Assemblage variation of mosquitoes (Diptera: Culicidae) in different land use and activity periods within a lowland tropical forest matrix in Campeche, Mexico

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Received 26 February 2020; Accepted 12 May 2020

ABSTRACT: Most mosquito species are active during a certain part of the day, but climatic factors such as light intensity and relative humidity play an important role in the control of their activity. We selected three types of land use that were sampled in state of Campeche in 2018 (low semi-evergreen forest, secondary low semi-evergreen forest, and mango plantation), using ten CDC light traps baited with CO_2, that were active during nine hours of three activity periods (dawn, noon, and nightfall). A GLM was used to investigate changes in the assembly of mosquitoes between different types of land use and temporal variations. Rank abundance curves were used to detect changes in the spatial and activity period of the mosquitoes and we then calculated the Exponential Shannon Index. A total of 6,110 mosquitoes belonging to 23 species were captured. The greatest richness and abundance were found in the secondary low semi-evergreen forest, with greater richness and lower abundance than the mango plantation which showed more abundance. Of the activity periods, dusk had the greatest abundance and richness followed by dawn and finally noon. ***Journal of Vector Ecology* 45 (2): 188-196. 2020.**

Keyword Index: Culicidae, activity periods, land use types, low semi-evergreen forest, diversity.

INTRODUCTION

Infectious diseases have significantly influenced human biology and society and have even determined the course of important historical events. Approximately three-quarters of the recognized emerging infectious diseases were once or are currently zoonotic, that is, transmissible between animals and humans (Wilcox and Gubler 2005). The control of zoonotic diseases is one of the most important concerns in the area of human health. Recent studies have shown that most pandemics have originated from zoonoses (Smith et al. 2007). Many diseases are typical of wild animals (enzootic cycles) that are spread with the participation of arthropod vectors (Wilcox and Gubler 2005). Mosquitoes are vectors of several zoonoses, including yellow fever, Venezuelan equine encephalitis, dengue, malaria, Chikungunya, and Zika.

More than 3,490 mosquito species have been described worldwide, of which 195 to 250 have been reported in Mexico. Of these species, approximately 43 are of medical importance and 115 of veterinary interest (Darsie 1996, Harbach 2007). As a result of the geographical location and topographic and vegetation diversity in the state of Campeche, Mexico, it shares a singular fauna with endemic elements with many taxa representing neotropical areas. However, there are few faunistic and ecological studies that have been carried out in the state of Campeche, as only 21 species of mosquitoes have been reported (Heinemann and Belkin 1977), but in neighboring states such as Quintana Roo (81 species) and Tabasco (104 species), many more species have been reported due to recent fauna studies (Ortega-Morales et al. 2010, Ortega-Morales et al. 2019). Most of these species can feed on humans and other animals (Harbach 2007).

Most mosquito species are active during a certain part of the day. In previous studies it was mentioned that the onset and cessation of activity were completely controlled by climatic factors such as light intensity and relative humidity. However, circadian rhythms play an important role in the control of mosquito activity, governed endogenously by periods of light and dark. Mosquito activity in search of hosts can be placed into one of four categories: nocturnal, twilight/nocturnal, twilight/diurnal, and diurnal (Kawada et al. 2005). Habitat alterations caused by changes in land use have the potential to impact the dynamics of vector-borne disease directly and indirectly, causing changes in the richness and abundance of mosquitoes, modifying hematophagous habits, and even altering activity patterns from dusk to dawn (Ndoen et al. 2011, Gottdenker et al. 2014, Abella-Medrano et al. 2018).

Research on the periods of mosquito activity in Mexico are few, and they do not include the component of land use type. This lack of information, coupled with human activities within conserved areas such as jungles, can contribute to the increased impact of vector-borne diseases as they could cause changes in the assembly of species and therefore alter the trophic interactions, which affects the increased risk of transmission (Alcaide et al. 2009, Keesing et al. 2010). Therefore, knowing changes in the assembly of mosquitoes among different types of land use and at different activity periods might provide valuable information to advance the understanding of the dynamics associated with zoonotic

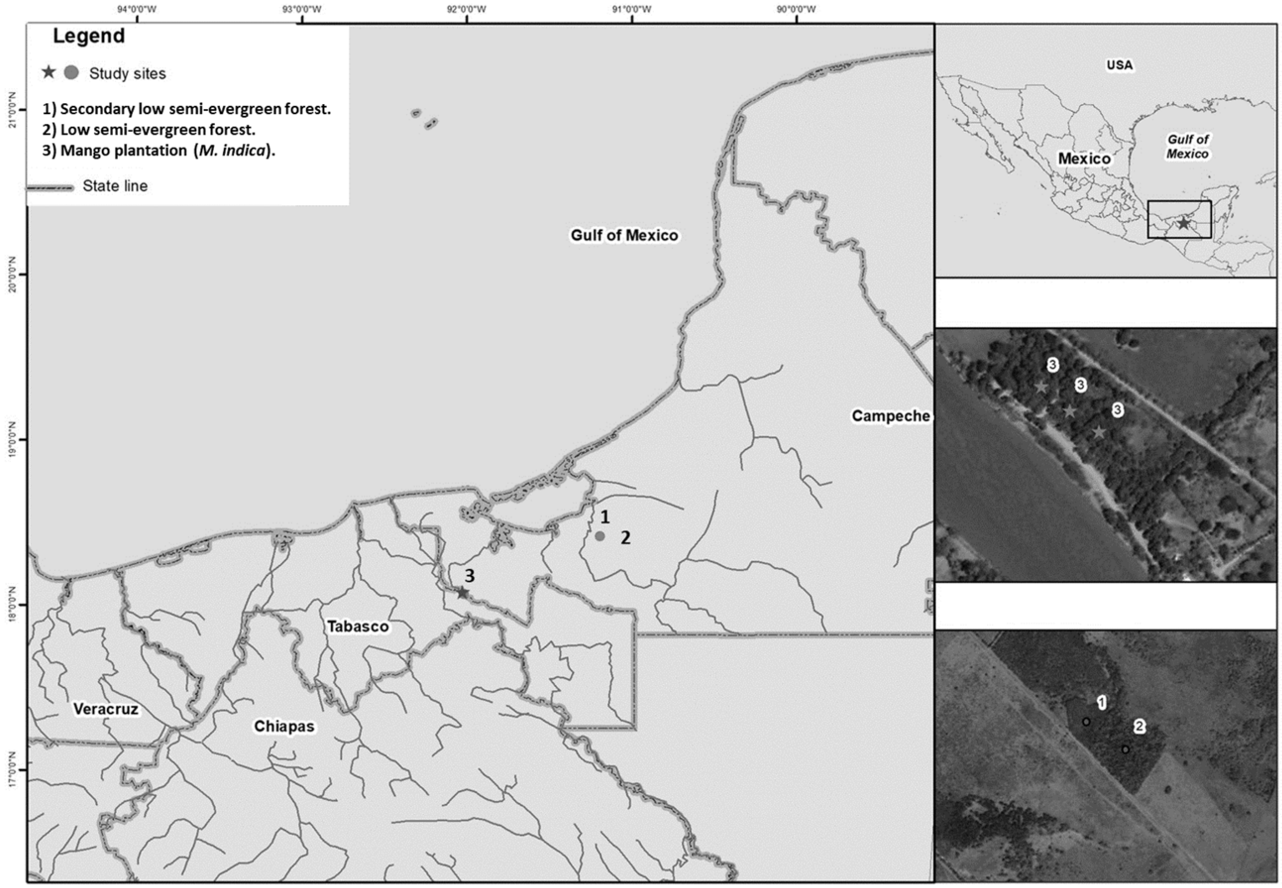

Figure 1. Study areas. Candelaria, (1) Secondary low semi-evergreen forest, (2) low semi-evergreen forest, and Santa Lucía, (3) Mango plantation (*M. indica*).

diseases.

MATERIALS AND METHODS

Study areas

Sampling was carried out from 30 July to 9 August 2018. Three types of land use were sampled in the north of the state of Campeche, Mexico: low semi-evergreen forest, secondary low semi-evergreen forest, and mango plantation (*Mangifera indica*). In the Candelaria location, the tropical low forest has primary vegetation with a predominance of *Haematoxylum campechianum*. There is also secondary tropical low forest with a predominance of herbaceous vegetation and *H. campechianum*. In Palizada, at the Santa Lucia ranch, there is the mango plantation (*M. indica*) and *H. campechianum* plantation, which is located within a reforestation project (Figure 1).

Mosquito samples

Sampling was conducted within a half-hectare square grid (100 × 50 m) at each site using ten CDC miniature incandescent light traps (model 512; John W. Hock Company) baited with CO_2 from yeast (*Saccharomyces cerevisiae*). Traps were placed in two transects of 100 m, separated 50 m from each other (five traps per transect), with a distance of 25 m between traps on the same transect to avoid competition between them and placed 60 cm above the ground (Silver 2007, Kirkeby et al. 2013). Traps were left active three hours during the dawn (starting one hour before sunrise, 17:30 to 08:30), at noon (from 12:30 to 15:30), and during nightfall (one hour before sunset, 17:30 20:30), for a total of nine hours of sampling per day; each site was sampled for two days. We used information provided by GPS to determine the exact time of sunrise and sunset. Collected mosquitoes were preserved at -20° C. All the material was first placed in Petri dishes and then kept frozen until identification in the laboratory. The observation of taxonomic characteristics was performed with a dissecting microscope. Individuals were separated by location and trap number, taxonomically identified by species, and subsequently stored in entomological boxes. Series of each species were mounted on entomological pins following the recommended procedure for their preservation (Belkin 1967). We used the morphological nomenclature of Harbach and Knight (1980).

Statistical analysis

Species accumulation curves and the Abundance-based Coverage Estimator (ACE) and Chao1 were used to determine sample efficiency (Colwell and Coddington 1994, Magurran 2003). This procedure was performed with EstimateS 8.2.0. A generalized linear model (GLM assuming a Negative Binomial distribution with log-link function for Abundance and Richness analysis) was used to investigate changes in the assembly of mosquitoes between different types of land use (tropical evergreen forest, secondary tropical evergreen forest, and mango plantation) and the period of activity (dawn, noon, and nightfall). Rank abundance curves were used to detect changes in the spatial and activity period of the mosquito assemblage (Magurran 2003) and we then calculated the Exponential Shannon Index using the SPADE program (Chao and Shen 2010) to determine whether diversity changes in each of the types of land use. (Jost 2006, 2010).

RESULTS

Mosquito assemblage description

In 2018, a total of 6,110 adult mosquitoes belonging to nine genera and 23 species was captured during the rainy season in three types of land use and in three periods of activity. As shown in the species accumulation curve, the ACE index estimates 23 species, while the Chao1 index estimates 22 species, suggesting that 100% of the species were obtained in the present study. The dominant species were *Aedes taeniorhynchus* (36.2%), *Culex nigripalpus* (29.4%), *Aedes scapularis* (18.1%), *Culex eastor* (9.2%), *Aedes angustivittatus* (1.8%), *Aedes tormentor* (1.4%), and *Uranotaenia lowii* (1.3%). Rare species occupy 2.6% of the sampling. The greatest richness and abundance were found in the secondary low semi-evergreen forest (SF) (20 spp., 2,954 individuals). The low semi-evergreen forest (CF) had greater richness and less abundance (17 spp., 1,045 individuals) than the mango plantation (MP) (11 spp., 2,111 individuals). With respect to the period of activity, dusk (NI) had the greatest abundance and richness (20 spp., 4,380 individuals), followed by dawn (DA) (14 spp., 1,127 individuals), and finally noon (NO) (12 spp., 603 individuals) (Table 1, Figure 2).

Assemblage analysis in types of land use and activity periods

The structure of the assembly of mosquito species changed during our study. There was a variation in the number of species and also with respect to abundance in each type of land use and for each period of activity. There were three dominant species for all sites and periods of activity, but the hierarchical position changes for the rest of the species (Figure 4). Shannon's exponential index is higher for less pronounced curves and therefore more equitable and may be a reason that the EF site has the highest value of this index. However, similar curves, and therefore values, of the nearby Shannon exponential are shown for periods of activity (Figure 2).

Assemblage structure

Significant effects were observed in the types of land use and in the periods of activity with respect to species richness (Table 2). Significant values regarding richness were found in the nightfall (NI) and noon (NO) periods and between low semi-evergreen forest (CF) in the NI period. Although the data show that secondary low semi-evergreen forest (SF) has a higher richness (19 spp.) compared to EF (17 spp.), the latter has a higher richness than SF during NI but less during NO, which is why significant values are reflected (Table 2, Figure 3). With respect to abundance, significant effects were detected in each type of land use and in each activity period (Table 2). Significant values were found in the NI and NO periods. There are significant effects of positive interaction between the EF in the NI and NO periods; the SE site was only significant for the NO period. There were no positive interactions at the SF site in the NI due to a very high abundance (2,390 individuals) with respect to the other periods of activity (Table 2, Figure 3).

DISCUSSION

This study focused on understanding the responses of a group of mosquitoes in different types of land use and periods of activity within a landscape originally dominated by a low semi-evergreen forest matrix. In general, our results showed that the region, regardless of the type of land use, was dominated by three species (*Aedes taeniorhynchus*, *Aedes scapularis,* and *Culex nigripalpus*) and that the communities were very similar in terms of species richness. More than half of the species were shared between the three types of land use and during periods of activity. In terms of abundance, the mosquito assembly showed greater variability and less similarity between types of land use and periods of activity, indicating that the resources for mosquito development varied according to space and time.

In particular, the hierarchy of dominant species changed in reference to the period of activity within each type of land use. Being immersed in the same matrix could explain the similarity in mosquito communities. The flight behavior of mosquito species, such as *Ae. taeniorhynchus* that can fly between 8-60 km (Ailes 1998), could explain why it was found in the three types of land use, and also for *Mansonia titillans* and *Coquillettidia perturbans* that can fly several kilometers from their oviposition sites (Carpenter and LaCasse 1955, Lounibos and Linley 1987). Therefore, high connectivity could be influencing the homogeneity in the local landscape and result in shared species in the types of land uses. However, when analyzing the periods of activity, we found subtle differences, since all species are related to a greater or lesser extent with the cycles of light and dark.

The abundance and richness of mosquitoes respond mainly to biotic factors (availability of hosts for food, plants as shelter, and oviposition) and to abiotic factors (relative humidity, seasonality, and temperature). However, light intensity is an important factor that regulates behavior, such as during the twilight period that can establish the beginning or end of mosquito activity (Forattini et al. 1981, Bona and Navarro-Silva 2008). Species like *Culex nigripalpus* had a greater abundance during the NI period, which coincides with other publications where it is considered as a nocturnal crepuscular species (Wright and Knight, 1968). On the other hand, *Psorophora ferox* presented a greater abundance during the NO period, as it is a tropical species that has daytime activity. *Aedes scapularis* had its greatest abundance in

Table 1. Species of mosquitoes captured in each land use type and each activity period.

*C	Spp	CF			SF			MP			Total
		DA	NO	NI	DA	NO	NI	DA	NO	NI	
At	*Aedes taeniorhynchus* (Wiedemann, 1821)	128	77	86	207	28	1,255	94	66	269	2,210
As	*Aedes scapularis* (Rondani, 1848)	142	95	28	194	79	184	83	148	155	1,108
Cn	*Culex nigripalpus* (Theobald, 1901)	30	1	193	10	4	553	141	0	863	1,795
Ao	*Aedes tormentor* (Dyar & Knab, 1906)	14	28	22	16	0	5	0	0	0	85
Ce	*Culex eastor* (Dyar, 1920)	7	0	50	4	0	273	8	0	219	561
Aa	*Aedes angustivittatus* (Dyar & Knab, 1907)	20	15	12	6	0	59	0	0	0	112
Pf	*Psorophora ferox* (Von Humboldt, 1819)	3	25	4	0	2	5	0	4	2	45
Ul	*Uranotaenia lowii* (Theobald, 1901)	1	2	27	0	0	27	0	0	25	82
Hr	*Haemagogus regalis* (Dyar & Knab, 1906)	0	13	0	0	2	2	0	0	0	17
Cp	*Coquillettidia perturbans* (Walker, 1856)	4	0	3	3	0	4	0	0	0	14
W	*Wyeomyia sp*	0	4	0	0	0	0	0	7	0	11
Af	*Aedes fulvus* (Ross, 1943)	0	0	2	1	0	5	0	0	0	8
Ap	*Anopheles pseudopunctipennis* (Dyar & Knab, 1906)	0	0	2	4	0	4	0	0	0	10
Mt	*Mansonia titillans* (Walker, 1848)	1	0	1	0	0	0	0	0	24	26
Pc	*Psorophora cyanescens* (Coquillett, 1902)	2	0	0	0	0	1	1	0	0	4
Ue	*Uranotaenia leucoptera* (Theobald, 1907)	0	1	1	0	0	0	0	0	1	3
Pi	*Psorophora ciliata* (Fabricius, 1794)	1	0	0	2	1	0	0	0	0	4
Ab	*Anopheles bradleyi* (King, 1939)	0	0	0	0	0	4	0	0	0	4
Av	*Anopheles vestitipennis* (Dyar & Knab, 1906)	0	0	0	0	0	4	0	0	0	4
Al	*Anopheles albimanus* (Wiedemann, 1820)	0	0	0	0	0	2	0	0	1	3
Po	*Psorophora confinnis* (Lynch Arribálzaga, 1891)	0	0	0	0	0	2	0	0	0	2
Mi	*Mansonia indubitans* (Dyar & Shannon, 1925)	0	0	0	0	0	1	0	0	0	1
Pv	*Psorophora varipes* (Coquillett, 1904)	0	0	0	0	1	0	0	0	0	1
	Richness	12	10	13	10	7	18	5	4	9	23
	Abundance	353	261	431	447	117	2,390	327	225	1,559	6,110

*CF low semi-evergreen forest, SF secondary low semi-evergreen forest, MP mango plantation, DA dawn, NO noon, NI nightfall, C species code.

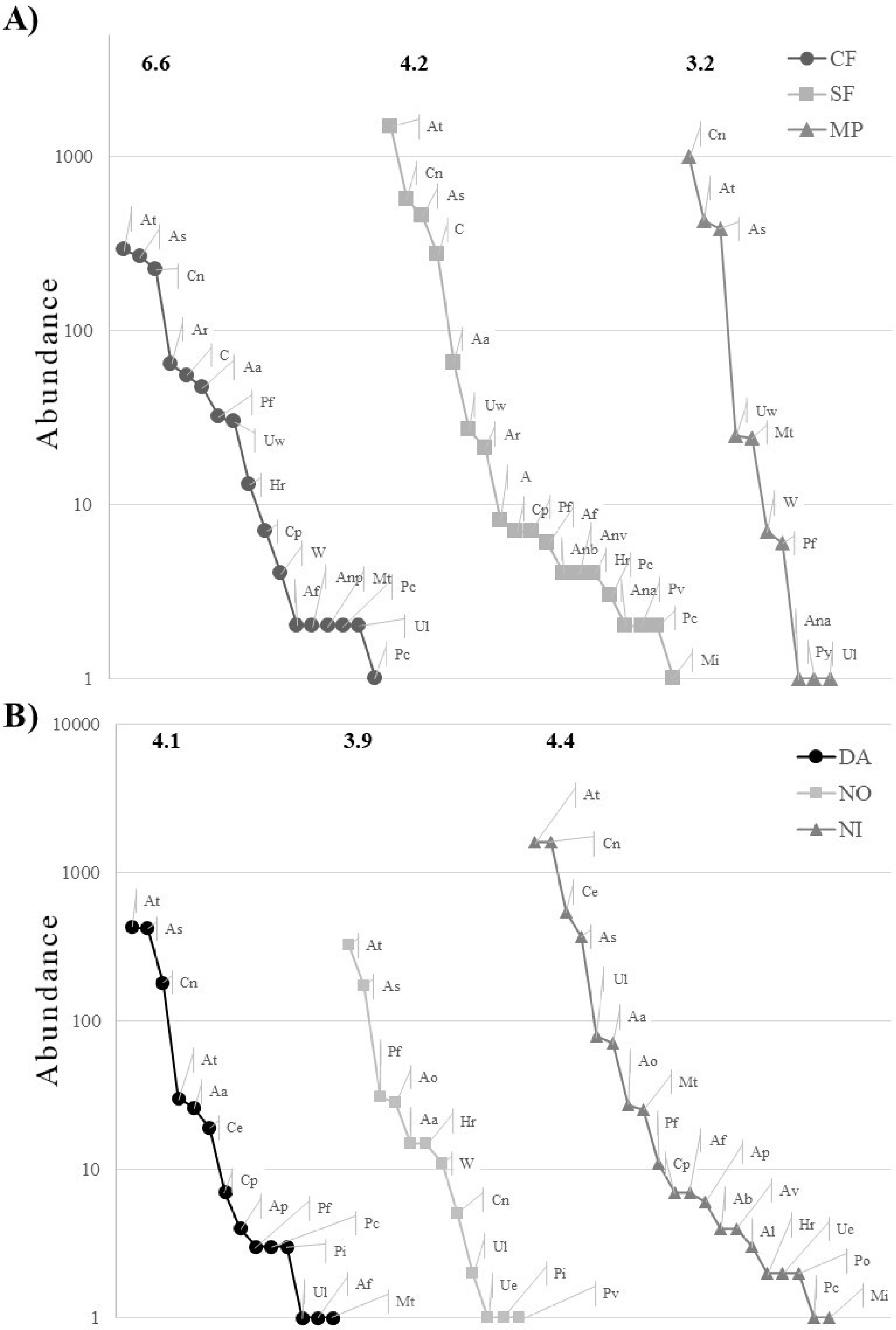

Figure 2. Rank-abundance curve. Numbers above graphs denote Exponential Shannon Index value for land use type (A) and activity period (B). Species codes (capital letters) are given in Table 1.

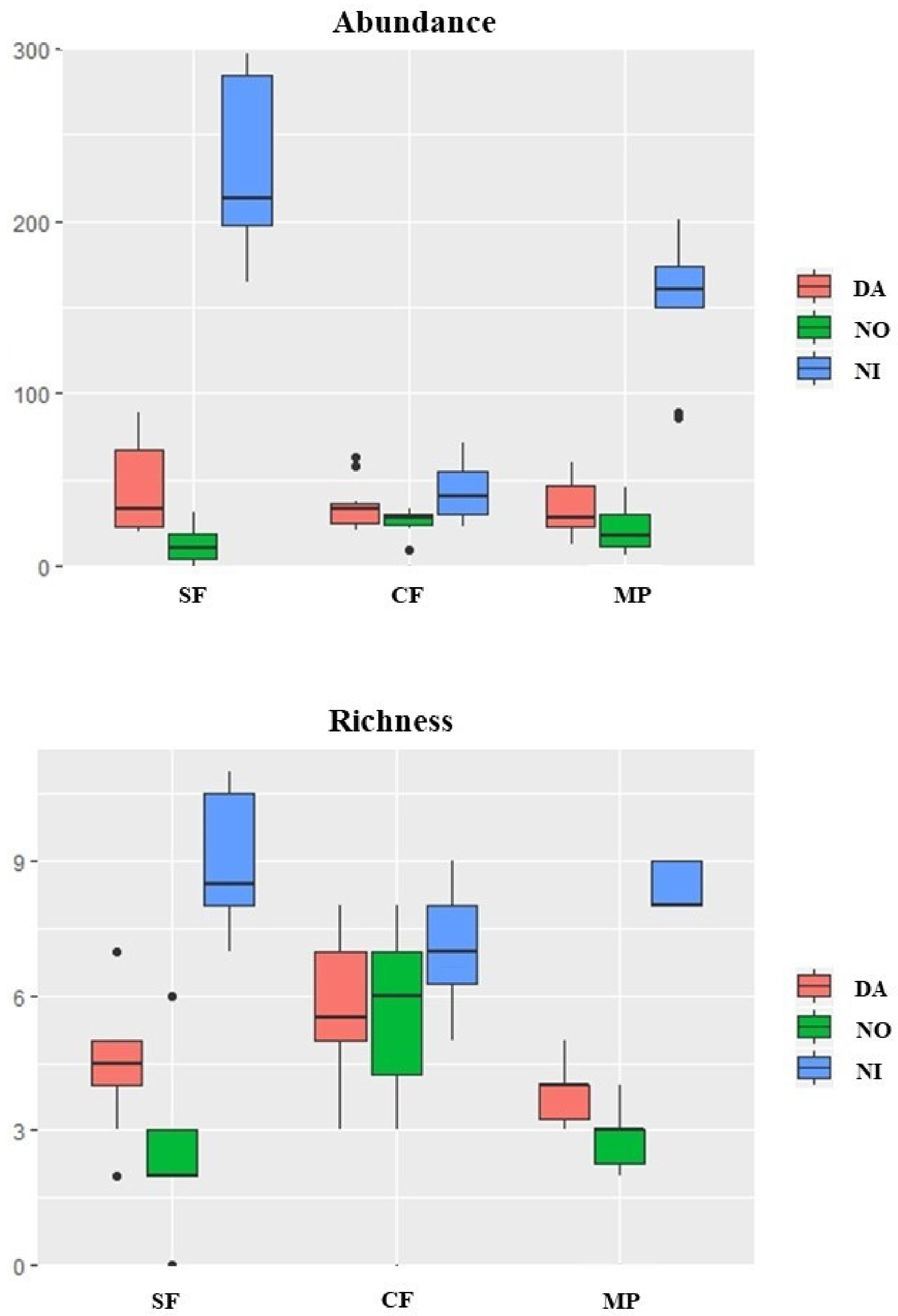

Figure 3. Mosquito richness and abundance in different land use type and activity periods. CF=low semi-evergreen forest, SF=secondary low semi-evergreen forest, MP=mango plantation, DA=dawn, NO=Noon, NI=nightfall activity period.

Table 2. A generalized linear model (GLM) assuming a Negative Binomial distribution with logit link function for Abundance and Richness analysis. Significant *P* values are in boldface and non-significant trends in italics.

Abundance

Components	Estimate	SE	*z*-value	*P*-value
Intercept	3.79549	0.1441	26.34	**< 2e-16**
Low semi-evergreen forest (CF)	-0.22596	0.20517	-1.101	*0.270771*
Secondary low semi-evergreen forest (SF)	-0.29596	0.20567	1.439	*0.150159*
Nightfall (NI)	1.68181	0.19924	8.441	**< 2e-16**
Noon (NO)	-1.31058	0.2182	-6.006	**1.90E-09**
CF:NI	-1.49714	0.28616	-5.232	**1.68E-07**
SF:NI	-0.06575	0.28346	-0.232	*0.81658*
CF:NO	0.99915	0.30217	3.307	**0.000945**
SF:NO	0.83634	0.30417	2.75	**0.005968**

Richness

Components	Estimate	SE	*z-value*	*P*-value
Intercept	1.4816	1.51E-01	9.828	**< 2e-16**
Low semi-evergreen forest (CF)	2.76E-01	2.00E-01	1.382	*0.167036*
Secondary low semi-evergreen forest (SF)	-1.21E-01	2.20E-01	-0.548	*0.58336*
Nightfall (NI)	7.04E-01	1.84E-01	3.822	**1.32E-04**
Noon (NO)	-6.49E-01	2.57E-01	-2.521	**0.011699**
CF:NI	-5.02E-01	2.56E-01	-1.965	**0.049364**
SF:NI	6.28E-02	2.67E-01	0.235	*0.814308*
CF:NO	6.14E-01	3.18E-01	1.928	*0.053875*
SF:NO	3.17E-01	3.57E-01	0.889	*0.374269*

the SF site, but in the MP it was more abundant in the NO period. This may be due to the ability of this species to adapt to regenerating sites or with intense changes, such as on a plantation (Orlandin et al. 2017).

With respect to the type of land use, *Haemagogus regalis* had its greatest abundance in EF during the NO period, possibly influenced by the presence of epiphytic plants such as bromeliads which are used as a site for oviposition (Berlin 1969, Lane 1953). Species in the genus *Anopheles* had mostly crepuscular activity (Astaiza et al. 1988) in the NI period except for *An. pseudopunctipennis* that was captured in the DA period. In turn, they had a greater presence and abundance in the SF site as some species of this genus have a predilection for disturbed sites (Rodríguez et al. 1996).

Some species of mosquitoes exhibit a high degree of specialization in their host selection and oviposition site, while others are generalists and opportunistic (Bentley and Day 1989). Changes in host abundance due to anthropogenic impacts can affect both host choice and habitat, especially if the species are generalists (Takken and Verhulst 2013, Abella-Medrano et al. 2015). Environments with some degree of disturbance, such as the SF and MP, can have a negative influence on biodiversity due to habitat loss, defaunation, and introduction of domestic fauna (Alberti 2008), that could cause mosquito species to adapt and therefore increase their abundance. For example, *Ae. scapularis* are attracted to humans and pets and feed on them, and in turn are a potential vector of Venezuelan equine encephalitis and yellow fever. On the other hand, *Cx. nigripalpus* had a greater abundance in the MP site that may be due to the proximity to the Usumacinta River, and as a consequence, environments are created for oviposition in permanent and semi-permanent water.

We show that land use types and periods of activity influence the structure of the mosquito assembly. However, our results also show that the assemblage of mosquitoes, despite being immersed in the same matrix and presenting three dominant species, is quite heterogeneous (that is, structure of different richness and abundance), which suggests that biotic and abiotic conditions are different for each type of land use. In turn, the periods of activity influence the presence of the species. Regenerating sites could host a greater abundance of species that could be disease vectors (*Ae. taeniorhynchus* and *Ae. scapularis*), but conserved sites could be more diverse. Finally, our work generates important information to understand the diversity of mosquitoes in reference to changes in land use in different periods of activity. We consider it a potentially useful tool in the development of epizootiological planning and surveillance programs focused mainly on species of mosquitoes of medical and veterinary importance.

Acknowledgments

We thank Simon Pierre Mokondoko-Delgadillo, Paulina Walbey, Citlali López, Brenda Maya, Guillermo Orta and Adrián Serrano for their assistance during fieldwork. We thank landowners (Roberto Calzada, Roberto Uribe Jacinto, Juan Carlos Garcia Martinez, and Sebastián Montejo Narváez) for allowing us to work on their private properties. Rafael Ojeda-Flores was supported by Consejo Nacional de Ciencia y Tecnología (CONACYT Problemas Nacionales #219), and Carlos Antonio Abella-Medrano was supported by a post-doctoral fellowship grant (DGAPA Dirección general de asuntos del personal académico, Departamento de Fortalecimiento Académico, Programa de Becas Posdoctorales, Universidad Nacional Autónoma de México UNAM).

REFERENCES CITED

Abella-Medrano, C.A., S. Ibáñez-Bernal, I. MacGregor-Fors, and D. Santiago-Alarcon. 2015. Spatiotemporal variation of mosquito diversity (Diptera: Culicidae) at places with different land-use types within a neotropical montane cloud forest matrix. Parasit.Vectors 8: 487.

Abella-Medrano, C.A., S. Ibáñez-Bernal, P. Carbó-Ramírez, and D. Santiago-Alarcon. 2018. Blood-meal preferences and avian malaria detection in mosquitoes (Diptera: Culicidae) captured at different land use types within a neotropical montane cloud forest matrix. Parasitol. Intl. 67: 313-320.

Alberti, M. 2008. *Advances in Urban Ecology: Integrating Humans and Ecological Processes in Urban Ecosystems*. Springer, NY, 366 pp.

Alcaide, M., C. Rico, S. Ruiz, R. Soriguer, J. Munoz, and J. Figuerola. 2009. Disentangling vector-borne transmission networks: a universal DNA barcoding method to identify vertebrate hosts from arthropod bloodmeals. PLoS ONE 4: e7092. doi:10.1371/journal.pone.0007092.

Ailes, M.C. 1998. Failure to predict abundance of saltmarsh mosquitoes *Aedes sollicitans* and *Ae. taeniorhynchus* (Diptera: Culicidae) by using variables of tide and weather. J. Med. Entomol. 35: 200-204.

Astaiza, R., C. Murillo, and P. Fajardo. 1988. Biología de *Anopheles* (*Kerteszia*) *neivai* HD&K (Diptera: Culicidae) en la costa pacífica de Colombia. Rev. Saude Publ. 22: 101-108.

Belkin, J.N., S.J. Heinemann, and W.A. Page. 1970. The Culicidae of Jamaica. Contrib. Am. Entomol. Inst. 6: 1-458 pp.

Bentley, M.D. and J.F. Day. 1989. Chemical ecology and behavioral aspects of mosquito oviposition. Annu. Rev. Entomol. 34: 401–421.

Berlin, O.G.W. 1969. Mosquito studies (Diptera, Culicidae) XII. A revision of the neotropical subgenus *Howardina* of *Aedes*. Estudios sobre zancudos (Diptera, Culicidae) XII. Revisión del género neotropical *Howardina* de *Aedes*. Contrib. Am. Entomol. Inst. 4: 1-190.

Brown, B.V., A. Borkent, J.M. Cumming, D.M. Wood, N.E. Woodley, and M. Zumbado. 2009. *Manual of Central American Diptera: Volume 1*. Canadian Sci. Publ. (NRC Research Press). 714 pp.

Bona, A.A. and M.A. Navarro-Silva. 2008. Diversidade de Culicidae durante os períodos crepusculares em bioma de Floresta Atlântica e paridade de *Anophles cruzii* (Diptera: Culicidae). Rev. Brasileira Zool. 25: 40-48. http://dx.doi.org/10.1590/S0101-81752008000100007.

Carpenter, S.J. and W.J. LaCasse. 1955. Mosquitoes of North America. Univ. Calif. Press. 360 pp.

Chao, A. and T.J. Shen. 2010. Program SPADE (Species Prediction and Diversity Estimation). http://chao.stat.nthu.edu.tw.

Colwell, R.K. and J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Phil. Trans. R Soc. B. 345: 101–118.Darsie Jr., R.F. 1996. A survey and bibliography of the mosquito fauna of Mexico (Diptera: Culicidae). J. Am. Mosq. Contr. Assoc. 12: 298-306.

Forattini, O.P., A.C. Gomes, J.L.F. Santos, E.A.B. Galati, E.X. Rabello, and D. Natal. 1981. Observações sobre atividade de mosquitos Culicidae, em mata residual no Vale do Ribeira, São Paulo, Brasil. Rev. Saúde Públ. 15: 557-586.

Gottdenker, N.L., D.G. Streicker, C.L. Faust, and C.R. Carroll. 2014. Anthropogenic land use change and infectious diseases: a review of the evidence. EcoHealth 11: 619-632.

Harbach, R.E. 2007. The Culicidae (Diptera): a review of taxonomy, classification and phylogeny. Zootaxa 1668: 91-538.

Harbach, R.E. and K.L. Knight. 1980. *Taxonomists' Glossary of Mosquito Anatomy*: Plexus Publishing Inc. Marlton, NJ. 415 pp.

Heinemann, S.J. and J.N. Belkin. 1977. Collection records of the project "Mosquitoes of Middle America." 7. Costa Rica (CR). Mosq. Syst. 9: 237-287.

Jost, L. 2006. Entropy and diversity. Oikos 113: 363–375.

Jost, L. 2010. The relation between evenness and diversity. Diversity 2: 207–232.

Kawada, H., S.Y. Takemura, K. Arikawa, and M. Takagi. 2005. Comparative study on nocturnal behavior of *Aedes aegypti* and *Aedes albopictus*. J. Med. Entomol. 42: 312-318.

Keesing, F., L.K. Belden, P. Daszak, A. Dobson, C.D. Harvell, R.D. Holt, P. Hudson, A. Jolles, K.E. Jones, C.E. Mitchell, S.S. Myers, T. Bogich, and R.S. Ostfeld. 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468: 647-652.

Kirkeby, C., K. Græsbøll, A. Stockmarr, L.E. Christiansen, and R. Bødker. 2013. The range of attraction for light traps catching Culicoides biting midges (Diptera: Ceratopogonidae). Parasit. Vectors 6: 67.

Lane, J. 1953. *Neotropical Culicidae. Volumes I & II.* Univ. Sao Paulo, Brazil. 1,112 pp.

Lounibos, L. and J. Linley. 1987. A quantitative analysis of underwater oviposition by the mosquito *Mansonia* *titillans*. Physiol. Entomol. 12: 435-443.

Magurran, A.E. 2003. *Measuring Biological Diversity*. Wiley. 264 pp.

Ndoen, E., C. Wild, P. Dale, N. Sipe, and M. Dale. 2011. Dusk to dawn activity patterns of anopheline mosquitoes in West Timor and Java, Indonesia. SE Asian J. Trop. Med. Publ. Hlth. 42: 550.

Orlandin, E., E.B. Santos, M. Piovesan, M.A. Favretto, A.H. Schneeberger, V.O. Souza, G.A. Muller, and G. Wagner. 2017. Mosquitoes (Diptera: Culicidae) from crepuscular period in an Atlantic Forest area in Southern Brazil. Brazilian J. Biol. 77: 60-67.

Ortega Morales, A.I., P. Mis Avila, A. Elizondo-Quiroga, R.E. Harbach, Q.K. Siller-Rodríguez, and I. Fernández-Salas. 2010. Los mosquitos del estado de Quintana Roo, México (Diptera: Culicidae). Acta Zoológ. Mexicana 26: 33-46.

Ortega-Morales, A. I., R. Méndez-López, J.A. Garza-Hernández, V.H. González-Álvarez, I. Ruiz-Arrondo, H. Huerta-Jiménez, L.M. Rodríguez-Martínez, and M.A. Rodríguez-Pérez. 2019. The mosquitoes (Diptera: Culicidae) of Tabasco, Mexico. J. Vector Ecol. 44: 57-67.

Rodriguez, A.D., M.H. Rodriguez, J.E. Hernandez, S.W. Dister, L.R. Beck, E. Rejmankova, and D.R. Roberts. 1996. Landscape surrounding human settlements and *Anopheles albimanus* (Diptera: Culicidae) abundance in Southern Chiapas, Mexico. J. Med. Entomol. 33: 39-48.

Smith, K.F., D.F. Sax, S.D. Gaines, V. Guernier, and J.F. Guégan. 2007. Globalization of human infectious disease. Ecology 88: 1903-1910.

Silver, J. B. 2007. *Mosquito Ecology: Field Sampling Methods*. Springer. 1,477 pp.

Takken, W. and N.O. Verhulst. 2013. Host preferences of blood-feeding mosquitoes. Annu. Rev. Entomol. 58: 433-453.

Wright, R.E. and K.L. Knight. 1968. Evening crepuscular activity of some Iowan mosquitoes (Diptera: Culicidae). J. Kansas Entomol. Soc. 45-47.

Wilcox, B.A. and D.J. Gubler. 2005. Disease ecology and the global emergence of zoonotic pathogens. Environ. Hlth. Prev. Med. 10: 263-272.