

# A comparative study of Odonata (Insecta) assemblages along an altitudinal gradient in the sierra de Coalcomán Mountains, Michoacán, Mexico

Rodolfo Novelo-Gutiérrez · José Antonio Gómez-Anaya

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**Abstract** Odonate diversity in the Coalcomán Mountain Range (CMR), Michoacán State, Mexico, was surveyed, and samplings were made during 2 years in eight streams along an altitudinal gradient. Presence–absence data were analyzed using non-parametric and parametric methods. Beta and gamma diversities were estimated using Whittaker’s and Lande’s formulae, respectively. A total of 2,526 adults and 489 larvae were captured, yielding 116 species ( $\gamma$  diversity), 44 genera and 9 families. Five new species were discovered. The genus *Argia* was the most important contributor to Zygoptera diversity and total richness ( $\gamma$  diversity), yielding 40.4 and 14.7%, respectively. The non-parametric estimator Chao2 provided the closest theoretical estimate of species richness, and Clench’s model fit the data well ( $R^2$  ranged from 99.44 to 99.99) to explain a high proportion of the variance (98.8). We conclude that beta diversity is important at the landscape scale, supporting the hypothesis that Mexico is a beta diverse country. Our results triple the number of known species of Odonata for Michoacán. Given the considerable richness of odonates at local and landscape scales, our results support the proposal of the Coalcomán Mountain Range as a priority area for conservation and related research.

**Keywords** Coalcomán mountain range · Conservation · Diversity · Odonata · Species richness · Western Mexico

## Introduction

Mexico is located between the Nearctic and the Neotropical biogeographic regions, and is considered one of the most mega diverse countries in the world (Mittermeier et al. 1997), with insects being important contributors to this richness (Kalkman et al. 2008). However,

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R. Novelo-Gutiérrez (✉) · J. A. Gómez-Anaya  
Departamento de Entomología, Instituto de Ecología, A.C., Km 2.5 Carretera Antigua a Coatepec  
# 351, Congregación El Haya, 91070 Xalapa, Veracruz, Mexico  
e-mail: rodolfo.novelo@inecol.edu.mx

J. A. Gómez-Anaya  
e-mail: antonio.gomez@inecol.edu.mx

the scarcity of expert taxonomists, the large spatial expanse, and the diverse topography of the territory have impeded satisfactory inventories of insect species. Western Mexico is one of the most interesting regions, primarily because of its high level of endemism (Ceballos and Rodríguez 1993). Unfortunately, the rate of habitat loss and degradation is faster than the capacities to systematically survey this region.

Although odonates in Mexico have been surveyed more or less continuously over the last 30 years (González-Soriano and Novelo-Gutiérrez 2007), complete records by region are still scarce. Furthermore, the odonates are an important link between land and freshwater food chains because larvae and adults are primary and secondary predators, as well as prey for vertebrates (Louton et al. 1996; Bried and Ervin 2005). In the Palaearctic region, they are commonly used as indicators of environmental quality (Sahlén and Ekkestubbe 2001), and recently have been proposed as indicators of environmental quality in tropical areas (Clausnitzer 2003; Suhling et al. 2006; Campbell and Novelo-Gutiérrez 2007), and ecological integrity in aquatic ecosystems (Stewart and Samways 1998).

Our objective was to survey the diversity of odonates in an unexplored area of Michoacán State to:

1. provide a georeferenced species list from the Sierra de Coalcomán Mountains based upon systematic collections,
2. define odonate assemblages using altitudinal clines, slope localization, and habitat structure,
3. determine the relative contribution of  $\alpha$  and  $\beta$  diversity at local and landscape scales, and
4. provide data to support conservation efforts.

## Study area

The Coalcomán Mountain Range (CMR), Michoacán, Mexico, is located at 18°35'659"–19°00'524"N and 102°27'786"–103°40'601"W (Fig. 1). The climate is predominantly tropical (annual average temperature 26.5°C), with the rainy period occurring in summer, and the average annual precipitation ranging from 700 mm in the lowlands to 1,300 mm in the highlands (Antaramián 2005). Surveys were made in eight streams ranging in altitude from 10 to 1,130 m asl. The collections were made in tropical deciduous forest, tropical sub-deciduous forest, cloud forest, and pine-oak forest. Three sites were located on the windward slope, one on a high plateau of the mountain range, and the remaining four sites on the leeward slope (Table 1). These sites represented three physiographic provinces: Pacific Coastal Plains, Sierra Madre del Sur, and Depresión del Balsas-Tepalcatepec (Antaramián and Correa 2003). The water channel data for the streams described below are provided in Table 2.

### El Ticuiz (TZ)

This stream is located near the seashore at 18°40'403"N, 103°40'601"W, and 10 m asl. Most of the riparian vegetation has been highly disturbed by banana plantations, and some segments of the water course are frequently altered by dragging. In the surveyed segment no riffles were observed, only small, shallow rapids. The substrate was predominantly composed of fine gravel and mud, and the aquatic vegetation was composed mostly of *Eichhornia crassipes* (Mart.), *Lemna gibba* L., *Pistia stratiotes* (L.), and *Typha latifolia* L.



### California (CF)

This site is located 10 km west of Apatzingán City on Rd. 120 (19°06'207"N, 102°27'786"W, 280 m asl) and is mostly a shaded stream surrounded by lemon-tree plantations. Only a few rapids were observed, and the substrate was composed mostly of mud and plant roots along the edges, and fine and coarse gravel in the center. Although floating or submerged aquatic vegetation was not observed, a few small patches of emergent plants were present, and patches of decaying leaves were present along the stream shore.

### La Estanzuela (EZ)

Located at 18°35'659"N, 103°27'135"W, and 408 m asl, the stream "Los Naranjos" runs through a moderately perturbed tropical subdeciduous forest with large patches of sunny and shaded areas. Riffles and rapids were very common, and the substrate was composed of boulders, rocks, cobble, gravel, sand, silt and mud, as well as banks of decaying leaves. The aquatic vegetation was represented by riparian plant roots and mats of filamentous algae in shallow zones.

### Río Pinolapa (RP)

Located on Rd. 120 (19°00'524"N, 103°01'456"W, and 616 m asl), this site has vegetation corresponding to a dry tropical deciduous forest, and is surrounded by pastures. Although the water channel generally runs into a wide canyon, riffles and rapids were common, as well as pools. The substrate was composed of boulders, rocks, cobble, gravel, sand, silt, mud, and decaying leaves. The aquatic vegetation was composed predominantly of emergent grasses on pool banks, roots of riparian shrubs and trees, and mats of filamentous algae.

### Villa Victoria (VV)

This site is located in a tropical subdeciduous forest at 18°45'370"N, 103°22'393"W, and 769 m asl, and is disturbed by low-density human settlements and corn crops in some areas. No riffles were observed, but rapids were present, as were two small waterfalls with big pools. The riparian vegetation cover was good and was composed mostly of trees 5–10 m tall. The substrate was composed principally of CaCO<sub>3</sub> rocks, gravel, sand, mud, and a few patches of decaying leaves along the banks. Roots of riparian vegetation (herbaceous plants and trees) and filamentous algae constituted the aquatic vegetation.

### Aguililla (AG)

This stream is located in a tropical deciduous forest at 18°43'503"N, 102°47'687"W, and 1,020 m asl, and runs into a wide and deep canyon with most of the riparian vegetation composed of shrubs and bushes. Riffles, rapids, and pools were very common, and the substrate was composed of big boulders, rocks, cobble, gravel, sand banks, silt, mud, and packs of litter. Aquatic vegetation was composed of riparian plant roots and mats of filamentous algae in some zones.

### El Colorín (CL)

This torrential stream (located at 18°39'540"N, 103°24'570"W, and 1,050 m asl) runs into a ravine covered by cloud forest, and is close to the village of La Nuez. It is mostly shaded, with riparian vegetation composed of tall trees, and with most of the ravine's vegetation in good condition. The substrate was composed mainly of big boulders, small rocks, coarse and fine gravel, sand and litter. Aquatic vegetation was absent, with only a few root-mats from hanging riparian vegetation observed. The stream is structured by repetitive terraces with waterfalls and pools.

### La Chichihua (CH)

The stream (located at 18°44'812"N, 103°13'379"W, and 1,130 m asl) runs into a highly perturbed pine-oak forest surrounded by crops, pasture land, and small human settlements. Riparian vegetation is scarce in some areas, but abundant in others. The substrate was composed of boulders, rocks, cobble, gravel, sand, mud and decaying leaves along the banks. The aquatic vegetation was almost absent except for some emergent grasses and roots of riparian woody and herbaceous vegetation.

## Materials and methods

Collections were made twice per season during 2005, and once per season during 2006 (excluding winter), by two people. Adults and larvae were collected at each site from 10:00 to 16:00 h (1 day per site), along 500 m stream segments using aerial nets for adults and a D-frame aquatic net for larvae. Some larvae were kept alive until adult emergence, while the remaining specimens were preserved in 96% ethanol. Physicochemical data (pH, temperature, dissolved oxygen, conductivity) were recorded during each trip using a digital water analyzer model ICM 5500 (forestry suppliers). Stream width, depth, and current velocity were measured using a metric power tape and a digital flow meter, respectively, and gradient was calculated according to Resh et al. (1996). Discharge was measured twice in three streams (CL, TZ and CH) during April (dry season) and July (rainy season) 2006, and once for CF and VV (July), and EZ and RP (April) (Table 2).

### Species richness estimators

Presence–absence data were analyzed using non-parametric and parametric methods in order to estimate gamma diversity. Since species lists were obtained from samples and not a census,  $S_{\text{obs}}$  often underestimates  $S$  (Colwell and Coddington 1994). To reduce this bias, species accumulation curves were constructed for each stream and for the whole area using Chao2, Bootstrap, and Jackknife2 provided in EstimateS, version 8.0 (Colwell 2006). These estimators differ in the way rare species are used to correct  $S_{\text{obs}}$ . Chao2 and Jack2 use  $L$  and  $M$ , the number of species in one sample (uniques) and the number of species in two samples (duplicates), respectively; while Bootstrap uses  $p_j$ , the proportion of sampling units containing each species  $j$  (Palmer 1990; Magurran 2004). Likewise, parametric richness estimation was performed to see if the cumulative data would fit the Linear Dependence Model (Soberón and Llorente 1993) or Clench's Model (Clench 1979).

To adjust the models, the mean number of species per sample was used from the results provided by EstimateS to obtain the ideal curve or statistical average of species added as

effort increased (Jiménez-Valverde and Hortal 2003). This was accomplished using the non-linear estimation module in STATISTICA (StatSoft 2006), and applying the Simplex and Quasi-Newton methods for parameter estimation. The sampling units for both parametric and non-parametric richness estimation were defined as hours/individual/day.

### Beta and gamma diversity

Following Wilson and Shmida (1984), Whittaker's formula for beta diversity was used for the construction of a pairwise similarity matrix among all sites. A cluster analysis was performed on the matrix using the complete linkage amalgamation method, which defines the distance between any two clusters as the maximum distance between them. The result was a dendrogram showing faunal similarities among sites. The software Statistica (Statsoft 2006) was used for this analysis. Complementarity analysis (Colwell and Coddington 1994) was made to compare the odonate fauna of both slopes.

Gamma diversity was estimated according to Lande (1996):

$$\beta = \sum_i q_j (S_T - S_j)$$

where  $S_T$  = species richness of the landscape ( $\gamma$  diversity),  $S_j$  = the richness of assemblage  $j$ , and  $q_j$  = the proportional weight of assemblage  $j$  based on its importance (here, importance was considered as the percentage of exclusive species in relation to the whole landscape).

## Results

### Physicochemical variables

The lowest and highest mean values were: water temperature at CL (22.6°C) and RP (28°C), pH at TZ (7.47) and RP (8.47), conductivity at CL (50.08) and RP (666.83), and oxygen at TZ (4.31) and AG (8.41) (Table 3). The highest gradient occurred at CL (close to 16° in some transects), whereas the lowest was at CF (1° in some transects) (Table 3). Maximum discharge at TZ was 36 m<sup>3</sup>/s, whereas the discharge in CF was 18 m<sup>3</sup>/s (Table 2).

### Richness and composition

A total of 3,015 specimens (larvae and adults) were collected, yielding 116 species ( $\gamma$  diversity), 44 genera and 9 families (Table 4). Five new species were discovered: two in *Argia*, two in *Progomphus* (*Progomphus marcelae* Novelo, Novelo-Gutiérrez 2007a; *P. lambertoi* Novelo, Novelo-Gutiérrez 2007b), and one in *Phyllogomphoides*. The most diverse genus was *Argia* (17 species), followed by *Hetaerina*, *Progomphus*, *Brechmorhoga* and *Macrothemis* (5 species each).

The highest and lowest alpha diversity was recorded at TZ (10 m asl) and CL (1,050 m asl) with 66 and 28 species, respectively. Alpha diversity for the remaining localities ranged from 38 to 51 species (Fig. 2). No significant Spearman rank correlation was observed between altitude and number of species ( $r_{\text{Spearman}} = -0.59$ ,  $P > 0.05$ ,  $n = 8$ ). Alpha diversity by altitudinal gradient was 92 (10–500 m), 61 (501–1,000 m), and 63 (1,001–1,130 m).

**Table 3** Averages and 95% confidence intervals (LL, lower limit; UL, upper limit) for the physicochemical variables recorded in the streams (?, data unavailable)

	AG	CF	CH	CL	EZ	RP	TZ	VV
Temperature (°C)								
Average	25.48	26.17	22.62	20.14	26.48	28.03	29.35	25.48
LL	24.62	25.24	21.69	19.29	25.56	27.02	28.42	24.62
UL	26.33	27.09	23.54	21.00	27.40	29.04	30.27	26.33
pH								
Average	8.33	7.91	8.16	7.54	8.08	8.47	7.47	7.78
LL	8.21	7.78	8.04	7.42	7.95	8.33	7.35	7.66
UL	8.45	8.03	8.29	7.66	8.21	8.61	7.60	7.90
Conductivity (µS/cm)								
Average	346.54	338.11	460.89	50.08	509.83	666.83	640.50	598.83
LL	324.45	314.25	437.03	28.00	485.97	640.70	616.60	576.75
UL	368.62	361.96	484.74	72.17	533.68	692.96	664.30	620.92
Oxygen (ppm)								
Average	8.41	7.79	7.74	8.37	7.53	7.78	4.31	6.60
LL	7.79	7.13	7.08	7.75	6.87	7.05	3.65	5.99
UL	9.03	8.46	8.41	8.98	8.20	8.51	4.98	7.22
<i>N</i>	42.00	36.00	36.00	42.00	36.00	30.00	36.00	42.00
Gradient								
Average	?	0°41'15"	1°49'58"	7°48'03"	4°44'41"	1°08'45"	1°08'45"	2°41'27"
Min	?	0°13'45"	0°48'72"	1°01'52"	1°08'45"	0°20'38"	0°27'30"	1°08'45"
Max	?	1°29'21"	4°34'26"	15°19'23"	6°37'00"	2°24'18"	2°24'18"	7°24'25"
<i>N</i>		7	7	7	7	7	7	7

Non-parametric estimators

A comparison of theoretical richness per site based on Chao2 and Clench’s model, and the observed richness is provided in Fig. 2. Chao2 predicted 120 species, Bootstrap 123, and Jackknife2 127 species for the CMR (Fig. 3; Table 5). Thus, the 116 observed species registered for the CMR ( $\gamma$  diversity) represents 96.7, 94.3, and 91.3% of the theoretical richness, respectively. The richness estimation by sampling locality (Fig. 4) provides some indication of where more sampling effort could be applied to get a more complete list for the CMR.

Parametric estimators

According to the Clench and Linear Dependence models, 124 and 110 species are expected for the CMR, respectively. The first model explained a higher proportion of the variance (98.90%), while the second one underestimated the number of species (Table 6). In general, our data better fit Clench’s model ( $R^2$  ranged from 99.44 to 99.99), than the Linear Dependence model ( $R^2$  ranged from 94.88 to 98.53), although the difference was small. As it can be seen in Table 6, CH more closely approximated theoretical richness when using the slope data from Clench’s model (0.33) in relation to total effort ( $n = 11$ ), while AG is still far from a complete list of species (slope = 1.07) because of the lower sampling effort ( $n = 8$ ). The species accumulation curves for each stream in accordance with Clench’s model are shown in Fig. 5.

**Table 4** Richness and composition of the Odonata among sampling locations in the Coalcomán Mountain Range, Michoacán, Mexico

Species/assemblage	TZ	CF	EZ	RP	VV	AG	CL	CH	Total	Frequency
Number of species	66	42	38	51	50	40	28	39	116	
<i>Hetaerina americana</i>	x	x	x	x	x	x		x	7	87.5
<i>H. capitalis</i>			x	x	x		x		4	50
<i>H. cruentata</i>							x	x	2	25
<i>H. occisa</i>	x	x	x		x		x		5	62.5
<i>H. titia</i>	x								1	12.5
<i>Archilestes grandis</i>			x	x	x	x	x	x	6	75
<i>Mecistogaster ornata</i>		x	x		x		x		4	50
<i>Palaemnema domina</i>			x	x	x	x	x	x	6	75
<i>Neoneura amelia</i>	x	x							2	25
<i>Protoneura cara</i>	x	x	x	x	x	x		x	7	87.5
<i>Protoneura rojiza</i>			x		x		x		3	37.5
<i>Apanisagrion lais</i>							x	x	2	25
<i>Argia anceps</i>				x	x	x		x	4	50
<i>A. carlcooki</i>	x	x	x	x					4	50
<i>A. cuprea</i>							x		1	12.5
<i>A. extranea</i>			x	x	x	x	x	x	6	75
<i>A. funcki</i>				x	x	x	x	x	5	62.5
<i>A. harknessi</i>		x		x				x	3	37.5
<i>A. lacrimans</i>							x		1	12.5
<i>A. oculata</i>		x	x	x	x	x	x	x	7	87.5
<i>A. oenea</i>	x	x	x	x	x	x		x	7	87.5
<i>A. pallens</i>			x	x	x	x		x	5	62.5
<i>A. plana</i>							x		1	12.5
<i>A. pulla</i>	x	x		x	x	x		x	6	75
<i>A. tarascana</i>	x	x		x	x	x		x	6	75
<i>A. tezpi</i>	x	x	x	x	x	x		x	7	87.5
<i>A. ulmeca</i>			x		x	x	x	x	5	62.5
<i>A. aff. pocomana</i>			x	x					2	25
<i>Argia sp.</i>							x		1	12.5
<i>Enallagma novaehispaniae</i>	x	x		x		x			4	50
<i>E. praevarum</i>								x	1	12.5
<i>E. semicirculare</i>	x	x		x	x	x		x	6	75
<i>Ischnura capreolus</i>	x								1	12.5
<i>I. hastata</i>	x								1	12.5
<i>I. ramburii</i>	x								1	12.5
<i>Leptobasis candelaria</i>		x							1	12.5
<i>Leptobasis vacillans</i>	x	x							2	25
<i>Neoerythromma cultellatum</i>	x								1	12.5
<i>N. gladiolatum</i>	x								1	12.5
<i>Telebasis fliola</i>	x								1	12.5
<i>T. griffini</i>	x								1	12.5



**Table 4** continued

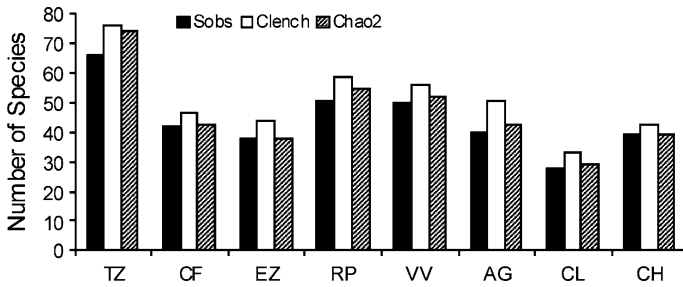
Species/assembly Number of species	TZ 66	CF 42	EZ 38	RP 51	VV 50	AG 40	CL 28	CH 39	Total 116	Frequency
<i>T. salva</i>	x	x	x	x	x	x		x	7	87.5
<i>Aeshna williamsoniana</i>							x		1	12.5
<i>Anax junius</i>	x								1	12.5
<i>A. walsinghami</i>						x			1	12.5
<i>Coryphaeschna adnexa</i>	x								1	12.5
<i>C. apeora</i>	x								1	12.5
<i>C. diapyra</i>			x		x		x		3	37.5
<i>C. viriditas</i>	x								1	12.5
<i>Gynacantha nervosa</i>	x	x			x				3	37.5
<i>Triacanthagyna septima</i>	x								1	12.5
<i>Remartinia luteipennis</i>	x								1	12.5
<i>Rhionaeschna psilus</i>				x	x				2	25
<i>Aphylla protracta</i>	x	x							2	25
<i>Erpetogomphus bothrops</i>	x		x	x					3	37.5
<i>E. cophias</i>							x		1	12.5
<i>E. elaps</i>		x	x	x	x	x	x	x	7	87.5
<i>E. sp.group agkistrodon</i>							x		1	12.5
<i>Phyllocyca elongata</i>	x	x							2	25
<i>Phyllogomphoides luisi</i>	x	x		x	x	x			5	62.5
<i>Ph. pacificus</i>		x	x	x	x	x			5	62.5
<i>Ph. apiculatus</i>	x		x	x	x	x		x	6	75
<i>Phyllogomphoides sp.</i>						x			1	12.5
<i>Progomphus clendoni</i>			x	x	x	x		x	5	62.5
<i>P. lambertoi</i>		x		x		x		x	4	50
<i>P. marcelae</i>				x					1	12.5
<i>P. mexicanus</i>					x				1	12.5
<i>P. zonatus</i>							x	x	2	25
<i>Anatya guttata</i>			x						1	12.5
<i>Brachymesia furcata</i>	x								1	12.5
<i>Brechmorhoga nubecula</i>			x		x				2	25
<i>B. praecox</i>	x	x	x	x	x	x		x	7	87.5
<i>B. rapax</i>							x	x	2	25
<i>B. tepeaca</i>							x		1	12.5
<i>B. vivax</i>			x						1	12.5
<i>Cannaphila insularis</i>		x							1	12.5
<i>Dythemis maya</i>				x	x	x	x		4	50
<i>D. multipunctata</i>								x	1	12.5
<i>D. nigrescens</i>	x	x		x	x	x		x	6	75
<i>D. sterilis</i>	x	x		x	x				4	50
<i>Erythemis mithroides</i>	x								1	12.5
<i>E. plebeja</i>	x	x	x	x					4	50

**Table 4** continued

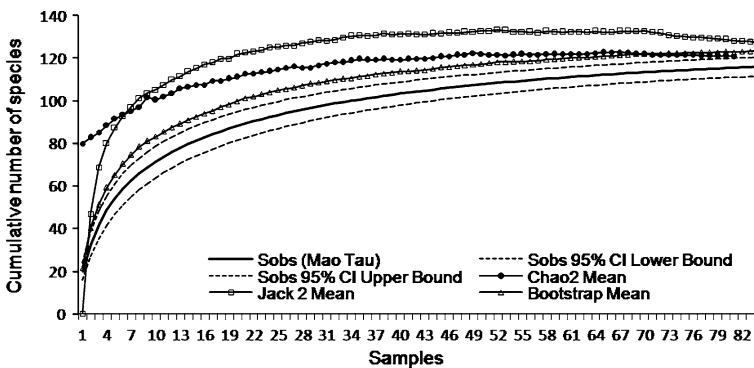
Species/assemblage	TZ	CF	EZ	RP	VV	AG	CL	CH	Total	Frequency
Number of species	66	42	38	51	50	40	28	39	116	
<i>E. simplicicollis</i>	x		x						2	25
<i>E. vesiculosa</i>	x	x			x				3	37.5
<i>Erythrodiplax basifusca</i>	x			x	x	x		x	5	62.5
<i>E. fervida</i>	x	x							2	25
<i>E. funerea</i>	x	x	x	x	x	x			6	75
<i>E. fusca</i>	x			x					2	25
<i>Libellula croceipennis</i>		x	x	x	x	x	x	x	7	87.5
<i>Macrothemis hemichlora</i>	x	x		x					3	37.5
<i>M. inacuta</i>	x			x	x	x			4	50
<i>M. inequilinguis</i>	x	x	x	x	x	x		x	7	87.5
<i>M. pseudimitans</i>		x	x	x	x	x		x	6	75
<i>M. ultima</i>							x		1	12.5
<i>Miathyria marcella</i>	x								1	12.5
<i>M. simplex</i>	x								1	12.5
<i>Micrathyria aequalis</i>	x								1	12.5
<i>M. debilis</i>		x							1	12.5
<i>M. didyma</i>	x								1	12.5
<i>M. ocellata</i>	x								1	12.5
<i>Orthemis discolor</i>	x	x	x	x	x	x		x	7	87.5
<i>O. ferruginea</i>	x	x		x	x	x			5	62.5
<i>O. levis</i>		x	x						2	25
<i>Paltothemis cyanosoma</i>							x		1	12.5
<i>P. lineatipes</i>			x	x	x	x		x	5	62.5
<i>Pantala flavescens</i>	x		x	x	x	x		x	6	75
<i>P. hymenaea</i>	x				x				2	25
<i>Perithemis domitia</i>	x			x	x			x	4	50
<i>P. intensa</i>	x			x	x				3	37.5
<i>P. mooma</i>	x								1	12.5
<i>Pseudoleon superbus</i>	x	x	x	x	x	x		x	7	87.5
<i>Tauriphila argo</i>	x								1	12.5
<i>T. australis</i>	x	x							2	25
<i>Tholymis citrina</i>	x								1	12.5
<i>Tramea abdominalis</i>	x			x					2	25
<i>T. onusta</i>	x			x	x	x		x	5	62.5

### Beta diversity

Maximum species turnover ( $\beta$  diversity) was observed between TZ and CL ( $\beta_w = 2.0$ ), with CL being the most dissimilar to all other localities. In contrast, the streams at RP and VV showed the lowest turnover ( $\beta_w = 1.21$ ) (Fig. 6). The three localities on the windward slope revealed a greater turnover of species ( $\beta_w = 2.41$ ) than the five localities on the



**Fig. 2** Number of species and richness estimation using parametric (Clench) and non-parametric (Chao2) methods for the sites surveyed during 2005–2006, in the Coalcomán Mountain Range, Michoacán, Mexico



**Fig. 3** Species accumulation curves of Odonata from the Coalcomán Mountain Range, Michoacán, Mexico, during 2005–2006

leeward slope ( $\beta_w = 1.80$ ). By altitudinal gradient, species turnover was  $\beta_w = 1.285$  (10–500/501–1,000 m),  $\beta_w = 1.451$  (10–500/1,001–1,130 m), and  $\beta_w = 1.295$  (501–1,000/1,001–1,130 m).

**Species exclusivity and distribution**

The highest number of exclusive species was recorded at TZ (24), representing 36% of the total species for this site, while 10 species were exclusive to CL and represented 36% of the richness for this site. The remaining sites had less than five exclusive species each. TZ represents one of the most anthropogenically disturbed streams, whereas CL could be considered the most naturally conserved stream among those surveyed. Most exclusive species at TZ were libellulids (10), followed by coenagrionids (7), aeshnids (6), and calopterygids (1). In contrast, at CL the coenagrionids had more exclusive species (4), followed by libellulids (3), gomphids (2) and aeshnids (1).

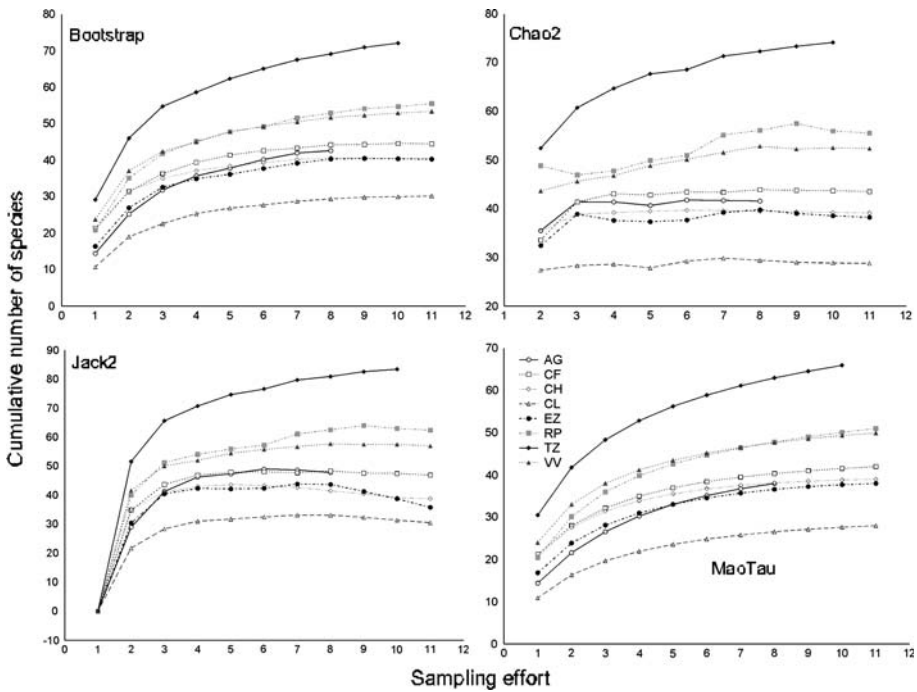
Vertical (altitudinal) and horizontal (geographical) distribution of species showed high variability. Eleven species, *Hetaerina americana*, *Argia oculata*, *A. oenea*, *A. tezpi*, *Telebasis salva*, *Erpetogomphus elaps*, *Brechmorhoga praecox*, *Libellula croceipennis*, *Macrothemis inequiunguis*, *Orthemis discolor* and *Pseudoleon superbus* showed wide geographical distributions in the CMR (frequency = 87.50%), supporting previous observations in Mexico (González-Soriano and Novelo-Gutiérrez 2007).

**Table 5** Non-parametric richness estimators and their variance

Sites	$S_{\text{obs}}$	IC 95%			Eff*			Bootstrap			Chao2			Jack2			
		IC 95%			Eff*			Bootstrap			Chao2			Jack2			
		Mean	SD	Eff	Mean	SD	Eff	Mean	SD	Eff	Mean	SD	Eff*	Eff	Mean	SD	Eff
TZ	66	60.27–71.73	1.64	92.01	72	1.64	91.67	74	1.64	91.67	74	68.52–92.65	71.24	89.19	83	3.45	79.52
CF	42	39.12–44.88	0.77	93.58	44	0.77	95.45	43	0.77	95.45	43	42.21–52.69	79.71	97.67	47	2	89.36
EZ	38	36.75–39.25	0.57	96.82	40	0.57	95	38	0.57	95	38	38.02–41.87	90.76	100	36	2.65	105.6
RP	51	46.57–55.43	1.14	92.01	55	1.14	92.73	55	1.14	92.73	55	52.11–69.58	73.3	92.73	62	2.62	82.26
VV	50	46.61–53.39	1.27	93.65	53	1.27	94.34	52	1.27	94.34	52	50.44–62.95	79.43	96.15	57	3.14	87.72
AG	40	36.46–43.54	1.61	91.87	44	1.61	90.91	43	1.61	90.91	43	40.58–54.06	73.99	93.02	48	4.1	83.33
CL	28	25.89–30.11	0.75	92.99	30	0.75	93.33	29	0.75	93.33	29	28.08–35.29	79.34	96.55	30	1.92	93.33
CH	39	37.82–40.18	0.67	97.06	40	0.67	97.5	39	0.67	97.5	39	39.01–42.36	92.07	100	39	2.97	100
CMR	116	111.48–120.52	0.65	96.25	123	0.65	94.31	120	0.65	94.31	120	117.26–134.47	86.26	96.67	127	1.98	91.34

L, Localities;  $S_{\text{obs}}$ , observed richness; IC, confidence interval; Eff, percentage of efficiency; SD, standard deviation

\*Estimated with the upper limit of IC



**Fig. 4** Non-parametric cumulative curves for sampled streams in the Coalcomán Mountain Range, Michoacán, Mexico

At a landscape scale, 45 species were exclusive to one particular site, representing 38.8% of the gamma diversity, with one site (TZ) achieving nearly 57%. Windward and leeward slopes were 43% complementary. No single species inhabited all the streams studied, although 53 species (45.6% of  $\gamma$ ) occurred at three or more streams (eurytopic). In contrast, 63 species (54.3% of  $\gamma$ ) were found in just one or two streams (stenotopic). According to Lande (1996), the relative contribution of alpha and beta diversity to gamma diversity was 41.58 and 58.41%, respectively.

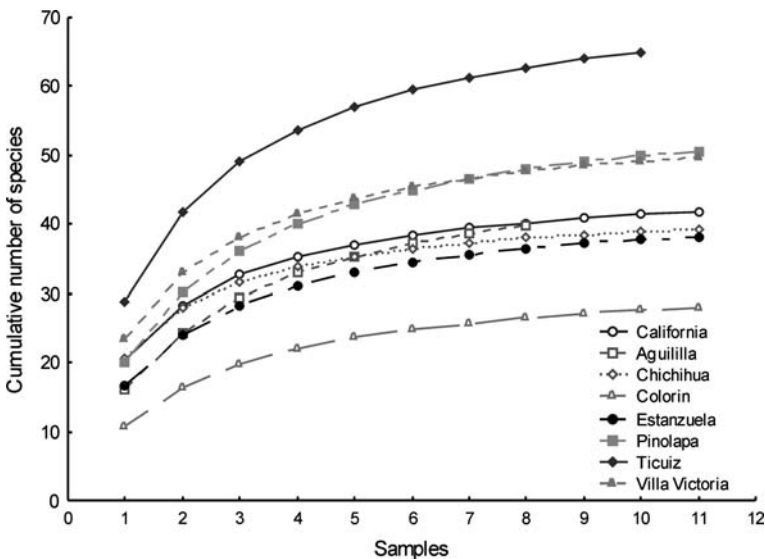
### Adult seasonality

Twenty-five species were present during all collecting periods, suggesting they flew throughout the year, while 17 species were collected only once, and most species flew for two or three seasons out of the year. Summer and autumn had similar numbers of species flying in four localities (Fig. 7), while in the other three localities autumn predominated. Only in CL were there more species flying in summer. In contrast, winter had the fewest species flying in five localities. In the two localities with the lowest elevations on the leeward slope (CF and RP), the number of species flying was more or less constant in summer, autumn and winter. Twelve species exhibited strong seasonality, with 10 favoring the rainy season (summer), one (*Progomphus lambertoi*) apparently restricted to the beginning of spring (the driest season), and one (*Progomphus marcelae*) to the last third of autumn.

**Table 6** Sites, number of species registered, parameters and predictions of two species accumulation models fitted for each odonate assemblage

Sites	#spp	Clench							Linear dependence					
		<i>n</i>	<i>a</i>	<i>b</i>	<i>a/b</i>	<i>R</i> <sup>2</sup>	sl	Eff	<i>a</i>	<i>b</i>	<i>a/b</i>	<i>R</i> <sup>2</sup>	sl	Eff
CF	42	11	36	0.77	47	99.71	0.40	89.36	15.61	0.38	41	95.57	0.24	89.362
AG	40	8	23.5	0.46	51	99.92	1.07	78.43	23.78	0.58	41	94.88	0.23	97.561
CH	39	11	39	0.90	43	99.90	0.33	90.70	24.92	0.66	38	96.16	0.02	102.632
CL	28	11	16.1	0.48	33	99.99	0.41	84.85	11.79	0.43	27	98.53	0.10	103.704
EZ	38	11	26.5	0.60	44	99.93	0.46	86.36	18.53	0.49	38	97.65	0.09	100.000
RP	51	11	30.3	0.51	59	99.94	0.69	86.44	22.00	0.44	50	97.76	0.17	102.000
TZ	66	10	47	0.62	76	99.44	0.91	86.84	33.01	0.52	63	95.23	0.18	104.762
VV	50	11	40.4	0.72	56	99.87	0.51	89.29	27.17	0.56	49	95.71	0.06	102.041
CMR	116	84	17.4	0.14	124	98.90	0.11	93.54	10.78	0.10	110	92.47	0.00	105.45

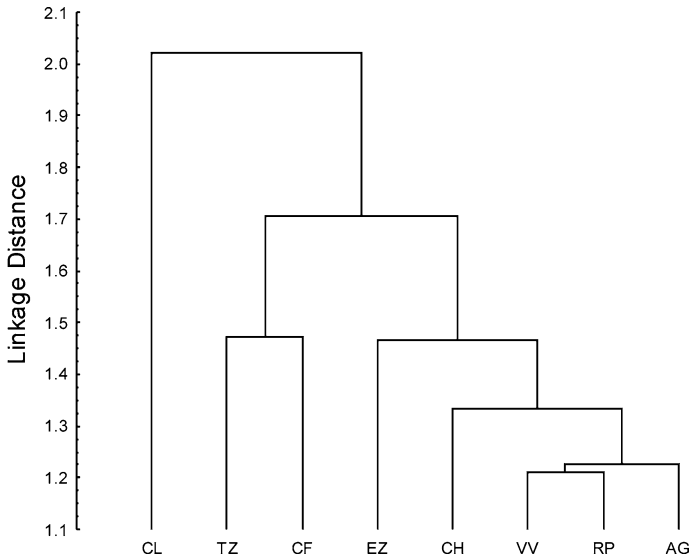
*a*, Slope at the beginning of sampling; *b*, a parameter related to the mode of accumulation of new species during sampling; *n*, sampling effort; *a/b*, asymptote; *R*<sup>2</sup>, coefficient of determination; sl, slope; eff, percentage of efficiency; The slope was estimated by the first derivative of Clench’s function  $[a/(1 + b \times n)^2]$ , and the first derivative of linear dependence  $[a \times \exp(-b \times n)]$



**Fig. 5** Species accumulation curves for the streams based on Clench’s model. Each point represents the average of 100 randomized samples (see estimated parameters in Table 6)

**Discussion**

González-Soriano and Novelo-Gutiérrez (1996) recorded 38 species for Michoacán. Ponce (2005) added 17 new records bringing the number to 55 species. Our survey provided 88 new state records, increasing the total number to 143 species for Michoacán, which represents 40.3% of the total cited for Mexico by González-Soriano and Novelo-Gutiérrez (2007).



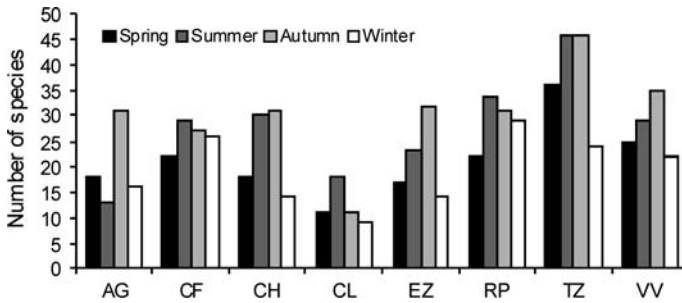
**Fig. 6** Cluster analysis dendrogram for the Odonata from the Coalcomán Mountain Range, Michoacán, Mexico, based on Whittaker's Similarity Matrix and the Complete Linkage Method. The CL assemblage is the most dissimilar while VV, RP and AG assemblages show great similarity

The odonate fauna of the CMR is composed of wide ranging species, species with distributions restricted to one or two biogeographic provinces (Costa Pacífica Mexicana and the Depresión del Balsas [*sensu* Morrone 2001]), and a few possible endemics (the five new species).

In six streams, the species richness of Anisoptera was greater than that for Zygoptera, in one stream the reverse was true (see below), and in one stream both suborders were practically equal (Table 4). The richest family was the Libellulidae (Anisoptera) (48 spp.), followed by the Coenagrionidae (Zygoptera) (31 spp.). These data reflect the general pattern for Mexico: a greater diversity of Anisoptera (58%) than Zygoptera (42%), as well as the predominance of Libellulidae in the Anisoptera and Coenagrionidae in the Zygoptera (González-Soriano and Novelo-Gutiérrez 2007). The genus *Argia* was the most important contributor to Zygoptera diversity, achieving a maximum total richness ( $\gamma$  diversity) of 40.4 and 14.7%, respectively. Moreover, *Argia* represented 41–60% of the Zygoptera  $\alpha$ -diversity in seven sites, and 20–29% of the total local richness in five sites. The site where *Argia* contributed least to both Zygoptera and total local richness is the most perturbed: TZ (23.8 and 7.6%, respectively). It would be interesting to test these *Argia* proportions in other regions to see if the ecological conditions of the streams correlate with *Argia* diversity.

### Species richness

Species richness (alpha diversity) is more or less similar in most of the streams studied, except for TZ and CL, which exhibited the highest and lowest richness, respectively. The higher richness in TZ could be explained by its near-sea level location, warm and wet conditions, presence of several types of aquatic macrophytes, and a relatively constant flow of water for most of the year, thus favoring the establishment of many tropical species. Also, this stream has been moderately to highly impacted by several human activities such



**Fig. 7** Adult seasonality in the Coalcomán Mountain Range study sites, Michoacán, Mexico

as the elimination of original riparian vegetation (practically no shade in the stream area studied), establishment of banana crops, and dredging of the water channel, thus enhancing the presence of “weed species” (opportunistic species of the Coenagrionidae, Aeshnidae and Libellulidae which take advantage of exposed, highly insolated lentic habitats (Louton et al. 1996; Clausnitzer 2003)). These species increase alpha richness (Halffter and Moreno 2005), as evidenced by the number of uniques (14) and duplicates (9) that form the third part of its total richness. In contrast, the lowest species richness in CL could be due to the fact that it is a mountainous, mostly shaded, less perturbed, narrow stream with most of the stream course occupied by big boulders, and repetitive terraces. Such closed canopy habitats can be less diverse than those containing mosaics of sun–shade and open–closed areas (Kinvig and Samways 2000; Dijkstra and Lempert 2003; Smith et al. 2007). CL was unique because the Zygoptera were more diverse than Anisoptera, probably because most Anisoptera species breed in lentic waters, and these habitats are rare in torrential streams (Brooks 1999), and because forested habitats may obstruct mobility (Schutte et al. 1997; Bried and Ervin 2005). It has been documented that more Zygoptera species than anisopterans occur in dense forests (O’Neill and Paulson 2001) or along shaded stretches of streams (Brooks and Jackson 2001). The dominance of Zygoptera under shaded conditions also may have a physiological explanation. Given their small size relative to anisopterans, they qualify as thermal conformers (May 1976), showing high conductance, and their body temperature varying with environmental temperature (De Marco and Resende 2002). In contrast, most of the anisopterans found at the CMR are probably heliotherms, having a larger size and consequently lower conductance, with their activity primarily determined by solar irradiation (De Marco and Resende 2002). We speculate that most of the anisopterans found at CL (e.g. *Progomphus zonatus*, *Brechmorhoga rapax*, *B. tepeaca*, *Macrothemis ultima*, *Paltothemis cyanosoma*) might be endotherms (May 1976), producing endogenous heat and controlling their hemolymph circulation in order to thermoregulate (May 1991). We base this supposition on the fact that these species are behaviorally classified as fliers (Corbet 1999), while zygopterans behave mostly as perchers. This classification is directly related to thermoregulation (De Marco and Resende 2002). However, because of the scarce ecological and biogeographical knowledge of tropical odonates, a conclusive explanation based on functional diversity is difficult to apply (Clausnitzer 2001). Nevertheless, these streams located in ravines in the mountainous areas of Mexico apparently have historically served as small refugia, contributing greatly to odonate beta diversity (Novelo personal observation). In this study, more than 30% of the local richness at CL was contributed by exclusive species not found at other surveyed localities.



## Theoretical richness

The number of rare species (uniques and duplicates) is the key factor on which two of the non-parametric estimators applied in this study are based. If a sampling protocol is efficient (holding the sampling area and time period constant), then the curve of uniques and duplicates should decrease as collecting effort increases (Toti et al. 2000).

Some of the species accumulation curves by stream (Fig. 4) do not completely reach the asymptote, which suggests those lists may not be complete. According to the Chao2 estimator, the more reliable lists correspond to CH and EZ (100%), while the most incomplete list corresponds to AG (93%), where the collecting effort was smaller. Of the three estimators used, Chao2 and Bootstrap more closely approximated the observed data, while Jackknife2 tends to overestimate in most cases. Also, the Mao Tau Upper Bound can be used as a good richness estimator, as evidenced by data provided in Table 5 which show great similarity with Chao2 and Bootstrap estimations.

According to Table 5, Chao2 provides the best sampling effort (measured as percentage of efficiency) when data averages are used for this purpose than with the other two estimators (Bootstrap and Jackknife2). However, this percentage of efficiency drops drastically if it is estimated by taking into account the upper limit of the confidence interval (see column with asterisk in Table 5). In this case, we think it is best to consider the results provided by the mean than those of the upper limit (for example, after 2 years of collecting adults and larvae at TZ it would be very unlikely to have missed 26 species).

As previously mentioned, sampling efficiency varied among sites and richness estimators. Maximum efficiency was observed at EZ and CH with 100% according to Chao2, and Jackknife2 for CH. Chao2 appears to perform more reliably for the majority of sites. However, when compared to parametric estimators, the percentages of efficiency of Jack2 (and to a lesser extent, those of Bootstrap) appear more consistent with those of Clench's model at five sites (Tables 5, 6).

We conclude that our sampling method was efficient, averaging more than 93%. Based upon the ecological and taxonomic knowledge of the rare species found in our data sets, many could be species particularly common in other areas, and were probably transient in our sampled streams.

## Beta diversity

The most contrasting odonate assemblages where species turnover was more drastic were those located on the windward slope, probably as a result of habitat heterogeneity and variation in climatic regime. In contrast, assemblages on the leeward slope had more or less the same geomorphologic and hydrological conditions, as well as similar habitat structure, resulting in similar richness and composition (Fig. 6). The exception was the assemblage for CF which was similar to that of TZ. Despite the greater distance between these two localities, and that they belonged to different biogeographic and physiographic provinces (Morrone 2001; Antaramián and Correa 2003), they share many species in common as shown by the similarity dendrogram (Fig. 6). A plausible explanation could be that both localities are at the lowest altitudinal range with respect to the other sites, and with the warmest temperatures. Moreover, they exhibit similar habitat structure (except that TZ is mainly an open-canopy stream, while CF is mainly a closed-canopy stream) with shallow and more or less narrow basins, most of the substrate composed of mud, sand and fine gravel, and no or very few small rapids. As such, the historical species pool in the region may have played an important role in the formation of these two assemblages (e.g. Halffter

and Moreno 2005). The great majority of species in the CF assemblage are very common and wide ranging, such that it could be considered a subunit of TZ, although located on the leeward slope. Overall, TZ and CL comprised 81% of the gamma diversity, with the other 6 assemblages providing the remaining 19%. We conclude that the beta component is important at the landscape scale; supporting the hypothesis that Mexico is a beta-diverse country (Arita 1997; Rodríguez et al. 2003).

## Conservation

The CMR has been proposed as a Terrestrial Priority Region by the National Commission for the Use and Knowledge of the Biodiversity (CONABIO), a federal Mexican government agency (Arriaga et al. 2000). Villaseñor-Gómez (2005) proposed that, based upon floristic and faunal criteria, an area comprising the municipalities of Coalcomán, Aquila and Coahuayana should be set aside as a priority area for the conservation of biodiversity. Our systematically collected data support this conservation proposal by revealing a considerable richness of odonate species at local and landscape scales, as well as endemic and newly recorded species.

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## References

- Antaramián HE (2005) Descripción física y biótica. Clima. In: Villaseñor-G LE (ed) La biodiversidad en Michoacán. Estudio de Estado, CONABIO-SUMA-UMSNH, México
- Antaramián HE, Correa G (2003) Fisiografía. In: Secretaría de Educación Pública en Michoacán y Universidad Michoacana de San Nicolás de Hidalgo. Atlas Geográfico de Michoacán, 2nd edn. EDDISA, México
- Arita HT (1997) The non-volant mammal fauna of Mexico: species richness in a mega diverse country. *Biodivers Conserv* 6:787–795. doi:10.1023/B:BIOC.0000010402.08813.ab
- Arriaga L et al (2000) Regiones Terrestres Prioritarias de México. CONABIO, México
- Bried JT, Ervin GN (2005) Distribution of adult Odonata among localized wetlands in East-central Mississippi. *Southeast Nat* 4(4):731–744. doi:10.1656/1528-7092(2005)004[0731:DOAOAL]2.0.CO;2
- Brooks SJ (1999) Field guide to the dragonflies and damselflies of Great Britain and Ireland. British Wildlife Publishing, Rotherwick
- Brooks SJ, Jackson KA (2001) The Odonata of Bioko, Republic of Equatorial Guinea, with the description of fan-shaped setae on early instar Libellulidae larvae. *Odonatologica* 30(1):29–38
- Campbell WB, Novelo-Gutiérrez R (2007) Reduction in odonate phylogenetic diversity associated with dam impoundment is revealed using taxonomic distinctness. *Fundam Appl Limnol/Archiv für Hydrobiol* 168(1):83–92
- Ceballos G, Rodríguez P (1993) Diversidad y conservación de los mamíferos de México: II. Patrones de endemidad. In: Medellín RA, Ceballos G (eds) Avances en el estudio de los mamíferos de México. Asociación Mexicana de Mastozoología, A.C., México
- Clausnitzer V (2001) Notes on the species diversity of East African Odonata, with a checklist of species. *Odonatologica* 30(1):49–66
- Clausnitzer V (2003) Dragonflies communities in coastal habitats of Kenya: indication of biotope quality and the need of conservation measures. *Biodivers Conserv* 12:333–356. doi:10.1023/A:1021920402913
- Clench H (1979) How to make regional lists of butterflies: some thoughts. *J Lepidopterists Soc* 33:216–231
- Colwell RK (2006) EstimateS: statistical estimation of species richness and shared species from samples. Version 8.0. Department of Ecology and Evolutionary Biology, University of Connecticut, USA—user's guide an application published at: <http://purl.oclc.org/estimates>

- Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. *Philos Trans R Soc Lond Ser B* 345:101–118. doi:[10.1098/rstb.1994.0091](https://doi.org/10.1098/rstb.1994.0091)
- Corbet PS (1999) Dragonflies. Behavior and ecology of Odonata. Comstock, Ithaca
- De Marco P, Resende DC (2002) Activity patterns and thermoregulation in a tropical dragonfly assemblage. *Odonatologica* 31(2):129–138
- Dijkstra K-DB, Lempert J (2003) Odonate assemblages of running waters in the Upper Guinean forest. *Arch Hydrobiol* 157(3):397–412. doi:[10.1127/0003-9136/2003/0157-0397](https://doi.org/10.1127/0003-9136/2003/0157-0397)
- González-Soriano E, Novelo-Gutiérrez R (1996) Odonata. In: Llorente-Bousquets J, García-Aldrete AN, González-Soriano E (eds) Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento. UNAM, México
- González-Soriano E, Novelo-Gutiérrez R (2007) Odonata of Mexico revisited. In: Tyagi BK (ed) *Odonata: biology of Dragonflies*. Scientific Publishers, India
- Halfpeter G, Moreno CE (2005) Significado biológico de las diversidades alfa, beta y gamma. In: Halfpeter G, Soberón J, Koleff P, Meliá A (eds) *Sobre diversidad biológica: El significado de las diversidades alfa, beta y gamma*. m3 m-Monografías Tercer Milenio, vol 4. SEA, CONABIO, Grupo DIVERSITAS & CONACYT, Zaragoza
- Jiménez-Valverde A, Hortal J (2003) Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Rev Iberica Aracnologia* 8:151–161
- Kalkman VJ et al (2008) Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia* 595:351–363. doi:[10.1007/s10750-007-9029-x](https://doi.org/10.1007/s10750-007-9029-x)
- Kinzig RG, Samways MJ (2000) Conserving dragonflies (Odonata) along streams running through commercial forestry. *Odonatologica* 29:195–208
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13. doi:[10.2307/3545743](https://doi.org/10.2307/3545743)
- Louton JA et al (1996) The Odonata of Parque Nacional Manu, Madre de Dios, Peru; natural history, species richness and comparisons with other Peruvian sites. In: Wilson DE, Sandoval A (eds) *Manu. The Biodiversity of Southeastern Peru*. Smithsonian Institution, Washington, DC
- Magurran AE (2004) *Measuring biological diversity*. Blackwell Publishing, Oxford
- May ML (1976) Thermoregulation in adaptation to temperature in dragonflies (Odonata: Anisoptera). *Ecol Monogr* 46:1–32. doi:[10.2307/1942392](https://doi.org/10.2307/1942392)
- May ML (1991) Thermal adaptations of dragonflies, revisited. *Adv Odonatol* 5:71–88
- Mittermeier RA et al (1997) Megadiversidad, los países biológicamente más ricos del mundo. CEMEX, México
- Morrone JJ (2001) *Biogeografía de América Latina y el Caribe*, vol 3. M&T- Manuales y Tesis SEA, Zaragoza
- Novelo-Gutiérrez R (2007a) *Progomphus marcelae* spec. nov. from western Mexico (Anisoptera: Gomphidae). *Odonatologica* 36(1):79–84
- Novelo-Gutiérrez R (2007b) *Progomphus lambertoii* (Odonata: Anisoptera: Gomphidae), a new species from Mexico. *Proc Entomol Soc Wash* 109(4):791–797
- O'Neill G, Paulson DR (2001) An annotated list of Odonata collected in Ghana in 1997, a checklist of Ghana Odonata, and comments on West African odonate biodiversity and biogeography. *Odonatologica* 30(1):67–86
- Palmer MW (1990) The estimation of species richness by extrapolation. *Ecology* 21:1195–1198. doi:[10.2307/1937387](https://doi.org/10.2307/1937387)
- Ponce JS (2005) Biodiversidad: Insectos y arácnidos. In: Villaseñor-G LE (ed) *La biodiversidad en Michoacán. Estudio de Estado*, CONABIO-SUMA-UMSNH, México
- Resh VH et al (1996) Macroinvertebrates as biotic indicators of environmental quality. In: Hauer FR, Lamberti GA (eds) *Methods in stream ecology*. Academic Press, San Diego
- Rodríguez P et al (2003) El componente Beta de la diversidad de mamíferos de México. *Acta Zoológica Mexicana* n.s. 89:241–259
- Sahlén G, Ekkestubbe K (2001) Identification of dragonflies (Odonata) as indicators of general species richness in boreal forest lakes. *Biodivers Conserv* 10:673–690. doi:[10.1023/A:1016681524097](https://doi.org/10.1023/A:1016681524097)
- Schutte G et al (1997) Mobility of the rheobiont damselfly *Calopteryx splendens* (Harris) in fragmented habitats (Zygoptera: Calopterygidae). *Odonatologica* 26(3):317–327
- Smith J et al (2007) Assessing riparian quality using two complementary sets of bioindicators. *Biodivers Conserv* 16:2695–2713. doi:[10.1007/s10531-006-9081-2](https://doi.org/10.1007/s10531-006-9081-2)
- Soberón J, Llorente J (1993) The use of species accumulation functions for the prediction of species richness. *Conserv Biol* 7:480–488. doi:[10.1046/j.1523-1739.1993.07030480.x](https://doi.org/10.1046/j.1523-1739.1993.07030480.x)
- StatSoft (2006) *STATISTICA (data analysis software system and computer program manual) Version 7.1*. StatSoft Inc., Tulsa

- Stewart DAB, Samways MJ (1998) Conserving dragonfly (Odonata) assemblages relative to river dynamics in an African savanna game reserve. *Conserv Biol* 12:683–692. doi:[10.1046/j.1523-1739.1998.96465.x](https://doi.org/10.1046/j.1523-1739.1998.96465.x)
- Suhling F et al (2006) Dragonfly assemblages in arid tropical environments: a case study from western Namibia. *Biodivers Conserv* 15:311–332. doi:[10.1007/s10531-005-2007-6](https://doi.org/10.1007/s10531-005-2007-6)
- Toti DS et al (2000) A structured inventory of Appalachian grass bald and heath bald spider assemblages and a test of species richness estimator performance. *J Arachnol* 28:329–345. doi:[10.1636/0161-8202\(2000\)028\[0329:ASIOAG\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2000)028[0329:ASIOAG]2.0.CO;2)
- Villaseñor-Gómez LE (2005) Conservación de la Biodiversidad. Las áreas potenciales para la conservación. In: Villaseñor-G LE (ed) *La biodiversidad en Michoacán. Estudio de Estado*, CONABIO-SUMA-UMSNH, México
- Wilson M, Shmida A (1984) Measuring beta diversity with presence–absence data. *J Ecol* 72:1055–1064. doi:[10.2307/2259551](https://doi.org/10.2307/2259551)