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Macrophytes and metaphyton as habitats for insects in temporary and permanent tropical aquatic ecosystems

Las Macrófitas y el metafiton como hábitats para insectos en ecosistemas acuáticos tropicales temporales y permanentes

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Insect community structures in tropical regions appear to be related to the hydrological regime and energy paths through autochthonous and allochthonous sources. Macrophyte and metaphyton permanent coverage throughout the year generate conditions and resources, such as food and refuge, allowing the establishment of a large number of aquatic insect species. The hydrological regime is based on rain seasonality and has a direct influence on insect lifecycles. We evaluated insect community structures in five systems with differences in macrophyte/metaphyton coverage and hydrological regimes (two temporary wetlands and three permanent cenotes) in the Sian Ka'an Biosphere Reserve in southeast Mexico. The insect diversity values highly correlated with metaphyton abundance but not with macrophyte coverage. We also found that cenote hydrological stability could produce higher insect diversity in comparison with temporary wetlands.

Keywords: Sian Ka'an; cenotes; wetlands; aquatic vegetation; diversity

La comunidad de insectos en regiones tropicales está relacionada con el régimen hídrico y las rutas de energía tanto alóctonas como autóctonas. A lo largo del año, la cobertura permanente de las macrófitas y el metafiton generan condiciones y recursos propicios para la sobrevivencia de insectos, lo que ayuda a establecer un mayor número de especies. Por su parte, el régimen hídrico basado en lluvias y secas, tiene un efecto directo en el ciclo de vida de los insectos. En este trabajo evaluamos la estructura de la comunidad de insectos en cinco sistemas con diferencias en la cobertura de los productores primarios y en el régimen hídrico (dos humedales temporales y tres cenotes con agua todo el año) en la Reserva de la Biosfera de Sian Ka'an al sudeste de México. Encontramos que la diversidad de insectos está relacionada con la abundancia de metafiton, pero no lo está con la cobertura de macrófitas. También encontramos que la estabilidad hídrica de los cenotes podría producir una mayor diversidad de insectos en comparación con los humedales más temporales.

Keywords: Humedales; Vegetación Acuática; Diversidad; Yucatán; Quintana Roo

Introduction

Aquatic insect diversity is positively related to environmental heterogeneity.[1,2] In aquatic systems, primary producers mostly generate spatial heterogeneity by modifying the local environment and increasing the number of microhabitats [3] for different animal species.[4–6] Nevertheless, each primary producer has different morphologies and physiologies that generate dissimilar local conditions, such as microclimate, stream flow, food source and shelter against predators,[7–10] which is related to the number of available habitats.[11]

In aquatic systems, primary producers can be grouped into the following four categories: (1) phytoplankton, (2) periphyton, (3) metaphyton and (4) macrophytes. Because most phytoplankton do not generate structures suitable for macroinvertebrates, this group mostly affects habitats as a food source.[12–14] In contrast, periphyton, metaphyton and macrophytes not only

provide a food source but also provide shelter and modify the microclimate for macroinvertebrates and fish.[7,8,10,15]

In tropical wetlands, temperature seasonal variation is lower than in temperate systems. This small temperature variability has been related to larger macrophyte biodiversity in the neotropics than in the rest of the world.[16] Nevertheless, a marked seasonal variation in rainfall exists in most tropical wetlands that provokes floods as well as affects populations and macrophyte community structures.[17,18]

The morphology of primary producers may also influence the aquatic fauna composition.[19–21] Macrophytes can be classified according to their morphology and growth form as emergent, free-floating or submerged.[22,23] Each morphological characteristic allows the establishment of different aquatic insect communities.[21,24]

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Metaphyton has been defined as a floating mat composed mainly by macroscopic filamentous cyanoprokaryotes, diatoms, detritus and other components.[25] These free-floating structures are formed by several types of algae, protozoans, bacteria, fungi and detritus that serve as food sources for aquatic insects.[6,26–30] The influence of metaphyton in aquatic systems in tropical systems has received relatively little attention, although this algae community greatly influences the aquatic ecosystem ecology dynamics, such as nutrient cycles,[31] primary production, fauna diversity,[15,31–35] and even the number of larvae of the emergent insects.[33]

Usually, complex structures generated by these primary producers contain higher richness and diversity values of aquatic insects within a lake or river in temperate zones. For example, in the St. Lawrence River, Canada, metaphyton show larger macroinvertebrate biomasses than less complex substrates, such as submerged plants, which in turn show larger insect biomasses than emergent plants with simpler structures.[25] Nevertheless, this relationship depends on local conditions. For example, in eutrophic ponds in Fleetwood, UK, macroinvertebrate diversity values were higher in emergent rather than submerged or free-floating macrophytes.[21] However, these studies were focused on temperate systems with high anthropogenic disturbances that may affect these relationships.

In tropical regions, hydrological lake dynamics may influence the relationship between insects and primary producers. Changes in the hydraulic regime can affect the insect life strategies, which alters their survival capabilities and, consequently, their diversity.[26]

In this study, we aimed to evaluate these relationships within a pristine tropical system, in the Sian Ka'an Biosphere Reserve (SKBR), the largest reserve in Mexico, to better understand the relationships between insects and different primary producers related to hydrological changes. Our main purpose was to determine the relationship between the diversity of aquatic insect community with metaphyton and emergent macrophytes in a pristine setting, using both permanent and temporary tropical water bodies.

Methods

The SKBR is located in the Quintana Roo state in south-east México between 20° 07' 28" and 18° 07' 28" latitude and 88° 12' 12" and 87° 24' 36" longitude (Figure 1). The reserve is 5517.5 km² in area and an average of nine meters above sea level.[34] The climate is tropical wet and dry seasons (AW); it is warm and sub-humid with a summer rainy season and an annual average temperature of 26 °C with between 1100 and 1200 mm of annual precipitation. The rainy season lasts from May to March, and it is divided in two periods. The first period, a warmer rainy season due to hurri-

canes, lasts from May to October with 70% (800–1000 mm) of the rainfall. The second period, with colder precipitation from the humidity from by the Gulf of Mexico nortes, lasts from November to March with 150–300 mm of rainfall. April to July is the dry season, with approximately 60 mm of rainfall.[34–36]

The SKBR is part of one of the biggest karst systems on the earth, with soil composed of sedimentary rocks including limestones and dolomites.[34–37] The characteristics of the soil permit the existence of karst formations from the weathering of calcium carbonate in the zone, generating complex hydrological systems in a small geographic area composed of temporal wetlands and permanent cenotes.[38–40]

Cenotes are formed when calcareous soil collapses over an underground river leaving the underground water supply open to the outside.[37,41] Seasonal changes have a small influence on these water bodies. In contrast, wetlands totally depend on the rainfall, which causes their size to vary by season throughout the year.[41] Wetlands are water-covered surfaces with a depth below two meters.[36] Their large surface and low depth makes these water bodies susceptible to changes in temperature throughout the day and higher evaporation rates; thus, they depend on a constant supply of water from rainfall.[42]

SKBR vegetation is characterized by semi-deciduous and flooded forests, in which the dominant species include *Brosimum alicastrum*, *Manilkara zapota*, *Thrinax radiata*, *Bursera simaruba*, *Caesalpinia gaumeri*, *Haematoxylum campechianum* and *Bucida buceras*. [34–36] The aquatic vegetation community is dominated by emergent plants such as *Typha domingensis*, *Cladium jamaicense*, *Phragmites australis* and *Echinodorus andrieuxii*. [43,44] According to metaphyton studies of areas close to the Reserve, the metaphyton is mainly composed of filamentous cyanoprokaryota with a high presence of diatoms.[45]

Two wetlands and three cenotes were sampled within a year in the following three seasons: (1) warm rainy season (June), (2) cold rainy season (November) and (3) dry season (April). One of the cenotes has no littoral vegetation, while aquatic vegetation is present in the other two cenotes. To avoid species–area relationships, wetlands sampled areas were similar to cenotes (500–7000 m²). We choose cenotes and wetlands to evaluate the role of macrophytes and metaphyton on insects in aquatic systems with different water regimes, permanent in cenotes and temporary in wetlands.

In each system, we evaluated physicochemical parameters with a multiparameter probe (Hanna HI9828); wetlands were not measured in dry season because depth was below 5 cm. In addition, the percent coverage by macrophytes and metaphyton was determined. We only evaluated the percentage of emergent macrophytes, as it is the dominant macrophyte community. For both

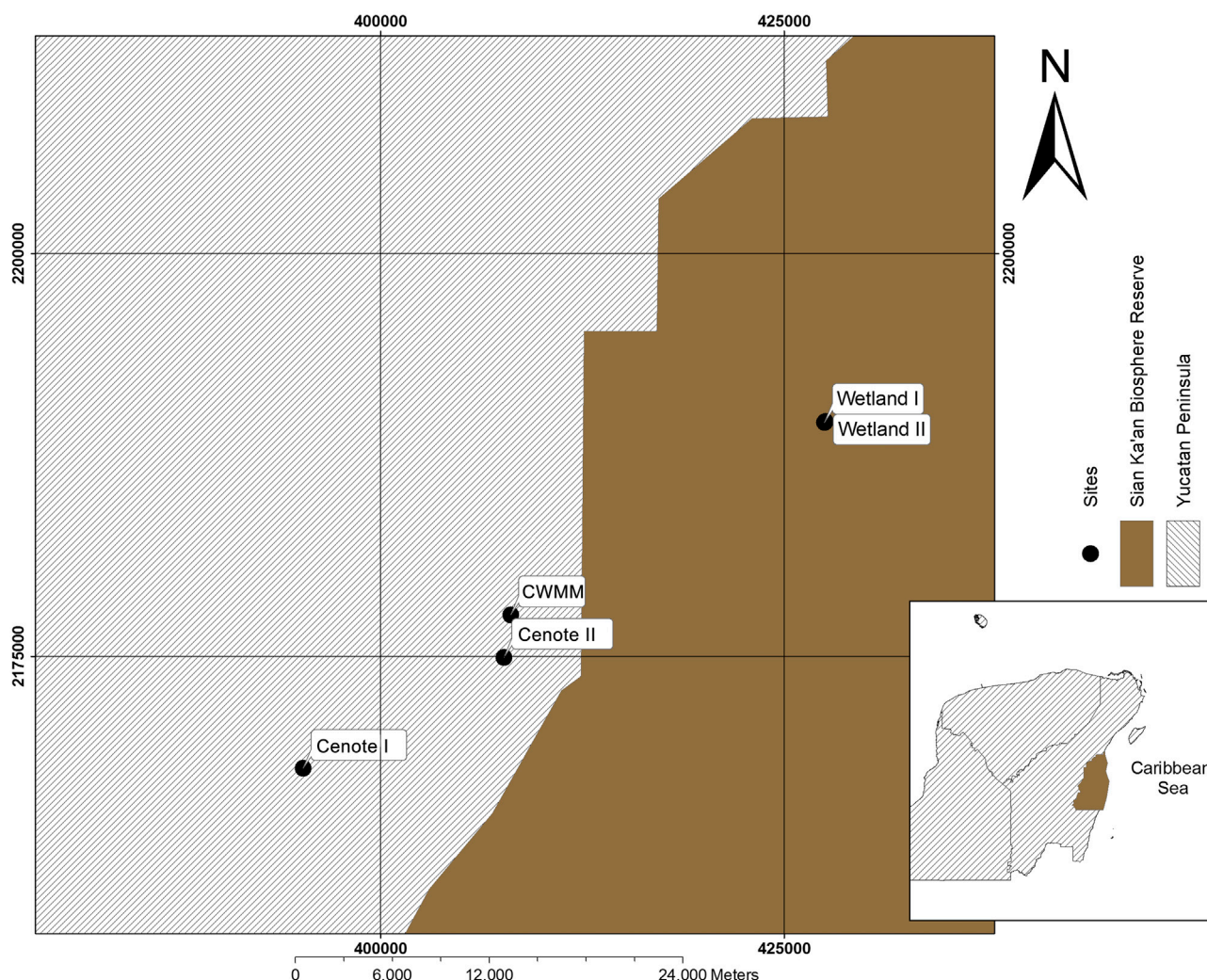


Figure 1. Geographical distribution of cenotes and wetlands sampled at Sian Ka'an Biosphere Reserve in the southeast of Mexico.

macrophytes and metaphyton, the percent coverage was evaluated with the naked eye within 1 m² quadrants.[46] We randomly placed 10 quadrants in the wetlands. In contrast, the quadrants were only placed in the littoral zones of the cenotes, as it is the only place macrophytes and metaphyton are established in the system.

The insects were sampled with a standard 30.5 cm D-frame aquatic net (mesh size of 0.25 mm). These nets are frequently used and recommended to sample macroinvertebrates on different kind of substrates in aquatic systems, allowing a homogenized sample.[47] In both cases, (wetlands and cenotes) macroinvertebrates were samples with 12 swings randomly placed on the wetland surface and in the littoral zones of cenotes, sampling nets were swung up from the substrate regardless of whether the substrate was soft or hard.

The collected insects were separated, preserved (in alcohol 80%) and transported to the laboratory. The

insects were then counted and identified down to the genus level with taxonomical keys.[48–59]

A non-metric multidimensional scaling (NMDS) was carried out in order to determine correlations among physicochemical variables. Aquatic primary producer coverage was compared among the sample sites with ANOVA, excluding the cenote without any primary producers. The insect community structure was characterized according to its total insect abundance and insect diversity using genus as a base unit and Fisher's alpha diversity index. We also looked for relationships among macrophytes, metaphyton and insect community attributes with correlation analyses using each sample season as a unit.

Results

Variability in physicochemical parameters was larger in wetlands than in cenotes. (Table 1). This last one

Table 1. Average of temperature, conductivity, dissolved oxygen and pH in the studied aquatic systems during the annual cycle in SKBR, Quintana Roo, Mexico.

Season	Aquatic system	Temperature (°C)	Conductivity ($\mu\text{S}/\text{cm}^2$)	Oxygen (mg/l)	pH
Early rainy	Cenote I	32.49	1.32	5.78	8.38
Early rainy	Cenote II	32.56	1.32	6.23	8.05
Early rainy	CWMM	28.6	2.52	6.46	7.76
Early rainy	Wetland I	30.28	1.24	0.72	7.99
Early rainy	Wetland II	31.33	1.32	1.27	7.91
Late rainy	Cenote I	27.07	1.44	1.79	9.1
Late rainy	Cenote II	25.77	1.27	1.57	9.08
Late rainy	CWMM	25.36	2.96	1.11	8.88
Late rainy	Wetland I	24.38	1.16	1.32	9.34
Late rainy	Wetland II	24.73	1.2	1.45	8.62
Dry	Cenote I	26.62	1.45	5.78	8.38
Dry	Cenote II	29.75	1.44	6.23	8.05
Dry	CWMM	25.63	3.23	6.46	7.76
Dry	Wetland I	—	—	—	—
Dry	Wetland II	—	—	—	—

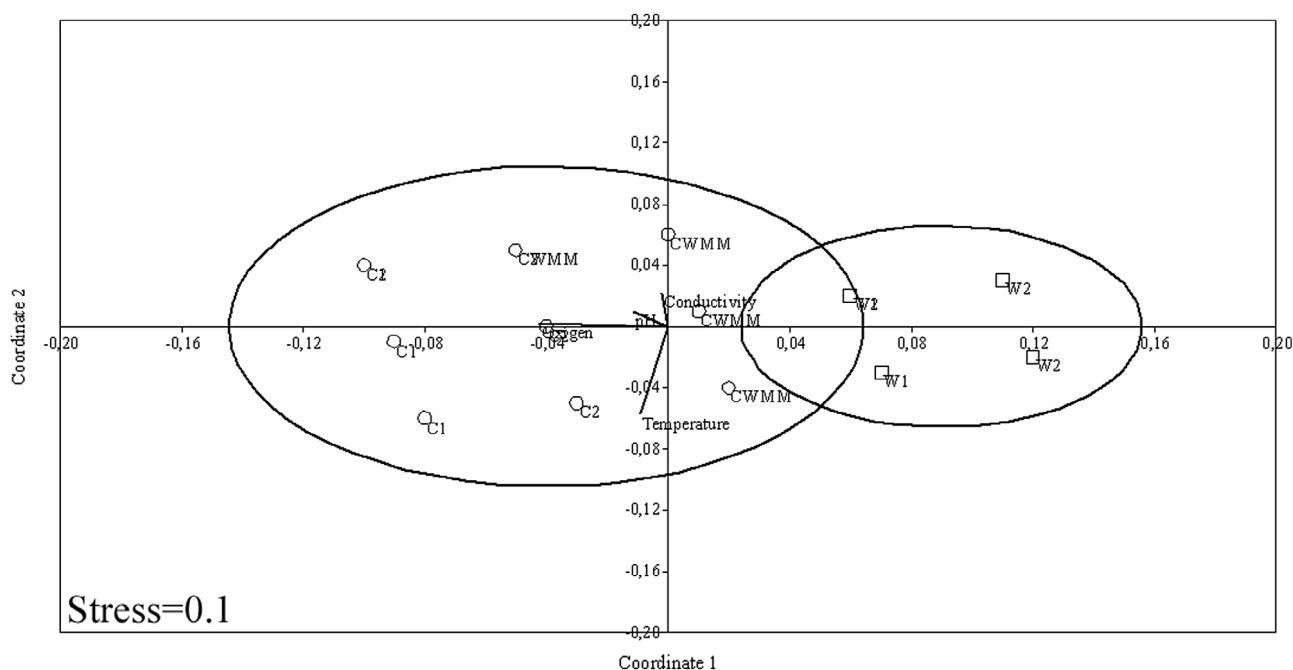


Figure 2. Non-metric multidimensional analysis, NMDS, for environmental variables of SKBR, Quintana Roo, Mexico. C1 = Cenote 1, C2 = Cenote 2, CWMM = Cenote without macrophytes and metaphyton, W1 = Wetland 1, W2 = Wetland 2.

presented higher values in oxygen concentration and pH and lower values in conductivity than wetlands. According to NMDS (Stress = 0.1; Figure 2) temperature and oxygen are the main factors of variance among sites and seasons.

Macrophyte coverage did not change among seasons (Table 2). However, there was significantly higher macrophyte coverage in the wetlands than in the cenotes ($H = 66.04$, $p < 0.05$). In contrast, metaphyton demon-

strated significant coverage differences among the seasons ($F = 3.06$, $p < 0.05$) and between the cenotes and the wetlands ($F = 4.43$, $p < 0.05$). A negative correlation was found between the macrophyte and metaphyton coverage (Figure 3).

We collected 790 unique aquatic insects distributed in 48 genera, with 22 (48.5%) belonging to the order Dipterans, 9 (18.8%) to Odonata, 8 (16.7%) to Coleoptera, 5 (10.4%) to Hemiptera and 4 (8.3%) to Ephemeroptera.

Table 2. Averages of the percentages of macrophytes covering periphyton mats in the aquatic systems studied, SKBR, Quintana Roo, Mexico.

Seasons Aquatic system	Warm rainy		Cold rainy		Dry	
	Metaphyton	Macrophytes	Metaphyton	Macrophytes	Metaphyton	Macrophytes
Cenote I	73	9	75	6	69	10
Cenote II	69	5	71	3	84	1
CWMM	—	—	—	—	—	—
Wetland I	61	38	75	23	51	25
Wetland II	68	32	64	29	48	23

Note: CWMM = cenote without macrophytes and metaphyton.

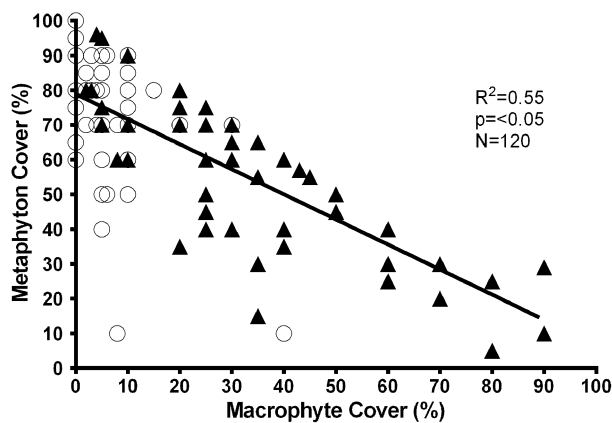


Figure 3. Correlation between coverage macrophytes and metaphyton in aquatic systems of SKBR, Quintana Roo, Mexico. Circles are cenotes and triangles are wetlands.

The total genus data by site is presented in the Appendix 1. The most abundant genera were Coleopterans *Enochrus* (Hydrophilidae) and *Laccophilus* (Dysticidae), with 129 and 91 organisms, respectively. The highest number of unique organisms, 487, was collected in the dry season, followed by the cold rainy season (189 organisms) and the rainy season (114 organisms). Nevertheless, the cumulative curve shows that it is important to have higher sampling to identify all genera present in the system (Figure 4).

There were no noticeable trends in the change in the diversity values during the year, and the cenotes have higher diversity values than the wetlands (Table 3). The insect diversity index showed a positive correlation with metaphyton coverage ($R^2 = 0.5$, $p = 0.01$), while there were negative correlations between macrophyte coverage and insect richness ($R^2 = 0.2$, $p = 0.07$, Figure 5).

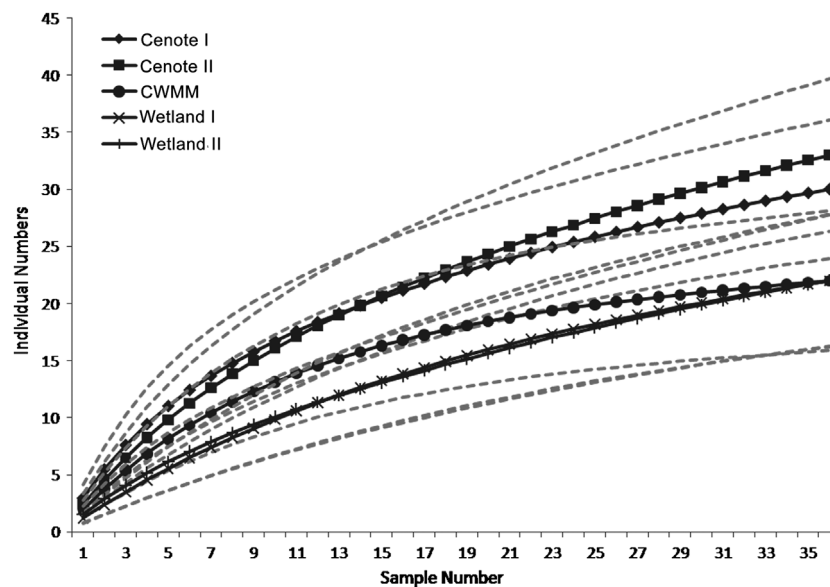


Figure 4. Accumulation curve of genus of aquatic insects' genus, SKBR, Quintana Roo, Mexico. Solid lines are the water bodies and the dotted lines are the range of 95% confidence.

Table 3. Fisher's alpha diversity index of aquatic insects for every season and annual in SKBR, Quintana Roo, Mexico.

Aquatic system	Early rainy	Late rainy	Dry	Annual Σ
Cenote I	12.01	13.47	10.76	14.33
Cenote II	8.92	8.1	5.48	9.95
CWMM	4	5.95	6.91	7.19
Wetland I	6.73	9.86	3.3	9.7
Wetland II	3.15	8.15	2.24	5.89

Note: CWMM = cenote without macrophytes and metaphyton.

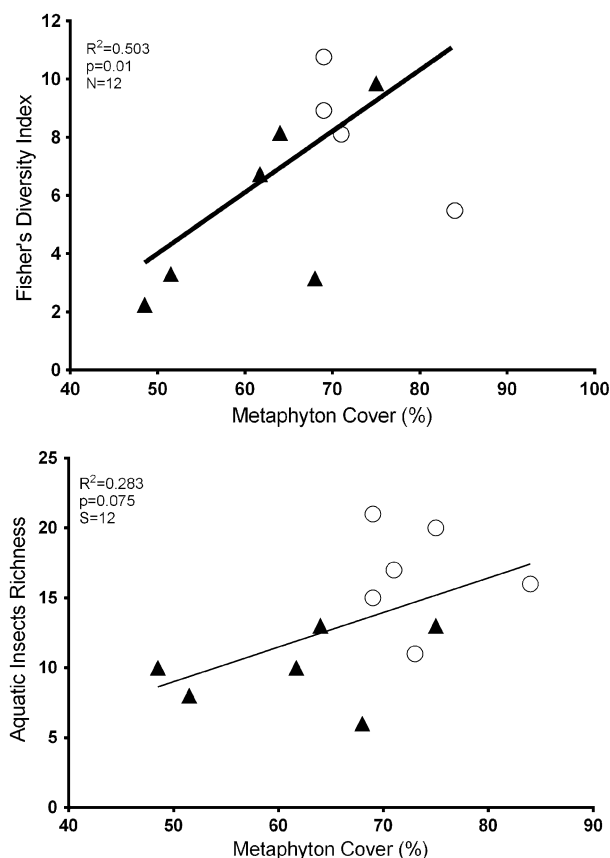


Figure 5. Correlation between Fisher's diversity and cover of macrophytes, as well as correlation between genus of aquatic insects' richness and cover of macrophytes in SKBR, Quintana Roo, Mexico. Circle represent cenotes and triangles represent wetlands.

Discussion

Cenotes have more stable physicochemical variables than wetlands because they are deep aquatic systems with permanent water sources along the year. Wetlands are temporal aquatic systems that only receive water during the rainy season. The small variation on abiotic factors in cenotes were well described in previously.[60] Other studies show that permanent and temporary wetlands in Sian Ka'an present similar abiotic conditions in rainy

seasons but differ significantly during dry season.[39,60] Nevertheless, nutrients and productivity variables such as chlorophyll *a* were low without any differences in all systems and seasons.[39]

The inverse relationship between macrophytes and metaphyton suggests a potential competitive exclusion pattern between these two types of primary producers.[61–63] Generally, plants present different strategies for competitor exclusion. During this competition, both macrophytes and metaphyton may exude allelopathic substances that inhibit the growth of their competitor.[64] The effect of allelopathy depends on the population density of the plants that produce the chemicals and the sensitivity of the plants that receive them as well as on environmental variables, such as the lack of nutrients.[65,66]

The SKBR wetlands have a low diversity and abundance aquatic insect families compared to other tropical systems.[67,68] This could be explained by the oligotrophic status of these water body types.[40] A low level of nutrients is directly related to the diversity and abundance of aquatic biota in similar systems, such as the subtropical Everglades in Florida.[68,69]

Macroinvertebrates abundance and richness increase with habitat complexity or morphology, as this is directly related to the number of microhabitats and therefore the number of biotic interactions and the greater availability of microclimates.[1] In our case, emergent plants compose the dominant macrophyte lifestyle which usually support lower macroinvertebrate diversity than other types of macrophytes.[19,70–72] This confirms that a less complex substrate may offer lower protection against predators and lower food sources.[10,11] The metaphyton is a more complex structure formed by filamentous cyanoprokaryotes, diatoms, detritus and other components.[45] This combination of elements make metaphyton wrinkled structures that produce more niches than emergent macrophytes, and therefore more aquatic insect diversity.[27] Metaphyton are usually a major component in the diet of diverse aquatic insects.[73] Nevertheless, the role of allochthonous energy on aquatic insects on SKBR must be clarified, since in others studies in the same area but on fish community, the allochthonous material is the most important mainly resource on their diet.[64]

Although the primary producers are important sources for insects, sampled cenotes without primary producers showed similar diversity to wetlands. This lack in differences suggests that other factors are playing important roles in insect diversity in tropical wetlands. One of these factors appears to be ecological stability caused by the hydrological regime. The wetland hydroperiod is unstable with long periods lacking water,[74] and wetland primary producers support only a limited insect larval community that is capable of surviving

through these harsh dry-season conditions. These larvae are the initial seeds for repopulation during the following rainy season.[75] In contrast, cenotes are a more stable system that allow the establishment of more stable aquatic communities compared with wetlands.[39,40]

The relationship between primary producers and aquatic insects in the RSBK is complex. Macrophytes and metaphyton have a negative correlation, which suggests a competitive relationship that must be further explored in later studies. However, these interactions appear to affect the aquatic insect community; in areas where metaphyton was abundant, insect communities were also more abundant and diverse than in communities with emergent macrophytes. Coupled with primary production, water supply and aquatic system hydrodynamics appear to have a strong relationship with aquatic insect diversity and abundance. This study is a first approach in identifying this three-actor relationship in the tropical calcareous system of the SKBR.

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Appendix 1

Number of individuals by genus of aquatic insects in different sites during an annual cycle in SKBR, Quintana Roo, Mexico.

Order	Genus	Cenote I	Cenote II	CWMM	Wetland I	Wetland II	Σ
Ephemeroptera	<i>Brachycercus</i>	7	1	0	0	0	8
	<i>Procloeon</i>	0	1	5	0	0	6
	<i>Cerobrachys</i>	15	0	0	0	1	16
	<i>Cloeon</i>	1	1	0	0	1	3
Odonata	<i>Erythemis</i>	9	5	1	1	1	17
	<i>Protoneura</i>	3	0	0	0	0	3
	<i>Argia</i>	8	12	6	5	4	35
	<i>Libellula (Belonia)</i>	12	3	4	1	0	20
	<i>Libellula (Holotania)</i>	9	6	3	2	0	20
	<i>Neoneura</i>	5	2	17	0	0	24
	<i>Acanthagrion</i>	1	0	8	4	0	13
	<i>Coryphaescna</i>	0	1	0	1	0	2
	<i>Nehalennia</i>	18	3	6	4	0	31
	<i>Pelocoris</i>	0	9	5	2	6	22
Hemiptera	<i>Trepobates</i> sp. 1	9	6	5	0	0	20
	<i>Trepobates</i> sp. 2	1	0	1	0	0	2
	<i>Platyvelia</i>	0	1	0	0	0	1
	<i>Mesovelia</i>	1	3	3	0	0	7
	<i>Belostoma</i>	0	0	1	0	0	1
	<i>Megadytis</i>	0	0	0	1	0	1
Coleoptera	<i>Gyrinus</i>	0	2	0	0	0	2
	<i>Laccophilus</i>	24	6	18	5	38	91
	<i>Hydaticus</i>	1	2	0	0	1	4
	<i>Anchytarsus</i>	0	1	0	1	0	2

(Continued)

Appendix1 (Continued).

Order	Genus	Cenote I	Cenote II	CWMM	Wetland I	Wetland II	Σ
Diptera	<i>Enochrus</i>	38	16	1	21	53	129
	<i>Hydrochus</i>	0	0	0	4	0	4
	<i>Prionocyphon</i>	0	6	21	1	2	30
	<i>Dasyhelea</i>	2	0	0	0	8	10
	<i>Chaoborus</i>	1	0	0	0	0	1
	Tipulidae	2	0	0	0	2	4
	<i>Anopheles</i>	6	1	4	0	2	13
	<i>Deinocerites</i>	1	0	0	0	3	4
	<i>Culex</i>	1	2	0	0	2	5
	<i>Ablabesmyia</i>	1	1	0	2	1	5
	<i>Goeldichironomus</i>	1	1	0	2	0	4
	<i>Axarus</i>	3	5	11	10	4	33
	<i>Parachironomus</i>	0	1	0	0	0	1
	<i>Polypedilum</i>	4	11	0	7	46	68
	<i>Natarsia</i>	0	0	3	0	1	4
	<i>Tribelos</i>	4	1	0	0	0	5
	<i>Zavreliella</i>	0	0	0	0	1	1
	<i>Beardius</i>	0	0	0	2	0	2
	<i>Dicrotendipes</i>	0	10	15	0	5	30
	<i>Chironomus</i>	2	3	0	0	1	6
	<i>Glyptotendipes</i>	0	0	0	2	0	2
	<i>Micropsectra</i>	0	1	0	3	58	62
	<i>Endotribelos</i>	0	0	1	0	0	1
	Tabanidae	2	2	0	2	0	6
	<i>Synendotendipes</i>	0	1	7	0	0	8
	Σ	193	129	146	84	241	793

Note: CWMM = cenote without macrophyte or metaphyton.