

## Research Article

# Temporal variation in the diversity of Cantharidae (Coleoptera), in seven assemblages in tropical dry forest in Mexico

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### Abstract

One aspect of cantharids that has received little attention is the analysis of temporal diversity patterns. For an approximation to this aspect, temporal variation in richness, abundance and temporal turnover in monthly species composition were analyzed for seven assemblages of Cantharidae associated to the Tropical Dry Forest (TDF), in Mexico. A search was also made for processes associated. High species richness and abundance for the rain season, high dissimilarity among the months of the inter-seasonal period, and common patterns of diversity in the assemblages, regardless of the species they included, were expected. The seven assemblages clearly displayed a seasonal pattern of abundance associated with the rain season, but the total expression of seasonality in each assemblage was determined by asynchronous emergence of genera and species, in addition to high temporal turnover in species composition. With few exceptions, abundance, richness and temporal turnover showed statistically significant correlation with variation in precipitation; temperature had apparently little or no influence. The results suggest that adult emergence could be determined by host plant phenology and, indirectly, by abiotic factors such as precipitation. The importance of conducting more comprehensive studies to provide accurate evidence to characterize temporal patterns of diversity in TDF insect assemblages and associated processes, not just indicating the presence-absence of species at given times and places is emphasized.

**Key words.** Soldier beetles, Insecta, phenology, temporal turnover.

### Resumen

Uno de los aspectos de Cantharidae que ha recibido poca atención es el análisis de sus patrones temporales de diversidad. Como una aproximación al tema, en este trabajo se analizó la variación temporal de la riqueza, abundancia y disimilitud en la composición de especies, dentro de siete ensambles de cantáridos asociados a bosque tropical caducifolio (BTC) en México, y procesos relacionados. Se esperaban altos valores de riqueza y abundancia durante la temporada de lluvias, una alta disimilitud en los meses del periodo interestacional, así como patrones similares entre los ensambles, independientemente de las especies que los componen. Los ensambles mostraron un patrón estacional de abundancia claramente asociado a la temporada de lluvias, pero la expresión total de la estacionalidad de cada uno estuvo determinada por la emergencia asincrónica de géneros y especies y por la alta disimilitud en la composición temporal de especies. Con algunas excepciones, la abundancia, riqueza y disimilitud temporal, tuvieron una relación significativa con la variación mensual de la precipitación; la temperatura tiene poca o ninguna influencia. Es posible que la emergencia de los adultos de cantáridos esté determinada por la fenología de sus plantas huéspedes e indirectamente por factores abióticos como la precipitación. Sin embargo, son necesarios estudios más integrales que provean evidencia robusta para caracterizar los patrones temporales de la diversidad de insectos en el BTC y los procesos implicados, que no sólo señalen la presencia-ausencia de las especies en ciertos lugares y momentos.

**Palabras clave:** cantáridos, Insecta, fenología, variación temporal.

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## Introduction

Cantharidae (Coleoptera), is the most diverse family of soft-bodied elateroids, with five subfamilies, nine tribes, approximately 150 genera and close to 5,700 species, which are found world-wide (except for the Antarctic region), in a great variety of habitats [1-3]. 223 Cantharidae species have been recorded in Mexico, representing 15-25% of the total estimated richness of the country [4]. This biological group also has high and complex morphological, taxonomic, ecological and evolutionary diversity [5].

One of the aspects of cantharids that has received little attention is the analysis of their temporal diversity patterns. Until now, there had been no studies analyzing this in detail, although several authors had recognized that some genera and species of the family could emerge at any time or at very specific times of the year, in spring or summer, usually in synchrony with seasonality [6, 7, 8]. This information is commonly obtained from labels of specimens found in collections [e.g. 9, 10], and is of no use in pinpointing how the cantharid species in the same assemblage appear through time and/or which processes are associated to phenology, leaving a significant information gap in the study of this family.

There are few studies that focus on patterns of temporal variation of insect diversity [e.g. 11-14], in comparison to those that evaluate spatial diversity patterns. One of the reasons to explain this difference is that, in general, a wide variety of collecting methods are used, or sampling is not systematic. This makes reliable comparison between assemblages impossible; moreover, sometimes communities are not even considered to change throughout time and space, and the study of temporal patterns is automatically discarded [12, 15].

Considering this, in the absence of accurate information as a starting point, it is difficult to distinguish temporal changes in biodiversity or the factors that modulated them [15]. However, when reliable data are available, the evaluation of temporal replacement of species can be accomplished through the most common ways of exploring biodiversity, like measurement of beta diversity [16].

Depending on the time scale of the study, it is also possible to analyze how seasonal and annual events, along with other cyclical phenomena, influence the expression of species richness and relative abundance. For example, monthly variation of precipitation and temperature has proven to be important for the emergence and synchronization of seasonal insect activity; temperature can be particularly decisive in the emergence of insects, determining both development rates and periods of reproductive activity [12].

These aspects can be more relevant in seasonal ecosystems, because the variation of certain environmental factors also determines availability of food resources and/or microhabitats for insects. An evident case for this phenomenon takes place at the Tropical Dry Forest (TDF), in which the annual gradient of temperature and precipitation is pronounced and clearly defines both the rain and dry seasons. The life cycles of TDF insects have adjusted according to these seasonal changes.

In the TDF, change in leaf coverage between both seasons is drastic, while the phenology of plants varies according to the seasonal gradient and the stratum or family concerned [see 17]. In insects, it has been observed that seasonal peaks of abundance and richness occur in the wet season, with the most leaf coverage, or in synchrony with flowering and/or fructification of a particular group of plants [e.g. 18-20].

Although this temporal pattern of TDF insects is widely known, most studies do not exhaustively evaluate events of species substitution within the same assemblage over time, or even associate them with seasonality. However, this type of evaluation would allow the analysis of how the entomofauna responds to the adversity of seasonality, to evaluate responses to spatial and temporal elements and to the limitation of resources, as well as to scrutinize behaviors facing the complexity of the environment in which it is immersed [*sensu* 21].

The purpose of this work was to analyze the temporal variation in richness and abundance of seven assemblages of Cantharidae associated to TDF on the Mexican Pacific Slope, as well as to search for temporal patterns in diversity and the processes associated. Considering pairs of sampled months, the temporal replacement within species composition (beta diversity) from one month to the next was also analyzed for each assemblage, along with its relationship with temporal variation in precipitation and temperature at each locality.

From the perspectives described above, it is possible to observe: the highest number of species (in the adult stage) interacting at a single point in time (species richness); how stable the species assemblages are in time in terms of quantity and quality (beta diversity), and how changes in diversity are related with the monthly variation of temperature and rainfall in TDF assemblages. Since seasonality is noticeable and adult cantharids live for only a few weeks –commonly during the wet season [10]– high values of species richness for the rain season and high dissimilarity in monthly species composition (temporal beta diversity) between the months of the inter-seasonal period were expected, as well as common patterns of diversity in the seven assemblages, regardless of the species they included.

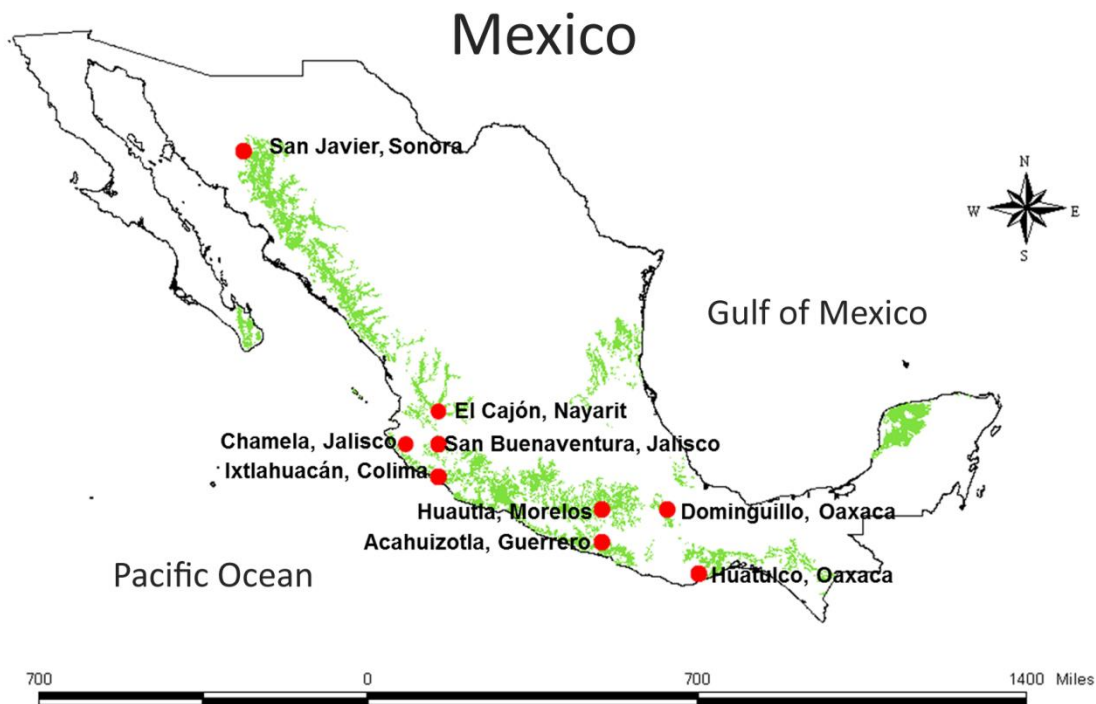
Analysis of temporal patterns of Cantharidae from Mexican TDF and possible causes does not only mean progress in the study of cantharids, but also allow to understand the TDF insect patterns. The study of temporal variation of diversity and associated processes is key to recognizing dynamics in that ecosystem, as well as establishing strategies for its conservation and restoration

[15]. Due to its nature, the TDF may be highly susceptible and unable to endure the impacts of climate change or human activity [22, 23].

## Methods

*Study areas and sampling design.* The cantharids utilized in this study were collected from seven localities within in the TDF along the Mexican Pacific Slope (Fig. 1). Each locality was sampled at different times from 1995 to 2009, as part of the long term project “*Los insectos del bosque seco*” (or “Dry forest insects”) [24], whose main purpose was to make an inventory of the Mexican TDF entomofauna and to roughly analyze phenological patterns.

The localities Santiago Dominguillo, Sierra de Huautla and San Buenaventura were the first ones visited; they were sampled monthly during a year. The other localities were sampled from seven to eight months, due to adjustments in insect collection dynamics according to the seasonality displayed by cantharids in the first sampled assemblages (Appendix 6), but always included both rain and dry seasons.



**Fig. 1. Localities with Tropical Dry Forest (TDF) from which Cantharidae (Coleoptera) were collected for this study. Green areas represent Mexican TDF according to [25].**

In each locality field work was performed: a) by two people using aerial insect nets and beat sheets, between 9:00 and 15:00 hours (or 10:00 to 16:00 in summer time); b) three Minnesota-type light traps [26] randomly placed at three sites in each locality; and c) six Malaise traps based on the Townes model were placed in each locality [27].

Light traps were equipped with a combination of one mercury-vapor lamp and two 15 watt UV bulbs (one of them unfiltered); this mechanism was placed over a 20-cm-diameter container filled with 70% ethanol. Light sources were installed against a white vertical sheet and were active each month for a five-day period, four hours a day, always with new moon on the third day of sampling. Malaise traps were active during 24 hours on the same days that light traps were active, but at different sites; in Acahuizotla, Guerrero this kind of trap was not used. For information on localities see Appendix 6. More information on trap location is found in Noguera et al. [28, 29], Rodríguez-Vélez et al. [30], and Zaragoza et al. [31, 32].

For each sampling period, monthly precipitation and temperature data were obtained from the Mexican National Meteorological Service, from the meteorological stations closest to each locality (Fig. 2). There is no precipitation and temperature data on Santiago Dominguillo, Oaxaca for the period of sampling, so the correlation analysis between these parameters and richness and abundance of Cantharidae from that locality was excluded.

*Data analysis.* For the analysis of temporal patterns of TDF diversity of Cantharidae, monthly variation in species richness and species abundance in each assemblage was considered. Because of differences in sampling effort among assemblages, the sample-based rarefaction curves with Past 3.10 software [33] were calculated; this method allows comparison among the seven assemblages at comparable levels of sampling effort [34].

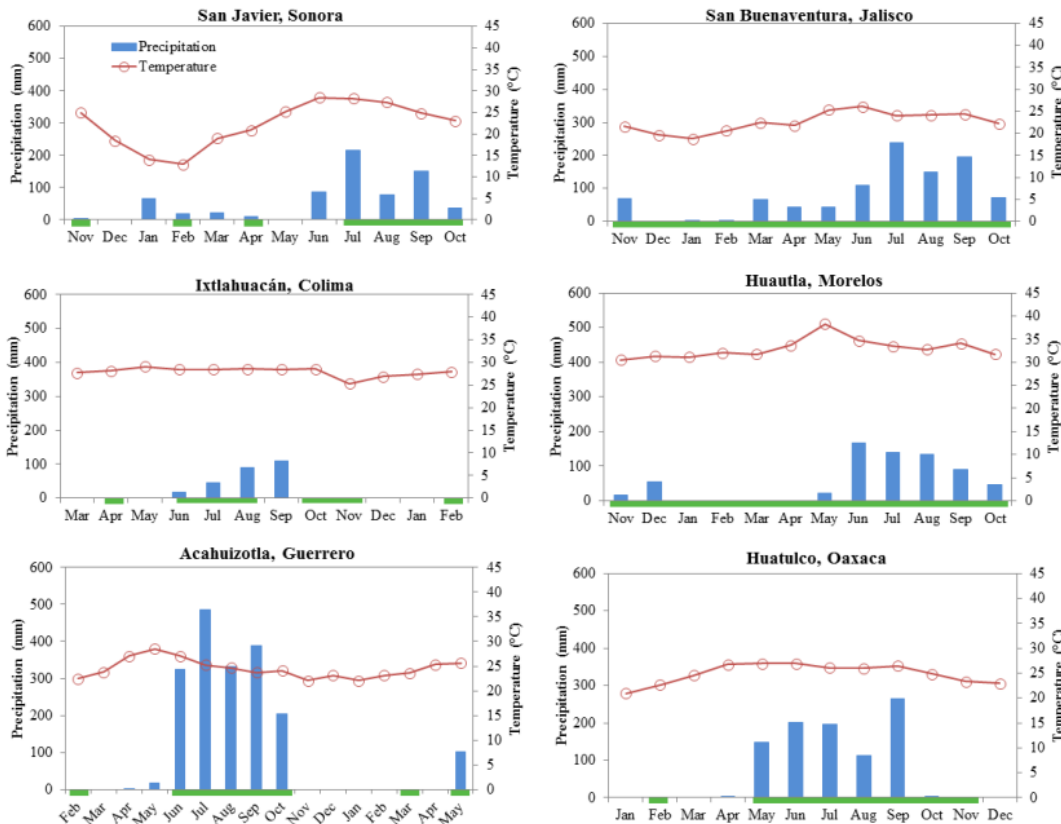


Fig. 2. Monthly variation of precipitation (bars) and temperature (lines) in the six localities with Tropical Dry Forest (TDF) on the Mexican Pacific Slope; data match the specific period of sampling in each locality. A horizontal green bar shows the actual sampling period.

The temporal turnover of TDF cantharid assemblages was analyzed using the proportion of cumulative  $\alpha$  diversity, represented by  $\alpha\% = (\bar{\alpha}/\alpha) * 100$ ; where  $\alpha$  is the cumulative alpha diversity or the total number of species in the total monthly samples, and  $\bar{\alpha}$  is the average number of species per sampling period (i.e. one month) [16, 35]. According to this measure, when  $\bar{\alpha}$  equals  $\alpha$ , no temporal turnover exists and values of  $\alpha\%$  will reach 100%.

We also calculated the dissimilarity in monthly species composition for each assemblage, using the Jaccard dissimilarity index ( $1 - \beta_{CC}$ , in this work), which only utilizes incidence data, and using the Bray-Curtis dissimilarity index ( $1 - \beta_{BC}$ , in this work), which also utilizes abundance data. This way of measuring beta diversity roughly describes the rate and magnitude of the changes in assemblage structures, and they can be associated to changes in the environment [36, 37].

To explore processes associated with temporal diversity patterns of Cantharidae, the relationship of monthly variation in temperature and precipitation with species richness and abundance was evaluated through the Pearson correlation coefficient with Past 3.10 software [33]. To evaluate the degree and direction of association between temporal turnover and temporal variation of precipitation and temperature, Mantel tests [37, 38] were conducted using 9999 random permutations of pairwise dissimilarity matrices (incidence and abundance matrices) against absolute pairwise difference in precipitation and temperature with the R package *vegan* [39].

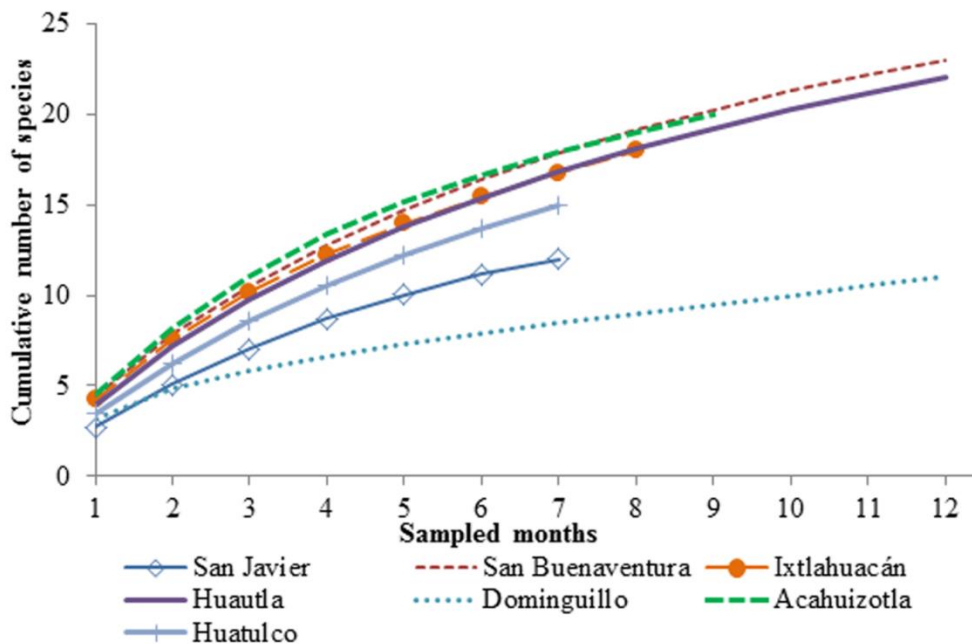
Since both environmental parameters are related with TDF resource availability [40] and had previously been proposed as important elements for the seasonality of Cantharidae [31, 32], in this study high richness and abundance were expected during the rainiest months. Temporal beta diversity was also expected to have been higher in inter-seasonal months, as a result of the variation in resource availability during that period due a higher precipitation and temperature.

## Results

71 species and 4063 specimens of Cantharidae were recorded at the seven localities of TDF sampled (Appendix 6, 7). Since the cantharid fauna of the country has been poorly studied, it was difficult to identify all the specimens to species level, so we used morphospecies in all the analyses. Sampled-based rarefaction curves (Fig. 3) demonstrate a similar pattern between San Buenaventura, Huautla, Acahuizotla and Ixtlahuacán despite of differences in sampling effort. The richest assemblages were San Buenaventura and Huautla, and the poorest was Dominguillo, the three assemblages with 12 months of sampling.

As expected, almost all the TDF Cantharidae assemblages displayed greatest abundance and species richness during the rain season (May to November) (Appendix 1). In San Buenaventura and Acahuizotla, the greatest specimen abundance also coincided with the highest precipitation of the year; in San Javier, two peaks of abundance in two distant months were recorded: April and August, during a different time of highest precipitation and temperature; in Huautla, abundance and species richness were concentrated between June and August; while in Dominguillo, where sampling was conducted under the influence of El Niño event, the maximum value of abundance was reached in October, after months of gradually increasing since March.





**Fig. 3. Sample-based rarefaction curves for seven TDF Cantharidae assemblages.**

In general, patterns of monthly richness and abundance coincided in most of the assemblages (Appendix 1), except for Ixtlahuacán and Dominguillo, which showed greatest richness in a different month than that of greatest abundance. Among the assemblages, the most pronounced abundance peaks were for Huautla and San Javier, with 414 and 331 specimens, respectively. The most prominent richness peaks were for Acahuizotla and Huautla, with 15 and 14 species, respectively.

In each assemblage, genera were being replaced by different genera over time, in such a way that only one would be dominant at a certain moment of sampling; then, its abundance would decrease gradually until another genus would replace it as dominant (Appendix 2). In San Buenaventura and Dominguillo, this phenomenon was clearly observed.

Among species, a high variety of temporal patterns were observed (Appendices 3, 7). When combined, these defined the seasonal pattern for the family and genera. Most of the taxa (85% of the species) were only associated with the wettest period of the year; only *Chauliognathus corvinus*, *Ditemnus tricornis* and *D. abdominalis* were exclusively recorded during the dry season (December to April), in one of the assemblages in which they had been collected; another eight species were registered in both seasons.

In each locality, more than 50% of species were recorded one or two times (months) through the sampling period (Appendix 7). In all, 48% of the species were recorded in a single sample during the entire sampling period; 21% in two monthly samples; 17% in three monthly samples, and 6% in four monthly samples; only eight species had more prolonged presence – between five and nine months–. *Belotus ca. bipunctatus* had the most extended presence, with nine monthly records in Dominguillo; *Belotus ca. bicolor* and *Ditemnus fossiger*, from the same assemblage, as well as *D. tricornis*, from San Buenaventura, had eight monthly records. It is interesting to point out that, at the aforementioned sites, the temporal pattern of these four species was quite different from that of other assemblages.

In general, cantharid species present in two or more assemblages showed different temporal patterns in each one, in relation to their monthly incidence and abundance (Appendices 3, 7). It was also observed that congeneric species of conspicuous genera like *Chauliognathus* (Appendix 4) substituted each other over time and displayed the greatest abundance at different times at the same assemblage.

The proportion of cumulative  $\alpha$  varied from 19.2 to 34.5, which indicates a high temporal turnover within each assemblage (Table 1). Compositional dissimilarity measured with Jaccard and Bray-Curtis indices was generally greater than 50% across pairs of compared months from the seven assemblages (Appendix 5). As expected, a noticeable increase in temporal turnover during the transition between seasons was observed; this high species replacement remains constant between months of the rain season in all the assemblages. Also, temporal turnover of the seven assemblages showed different patterns, while the most similar were Ixtlahuacán - Huatulco and San Buenaventura - Dominguillo.

With the exception of Huatulco, abundance always had a positive and statistically significant relationship with temporal variation in precipitation (Table 2); temperature, on the other hand, apparently had no influence on cantharid abundance. Species richness seems to have the same response in most of the assemblages, except for San Javier. Unlike abundance, temperature seems to influence this aspect of richness at San Buenaventura.

Dissimilarity in temporal species composition only displayed a significant relationship with the variation of precipitation in San Buenaventura, Huautla, Dominguillo (Jaccard), Ixtlahuacán and Huatulco (Bray-Curtis) (Table 2); variation in temperature seemed to have influence in Ixtlahuacán (Jaccard) and Acahuizotla (both measures of beta). The only assemblages that always maintained a positive and significant relationship between both environmental factors, and all of the diversity parameters included here, were San Buenaventura and Huautla.

Table 1. Temporal diversity of seven assemblages of TDF Cantharidae. Where  $\alpha$ : cumulative species richness;  $\bar{\alpha}$ : average species richness; and  $\alpha\%$ : proportion of cumulative  $\alpha$  represented by average  $\bar{\alpha}$  diversity, according to  $\alpha\% = (\bar{\alpha} / \alpha) * 100$ . When  $\bar{\alpha}$  equals  $\alpha$ , no temporal turnover must exist and values of  $\alpha\%$  will reach 100%.

Assemblage	$\alpha$	$\bar{\alpha}$	$\alpha\%$
San Javier, Sonora,	12	3.8	31.6
San Buenaventura, Jalisco	23	4.4	19.2
Ixtlahuacán, Colima	18	4.8	26.9
Huautla, Morelos	22	4.3	19.8
Dominguillo, Oaxaca	11	3.8	34.5
Acahuizotla, Guerrero	21	4.5	21.6
Huatulco, Oaxaca	15	3.4	22.8

The seven TDF Cantharidae assemblages displayed a seasonal pattern of abundance associated with the rain season. In other regions of the world, seasonality of most cantharids is a frequent pattern; regardless of the type of vegetation inhabited, emergence periods are short and are also associated to a particular season of the year, generally the warmest [6-10, 41].



In this study, species of genera like *Chauliognathus* were recorded in the same period in which congeneric species from the Nearctic region can usually be found [see 8]. On the contrary, other species were distinctive because of more prolonged permanence in the TDF, suggesting they could be multivoltine and possibly generalists that uses resources available throughout the year. Lack of information about natural history of the genera does not permit more convincing conclusions; however, it is interesting to point out that this pattern has been typically recorded for cantharid species associated with temperate mountain regions [5].

It is noteworthy that the total expression of seasonality in each assemblage of Cantharidae was determined by the asynchronous emergence of genera and species, whose abundance decreased steadily and was slightly overlapping; this can be notice in the high dissimilarity found in temporal species composition. It has been suggested that this pattern could be considered a phenological strategy providing protection for less abundant species, or a strategy of adequate resource distribution and reduction of interspecific competition [6, 8, 12, 42].

In the Mexican TDF, the moment of adult emergence, duration of presence throughout the sampling period, and the temporal distribution of abundance remarkably varied within the same assemblage, even genus level. In San Buenaventura and Domingullo, the way in which genera substituted each other in the short time of the rain season was evident, as well as how only one genus was dominant at a given point of the sampling.

Temporal Cantharidae assemblages were constituted by non-congeneric species and shared few or no species. This demonstrates a taxonomic and ecological richness as high as the species number in the assemblage at any given moment of sampling and a high dissimilarity in temporal species composition. In relation to this, the TDF Cantharidae assemblages may in fact be made of smaller temporal assemblages, as has been previously proposed for other taxonomic groups [18].

Until now, there has been little information on the feeding habits of Cantharidae, but a recent review by Pérez-Hernández (pers. comm.) seems to indicate that the association between cantharids and specific plant species is closer than previously thought. If this is true, adult emergence would be determined by host plant phenology and indirectly by abiotic factors such as precipitation. This pattern was also observed by Miskimen in Colombian dry forest Chauliognathinae: “phenology of *Chauliognathus proteus* was almost perfectly coincident with flowering of host plants” [sensu 5]. In the Mexican TDF we have observed synchrony between emergence of *Chauliognathus* species and the flowering of *Tridax coronopifolia* (Kunth) Hemsl., 1881 (Asteraceae), to mention one example.

Analysis of the TDF flowering plant phenology and direct observations made during the sampling of Cantharidae could provide evidence to support the hypothesis of a close relation between both groups. According to Zaragoza-Caballero (pers. comm.), most cantharids were collected from inflorescences and, according to other studies, most adults generally emerged throughout the flowering period of the majority of plants [43]. It is necessary to conduct more studies to corroborate whether host plant phenology and the diversity of TDF Cantharidae are correlated.

It had been suggested that in the TDF, the seasonality of Coleoptera is related to feeding habits and availability of resources [18]. For example, adult longhorned beetles (Cerambycidae) from the TDF presented a seasonal pattern similar to Cantharidae [29, 31] and have also similar feeding habits to those of adult cantharids [44]; however, Noguera et al., proposed that the seasonality of cerambycids could be associated to larval requirements (decaying wood). The presence of predator

rove beetles (Staphylinidae) in the TDF of Huautla, Morelos, was not particularly associated with one season or another [45], and dung beetle species (Scarabaeidae and Trogidae) from the TDF of Acahuizotla, Guerrero had a temporal pattern of abundance closely related to the rainfall period [46].

Table 2. Relationship between species richness, abundance and temporal turnover of seven TDF Cantharidae (Coleoptera) assemblages and monthly variation of precipitation and temperature. Values and P-values were calculated through Pearson correlation coefficient and Mantel test.

<b>Assemblage</b>	<b>Factor</b>	<b>Abundance</b>	<b>Richness</b>	<b>Incidence dissimilarity</b>	<b>Abundance dissimilarity</b>
San Javier, Sonora	Prec	0.925**	0.595	-0.420	-0.041
	Temp	0.535	0.602	-0.378	0.088
San Buenaventura, Jalisco	Prec	0.807**	0.858**	0.472**	0.345**
	Temp	0.442	0.5742*	0.078	0.035
Ixtlahuacán, Colima	Prec	0.939**	0.757*	0.283	0.497*
	Temp	0.385	0.548	0.326**	0.163
Huautla, Morelos	Prec	0.813**	0.879**	0.544**	0.684**
	Temp	0.135	0.162	0.076	0.013
Acahuizotla, Guerrero	Prec	0.761**	0.786**	-0.091	0.055
	Temp	0.116	0.339	0.553**	0.514**
Huatulco, Oaxaca	Prec	0.548	0.688*	0.351	0.514**
	Temp	0.360	0.471	0.022	0.224

\*\* P< 0.01, \*P<0.05

The lack of information on the feeding habits and habitats of the TDF Cantharidae and other species of Coleoptera, makes it difficult to ascertain whether adult emergence depends on guilds, if it is triggered by abiotic factors, or whether both elements act as important factors. This emphasizes the importance of more comprehensive studies that provide accurate evidence to characterize the TDF insect assemblages in detail –not just the presence-absence of species in particular moments and places–.

Even though a positive relationship between cantharid seasonal patterns and variation of precipitation has been corroborated in this work, we are still a long way from understanding how a certain quantity of rainfall can determine the presence or absence of species; not only for Cantharidae, but for most TDF insects. For example, in San Javier some atypical rain was recorded

from January to April, which would have triggered an adult explosive emergence if this factor was indeed a key to the emergence of Cantharidae; however, samplings in February and in April did not get a single specimen of that family.

In the TDF Cantharidae, some species can be found in two or more assemblages, displaying different seasonal patterns in each one: not always emerging in the same month, being present for different periods of time, and having unequal abundance distribution. It is possible that the variation in precipitation and temperature patterns among assemblages could influence the seasonality of these coleopterans and at the same time, these variations could be the result of differences in altitude, latitude and cyclical events such as El Niño Southern Oscillation (ENSO).

In this work, sampling in Dominguillo was conducted during a year in which ENSO was particularly severe (1997-1998); however, as mentioned before, precipitation and temperature data from Dominguillo were not available. Even so, it was evident that from the seven assemblages, the abundance distribution of cantharids in Dominguillo was atypical and was probably a result of the ENSO effects.

To establish implicated processes in spatial and temporal patterns of TDF insect diversity and other tropical ecosystems, it is necessary to evaluate more factors that might influence the structure and functionality of the assemblages. For example, although temperature showed limited influence in temporal variation of TDF diversity of Cantharidae, it may exert influence at shorter time scales, because daily adult activity of diurnal cantharids, and generally in larvae, seems to be determined by temperature variation throughout the day [6, 47-48].

The study of relations between plant species composition and the structure of Cantharidae assemblages is also essential, particularly because of their potential relationship, as it has been mentioned before about spatial patterns of the family [49].

The TDF environmental heterogeneity is a factor that should also be analyzed at great length. It has been observed that assemblages from habitats with more homogeneous environmental parameters show low temporal beta diversity, in spite of the high species richness [16]. In the case of the TDF, temporal environmental heterogeneity is high, mainly because of variation in precipitation throughout the year. The influence of this factor upon the temporal structure of insect assemblages is clear.

Other important factors for the analysis of temporal patterns of the TDF Cantharidae are coexistence between this family and other insects, inter- and intraspecific competition, presence of natural enemies, and other biological interactions, as well as the structure of the complete life cycle [12, 14].

Availability of resources upon which insects feed as a determining factor to seasonality of the TDF insects has practically been forgotten, but whatever speculation there has been leads to important questions.

Finally, it is important to note that seasonal patterns in the Mexican TDF Cantharidae analyzed here corroborate the high ecological diversity previously proposed for the family by Crowson [5], and also reveals the absence of information concerning implicated processes in the seasonality of Coleoptera from the TDF.

## Implications for conservation

This work represents a breakthrough in the study of the temporal arrangement of TDF insects, and proves that ecological diversity is higher than suspected; not only because TDF certainly possesses high spatial beta diversity [50], but high temporal beta diversity as well. This gives more relevance to the TDF and could also mean greater susceptibility to climate change and anthropogenic activities. In this study, big differences were found in temporal diversity and turnover between assemblages visited under strong ENSO events (e.g. Dominguillo) and assemblages with more normal climate (e.g. San Buenaventura), which suggest an important effect of climate change on the diversity of Cantharidae. Temporal turnover should be taken into account to assess resilience of natural communities to face climate change [51]. Furthermore, the resistance of insects against TDF adverse seasons may have precisely provided them with greater resilience to those changes. Temporal turnover in species abundances and richness could be critical in ecosystem functioning and deserves more attention [51].

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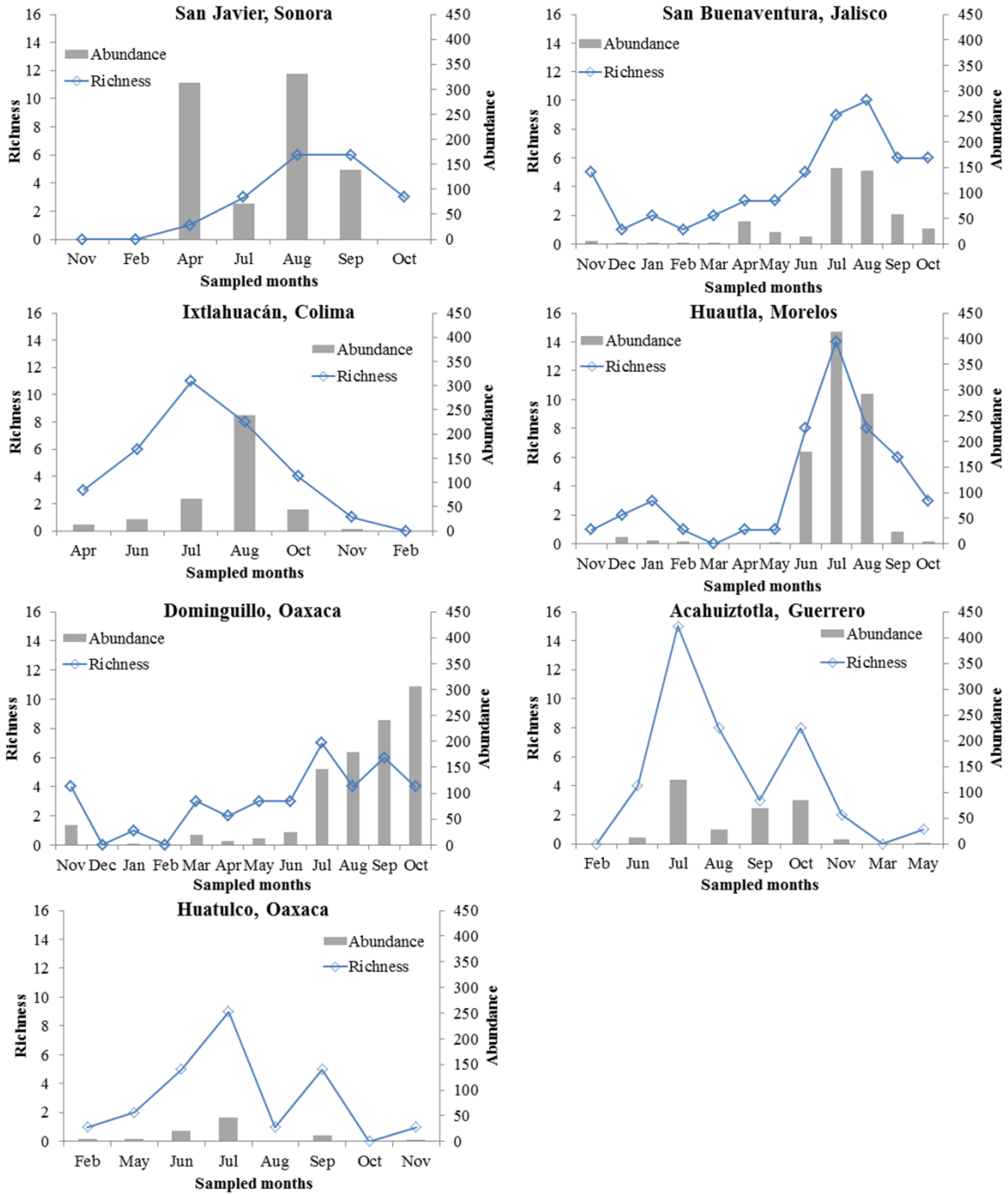
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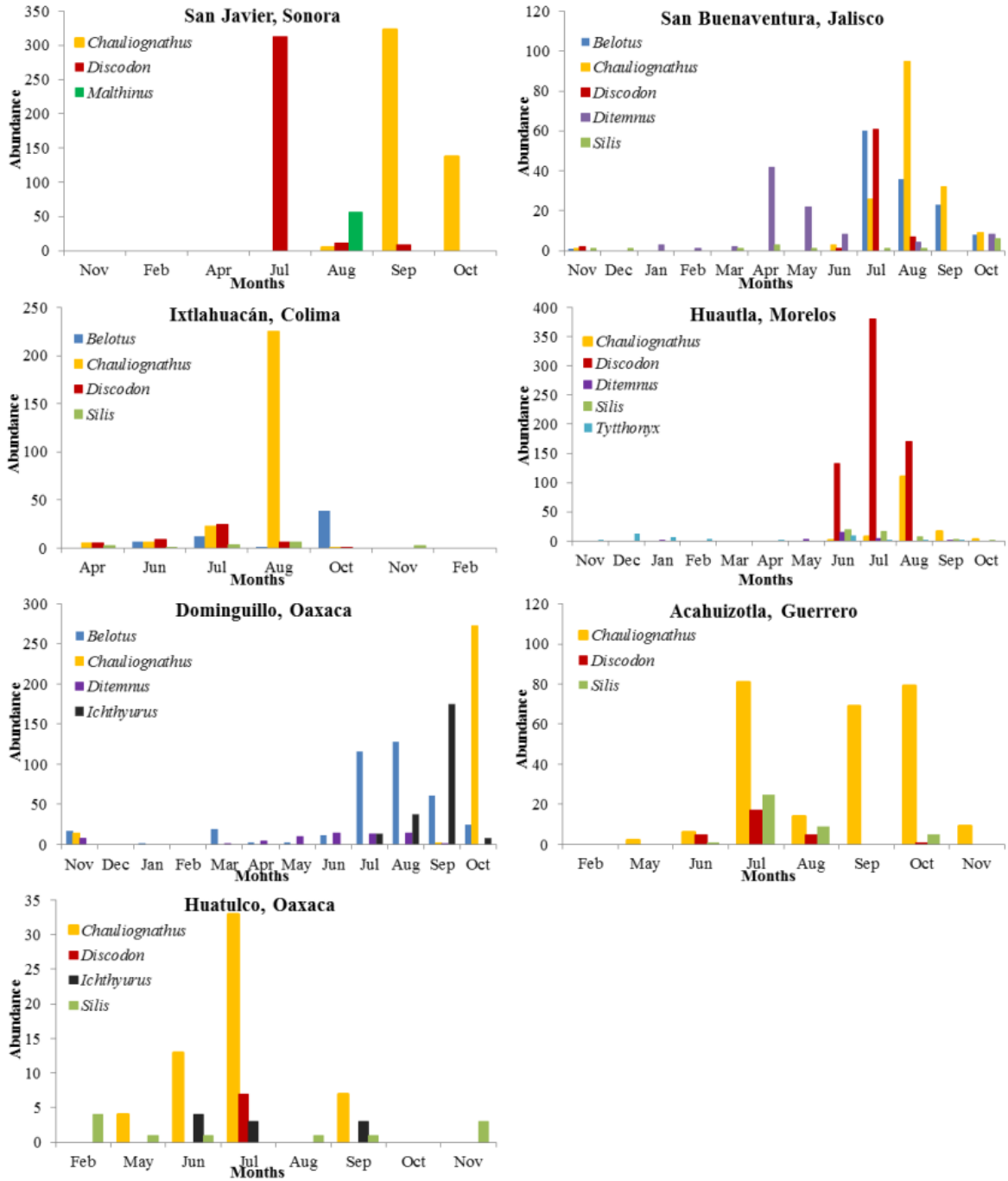
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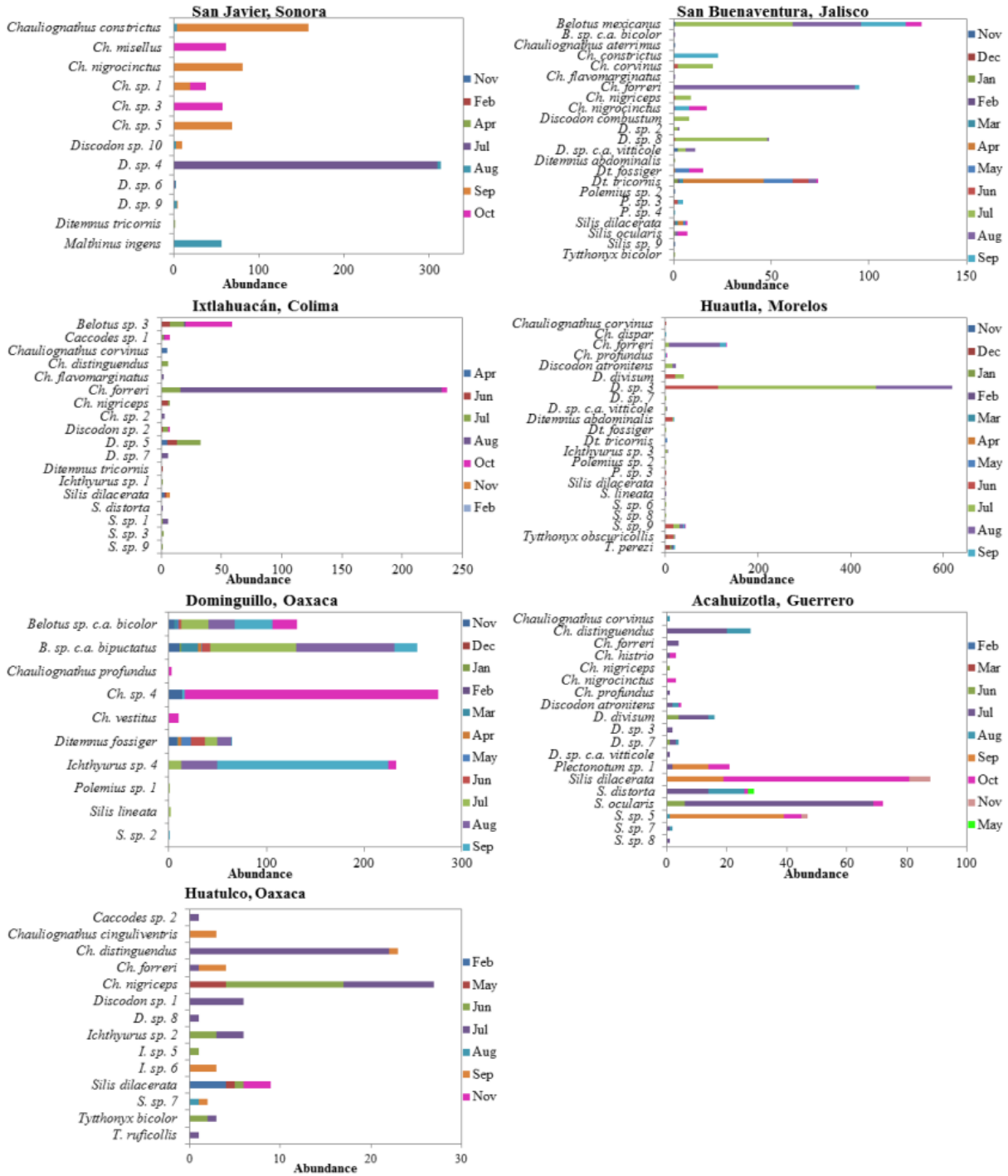
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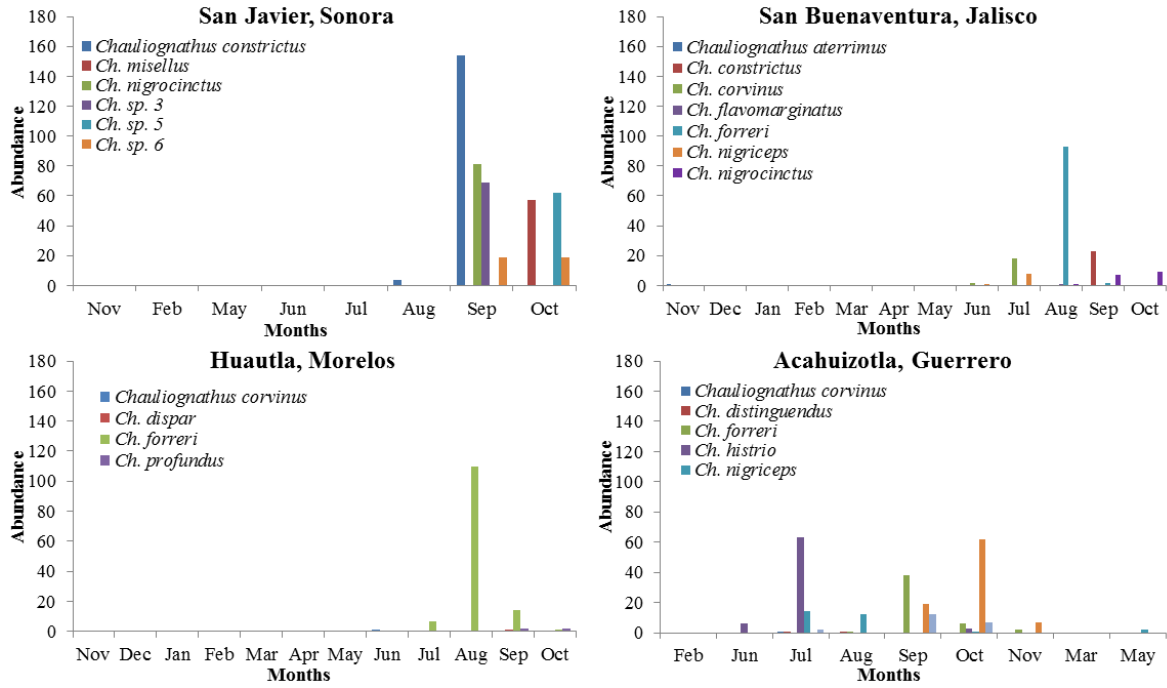
Appendix 1. Temporal variation of species abundance and richness of seven Cantharidae assemblages, in the Mexican TDF, during the sampled months at each locality.



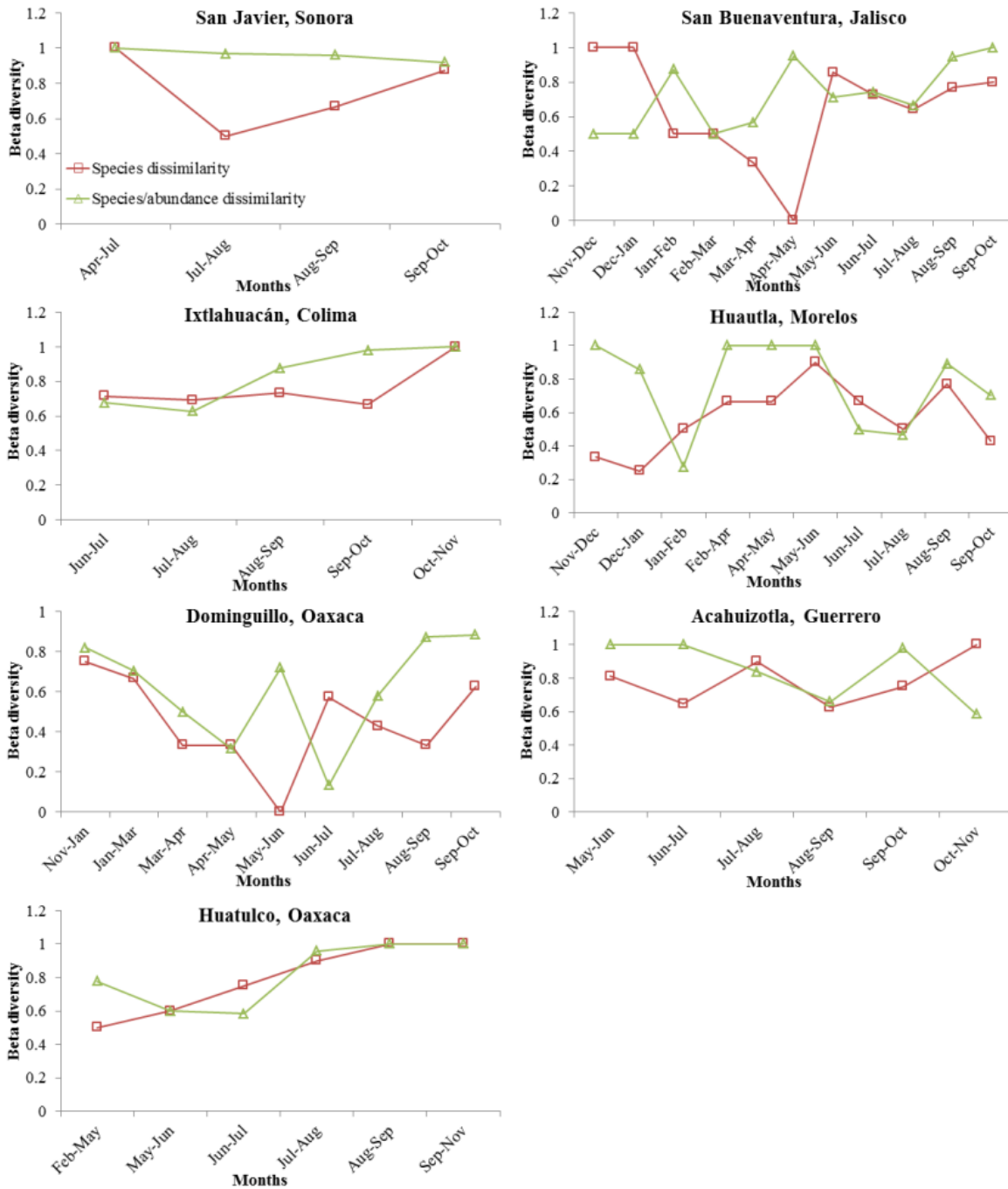
Appendix 2. Monthly variation of TDF Cantharidae genera abundance. For a better visualization of data, only genera with more than ten specimens collected at each locality are included.



Appendix 3. Temporal incidence and abundance variation of Cantharidae (Coleoptera) species in seven assemblages of Mexican TDF.



Appendix 4. Temporal abundance variation of *Chauliognathus* species in four assemblages of Mexican TDF.



Appendix 5. Dissimilarity in species composition between pairs of sampling months of seven TDF Cantharidae assemblages.



Appendix 6. Data from TDF assemblages on the Mexican Pacific Slope in which cantharids were collected. Localities were ordered according to latitude, from North to South. Months are in Roman numerals. Average altitude is expressed for each study area. MAP: Mean annual precipitation; MAT: Mean annual temperature; N: total abundance; S: total species richness; climate according to [53].

Assemblage	Sampled months	Geographic location	Average altitude (masl)	MAP (mm)	MAT (°C)	Climate	N	S
San Javier, Sonora	XI/2003; II, IV, VII, VIII, IX and X/2004	28°34'53" N -109°44'51.5" W	614	685	22.3	(A)Ca(w <sub>0</sub> )(x')(e)	855	12
San Buenaventura, Jalisco	XI/1996 to X/1997	19°47'37" N -104°03'19" W	810	991	22.6	Aw <sub>0</sub> (w)(i')g	478	23
Ixtlahuacán, Colima	IV, VI to XI/2006, and II/2007	18°59'10.2" N -103°42'13.5" W	258	261	27.9	Aw <sub>0</sub> (w)ig	391	18
Sierra de Huautla, Morelos	XI/1995 to X/1996	18°27'26" N -99°07'33" W	1000	666	32.9	Aw'' <sub>0</sub> (w)(i')g	942	22
Santiago Dominguillo, Oaxaca	XI/1997 to X/1998	17°39'23" N -96°54'39.6" W	845	242	22.3	Bs <sub>0</sub> (h')w''(w)(i')g	977	11
Acahuizotla, Guerrero	II, VI to XI/2008, III and V/2009	17°22'44" N -99°27'16" W	881	1749	24.5	A(C)w <sub>2</sub> (w)ig	330	20
Huatulco, Oaxaca	II, V to XI/2005	15°46'10.4" N -96°11'40.6" W	103	928	24.9	Aw <sub>0</sub> ''(w)i	90	15

Appendix 7. Monthly abundance of 71 species of Cantharidae (Coleoptera) from seven assemblages of Mexican TDF. From North to South: SJ: San Javier, Sonora; SB: San Buenaventura, Jalisco; IX: Ixtlahuacán, Colima; HU: Sierra de Huautla, Morelos; DO: Santiago Domingullo, Oaxaca; AC: Acahuizotla, Guerrero; HT: Huatulco, Oaxaca. A cell without numbers means no sampling.

Cantharidae		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Chauliognathinae														
Chauliognathini														
<i>Belotus mexicanus</i>	SB	0	0	0	0	0	0	60	35	23	8	1	0	127
<i>B. sp. c.a. bicolor</i>	SB	0	0	0	0	0	0	0	1	0	0	0	0	1
	DO	0	0	2	0	2	3	28	27	38	25	6	0	131
<i>B. sp. c.a. bipuctatus</i>	DO	2	0	17	3	1	8	88	101	23	0	11	0	254
<i>B. sp.</i>	IX		0		0		7	12	1		39	0		59
<i>Chauliognathus aterrimus</i>	SB	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Ch. cinguliventris</i>	HT		0			0	0	0	0	3	0	0		3
<i>Ch. constrictus</i>	SJ		0		0			0	4	154	0	0		158
	SB	0	0	0	0	0	0	0	0	23	0	0	0	23
<i>Ch. corvinus</i>	SB	0	0	0	0	0	2	18	0	0	0	0	0	20
	IX		0		5		0	0	0		0	0		5
	HU	0	0	0	0	0	1	0	0	0	0	0	0	1
	AC		0			0	0	1	0	0	0	0		1
<i>Ch. dispar</i>	HU	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Ch. distinguendus</i>	IX		0		0		0	6	0		0	0		6
	HT		0			0	0	22	0	1	0	0		23
	AC		0			0	0	1	1	0	0	0		2
<i>Ch. flavomarginatus</i>	SB	0	0	0	0	0	0	0	1	0	0	0	0	1
	IX		0		0		0	0	2		0	0		2
<i>Ch. forreri</i>	SB	0	0	0	0	0	0	0	93	2	0	0	0	95
	IX		0		0		0	16	217		4	0		237
	HU	0	0	0	0	0	0	7	110	14	1	0	0	132
	AC		0			0	0	0	1	38	6	2		47
	HT		0			0	0	1	0	3	0	0		4

<i>Ch. histrio</i>	AC		0		0	6	63	0	0	3	0		72
<i>Ch. misellus</i>	SJ		0		0		0	0	0	57	0		57
<i>Ch. nigriceps</i>	SB	0	0	0	0	0	1	8	0	0	0	0	9
	IX		0		0		6	1	0		0	0	7
<i>Ch. nigrocinctus</i>	AC		0			2	0	14	12	0	1	0	29
	HT		0			4	13	10	0	0	0	0	27
	SJ		0		0			0	0	81	0	0	81
<i>Ch. profundus</i>	SB	0	0	0	0	0	0	0	1	7	9	0	17
	AC		0			0	0	0	0	19	62	7	88
	HU	0	0	0	0	0	0	0	0	2	2	0	4
<i>Ch. vestitus</i>	DO	0	0	0	0	0	0	0	0	0	3	0	3
	AC		0			0	0	2	0	12	7	0	21
<i>Ch. sp. 2</i>	DO	0	0	0	0	0	0	0	0	0	10	0	10
<i>Ch. sp. 3</i>	IX		0		0		0	0	3		0	0	3
<i>Ch. sp. 4</i>	SJ		0		0			0	0	69	0	0	69
<i>Ch. sp. 5</i>	DO	0	0	0	0	0	0	0	0	2	260	14	276
<i>Ch. sp. 6</i>	SJ		0		0			0	0	0	62	0	62
<i>Ch. sp. 6</i>	SJ		0		0			0	0	19	19	0	38
Ichthyurini													
<i>Ichthyurus sp. 1</i>	IX		0		0		0	1	0		0	0	1
<i>I. sp. 2</i>	HT		0			0	3	3	0	0	0	0	6
<i>I. sp. 3</i>	HU	0	0	0	0	0	0	3	2	0	0	0	5
<i>I. sp. 4</i>	DO	0	0	0	0	0	0	13	37	175	8	0	233
<i>I. sp. 5</i>	HT		0			0	1	0	0	0	0	0	1
<i>I. sp. 6</i>	HT		0			0	0	0	0	3	0	0	3
Malthinae													
Malthinini													
<i>Caccodes sp. 1</i>	IX		0		0		0	2	1		4	0	7
<i>C. sp. 2</i>	HT		0			0	0	1	0	0	0	0	1
<i>Malthinus ingens</i>	SJ		0		0			0	56	0	0	0	56

<i>Plectonotum</i> sp.	AC	0	0	0	0	0	1	0	0	0	0	0	1	
Silinae														
Silini														
<i>Discodon atronitens</i>	HU	0	0	0	0	0	0	16	6	0	0	0	0	22
	AC	0			0	0	1	0	0	0	0		1	
<i>D. combustum</i>	SB	0	0	0	0	0	0	8	0	0	0	0	0	8
<i>D. divisum</i>	HU	0	0	0	0	0	20	19	0	0	0	0	0	39
	AC	0			0	1	2	1	0	0	0		4	
<i>D. sp. c.a. vitticole</i>	SB	0	0	0	0	0	0	4	5	0	0	2	0	11
	HU	0	0	0	0	0	0	2	1	0	0	0	0	3
	AC	0			0	0	2	2	0	1	0		5	
<i>D. sp. 1</i>	HT	0			0	0	6	0	0	0	0		6	
<i>D. sp. 2</i>	SB	0	0	0	0	0	0	2	1	0	0	0	0	3
	IX	0		0		1	5	0		1	0		7	
<i>D. sp. 3</i>	HU	0	0	0	0	0	113	342	164	0	0	0	0	619
	AC	0			0	0	2	0	0	0	0		2	
<i>D. sp. 4</i>	SJ	0		0			310	4	0	0	0		314	
<i>D. sp. 5</i>	IX	0		5		8	20	0		0	0		33	
<i>D. sp. 6</i>	SJ	0		0			2	1	0	0	0		3	
<i>D. sp. 7</i>	IX	0		0		0	0	6		0	0		6	
	HU	0	0	0	0	0	0	1	0	0	0	0	0	1
	AC	0			0	4	10	2	0	0	0		16	
<i>D. sp. 8</i>	SB	0	0	0	0	0	1	47	1	0	0	0	0	49
	HT	0			0	0	1	0	0	0	0		1	
<i>D. sp. 9</i>	SJ	0		0			1	3	1	0	0		5	
<i>D. sp. 10</i>	SJ	0		0			0	3	7	0	0		10	
<i>Ditemnus abdominalis</i>	SB	1	0	0	0	0	0	0	0	0	0	0	0	1
	HU	0	0	0	0	0	15	3	0	1	0	0	0	19
<i>Dt. fossiger</i>	SB	0	0	0	1	7	0	0	0	0	7	0	0	15
	HU	0	0	0	0	0	0	1	0	0	0	0	0	1

<i>Dt. tricornis</i>	DO	0	0	1	4	10	14	13	14	1	0	8	0	65
	SJ		0		2			0	0	0	0	0		2
	SB	2	1	2	41	15	8	0	4	0	1	0	0	74
	IX		0		0		1	0	0		0	0		1
	HU	1	0	0	0	3	0	0	0	0	0	0	0	4
<i>Polemius sp. 1</i>	DO	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>P. sp. 2</i>	SB	0	0	0	0	0	0	0	0	0	0	1	0	1
	HU	0	0	0	0	0	0	2	0	0	0	0	0	2
<i>P. sp. 3</i>	SB	0	0	0	0	0	2	0	0	3	0	0	0	5
	HU	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>P. sp. 4</i>	SB	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Silis dilacerata</i>	SB	0	0	1	3	1	0	0	0	0	1	0	1	7
	IX		0		3		1	0	0		0	3		7
	HU	0	0	0	0	0	1	0	0	0	0	0	0	1
	AC		0			0	0	0	0	0	3	0		3
	HT		4			1	1	0	0	0	0	3		9
<i>S. distorta</i>	IX		0		0		0	0	1		0	0		1
	AC		0			0	1	0	0	0	0	0		1
<i>S. lineata</i>	HU	0	0	0	0	0	0	0	1	0	0	0	0	1
	DO	0	0	0	0	0	0	2	0	0	0	0	0	2
<i>S. ocularis</i>	SB	0	0	0	0	0	0	1	1	0	5	0	0	7
	AC		0			0	0	1	0	0	2	0		3
<i>S. sp. 1</i>	IX		0		0		0	1	5		0	0		6
<i>S. sp. 2</i>	DO	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>S. sp. 3</i>	IX		0		0		0	2	0		0	0		2
<i>S. sp. 4</i>	DO	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>S. sp. 5</i>	AC		0			0	0	4	0	0	0	0		4
<i>S. sp. 6</i>	HU	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>S. sp. 7</i>	AC		0			0	0	20	8	0	0	0		28
	HT		0			0	0	0	1	1	0	0		2

S. sp. 8	HU	0	0	0	0	0	0	2	0	0	0	0	0	2	
	AC		0			0	0	0	1	0	0	0		1	
S. sp. 9	SB	0	0	0	0	0	0	0	0	0	0	1	0	1	
	IX		0		0		0	1	0		0	0		1	
	HU	0	0	0	0	0	18	13	7	3	1	0	0	42	
Tytthonyxini															
<i>Tytthonyx bicolor</i>	SB	0	0	0	0	0	0	1	0	0	0	0	0	1	
	AC		0			0	0	1	0	0	0	0		1	
	HT		0			0	2	1	0	0	0	0		3	
<i>T. obscuricollis</i>	HU	1	0	0	1	0	10	2	2	0	0	1	4	21	
<i>T. perezii</i>	HU	5	4	0	0	0	0	0	0	2	0	0	9	20	
<i>T. ruficollis</i>	HT		0			0	0	1	0	0	0	0		1	
Total			12	9	23	68	46	274	1260	951	736	609	61	14	4063