-515-7746; E-mail: mhreiski@ncsu.edu

to local habitats and focal exposures (Traub & Wisseman, 1974; Wilson *et al.*, 1990). However, variation in fine-scale habitat preferences across mosquitoes (Diptera: Culicidae) has scarcely been explored (Reisen, 2010). In a study limited to two sites and 9 days of sampling, comparisons of flying mosquitoes at night with resting mosquitoes during the day suggested that most species rest and host seek in similar habitats (pasture or forest) (Bidlingmayer & Hem, 1981). Other studies have focused on the vector of Western equine encephalitis in California, *Culex tarsalis* (Diptera: Culicidae), and describe a significant edge effect whereby more mosquitoes were captured at the ecotone between two habitats than within either habitat (Lothrop & Reisen, 2001; Thiemann *et al.*, 2011). More recently, several studies have examined assemblages of adult mosquitoes and demonstrated that certain species are consistently found in forested areas, whereas others are found in pasture or disturbed areas in the midwestern U.S.A. (O'Brien & Reiskind, 2013), tropical Australia (Steiger *et al.*, 2012), Thailand (Thongsripong *et al.*, 2013) and Japan (Hoshi *et al.*, 2014). This may have important consequences for the risk for mosquito-borne disease transmission, as has been described for West Nile virus vector *Culex* spp. in Illinois (Gardner *et al.*, 2014). However, these studies were not spatially explicit and thus cannot determine the scale over which mosquito distributions and diversity vary. Indeed, the distribution of host-seeking mosquitoes across habitats has scarcely been examined at a fine spatial scale (10s–100s of metres), although studies focusing on single species have examined dispersal in relatively homogeneous habitats (e.g. a scrapyard, a suburban neighbourhood) at this scale (Pumpuni & Walker, 1989; Maciel-de-Freitas *et al.*, 2010; Hamer *et al.*, 2014). Taken collectively, these studies suggest that adult host-seeking mosquitoes of different species may be more closely tied to certain habitats than has previously been appreciated, which has important consequences for patterns of vector diversity, risk for disease transmission, and control efforts (Lothrop *et al.*, 2002; Reisen, 2010).

To elucidate the importance and spatial scale of variation in mosquito species distributions across habitats, the hypothesis that host-seeking mosquito species are faithful to grassland, edge or forest habitats was tested herein. Habitat fidelity in multiple mosquito species was assessed by creating transects from grassland to woodlots. Based upon previous work, it was predicted that most mosquito species would show a high degree of habitat fidelity at a scale of less than 100 m (O'Brien & Reiskind, 2013). As previous authors have reported edge or ecotonal effects for mosquitoes, and edge effects are important for the fine-scale distribution of many taxa (Bidlingmayer & Hem, 1981; Lothrop & Reisen, 2001; Ries *et al.*, 2004), the present study also sampled near the edges between grassland and woodlot to investigate the importance of habitat edges in determining mosquito distributions.

Materials and methods

Study locations

Three agricultural/mixed-use landscapes ('sites') were selected for examination of habitat use by host-seeking female mosquitoes. These were the Lake Wheeler Experimental Farm on the North Carolina State University (NCSU) campus, the Prairie Ridge area (in sites controlled by both NCSU and the North Carolina Museum of Natural Sciences), and a private beef cattle farm near Durham, NC (Fig. 1A–C). Using aerial images (Google Earth, accessed between 1 April and 15 May 2014), three 200-m transects each encompassing 100 m of forest and 100 m of open grassland ('transects') were plotted within each landscape (Fig. 1D). Five sampling locations ('locations') were placed on each transect, including one at each end, one in each of the forest and field sides at 10 m from the forest/grassland

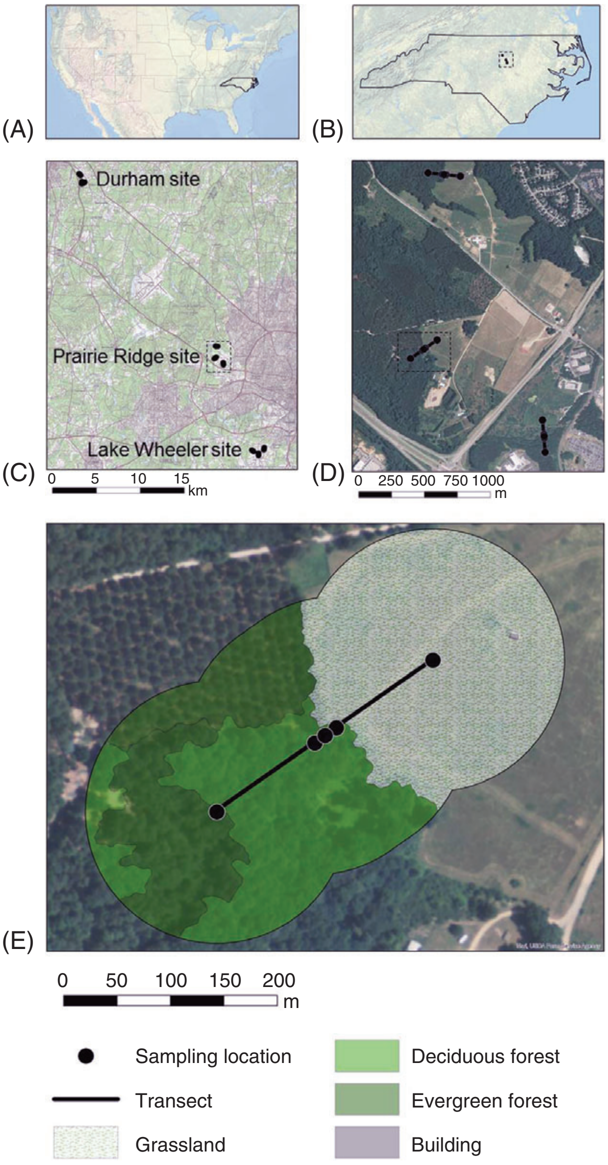

Fig. 1. (A, B) Location of study sites in North Carolina, U.S.A.. (C) Three study sites within the Raleigh–Durham metropolitan area (note black transect markers). (D) Three transects (black lines) at the Prairie Ridge study site. (E) One transect at the Prairie Ridge site, showing 100-m circles around each sampling location (black dots) with hand-digitized land classifications.

edge, and one at the forest/grassland edge (Fig. 1E). At each sampling location, a 1.3-m piece of steel rebar was placed. As several of the grassland locations were active pastures for cows or horses, each piece of rebar was covered with a piece of PVC pipe between uses.

Trapping protocol

Following O'Brien & Reiskind (2013), a Centers for Disease Control and Prevention (CDC) miniature light trap (John W. Hock & Co. Gainesville, FL, U.S.A.) was set at each location (without the light enabled) once every 2 weeks from 5 June to 21 October 2014. The trap was baited with 1 kg of solid carbon dioxide (CO_2) placed in a 1-gallon, insulated drink cooler. Both the trap and cooler were hung on a T-shaped PVC frame mounted on the preinstalled rebar. Traps were set between 14.00 hours and 16.00 hours and collected between 08.00 hours and 11.00 hours the following day. Over the course of the sampling period, 10 trap failures occurred over 459 trap nights (a 2.2% failure rate).

Sample sorting and identification

After trapping, samples were brought to the laboratory where they were killed and stored at −20 °C until processing. Samples were sorted into mosquitoes and non-mosquitoes. Mosquitoes were identified to species following Darsie & Ward (2005) and Burkett-Cadena (2013). The area sampled falls within a hybrid zone between *Culex pipiens* and *Culex quinquefasciatus*, and these species could not be separated (Huang *et al.*, 2011). Likewise, *Anopheles quadrimaculatus* and *Anopheles smaragdinus* (Diptera: Culicidae) were not distinguished, and *An. quadrimaculatus s.l.* was used to designate both of these species.

Land use classification

Aerial 6-in. ground resolution imagery was gathered from U.S. Geological Survey (USGS) Earth Explorer [http://earthexplorer.usgs.gov; North Carolina Center for Geographic Information & Analysis (NC CGIA)] for each site. ESRI ARCMAP Version 10.2.2 (Environmental Systems Research Institute, Redlands, CA, U.S.A.) was used to quantify land cover types within 100 m of each sampling location. A circle with a radius of 100 m was drawn around each trap location, and all features within the circle were digitally classified into one of eight categories: grassland; deciduous tree canopy; evergreen tree canopy; mixed tree canopy; shrub; cultivated crops; barren land, and pavement and buildings.

Statistical analysis

Because this study was focused on testing an explicit spatial hypothesis, total catches per mosquito species were pooled for each location across the 11 sampling periods, yielding a site × species mosquito abundance matrix. Although there are seasonal patterns of species activity (Carpenter & LaCasse, 1955; Lampman & Novak, 1996), the present study focused strictly on spatial, rather than temporal, species segregation. Over the 11 sampling periods, five habitats experienced a single failure ($n = 10$ trap nights), two habitats experienced two trap failures ($n = 9$ trap nights), and the remaining 38 traps experienced no failure ($n = 11$ trap nights). A square root transformation was applied to the raw mosquito species counts to dampen the effect of dominant species and the transformed counts were then divided by the number of trap nights to control for differing numbers of trap nights (caused by trap failures). One-way analysis of variance (ANOVA) was used to test for differences across habitat types in three measures of community diversity: (a) species richness, defined as the total number of species caught; (b) the Shannon–Weiner index, a measure of species diversity weighted by relative abundance (Magurran, 2004), and (c) rarefied species richness, which estimates species richness using rarefaction to account for differences in abundances of mosquitoes between trap locations (Hurlburt, 1971; Heck *et al.*, 1975). A sample size of 15, the lowest total trap count for any site, was used to estimate rarefied richness.

All statistical analyses were performed in R Version 3.2.2 (R Core Team, 2014), with community diversity estimation and ordination methods implemented in the R package 'vegan' (Oksanen *et al.*, 2015). The segregation of mosquito species along environmental gradients was explored with a partial canonical correspondence analysis (pCCA), which treats a site × species abundance matrix as the response and an environmental data matrix as the predictor in multivariate multiple regression, with gradient axes constrained as linear combinations of the environmental variables (Ter Braak, 1987). A key advantage of pCCA is that the influence of some environmental variables (i.e. covariables) can be partialled out, making it possible to assess the effects of those environmental variables that are of primary interest while controlling for other between-site differences. A pCCA was run with the site × species abundance matrix as the response, the environmental variables %DeciduousForest, %EvergreenForest, %MixedForest, %Grassland and %Shrub as predictor variables, and the environmental variables %BarrenLand, %Buildings, %CultivatedCrops and %Pavement as covariables.

Finally, generalized linear mixed models (GLMMs) were used to test the hypothesis that the abundance of each mosquito species differs across habitat types. Mosquito abundance was regressed against distance from the field, fitting models with negative binomial errors and log link functions. Because overall abundance may vary at the scale of transects, intercepts were allowed to vary randomly across transects. Akaike's information criterion (AIC) was used to compare the fit of two model structures for each species: firstly, a linear function was used to model an increase or decrease in abundance along transects ($y = \beta_1 x + \varepsilon$); secondly, a quadratic function was used to allow for an 'edge effect,' in which species abundance is highest at intermediate distances along transects ($y = \beta_1 x + \beta_2 x^2 + \varepsilon$), as has been reported for some species in previous studies (Bidlingmayer & Hem, 1981; Lothrop & Reisen, 2001). For the linear function, a significant positive slope indicates that the species favours forested habitat, and a negative slope indicates the species favours field habitat. As a test statistic for model comparison, the AIC of the linear model was subtracted from the AIC of the quadratic model and differences of < -2 were considered to indicate support for a model, < -5 to indicate strong support, and < -10 to indicate very strong support. All GLMMs were fit using the R package glmmADMB (Fournier *et al.*, 2012; Skaug & Yu, 2014).

For all GLMMs, residuals were inspected visually to assess model adequacy. If residuals appeared to deviate from normality, then, according to the nature of the deviation, some combination of log-transforming of abundance data, removal of outliers, and fitting of a zero-inflated model was attempted. If it proved impossible to model a given species adequately, as was anticipated for some rare species, that species was excluded from the GLMM analysis. For species that were excluded, a conservative approach was used to test the hypothesis that species abundance differs across habitat types using Mood's median test (Mood, 1954). This approach counts the number of observations within each group that fall above and below the global median of the dataset, and then employs a Fisher's exact test to determine whether one or more groups have a significantly different number of observations falling above or below the global median. Although this test has low power compared with alternatives such as regression, ANOVA and the Kruskal–Wallis test, it is robust to heteroscedasticity, non-normality and outliers as encountered with more rare species (Siegal & Castellan, 1988; Freidlin & Gastwirth, 2000).

Table 1. Abundances and percentages of mosquito species across all sites, all transects, from 1 June 2014 to 15 October 2014.

Genus	Species	Specimens *n*	%
Aedes	*vexans* (Meigen)	466	5.8
	cinereus (Meigen)	112	1.4
Anopheles	*crucians s.l.* Wiedmann	21	0.3
	punctipennis (Say)	102	1.3
	quadrimaculatus s.l. Say	62	0.8
Coquillettidia	*perturbans* (Walker)	24	0.3
Culex	*erraticus* (Dyar and Knab)	3460	43.1
	pipiens/quinquefasciatus L./Say	415	5.2
	salinarius Coquillett	563	7.0
Ochlerotatus	*atlanticus* Dyar and Knab	332	4.1
	canadensis (Theobald)	91	1.1
	dupreei (Coquillett)	36	0.5
	hendersoni Cockerell	26	0.3
	infirmatus Dyar and Knab	11	0.1
	triseriatus (Say)	65	0.8
	japonicus (Theobald)	12	0.2%
Psorophora	*ciliata* (Fabricius)	10	0.1
	columbiae (Dyar and Knab)	1033	12.9
	cyanescens (Coquilllett)	3	< 0.1
	ferox (Von Humboldt)	635	7.9
	howardi Coquillett	5	< 0.1
Stegomyia	*albopicta* (Skuse)	537	6.7%
Uranotaenia	*sapphirina* (Osten Sacken)	7	< 0.1
	Total	**8028**	**100**

Results

A total of 8028 female mosquitoes were captured, representing 23 species. Eight species accounted for ∼93% of the total collection (Table 1). The most common species was *Culex erraticus* (∼43% of the total), followed by *Psorophora columbiae* (Diptera: Culicidae) (∼13%), *Psorophora ferox* (∼8%), *Culex salinarius* (∼7%), *Stegomyia albopicta* (=*Aedes albopictus*) (Diptera: Culicidae) (∼7%), *Aedes vexans* (Diptera: Culicidae) (∼6%), *Cx. pipiens/quinquefasciatus* (∼5%), and *Ochlerotatus atlanticus* (=*Aedes atlanticus*) (Diptera: Culicidae) (∼4%). There was a significant association between richness and habitat, with mean richness increasing along transects from field to forest ($F = 2.95$, $P < 0.05$) (Fig. 2A). Shannon–Wiener diversity followed a similar pattern, although results were not significant ($F = 2.4$, $P = 0.07$) (Fig. 2B). Like richness, rarefied species richness showed a clear increase from field to forest ($F = 2.9$, $P < 0.05$) (Fig. 2C).

The pCCA results revealed that environmental variables explained a significant amount of variation in mosquito assemblages (ANOVA-like test conditioned on four covariables, 999 permutations; $F = 4.45$, $P < 0.001$) (Fig. 3A). After controlling for covariables, environmental variables explained 33.63% of variation in the current data. The first pCCA axis accounted for 65.16% of the total explained variation (eigenvalue: 0.25), and the second pCCA axis accounted for an additional 18.92% of the explained variance (eigenvalue: 0.07). Together, the first two pCCA axes accounted for 84.08% of the explained variation, or 28.28% of total variation in the data. The first pCCA axis represented a tree density gradient from field to forest sites, and the second pCCA axis reflected differences at the transect level (Fig. 3A). This second gradient corresponded with the characteristics of one site that had more grassland than shrub in the field sites, and more mixed and evergreen forest than deciduous forest in the forest habitats. Mosquito species segregated along both gradients, with stronger differentiation occurring along the tree density gradient (Fig. 3B). Over a third of the species showed a clear preference for forested habitat, particularly *Stegomyia*, *Aedes* and *Ochlerotatus* species. Of the forest-dwelling mosquitoes, *Ochlerotatus hendersoni* (=*Aedes hendersoni*), *Ochlerotatus triseriatus* (=*Aedes triseriatus*), *Uranotaenia sapphirina* (Diptera: Culicidae) and *S. albopicta* were more frequent in deciduous forest, *Ochlerotatus dupreei* (=*Aedes dupreei*), *O. atlanticus* and *Ochlerotatus japonicus* (=*Aedes japonicus*) were more frequent in mixed or evergreen forest, and *Ochlerotatus canadensis* (=*Aedes canadensis*), *Aedes cinerius*, *Ps. ferox* and *Psorophora howerdi* were forest generalists. Seven species were more common in field sites, with *Cx. pipiens/quinquefasciatus* and *Ochlerotatus infirmatus* (=*Aedes infirmatus*) occurring more frequently in shrub, *Psorophora ciliata*, *Ps. columbiae* and *Psorophora cyanescens* occurring more frequently in grassland, and *Cx. salinarius* and *An. quadrimaculatus* occurring equally in shrub and grassland. The remaining species clustered near the centre of the plot, indicating a lack of strong habitat association in the dataset, and included *Ae. vexans*, *Coquillettidia*

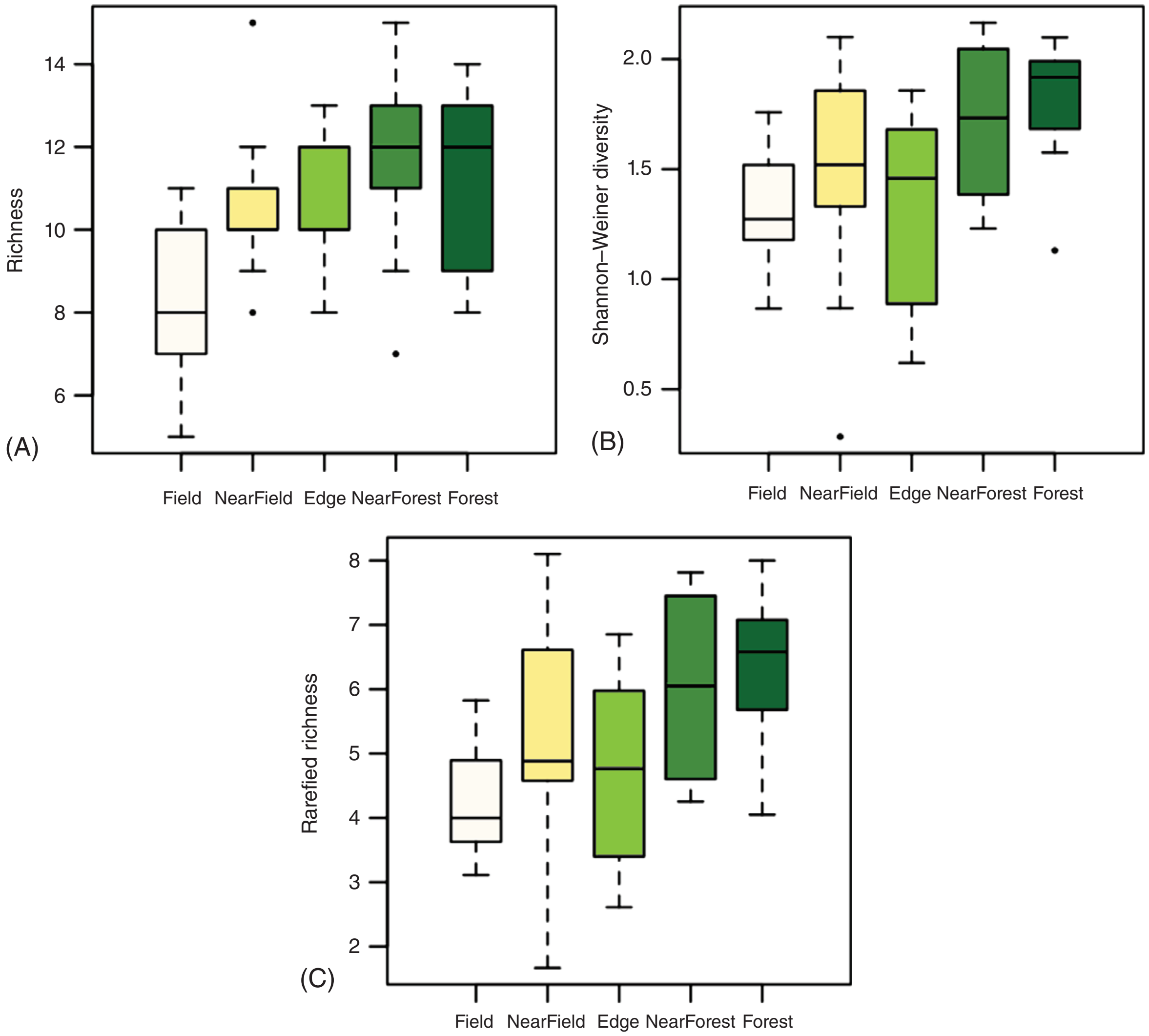

Fig. 2. (A) Mean species richness by habitat type ($n=9$). (B) Mean Shannon–Weiner diversity by habitat type ($n=9$). (C) Mean rarefied species richness by habitat type ($n=9$).

perturbans (Diptera: Culicidae), *Anopheles crucians*, *Anopheles punctipennis* and *Cx. erraticus*.

The GLMMs of species distributions in relation to the field–forest habitat gradient supported the results of the pCCA (Fig. 4, Table 2). It was possible to fit adequate models for 11 of the 23 species, which corresponded to all species with fewer than 18 non-zero abundances across the 45 trap sites. Log transformation improved model fit for all but two species (*Ae. cinereus* and *Cx. erraticus*), and fitting a zero-inflated model was necessary for one species because the optimization routine failed to converge without it (*Ps. ferox*, 24/45 zeroes). The quadratic model was strongly supported for one species, *S. albopicta*, and exhibited a maximum abundance at 58 m from the edge, indicating a preference for the interior of the forest, but near the edge (AIC difference > 6) (Table 2, Fig. 4). The linear model was favoured for all other species (Table 2). *Culex salinarius*, *Ps. columbiae*, *Cx. quinquefasciatus* and *An. quadrimaculatus* were significantly associated with grassland/field habitats, whereas *Ae. cinereus*, *Ps. ferox* and *O. triseriatus* were significantly associated with forested habitat (Table 2, Fig. 4). Three species examined, *Ae. vexans*, *An. punctipennis* and the abundant *Cx. erraticus*, showed no significant association with habitat ($P > 0.05$) (Table 2, Fig. 4). Among the rare species, *O. canadensis*, *O. atlanticus*, *O. hendersoni* and *O. dupreei* were significantly associated with forest habitats when examined with Mood's median test ($P < 0.05$). No other rare species were significantly associated with habitat (Figure S1).

Discussion

The present findings support the hypothesis that many host-seeking mosquitoes are faithful to habitats at a scale of less than 100 m, with 12 of 23 species showing significant habitat associations. The pCCA analysis revealed that mosquito species segregated along a tree density gradient that accounted

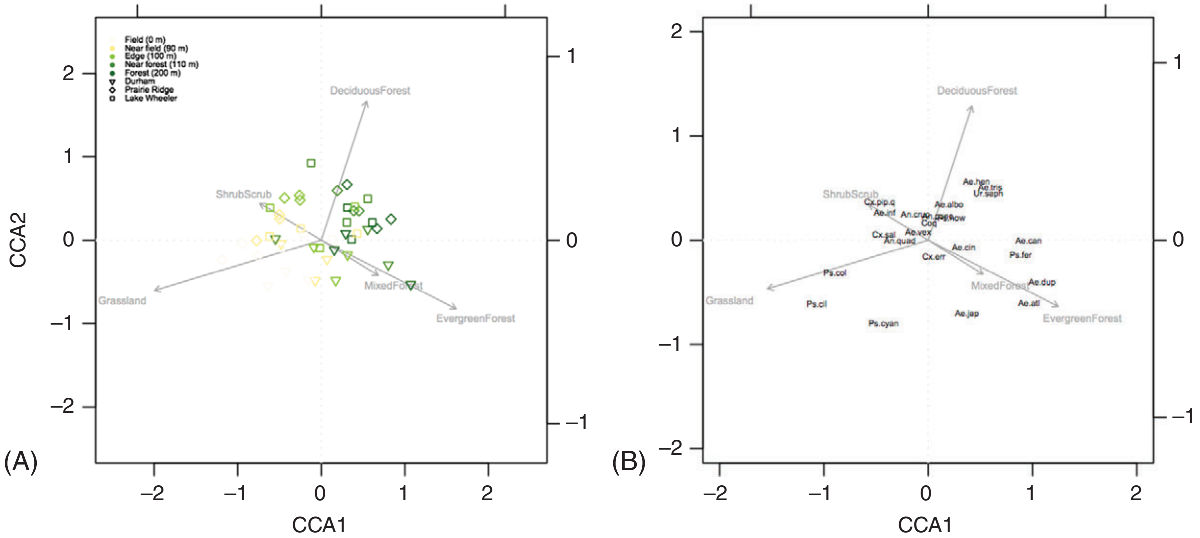

Fig. 3. (A) Partial canonical correlation analysis showing sites along the first two canonical correlations. The colour ramp denotes habitat: off-white, 100 m into field; yellow, 10 m into field; bright green, edge; medium green, 10 m into forest; dark green, 100 m into forest. Shape denotes the study site: triangle, Durham; diamond, Prairie Ridge; square, Lake Wheeler. (B) Mosquito species distribution with respect to measured environmental variables for all mosquito species.

for nearly two-thirds of explained variation in the mosquito abundance data. Although many rare species showed no significant association with habitat, this may be a function of the small numbers of mosquitoes captured for these uncommon species. Among common species, only *Ae. vexans*, *An. punctipennis* and *Cx. erraticus* were not associated with field, forest or edge habitats. Interestingly, *An. punctipennis* and *Ae. vexans* were noted to lack strong habitat associations in earlier studies (Bidlingmayer & Hem, 1981; O'Brien & Reiskind, 2013). Previous studies have shown that at least some mosquitoes have a preference for habitat edges (Bidlingmayer & Hem, 1981; Lothrop & Reisen, 2001), and the present study provides limited evidence that the invasive, anthropophilic *S. albopicta* favours forest edges. This species is common in suburban environments, and the ecotone between field and forest may be similar to a suburban habitat (Barker *et al.*, 2003). Patterns of diversity in the present study reflected the species' distributions, with higher species richness and rarefied richness in forest habitats, although Shannon's diversity index was not significantly associated with habitat.

The different sites segregated along the second pCCA axis, with two sites closer together (Prairie Ridge and Lake Wheeler) and distinct from the furthest site (in Durham). The pattern was consistent with the physical distance between sites (Fig. 1). Both the Prairie Ridge and Lake Wheeler sites are within the Northern Outer Piedmont level IV ecoregions, whereas the Durham site lies within the Triassic Basin Piedmont level IV ecoregion (Griffith *et al.*, 2002). The difference in species composition between Durham and the other two sites seemed to be driven by a relatively high abundance of *O. atlanticus* and *O. dupreei* in Durham woodlands, and *Cq. perturbans* at Lake Wheeler and Prairie Ridge. Both *O. atlanticus* and *O. dupreei* develop in rain-filled woodland pools, but otherwise little is documented about their ecology (Carpenter & LaCasse, 1955). *Coquillettidia perturbans* is an obligate pond-breeding species, but there are ponds near transects at all three sites. Why abundances of these three species should differ between Durham and the other sites is unclear, but the overwhelming pattern of variation in species assemblages was driven by vegetative habitat, not site.

The present study demonstrates that many mosquito species are constrained to seek hosts in certain habitats, as defined by vegetative structure. The majority of species were faithful to core grassland or woodlot habitats. Models of edge effects predict that habitat preferences are driven by superior resources in a given habitat, and no or at best supplementary resources in the alternative habitat (Ries & Sisk, 2004, 2008). In general, adult mosquitoes have broadly similar resource needs that may differ in the specifics, such as in blood, nectar (or other carbohydrate), and oviposition/larval habitat. Each of these three resources may drive the patterns observed in host-seeking mosquito abundance. Below, three possible drivers are weighed, based upon the patterns observed and knowledge of the natural history of these insects.

Mosquitoes show different preferences for blood hosts (Apperson *et al.*, 2004; Richards *et al.*, 2006; Hamer *et al.*, 2009; Simpson *et al.*, 2012). The blood-feeding preferences of many of the mosquitoes in the present study are not well characterized but, among both forest and field mosquitoes previously captured, they have been described as broadly mammalophilic or generalist feeders (Washino & Tempelis, 1983). Furthermore, mosquitoes are rarely faithful to hosts even at the level of taxonomic class (Washino & Tempelis, 1983; Chaves *et al.*, 2010). Host distribution has been considered important in arthropod parasite distributions, but only with highly specialized feeders, such as the amphibian-loving mosquito *Culex territans* (Walker) and less mobile ectoparasites, like ticks (Wilson *et al.*, 1990; Burkett-Cadena *et al.*, 2013). Although data on the distribution of potential blood hosts across the transects studied were not obtained, given the catholic feeding behaviour of most

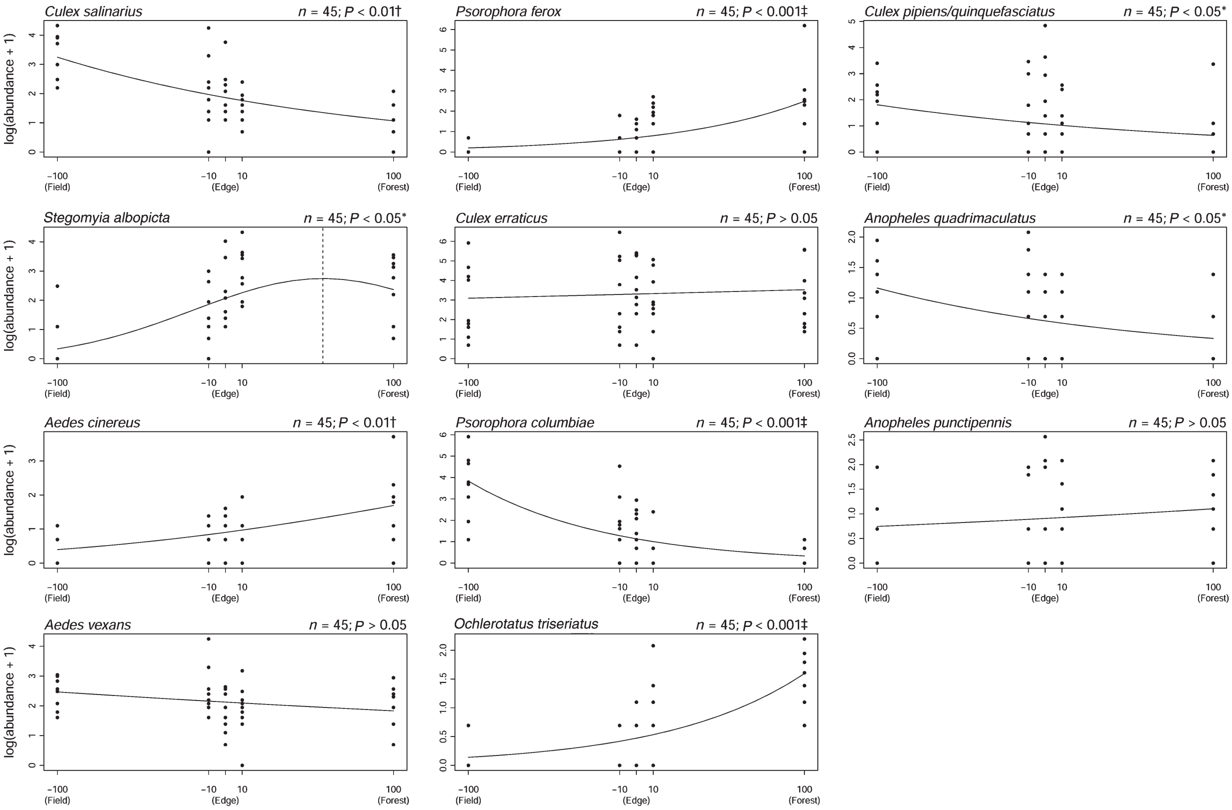

Fig. 4. Abundances of each species (with > 60 individuals) across transects. The *y*-axes denote metres; the *x*-axes show untransformed counts (note changes in scale for different species). Lines are generated from the best fit model (Table 2).

Table 2. Individual species responses to the forest–field habitat edge.

Species	AIC (quadratic) – AIC (linear)	Linear coefficient	Quadratic coefficient	Favoured habitat
Culex salinarius	1.97	**−0.00556†**	−4.00e−06	Field
Stegomyia albopicta	**−6.34**	**0.00585†**	**−8.42e−05***	Edge
Aedes cinereus	1.70	**0.01106‡**	1.95e−05	Forest
Aedes vexans	1.96	−0.00149	4.18e−06	None
Psorophora ferox	1.07	**0.01262‡**	−4.91e−05	Forest
Culex erraticus	0.24	0.00226	−3.28e−05	None
Psorophora columbiae	0.01	**−0.01217‡**	−5.81e−05	Field
Ochleratus triseriatus	1.01	**0.01217‡**	−6.76e−05	Forest
Culex pipiens/quinquefasciatus	0.89	**−0.00521***	−3.06e−05	Field
Anopheles quadrimaculatus	1.20	**−0.00625***	−3.92e−05	Field
Anopheles punctipennis	2.00	0.00196	−7.42e−07	None

For each species, data show the difference in Akaike information criterion (AIC) scores for the quadratic and linear models, the linear coefficient from the linear model, the quadratic coefficient from the quadratic model, and the inferred habitat preference. Positive linear coefficients indicate that a species prefers forest habitat, whereas negative coefficients indicate that a species prefers field habitat (Fig. 4). Positive quadratic coefficients indicate that the species is less abundant near the edge, and negative coefficients indicate that the species is more abundant near the edge. A significant AIC test score (AIC <−2) indicates the quadratic model is favoured over the linear model. All significant AIC test statistics and model coefficients are shown in bold. Significance levels for coefficients:$^*P < 0.05$; †$P < 0.01$; ‡$P < 0.001$.

mosquitoes, it seems likely that adequate sources of blood exist in both forest and field habitats for most species. Although bird and small mammal species are likely to change across forest and field habitat edges (Coppedge *et al.*, 2001; Horncastle *et al.*, 2005), the generalist nature of most mosquito feeding behaviour is not likely to result in the driving of mosquito distributions by specific host distributions. Variation in overall host biomass may have a profound effect on mosquito distribution, but this would tend to moderate habitat associations as grassland-loving mosquitoes are drawn into host-dense forests or forest-preferring mosquitoes are pulled into grasslands containing many birds or mammals. Consequently, bloodmeal host distribution does not seem to represent a likely driver of host-seeking mosquito habitat preference.

A second potential driver of mosquito distribution is the availability of plant nectar, which is consumed by most female mosquitoes during their lifetimes (Foster, 1995). The distribution of flowering species was not measured, but it is possible that these may contribute to the associations between habitats and mosquitoes. However, although some field and bioassay work suggests that mosquitoes prefer certain plants, there is no evidence that these preferences vary across different species of mosquito (Nikbakhtzadeh *et al.*, 2014), and there is no current evidence for mosquito–flora coevolution that might help explain the habitat associations of particular mosquito species. Alternatively, the overall availability of plant nectar in different habitats may influence mosquito distributions, but, as with host distributions, unequal distributions of sugar sources would be more likely to disrupt habitat associations as woodland mosquitoes are pulled into grassland environments or vice versa. Thus, it seems unlikely that the availability of either specific or general plant resources drives the distribution of blood-seeking mosquitoes. Still, it is possible that the habitat associations of carbohydrate-seeking mosquitoes differ from those of blood-seeking mosquitoes as many mosquito species choose between sugar and blood feeding depending on their nutritional status (Hancock & Foster, 1997; Gary & Foster, 2006). As the trapping methodology mimicked host cues, it was only possible to characterize the distribution of blood-seeking mosquitoes. Experiments using carbohydrate cues (e.g. floral volatiles) to attract and trap mosquitoes alongside host-cue traps may reveal differences in habitat associations between blood- and carbohydrate-seeking females (Nyasembe *et al.*, 2014).

The final potential resource driving mosquito distribution is the appropriate larval environment. After emergence and mating, adult female mosquitoes follow a lifecycle of blood and sugar seeking, blood feeding, resting while producing eggs, oviposition, and then blood seeking again. It is well known that gravid mosquitoes seeking oviposition sites are sensitive to a number of chemical, visual and physical cues (Bradshaw & Holzapfel, 1988; Bentley & Day, 1989; Reiskind & Zarrabi, 2012), and recent studies have found distinct larval assemblages of mosquito species in different habitats (Yee & Yee, 2007; Beketov *et al.*, 2010). Thus, it is possible that adult female distributions are driven by larval habitat preferences if females are unwilling to stray far from preferred larval habitats when seeking hosts. Although the natural history of most of the species cited in the present study is poorly documented, the patterns observed roughly correspond to known larval preferences (Carpenter & LaCasse, 1955; Laird, 1988; Ellis, 2008). Several species associated with forested habitats are known to rely on tree holes as larval habitats, such as *O. triseriatus* and *O. hendersoni* (Frank & Lounibos, 1983; Bradshaw & Holzapfel, 1988), and the three abundant species that showed no habitat association (*Cx. erraticus*, *An. punctipennis* and *Ae. vexans*) have been described as larval habitat generalists (Carpenter & LaCasse, 1955; Horsfall *et al.*, 1973). However, some species that showed a host-seeking habitat preference in the present study, such as *Cx. salinarius*, are also considered larval habitat generalists (Carpenter & LaCasse, 1955). Basic research on the larval habitats of poorly studied mosquito species is needed and might be combined with the sampling of adult populations to determine the extent to which ecological requirements of the larval stage affect the distributions of adult host-seeking mosquitoes.

Foraging mosquitoes may be bound to stay close to oviposition sites, given the fluctuating risks that pertain to adult female mosquitoes. Female mosquitoes face high mortality risks when attempting to blood feed, and it is well known that hosts vary in degrees of defensive behaviour and thus in the risk they pose to host-seeking mosquitoes (Walker & Edman, 1985, 1986; Edman & Scott, 1987). However, host seeking may not be as dangerous as post-prandial movement after a mosquito has taken in as much as three times her body weight in blood (Clements, 1992). Blood-fed mosquitoes are more susceptible to predation, although whether the risk for mortality is higher in mosquitoes that are blood-fed from other sources (i.e. tolerance of extreme abiotic conditions) has not been investigated (Roitberg *et al.*, 2003; Jackson *et al.*, 2005). Foraging far from larval habitats may exert such a high cost that it is not worth moving to a habitat to find a blood source if there are no appropriate places to oviposit. Indeed, this may help to explain why mosquitoes are such opportunistic catholic feeders despite their high mobility. There has been little examination of the relative risks of different life history stages within adult mosquitoes (Stone *et al.*, 2011), but the present results point to the importance of oviposition in the local distribution of host-seeking mosquitoes. More research on the relative risks associated with host seeking and oviposition in female mosquitoes is required to test the hypothesis that adult distribution is driven by larval habitat specialization.

There are several weaknesses to the present study. Firstly, as data across the entire season were pooled, it was not possible to see any seasonal segregation in species, which may further understanding of ecological specialization in the Culicidae (Lampman & Novak, 1996; Reiskind & Lounibos, 2013). Secondly, only three distinct sites were sampled and there was some site specificity for mosquito assemblages. Nevertheless, the present results, coupled with general findings of habitat specialization within the Culicidae, suggest that the broad patterns are universal. Finally, the traps were placed on the same nights in proximity to one another. This may have resulted in trap competition, although no evidence of this was detected in the data.

The findings of this study can be applied in several specific contexts. The building of spatially explicit models of pathogen transmission risk is highly dependent upon the accurate estimation of specific vector distributions (Reisen, 2010). For example, West Nile virus is transmitted primarily by field-favouring *Culex* spp. mosquitoes, including *Cx. pipiens* and *Cx. salinarius* (Anderson *et al.*, 2006; Mackay *et al.*, 2008). The knowledge that these vectors are restricted to grassland habitats allows for the fine-scale prediction of risk for exposure. Likewise, the LaCrosse encephalitis vector, *O. triseriatus*, is highly restricted to forested habitats (Leisnham & Juliano, 2012). Consequently, control of critical vectors may be tailored to certain habitats, limiting non-target impacts and minimizing the costs of controlling mosquitoes. The habitat-specific distribution of species can be coupled with predictions of changes in land use, which allow the prediction of mosquito-borne transmission across future landscapes for a variety of pathogens (Terando *et al.*, 2014). Landscapes may also be managed to limit certain species, such as the pestiferous *Ps. columbiae* or the *Culex* spp. West Nile vectors, by allowing grasslands to convert to forested areas. Examination of mosquito diversity may also be important. Although an enormous body of research has focused on mosquito species that are of singular importance in the transmission of major human pathogens, such as the *Anopheles* vectors of the human malarias, less research has focused on entire communities of mosquitoes. This is despite the fact that many vector-borne pathosystems, such as those of West Nile virus, Rift Valley fever, Venezuelan equine encephalitis, avian malaria, dog heartworm and human lymphatic filariasis, involve a variety of mosquito vectors of variable importance (Weaver, 2005; Turell *et al.*, 2008; Kimura *et al.*, 2010; Manguin *et al.*, 2010; Farajollahi *et al.*, 2011; Ledesma & Harrington, 2011). For these pathosystems, the habitat fidelity of various vectors, when combined with host habitat use, can dramatically influence the spatial distribution of pathogen transmission and disease risk. The results presented herein indicate that the scale of vector–habitat associations for mosquitoes is relatively fine, with collections of many species showing differences between core forest or field traps and those at the edge. This may be critical in associating remotely sensed landscape data with risk for pathogen transmission as much satellite imagery is presented at a 30-m pixel resolution (Cohen & Goward, 2004). A finer-scale assessment of habitat may be necessary to correctly predict the distributions of vector species. Additionally, the results suggest that identifying the distribution of larval habitats may be critical to determining the distribution of biting mosquitoes, and research on the larval habitats of mosquito species involved in multi-vector pathosystems is urgently needed.

Data availability

Upon acceptance for publication, data from this study will be deposited at Dryad (www.datadryad.org). R packages with data and variables will be deposited at GitHub (https://github.com/rgriff23/Mosquito_ecology) for public access.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/mve.12193

Figure S1. Frequencies of the 12 least common mosquito species along field–forest transects. *P*-values are derived from Mood's median test.

Acknowledgements

The authors wish to thank Oglesby Barrett III and Erin McDermott, Department of Entomology, NCSU, for assistance in the field collection of mosquitoes, and Cole Keenan, Department of Entomology, NCSU, for assistance in hand-digitizing land cover. They also thank Rick Kern (Department of Animal Science, NCSU) for allowing access to sites in Durham and at Lake Wheeler Farm, and Lawson Walston (Department of Animal Science, NCSU), Glen Catts (Department of Forestry, NCSU) and the North Carolina Museum of Natural Sciences for access to sites in the Prairie Ridge area. This manuscript was improved through the input of two anonymous reviewers and the editors at *Medical and Veterinary Entomology*. This work was supported by the North Carolina Agricultural Research Service (project NC-02404).

References

Anderson, J.F., Andreadis, T.G., Main, A.J., Ferrandino, F.J. & Vossbrinck, C.R. (2006) West Nile virus from female and male mosquitoes (Diptera: Culicidae) in subterranean, ground, and canopy habitats in Connecticut. *Journal of Medical Entomology*, **43**, 1010–1019.

Apperson, C.S., Hassan, H.K., Harrison, B.A. *et al.* (2004) Host feeding patterns of established and potential mosquito vectors of West Nile virus in the Eastern United States. *Vector-Borne and Zoonotic Diseases*, **4**, 71–82.

Barker, C.M., Brewster, C.C. & Paulson, S.L. (2003) Spatiotemporal oviposition and habitat preferences of *Ochlerotatus triseriatus* and *Aedes albopictus* in an emerging focus of La Crosse virus. *Journal of the American Mosquito Control Association*, **19**, 382–391.

Beketov, M.A., Yurchenko, Y.A., Belevich, O.E. & Liess, M. (2010) What environmental factors are important determinants of structure, species richness, and abundance of mosquito assemblages? *Journal of Medical Entomology*, **47**, 129–139.

Bentley, M.D. & Day, J.F. (1989) Chemical ecology and behavioural aspects of mosquito oviposition. *Annual Review of Entomology*, **34**, 401–421.

Bidlingmayer, W.L. & Hem, D.G. (1981) Mosquito flight paths in relation to the environment: effect of the forest edge upon trap catches in the field. *Mosquito News*, **41**, 55–59.

Bradley, D.J. (1994) Watson, Swellengrebel and species sanitation: environmental and ecological aspects. *Parassitologia*, **36**, 137–147.

Bradshaw, W. & Holzapfel, C. (1988) Drought and the organization of treehole communities. *Oecologia*, **74**, 507–514.

Burkett-Cadena, N.D. (2013) *Mosquitoes of the Southeastern United States*. University of Alabama Press, Tuscaloosa, AL.

Burkett-Cadena, N.D., McClure, C.J.W., Estep, L.K. & Eubanks, M.D. (2013) Hosts or habitats: what drives the spatial distribution of mosquitoes? *Ecosphere*, **4**, 30.

Carpenter, S.J. & LaCasse, W.J. (1955) *Mosquitoes of North America (North of Mexico)*. University of California Press, Berkeley and Los Angeles, CA.

Chaves, L.F., Harrington, L.C., Keogh, C.L., Nguyen, A.M. & Kitron, U.D. (2010) Blood feeding patterns of mosquitoes: random or structured? *Frontiers in Zoology*, **7**, 11.

Clements, A.N. (1992) *The Biology of Mosquitoes*. Chapman & Hall, London; New York, NY.

Cohen, W. & Goward, S. (2004) Landsat's role in ecological applications of remote sensing. *Bioscience*, **54**, 535–545.

Coppedge, B.R., Engle, D.M., Masters, R.E. & Gregory, M.S. (2001) Avian response to landscape change in fragmented southern great plains grasslands. *Ecological Applications*, **11**, 47–59.

Darsie, R. & Ward, R. (2005) *Identification and Geographical Distribution of the Mosquitoes of North America, North of Mexico*. University Press of Florida, Gainesville, FL.

Edman, J. & Scott, T. (1987) Host defensive behavior and the feeding success of mosquitoes. *Insect Science and its Application*, **8**, 617–622.

Ellis, A.M. (2008) Linking movement and oviposition behaviour to spatial population distribution in the tree hole mosquito *Ochlerotatus triseriatus*. *Journal of Animal Ecology*, **77**, 156–166.

Farajollahi, A., Fonseca, D.M., Kramer, L.D. & Kilpatrick, A.M. (2011) 'Bird biting' mosquitoes and human disease: a review of the role of *Culex pipiens* complex mosquitoes in epidemiology. *Infection, Genetics and Evolution*, **11**, 1577–1585.

Foley, J. & Piovia-Scott, J. (2014) Vector biodiversity did not associate with tick-borne pathogen prevalence in small mammal communities in northern and central California. *Ticks and Tick-Borne Diseases*, **5**, 299–304.

Foster, W.A. (1995) Mosquito sugar feeding and reproductive energetics. *Annual Review of Entomology*, **40**, 443–474.

Fournier, D.A., Skaug, H.J., Ancheta, J. *et al.* (2012) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods & Software*, **27**, 233–249.

Frank, J.H. & Lounibos, L.P. (1983) *Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities*. Plexus Publishing, Medford, NJ.

Freidlin, B. & Gastwirth, J. (2000) Should the median test be retired from general use? *American Statistician*, **54**, 161–164.

Gardner, A.M., Lampman, R.L. & Muturi, E.J. (2014) Land use patterns and the risk of West Nile virus transmission in central Illinois. *Vector-Borne and Zoonotic Diseases*, **14**, 338–345.

Gary, R.E. Jr. & Foster, W.A. (2006) Diel timing and frequency of sugar feeding in the mosquito *Anopheles gambiae*, depending on sex, gonotrophic state and resource availability. *Medical and Veterinary Entomology*, **20**, 308–316.

Griffith, G.E., Omernik, J.M., Comstock, J.A. *et al.* (2002) Ecoregions of North Carolina and South Carolina. [Colour poster with map, descriptive text, summary tables, and photographs.] ftp://newftp.epa.gov/EPADataCommons/ORD/Ecoregions/nc/ncsc_front.pdf [accessed on 11 May 2015].

Hamer, G.L., Kitron, U.D., Goldberg, T.L. *et al.* (2009) Host selection by *Culex pipiens* mosquitoes and West Nile virus amplification. *American Journal of Tropical Medicine and Hygiene*, **80**, 268–278.

Hamer, G.L., Anderson, T.K., Donovan, D.J. *et al.* (2014) Dispersal of adult *Culex* mosquitoes in an urban West Nile virus hotspot: a mark–capture study incorporating stable isotope enrichment of natural larval habitats. *PLoS Neglected Tropical Diseases*, **8**, e2768.

Hancock, R. & Foster, W. (1997) Larval and adult nutrition effects on blood/nectar choice of *Culex nigripalpus* mosquitoes. *Medical and Veterinary Entomology*, **11**, 112–122.

Harrison, G.A. (1978) *Mosquitoes, Malaria, and Man: A History of the Hostilities since 1880*. John Murray, London.

Heck, K.L., Van Belle, G. & Simberloff, D. (1975) Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology* **56**, 1459–1461.

Horncastle, V.J., Hellgren, E.C., Mayer, P.M., Ganguli, A.C., Engle, D.M. & Leslie, D.M. (2005) Implications of invasion by *Juniperus virginiana* on small mammals in the southern great plains. *Journal of Mammalogy*, **86**, 1144–1155.

Horsfall, W.R., Fowler, H.W., Moretti, L.J. & Larsen, J.R. (1973) Bionomics and Embryology of the Inland Floodwater Mosquito, *Aedes vexans*. University of Illinois Press, Urbana, IL.

Hoshi, T., Imanishi, N., Higa, Y. & Fernando Chaves, L. (2014) Mosquito biodiversity patterns around urban environments in south-central Okinawa island, Japan. *Journal of the American Mosquito Control Association*, **30**, 260–267.

Huang, S., Molaei, G. & Andreadis, T.G. (2011) Re-examination of *Culex pipiens* hybridization zone in the eastern United States by ribosomal DNA-based single nucleotide polymorphism markers. *American Journal of Tropical Medicine and Hygiene*, **85**, 434–441.

Hurlburt, S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**, 577–586.

Jackson, R.R., Nelson, X.J. & Sune, G.O. (2005) A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15155–15160.

Keesing, F., Holt, R. & Ostfeld, R. (2006) Effects of species diversity on disease risk. *Ecology Letters*, **9**, 485–498.

Kimura, M., Darbro, J.M. & Harrington, L.C. (2010) Avian malaria parasites share congeneric mosquito vectors. *Journal of Parasitology*, **96**, 144–151.

Laird, M. (1988) *The Natural History of Larval Mosquito Habitats*. Academic Press, London.

Lampman, R.L. & Novak, R.J. (1996) Oviposition preferences of *Culex pipiens* and *Culex restuans* for infusion-baited traps. *Journal of the American Mosquito Control Association*, **12**, 23–32.

Ledesma, N. & Harrington, L. (2011) Mosquito vectors of dog heartworm in the United States: vector status and factors influencing transmission efficiency. *Topics in Companion Animal Medicine*, **26**, 178–185.

Leisnham, P.T. & Juliano, S.A. (2012) Impacts of climate, land use, and biological invasion on the ecology of immature *Aedes* mosquitoes: implications for La Crosse emergence. *EcoHealth*, **9**, 217–228.

Lothrop, H. & Reisen, W. (2001) Landscape affects the host-seeking patterns of *Culex tarsalis* (Diptera: Culicidae) in the Coachella Valley of California. *Journal of Medical Entomology*, **38**, 325–332.

Lothrop, H., Lothrop, B. & Reisen, I. (2002) Nocturnal microhabitat distribution of adult *Culex tarsalis* (Diptera: Culicidae) impacts control effectiveness. *Journal of Medical Entomology*, **39**, 574–582.

Maciel-de-Freitas, R., Souza-Santos, R., Codeco, C.T. & Lourenco-de-Oliveira, R. (2010) Influence of the spatial distribution of human hosts and large size containers on the dispersal of the mosquito *Aedes aegypti* within the first gonotrophic cycle. *Medical and Veterinary Entomology*, **24**, 74–82.

Mackay, A.J., Roy, A., Yates, M.M. & Foil, L.D. (2008) West Nile virus detection in mosquitoes in East Baton Rouge parish, Louisiana, from November 2002 to October 2004. *Journal of the American Mosquito Control Association*, **24**, 28–35.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Malden, MA.

Manguin, S., Bangs, M.J., Pothikasikorn, J. & Chareonviriyaphap, T. (2010) Review on global co-transmission of human *Plasmodium* species and *Wuchereria bancrofti* by *Anopheles* mosquitoes. *Infection, Genetics and Evolution*, **10**, 159–177.

Mood, A.M. (1954) On the asymptotic efficiency of certain nonparametric two-sample tests. *Annals of Mathematical Statistics*, **25**, 514–522.

Nikbakhtzadeh, M.R., II Terbot, J.W., Otienoburu, P.E. & Foster, W.A. (2014) Olfactory basis of floral preference of the malaria vector *Anopheles gambiae* (Diptera: Culicidae) among common African plants. *Journal of Vector Ecology*, **39**, 372–383.

Nyasembe, V.O., Tchouassi, D.P., Kirwa, H.K. *et al.* (2014) Development and assessment of plant-based synthetic odor baits for surveillance and control of malaria vectors. *PLoS One*, **9**, e89818.

O'Brien, V.A. & Reiskind, M.H. (2013) Host-seeking mosquito distribution in habitat mosaics of southern Great Plains cross-timbers. *Journal of Medical Entomology*, **50**, 1231–1239.

Oksanen, J., Blanchet, F.G., Kindt, R. *et al.* (2015) *'Vegan' Community Ecology Package*. R package 2.3–0. https://cran.r-project.org, https://github.com/vegandevs/vegan [accessed on 1 November 2015].

Ostfeld, R.S. & Keesing, F. (2012) Effects of host diversity on infectious disease. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 157–182.

Pavlovsky, N. (1966) *The Natural Nidality of Transmissable Disease with Special Reference to the Landscape Ecology of Zooanthroposes*. University of Illinois Press, Urbana, IL.

Pumpuni, C.B. & Walker, E.D. (1989) Population-size and survivorship of adult *Aedes triseriatus* in a scrap tireyard in northern Indiana. *Journal of the American Mosquito Control Association*, **5**, 166–172.

R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Reisen, W.K. (2010) Landscape epidemiology of vector-borne diseases. *Annual Review of Entomology*, **55**, 461–483.

Reiskind, M.H. & Lounibos, L.P. (2013) Spatial and temporal patterns of abundance of *Aedes aegypti* L. (*Stegomyia aegypti*) and *Aedes albopictus* (Skuse) [*Stegomyia albopictus* (Skuse)] in southern Florida. *Medical and Veterinary Entomology*, **27**, 421–429.

Reiskind, M.H. & Zarrabi, A.A. (2012) Water surface area and depth determine oviposition choice in *Aedes albopictus* (Diptera: Culicidae). *Journal of Medical Entomology*, **49**, 71–76.

Richards, S.L., Ponnusamy, L., Unnasch, T.R., Hassan, H.K. & Apperson, C.S. (2006) Host-feeding patterns of *Aedes albopictus* (Diptera: Culicidae) in relation to availability of human and domestic animals in suburban landscapes of central North Carolina. *Journal of Medical Entomology*, **43**, 543–551.

Ries, L. & Sisk, T. (2004) A predictive model of edge effects. *Ecology*, **85**, 2917–2926.

Ries, L. & Sisk, T.D. (2008) Butterfly edge effects are predicted by a simple model in a complex landscape. *Oecologia*, **156**, 75–86.

Ries, L., Fletcher, R., Battin, J. & Sisk, T. (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 491–522.

Roitberg, B.D., Mondor, E.B. & Tyerman, J.G.A. (2003) Pouncing spider, flying mosquito: blood acquisition increases predation risk in mosquitoes. *Behavioral Ecology*, **14**, 736–740.

Siegal, S. & Castellan, N.J. (1988) *Nonparametric Statistics for the Behavioural Sciences*, 2nd edn. McGraw-Hill, New York, NY.

Simpson, J.E., Hurtado, P.J., Medlock, J. *et al.* (2012) Vector host-feeding preferences drive transmission of multi-host pathogens: West Nile virus as a model system. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, **279**, 925–933.

Skaug, H.J. & Yu, J. (2014) A flexible and automated likelihood-based framework for inference in stochastic volatility models. *Computational Statistics & Data Analysis*, **76**, 642–654.

Steiger, D.M., Johnson, P., Hilbert, D.W., Ritchie, S., Jones, D. & Laurance, S.G.W. (2012) Effects of landscape disturbance on mosquito community composition in tropical Australia. *Journal of Vector Ecology*, **37**, 69–76.

Stone, C.M., Hamilton, I.M. & Foster, W.A. (2011) A survival and reproduction trade-off is resolved in accordance with resource availability by virgin female mosquitoes. *Animal Behaviour*, **81**, 765–774.

Terando, A.J., Costanza, J., Belyea, C., Dunn, R.R., McKerrow, A. & Collazo, J.A. (2014) The southern megalopolis: using the past to predict the future of urban sprawl in the southeast US. *PLoS One*, **9**, e102261.

Ter Braak, C. (1987) The analysis of vegetation–environment relationships by canonical correspondence analysis. *Vegetatio*, **69**, 69–77.

Thiemann, T., Nelms, B. & Reisen, W.K. (2011) Bloodmeal host congregation and landscape structure impact the estimation of female mosquito (Diptera: Culicidae) abundance using dry ice-baited traps. *Journal of Medical Entomology*, **48**, 513–517.

Thongsripong, P., Green, A., Kittayapong, P., Kapan, D., Wilcox, B. & Bennett, S. (2013) Mosquito vector diversity across habitats in central Thailand endemic for dengue and other arthropod-borne diseases. *PLoS Neglected Tropical Diseases*, **7**, e2507.

Traub, R. & Wisseman, C. (1974) Ecology of chigger-borne rickettsiosis (scrub typhus) 1, 2. *Journal of Medical Entomology*, **11**, 237–303.

Turell, M.J., Dohm, D.J., Mores, C.N. *et al.* (2008) Potential for North American mosquitoes to transmit Rift Valley fever virus. *Journal of the American Mosquito Control Association*, **24**, 502–507.

Walker, E. & Edman, J. (1985) The influence of host defensive behaviour on mosquito (Diptera, Culicidae) biting persistence. *Journal of Medical Entomology*, **22**, 370–372.

Walker, E. & Edman, J. (1986) Influence of defensive behaviour of eastern chipmunks and gray squirrels (Rodentia, Sciuridae) on feeding success of *Aedes triseriatus* (Diptera, Culicidae). *Journal of Medical Entomology*, **23**, 1–10.

Washino, R.K. & Tempelis, C.H. (1983) Mosquito host bloodmeal identification – methodology and data analysis. *Annual Review of Entomology*, **28**, 179–201.

Weaver, S.C. (2005) Host range, amplification and arboviral disease emergence. *Archives of Virology*, **19**, 33–44.

Wilson, M.L., Ducey, A.M., Litwin, T.S., Gavin, T.A. & Spielman, A. (1990) Microgeographic distribution of immature *Ixodes dammini* ticks correlated with that of deer. *Medical and Veterinary Entomology*, **4**, 151–159.

Yee, D.A. & Yee, S.H. (2007) Nestedness patterns of container-dwelling mosquitoes: effects of larval habitat within variable terrestrial matrices. *Hydrobiologia*, **592**, 373–385.

Accepted 8 August 2016