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Diversity and Composition of Caddisflies (Insecta: Trichoptera) along an Elevation Gradient in Southeastern Mexico

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Abstract: We analyzed the alpha and beta components of male Trichoptera diversity along an altitudinal gradient ranging from 136 to 2432 m a.s.l. by studying five assemblages of adult male caddisflies in five streams of the Sierra de Juárez, Oaxaca, Mexico. Samples were collected with light traps in the "nortes" (February) and rainy (October) seasons of 2016, recording air temperature and relative humidity. The assemblages showed an abundance pattern clearly associated with the rainy season, and a high dissimilarity in their species composition. Species richness and abundance were significantly higher at lower altitudinal levels. The highest alpha diversity was recorded in the Flor de Azahar stream; beta diversity increased with altitude and made an important contribution to gamma diversity. These results suggest that temporal and altitudinal variations affect environmental variables, which influence the structure of Trichoptera assemblages. Temperature was the primary factor determining spatial and temporal distribution patterns of caddisfly assemblages in the study area. However, in the rainy season, this factor explained a smaller proportion of the observed changes. Therefore, it is necessary to evaluate other environmental variables and explore other ecosystems to provide additional evidence on the factors affecting the diversity patterns of the Trichoptera in the Sierra de Juárez.

Keywords: caddisflies; true diversity; altitude; temperature; mountain streams; Oaxaca

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1. Introduction

In aquatic macroinvertebrate communities, caddisflies are particularly interesting as they form the most diverse order among exclusively aquatic insects. Their larvae display a wide range of feeding habits and are food for different organisms, thus contributing to trophic dynamics and energy flow between aquatic and the adjacent terrestrial systems [1–3]. In addition, they have been widely used in water quality biological assessment and monitoring [2,4].

Ecological diversity results from the interactions among groups of species, the relationships between species and the environment, and the evolutionary and biogeographical history of the areas and the biota inhabiting them [5]. To infer the contribution of all these elements, it is necessary to study alpha, beta, and gamma diversity [5]. Alpha diversity is defined as the variety and abundance of species at a specific study point [6] as a result of the ecological relationships in a particular area [5]. Beta diversity represents the replacement of species between communities located in different localities [7] due to the interaction between environmental, spatial, and historical factors [8]. Total beta diversity (β_{cc}) can be divided into two elements: replacement (β_{-3}), which involves the substitution of some species by others between assemblages, and nesting (β_{rich}), which reflects the loss of species from the richest to the poorest assemblage [9]. Gamma diversity is defined by the species richness of a set of localities within a landscape [5].

Several studies conducted in Europe and North America have analyzed altitudinal distribution patterns of caddisflies [10–13]. Studies of this sort have recently been conducted in Central and South American countries [14–18], but none had been performed in Mexico to date.

In the mid-20th century, Janzen [19] noted that species richness is higher in tropical areas than in temperate areas, particularly in mountainous regions, because seasonal changes in temperature act as a selection factor for tighter thermal tolerances for organisms located along a tropical elevation gradient. Thermal gradation prevents dispersal and results in higher reproductive isolation and speciation rates [19]. This proposal prompted several studies on the subject [20,21], which generally confirmed Janzen's prediction.

According to Jacobsen [22], the study of macroinvertebrate richness patterns along altitudinal gradients has shown variable results, and no general pattern has been detected. If such a pattern exists, it may be masked by methodological complexities, the intrinsic characteristics of the system studied, or anthropogenic effects [22]. However, temperature is one of the key factors in structuring river fauna [23]. In terms of diversity, it has been observed that alpha diversity can be positively [15] or negatively correlated [14,18] with altitude, and, in some cases, low diversity values are observed at the ends of the gradient, being highest at intermediate sites [10,12]. Beta diversity increases with altitude [18] and may have a greater contribution to gamma diversity than alpha diversity [24].

The Sierra de Juárez is a mountain range located in the north-central part of the state of Oaxaca, Mexico. Due to its geographic location and geological history, this area shows a high environmental heterogeneity, with the predominance of temperate forests, evergreen tropical forests, and mountain cloud forests. The presence of the tree *Oreomunnea mexicana* (Standl.) J. F. Leroy (Juglandaceae), a relict species that emerged in the late Miocene about 23 mya [25], has been recorded in the area, which is evidence of its age. This region is home to numerous species of plants and animals and several endemic species [26]. The highly uneven relief is associated with a complex hydrological network comprising a wide range of aquatic environments with the potential to host a large variety of caddisflies, among other taxa.

Although caddisflies in Mexico have been continuously studied over the past 45 years, information is still scarce due to the lack of specialists and because most studies have focused on the systematics and taxonomy of the order [27], while little work has been conducted on the ecology of caddisfly communities. The objective of the present study was to examine the diversity of caddisflies in the Sierra de Juárez eastern slope by analyzing five assemblages located at different altitudes, in relation to temporal variations and some environmental factors. According to the current knowledge on the Trichoptera, we expect that: (i) species richness will be higher at study sites located at low altitudes and lower at higher sites; (ii) alpha diversity will decrease as altitude increases, considering that the study sites are located in a tropical region; (iii) beta diversity will increase along the altitudinal gradient, and (iv) temperature will play a key role on the modeling of the assemblages studied.

2. Materials and Methods

2.1. Study Area

Sierra de Juárez is located in the north of the state of Oaxaca, in the district of Ixtlán de Juárez, delimited by the geographic coordinates 17°46′ N, 96°30′ W and 17°02′ N, 96°16′ W (Figure 1). Temperate climate predominates in the region, although there is a vast mosaic of climates on a local scale, ranging from semi-warm humid and sub-humid to semi-cold and temperate humid in the highest parts [28]. These are associated with a gradient of temperature and particular vegetation types, where pine forests predominate, followed by high evergreen tropical forests and mountain cloud forests, among others [29]. The mean annual temperature ranges between 12 °C and 18 °C, but it may drop to less than 12 °C at higher altitudes, and frost events may occur. Precipitation varies from 800 mm to 1200 mm per year, with a summer rainfall pattern. The five collection sites correspond to different streams distributed along an altitudinal gradient [22,23] ranging from 136 m a.s.l. (Soyolapam stream) to 2432 m a.s.l. (Cascadas de Comaltepec) (Table 1). These streams are located within the Papaloapan River hydrological basin (RH28) and in the subbasins of the Valle Nacional River [Soyolapam stream (SS), Bobo stream (BS), Cascadas de Comaltepec (CC)] and the Playa Vicente River [Yegu-Iag-Lagu stream (YS), Flor de Azahar stream (FA)] [30].

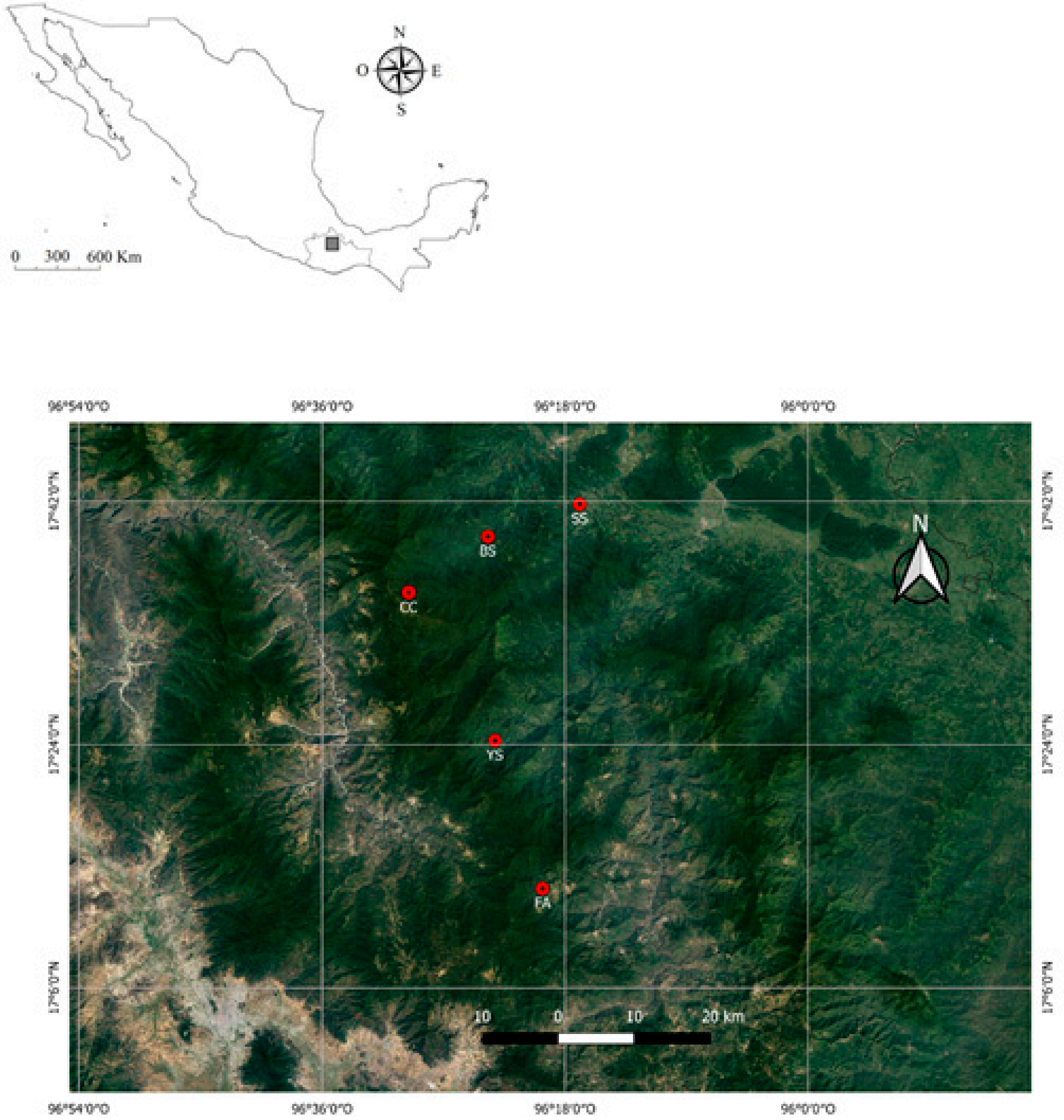

Figure 1. Geographic location of the Sierra de Juárez, Oaxaca, Mexico, and five study sites. SS = Soyolapam stream; BS = Bobo stream; CC = Cascadas de Comaltepec; YS = Yegu-Iag-Lagu stream; FA = Flor de Azahar stream. Modified from Google Earth.

Table 1. Study sites in the Sierra de Juárez, Oaxaca, Mexico. MAP = mean annual precipitation; MAT = mean annual temperature. Climate according to García notation [31].

Stream	Geographic Location	Altitude (msnm)	MAP (mm)	MAT (°C)	Vegetation Type	Climate
Soyolapam (SS)	17°41′47′′ N 96°16′54′′ W	136	3000–3500	24.9	Evergreen rainforest	Aw
Bobo (BS)	17°39′23′′ N 96°23′43′′ W	460	2500–3000	30	Evergreen rainforest	Af
Yegu-Iag-Lagu (YS)	17°24′18′′ N 96°23′11′′ W	1320	1200–2300	21	Cloud forest	(A)c(m)
Flor de Azahar (FA)	17°13′21′′ N 96°19′39′′ W	1967	800–1200	22.5	Oak-pine forest	Cw
Cascadas Comaltepec (CC)	17°35′15′′ N 96°29′35′′ W	2432	2000–2500	9	Pine forest	Cw

2.2. Field Data Collection and Insect Identification

To record the diversity of caddisflies in Sierra de Juárez, two sampling events were carried out during 2016; one during the “nortes” season (February) and the other at the end of the rainy season (October). Sampling was conducted by three persons over two consecutive days in each stream. Since many (but not all) adult caddisflies are of nocturnal or crepuscular habits and are also attracted by light, specimens were collected using two black-light traps. Each trap consisted of a 2.2 m × 1.5 m white sheet secured with ropes, illuminated with a 15-watt blacklight lamp and an energy source [32]. Light traps were placed on the banks of each of the five streams, with a minimum separation of 25 m between them, and operated for four hours from twilight. Caddisflies caught in the blacklight trap at each site were collected at 30-min intervals (considered sample units) between 18:30 and 22:30 during the winter and from 18:00 to 22:00 in the autumn. An amount of 32 samples were collected per site and 160 samples for the entire study area per season. In addition, some caddisflies were sacrificed in lethal chambers with ethyl acetate [33] to build a reference collection of pin-mounted specimens [32]. The remaining caddisflies collected were preserved in 96% alcohol bottles for subsequent identification. Similarly, air temperature and relative humidity were recorded at the same time intervals (every 30 min) using a HOBO Pro v2 thermo-hygrometer. Systematic sampling was carried out with four replicates obtained by placing two light traps on two consecutive days at each collection site. Additionally, an entomological net was used for one hour during daylight hours to capture diurnal caddisflies, such as those in the family Xiphocentronidae [34]. These were collected by sweeping the riverbank vegetation between 12:00 and 13:00 h.

For species identification, the genital structures of adult males were processed according to the technique described by Blahnik and Holzenthal [32]. The specimens collected were properly curated and deposited in the Colección Nacional de Insectos (National Insect Collection) of the Instituto de Biología (Institute of Biology) at Universidad Nacional Autónoma de México (CNIN-IBUNAM).

2.3. Data Analysis

The effects of the site and the collection season on air temperature and relative humidity were determined through a two-way ANOVA and a multiple correlation analysis to determine the direction of the relationship using the STATISTICA Ver. 6 program [35]. The overall sex ratio and the one for the most abundant species were calculated, and Chi^2 values were obtained to demonstrate the significance of the differences observed. Species presence-absence matrices were constructed for each site, each season, and the entire region; these matrices were analyzed with Clench’s parametric model and the Chao2 non-parametric model to evaluate sampling efficiency and estimate the expected richness. These analyses were carried out with the programs EstimateS ver 9.1.0 [36] and STATISTICA ver. 6 [35]. Model performance was evaluated according to Jiménez-Valverde and Hortal [37] in the case of the Clench model and to González-Oreja et al. [38] for the Chao2 model. Sampling units were defined as 30-min sampling intervals. The similarities in species composition between the five assemblages and the two seasons were assessed by constructing a presence-absence matrix and a dendrogram using the unweighted pair group method with arithmetic mean (UPGMA) and performing a similarity analysis (ANOSIM) with the Jaccard index. The similarity between groups was statistically tested ($p < 0.05$) using 1000 permutations [39]. These analyses were carried out with the BioDiversity Pro ver. 2 program [40]. The different diversity components were analyzed by recording the number of species (richness) and estimating the "true diversity" using the exponential of the Shannon index [41] corresponding to order 1 (alpha). The unit of measurement is the effective number of species representing the diversity of a hypothetical community in which all species have exactly the same abundance [41], allowing direct comparison of the diversity of different assemblages. Only male abundances were considered for calculating diversity indices, since there is insufficient taxonomic information to classify females and assign them to the different species, because the species level taxonomy of the order is mainly based on structures of the adult male genitalia [2]. Beta diversity between assemblages and their components was calculated using the betapart package in R [42], and beta diversity between seasons was calculated using the SPADE program [43]. True gamma diversity uses multiplicative diversity partitioning proposed by Whittaker [7] and was calculated as the product of mean alpha diversity by total beta diversity [44]. A two-way ANOVA was performed to determine the effects of the site and the collection season on the total caddisfly richness and abundance, and a multiple correlation analysis to determine the direction of the relationship using the STATISTICA ver. 6 program [35]. To understand the relationship between temperature, relative humidity, and caddisfly assemblages, discriminant analyses were performed by season and taxonomic level (family, genus, and species) using the STATISTICA ver. 6 program [35]. For this and the previous analysis, the data were normalized by a $\sqrt{x} + 0.5$ correction for temperature and abundance data and an arcsine$\sqrt{(x/100)}$ correction for relative humidity [45].

3. Results

3.1. Environmental Factors

The minimum and maximum air temperatures were recorded in CC (2432 m a.s.l.) during the "nortes" season (1.4 °C) and in SS (136 m a.s.l.) during the rainy season (29.2 °C), respectively. The lowest relative humidity was recorded in SS during the rainy season (68.7%) and the highest in CC during the rainy season (98%) (Table 2).

Table 2. Mean, standard error (±SE), minimum and maximum values of air temperature (T °C) and relative humidity (RH) of the five study sites in the Sierra de Juárez, Oaxaca, Mexico. n = "nortes", r = rainy. N = 50.

Stream	**SS**		**BS**		**YS**		**FA**		**CC**	
Season	**n**	**r**	**n**	**r**	**n**	**r**	**n**	**r**	**n**	**r**
T °C	16.74	21.90	15.73	19.71	10.31	19.42	9.43	14.89	2.26	11.77
(±SE)	(0.13)	(0.24)	(0.04)	(0.14)	(0.07)	(0.33)	(0.26)	(0.37)	(0.13)	(0.11)
Minimum	15.61	20.22	15.41	18.72	9.46	17.08	6.08	12.94	1.40	10.88
Maximum	18.18	29.24	16.39	23.62	11.66	24.77	14.19	20.89	3.49	14.65
RH%	90.87	88.60	91.62	91.49	91.35	92.13	80.71	93.19	84.84	94.45
(±SE)	(0.15)	(0.85)	(0.10)	(0.49)	(0.09)	(0.26)	(0.95)	(0.36)	(0.87)	(0.53)
Minimum	88.33	68.74	89.87	80.87	89.65	87.21	69.25	81.89	72.32	87.33
Maximum	92.53	92.74	92.72	93.75	92.26	94.30	91.47	96.73	90.39	98.00

According to the two-way ANOVA, the site, the month of collection, and the interaction between both factors exerted a significant effect on temperature (site: $F = 940.104$, $p < 0.005$; month of collection: $F = 2280.001$, $p < 0.005$; interaction: $F = 157.401$, $p < 0.005$) and relative humidity (site: $F = 25.204$, $p < 0.005$; month of collection: $F = 232.801$, $p < 0.005$; interaction: $F = 56.301$, $p < 0.005$, respectively). Altitude was negatively correlated with temperature ($r^2 = -0.43$, $p < 0.001$) and positively correlated with relative humidity ($r^2 = 0.22$, $p < 0.001$).

3.2. Richness and Composition

From the analysis of 320 samples from the five streams, a total of 19,479 adult caddisflies were collected, belonging to 13 families, 37 genera, and 121 species (Table 3). Eighteen new species for the science were recorded: three in the genus *Lepidostoma* Rambur, two in *Hydropsyche* Pictet, two in *Ochrotrichia* Mosely, two in *Metrichia* Ross, one each in the genera *Helicopsyche* Siebold, *Ithytrichia* Eaton, *Rhyacopsyche* Müller, *Zumatrichia* Mosely, *Oecetis* McLachlan, *Triaenodes* McLachlan, and *Cnodocentron* Schmid, and the species *Atopsyche bifurcata* Razo-González and Novelo-Gutiérrez and *A. jujmi* Razo-González and Novelo-Gutiérrez. SS presented 71 species, while BS, YS, and FA showed lower richness, with 44, 40, and 28 species, respectively. CC showed only eight species. There was a negative and significant correlation between altitude and the number of species ($r = -0.94$, $p < 0.005$), while the correlation between altitude and abundance was not significant ($r = -0.76$, $p = 0.14$).

Table 3. Richness and composition of adult Trichoptera assemblages in the Sierra de Juárez, Oaxaca, Mexico. Taxa are alphabetically arranged. x = "nortes", * = rainy, + = new species for the science; in bold the new record for state of Oaxaca; Freq = capture frequency (percentage of catch of each species in the ten samplings).

Species/Assemblage	SS	BS	YS	FA	CC	Freq
Calamoceratidae						
Phylloicus aeneus (Hagen, 1861)	*	*		*		30
Glossosomatidae						
***Culoptila jamapa* Bueno-Soria and Santiago-Fragoso, 1996**			x *	x *		40
Culoptila pararusia Blahnik and Holzenthal, 2006	x *					20
Mortoniella falcicula Blahnik and Holzenthal, 2008			*			10
Mortoniella meralda (Mosely, 1954)	x *					20
***Mortoniella mexicana* Blahnik and Holzenthal, 2008**	*	x				20
Protoptila bicornuta Flint, 1963	*					10
Protoptila ixtala Mosely, 1937	x *					20
***Protoptila liqua* Mosely, 1954**	x *					20
Protoptila resolda Mosely, 1937	*					10
Protoptila rota Mosely, 1937	*					10
***Protoptila spangleri* Flint, 1967**	x *					20
Helicopsychidae						
Cochliopsyche vazquezae Flint, 1986	*					10
Helicopsyche borealis (Hagen, 1861)	x *	*	*			40
***Helicopsyche dampfi* Ross, 1956**		*				10
Helicopsyche planata Ross, 1956	x	x	*			30
Helicopsyche tuxtlensis Bueno-Soria, 1983	x	*	*			30
***Helicopsyche* sp.**$^{+}$				*		10
Hydrobiosidae						
***Atopsyche bifurcata* Razo-González and Novelo-Gutiérrez, 2021**					*	10
Atopsyche calopta Ross and King, 1952		x		x		20
Atopsyche dampfi Ross and King, 1952	x	x	x *	x *		60
Atopsyche erigia Ross, 1947	*					10
***Atopsyche huenga* Flint, 1974**			*			10
***Atopsyche japoda* Ross and King, 1952**		x	x			20
***Atopsyche jujmi* Razo-González and Novelo-Gutiérrez, 2021**					*	10
***Atopsyche majada* Ross, 1947**	x *	*				30
Atopsyche pilcomayo Schmid, 1989					*	10
Hydropsychidae						
Cheumatopsyche gelita Denning, 1952	x					10
Diplectrona chiapensis Flint, 1967		x	x	x *	*	50
Hydropsyche toschiae (Denning, 1965)	x	x *	x *	x *		70
***Hydropsyche* sp. 1**$^{+}$			x *	x *	*	50
***Hydropsyche* sp. 2**$^{+}$	x *	*				30
Leptonema albovirens (Walker, 1852)	x *					20
Leptonema championi Mosely, 1933		x				10
Leptonema crassum Ulmer, 1905	*					10
Leptonema pinotepa Bueno-Soria et al., 2001		x *				20
Leptonema simulans mayanum Flint et al., 1987		x *				20
Plectropsyche hoogstraali Ross, 1947	x *	x *				40
***Smicridea bulara* Flint and Denning, 1989**	*					10
***Smicridea dampfi* Flint, 1974**		*				10
***Smicridea dithyra* Flint, 1974**	x *	x *	*			50
***Smicridea lachanha* Bueno-Soria and Hamilton, 1986**	x *					20
Smicridea radula Flint, 1974	x *	x *	*			50
Smicridea signata (Banks, 1903)	*					10

Table 3. *Cont.*

Species/Assemblage	SS	BS	YS	FA	CC	Freq
Hydroptilidae						
***Anchitrichia spangleri* Flint, 1970**	x *					20
***Costatrichia lodora* Mosely, 1937**	x *					20
Hydroptila denza Ross, 1948	*					10
Hydroptila mexicana Mosely, 1937	x *					20
Hydroptila misolha Bueno-Soria, 1984	*					10
Ithytrichia mexicana Harris and Contreras-Ramos, 1989			*	*		20
Leucotrichia imitator Flint, 1970		x				10
***Mayatrichia rualda* Mosely, 1937**			x *	*		30
***Metrichia cf. circulatrix* Bueno-Soria 2002**			*			10
***Metrichia crenula* Bueno-Soria 2002**			x			10
Metrichia yavesia Bueno-Soria, 2002				x *		20
***Metrichia* sp. 1^{+}**			*			10
***Metrichia* sp. 2^{+}**	*					10
***Neotrichia exicoma* (Mosely, 1937)**	*					10
***Neotrichia xicana* (Mosely, 1937)**	*	x				20
Neotrichia cf. *maria* Bueno and Hamilton, 1986		x				10
***Ochrotrichia pacifica* Flint, 1972**	x *					20
Ochrotrichia yavesia Bueno and Holzenthal, 2004			*	x		20
Ochrotrichia yetla Bueno-Soria, 2009	*	x *				30
***Ochrotrichia* sp. 1^{+}**			*			10
***Ochrotrichia* sp. 2^{+}**			*	*		20
Oxyethira azteca (Mosely, 1937)	x	x				20
***Oxyethira tica* Holzenthal and Harris, 1992**	*					10
***Rhyacopsyche mexicana* (Flint, 1967)**	*					10
***Rhyacopsyche* sp.$^{+}$**			*			10
***Zumatrichia filosa* Mosely, 1937**	*					10
***Zumatrichia multisetosa* Flint, 1970**	*					10
***Zumatrichia* sp.$^{+}$**	*	x				20
Lepidostomatidae						
Lepidostoma bakeri Flint, 1965				x *		20
Lepidostoma frontale (Banks, 1901)			x	x *		30
Lepidostoma zapoteca Razo-González, 2018				x		10
***Lepidostoma* sp. 1^{+}**			x *	x		30
***Lepidostoma* sp. 2^{+}**					x *	20
***Lepidostoma* sp. 3^{+}**		*	*			20
Leptoceridae						
***Nectopsyche dorsalis* (Banks, 1901)**	x *					20
Nectopsyche gemmoides Flint, 1981	x *	x *	*			50
***Nectopsyche pavida* (Hagen, 1861)**	x					10
***Oecetis disjuncta* (Banks, 1920)**	x *	x *				40
***Oecetis metlacensis* Bueno-Soria, 1981**	x *	x *	*	*		60
***Oecetis silviae* Bueno-Soria, 1981**		*	*			20
Oecetis sordida Blahnik and Holzenthal, 2014				x *		20
***Oecetis* sp.$^{+}$**	*					10
***Triaenodes* sp.$^{+}$**					*	10
Odontoceridae						
Marilia flexuosa Ulmer, 1905	*					10
Philopotamidae						
Chimarra acuta Ross, 1959	*					10
Chimarra barrettae (Banks, 1900)	x *	*				30
Chimarra bicolor (Banks, 1901)	*	*	*			30
Chimarra dentosa Ross, 1948	*					10
Chimarra laguna Ross, 1951	*					10
Chimarra mexicana (Banks, 1900)		x	x *	*		40
Chimarra oaxaca Blahnik, 1998			*			10
Chimarra ortiziana Flint, 1967	*					10
Chimarra pelaezi Bueno-Soria, 1985	*	x *	*			40
Chimarra ridleyi (Denning, 1941)	*					10
Chimarra setosa Ross, 1959	*					10
Wormaldia barbai Muñoz-Quesada and Holzenthal, 2015	*	x *	*	*		50
Wormaldia noveloi Razo-González, 2018			*		*	20
Wormaldia planae Ross and king, 1956	x					10
Wormaldia tarasca Bueno-Soria and Holzenthal, 1986				*		10
Polycentropodidae						
***Cernotina calcea* Ross, 1938**	*					10
***Cernotina chiapaneca* Bueno-Soria, 2010**	*					10
Polycentropus aliciae Barba-Álvarez and Bueno-Soria, 2005				*		10
Polycentropus aztecus Flint, 1967				x *		20
Polycentropus casicus Denning and Sykora, 1966				*		10
***Polycentropus mayanus* Flint, 1981**	x *	*				30
Polycentropus mexicanus (Banks, 1901)				x *		20
Polycentropus veracruzensis Flint, 1981		*	*			20
***Polyplectropus carolae* Bueno-Soria, 1990**		*				10
Polyplectropus charlesi (Ross, 1941)	*					10
Psychomyiidae						
Tinodes sp.	x *					20
Xiphocentronidae						
***Cnodocentron* sp.$^{+}$**	*					10
***Xiphocentron aureum* Flint, 1967**		*				10

From the active sampling with the entomological net, we also collected the species *Ithytrichia* sp. in FA, *Leucotrichia melleopicta* Mosely in SS, and *Oxyethira desadorna* Moulton and Harris in YS and FA.

The geographic distribution of the species widely varied across sampling sites. At the landscape scale, 65.25% of the species were unique to a particular site (Table 4); most were recorded in SS, and ten or fewer species were unique to any other streams. No species were found in all streams, but five were found in four streams, and thirty-four (28.81%) occurred in two or three streams.

Table 4. Observed, estimated, and exclusive richness, and observed and estimated true diversity of Trichoptera in an altitudinal gradient from the Sierra de Juárez, Oaxaca, Mexico. In parentheses the percentage of richness and diversity obtained in the field with respect to those estimated.

		Richness				True Diversity	
Site	**♂Abundance**	**Obs.**	**Clench**	**Chao2**	**Excl.**	**Obs.**	**Est.**
SSn	504	34	47 (72.34)	39 (87.18)	13(11.02)	6.60	6.90 (95.65)
BSn	191	27	40 (67.50)	69 (39.13)	4(3.39)	10.76	12.08 (89.07)
YSn	25	12	24 (50.00)	13 (92.31)	1(0.85)	10.80	14.57 (74.12)
Fan	29	16	35 (45.71)	30 (53.33)	6(5.08)	13.65	23.13 (59.01)
CCn	1	1	-	-	1(0.85)	1	-
SSr	5038	61	67 (91.04)	66 (92.42)	41(34.75)	11.68	11.77 (99.24)
BSr	1138	32	38 (94.12)	62 (51.61)	6(5.08)	4.86	4.99 (97.39)
YSr	527	37	55 (67.27)	55 (67.27)	8(6.78)	10.41	10.94 (95.16)
Far	283	25	30 (83.33)	29 (86.21)	10(8.47)	10.85	11.43 (94.93)
CCr	44	8	11 (72.73)	8 (100)	5(4.24)	5.05	5.50 (91.82)
SJ	7402	118	133 (88.72)	134 (88.06)	77(65.25)	17.22	19.45 (88.53)

The most abundant species were *Smicridea radula* and *Nectopsyche gemmoides*. The families with the largest number of species unique to any sampling site were Hydroptilidae (20) and Hydropsychidae (10), in accordance with their high abundance. Seven species showed a wide distribution in Sierra de Juárez: *Atopsyche dampfi*, *Hydropsyche toschiae*, *Hydropscyhe* sp. 1, *Smicridea dithyra*, *Oecetis disjuncta*, *O. metlacensis*, and *Wormaldia barbai*. In contrast, we collected only a single specimen of the following species: *Protoptila bicornuta*, *P. resolda*, *Helicopsyche dampfi*, *Atopsyche huenga*, *Leptonema championi*, *Smicridea dampfi*, *Metrichia circulatrix*, *Metrichia* sp. 1, *Metrichia*. sp. 2, *Neotrichia exicoma*, *Ochrotrichia* sp. 1, *Lepidostoma zapoteca*, *Nectosyche pavida*, *Marilia flexuosa*, *Cernotina calcea*, *C. chiapaneca*, *Polycentropus casicus*, *Polyplectropus carolae*, *Cnodocentron* sp., and *Xiphocentron aureum*. Thirty-eight additional species were rare; i.e., between two and five specimens were collected over the entire sampling.

The overall sex ratio was significantly skewed toward females (60.24%, Chi^2 = 788.36, $p < 0.05$). However, it was skewed toward males for some of the most abundant species, i.e., *Smicridea radula* (55.58%, Chi^2 = 43.22, $p < 0.05$), *S. lacanha* (73.56%; Chi^2 = 287.89, $p < 0.05$), and *Oecetis disjuncta* (74.24%, Chi^2 = 175.96, $p < 0.05$). On the other hand, it was biased toward females for other abundant species, such as *Nectopsyche gemmoides* (85.10%, Chi^2 = 1681.06, $p < 0.05$), *S. dithyra* (61.81%, Chi^2 = 110.34, $p < 0.05$), *Ochrotrichia pacifica* (63.83%, Chi^2 = 118.11, $p < 0.05$), *Anchitrichia spangleri* (58.81%, Chi^2 = 15.86, $p < 0.05$), and *Ochrotrichia* sp. 2 (84.38%, Chi^2 = 343.84, $p < 0.05$).

Regarding seasonality, fifty-seven species were recorded in the two seasons, only eight in the "nortes" season, and only fifty-eight in the rainy season. During the "nortes" season, 1697 caddisflies were collected, classified into 10 families, 28 genera, and 65 species; in the rainy season, 17,782 adults were collected, belonging to 13 families, 37 genera, and 115 species. At SS, 13 families, 34 genera, and 71 species were recorded; the dominant species were *Nectopsyche gemmoides*, *Smicridea radula*, and *S. dithyra*, representing 51.18% of the total abundance at the site. At BS, we recorded 44 species belonging to 11 families and 26 genera; *Smicridea radula* and *Leptonema pinotepa* were the dominant species, accounting for 56.58% of the abundance. At YS, forty species belonging to nine families and twenty-three genera were recorded; the dominant species were *Chimarra mexicana* and *Leucotrichia* sp., representing 38.23% of the abundance at the site. The 28 species recorded at FA belonged to 10 families and 18 genera; the dominant species were *Ochrotrichia* sp. 2 and *Hydropsyche toschiae*, accounting for 60.41% of the total. At CC, we collected fifty-four individuals classified into five families, six genera, and eight species; the dominant species were *Lepidostoma* sp. 3 and *Wormaldia noveloi*, which account for 64.81% of the total abundance at the site.

The dendrogram constructed with the Jaccard index showed that caddisfly assemblages were particular for each altitude (Figure 2). Cascadas de Comaltepec (CCll, CCn)—the site located at the highest altitude—was separated from the rest of the streams, which were clustered in two groups. On the one hand, samples of FA and YS were separated; on the other, samples of BS and YSr were separated, and, finally, the samples of SS, located at the lower part of the gradient. These results reveal that the composition of caddisfly assemblages is unique to each stream and season of the year, although the similarity analysis (ANOSIM) showed no significant differences between groups ($R = 0.90$, $p > 0.05$).

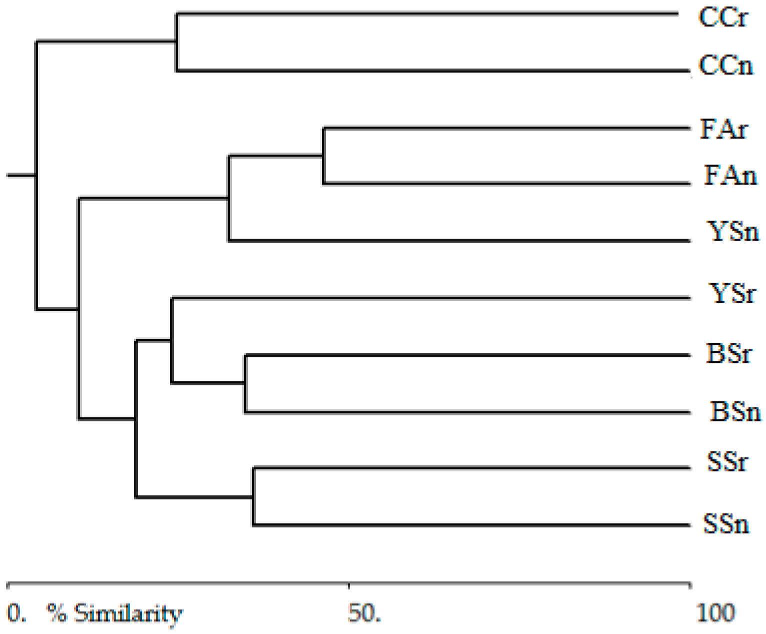

Figure 2. Cluster analysis based on the Jaccard index and UPGMA representing the faunistic relationships between the rivers sampled from the Sierra de Juárez, Oaxaca, Mexico.

The richness estimated with the Clench and Chao2 models was very similar (133 and 134 species, respectively), so the 118 collected species represent 88.72% and 88.06% of the theoretical richness, respectively. The data showed a better fit to the Clench model ($R^2 \geq 0.99$, Figure 3), indicating that the inventory was still incomplete (slope greater than 0.01) as the proportion of diversity sampled at each site varied between 44.50% (FA) and 71.98% (SS) in the "nortes" season, and between 67.23% (YS) and 90.89% (SS) in the rainy season (Table 5).

In contrast to the number of species, true alpha diversity per site was 2.57-fold higher at FA (12.82 effective species) than at CC, where the lowest diversity was recorded (4.99 effective species, Figure 4).

True alpha diversity was generally lower in the "nortes" season (15.26 effective species) than in the rainy season (17.05 effective species). At each stream, the effective number of species was higher in the "nortes" than in the rainy season, except for SS and CC, which showed the opposite trend (Table 4, Figure 5). The highest true alpha diversity was recorded at FA during the "nortes" season (13.65 effective species) and the lowest at CC during the rainy season (5.05 effective species), disregarding that only a single specimen was collected at CC during the “nortes” season. True alpha diversity was similar to the expected value in most cases, except for FA in the “nortes” season (Figure 5).

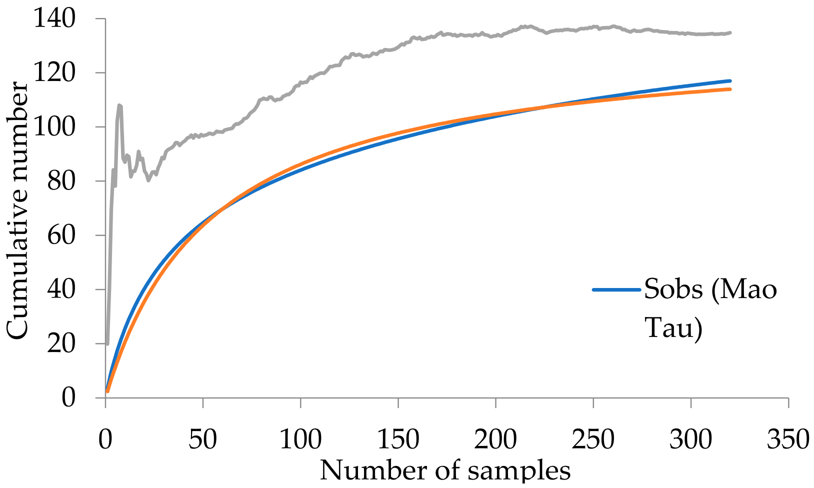

Figure 3. Species accumulation curve of Trichoptera from the Sierra de Juárez, Oaxaca, Mexico.

Table 5. Recorded species richness (S), parameters *a* (rate of increase of new species), *b* (slope of the curve), and predictions of Clench’s species accumulation model by season in Trichoptera assemblages from the Sierra de Juárez, Oaxaca, Mexico.

		Clench						
Stream	***S***	***n***	***a***	***b***	***a*/*b***	***R*^{2}**	**Slope**	**%**
SSn	34	32	3.76	0.08	47.24	0.99	0.30	71.98
BSn	27	32	2.42	0.06	40.05	0.99	0.28	67.42
YSn	12	32	0.76	00.03	24.25	0.99	0.19	49.49
FAn	16	32	0.89	0.02	35.95	0.99	0.28	44.50
CCn	1	16	-	-	-	-	-	-
SSr	61	32	16.54	0.25	67.12	0.99	0.21	90.89
BSr	32	32	4.79	0.12	38.93	0.99	0.20	82.21
YSr	37	32	3.27	0.06	55.03	0.99	0.39	67.23
FAr	25	32	3.72	0.12	30.86	0.99	0.16	81.01
CCr	8	32	0.98	0.09	11.19	0.99	0.07	71.50
SJtotal	118	320	2.44	0.02	133.41	0.99	0.97	87.70

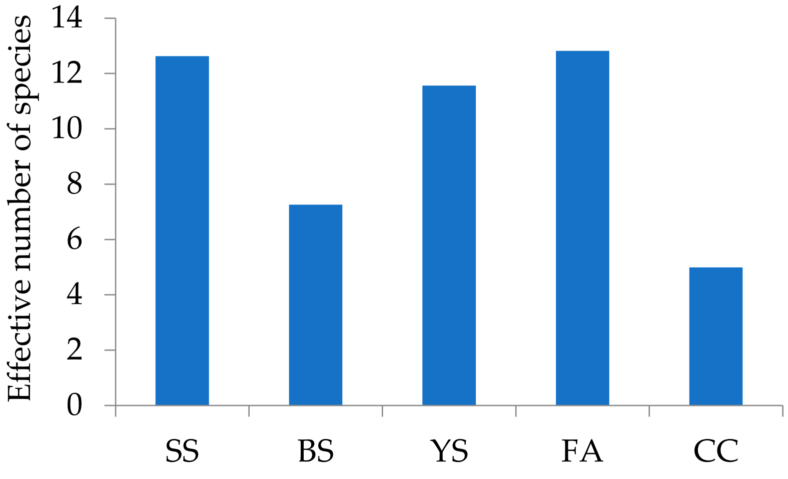

Figure 4. True alpha diversity of Trichoptera in the Sierra de Juárez, Oaxaca, Mexico.

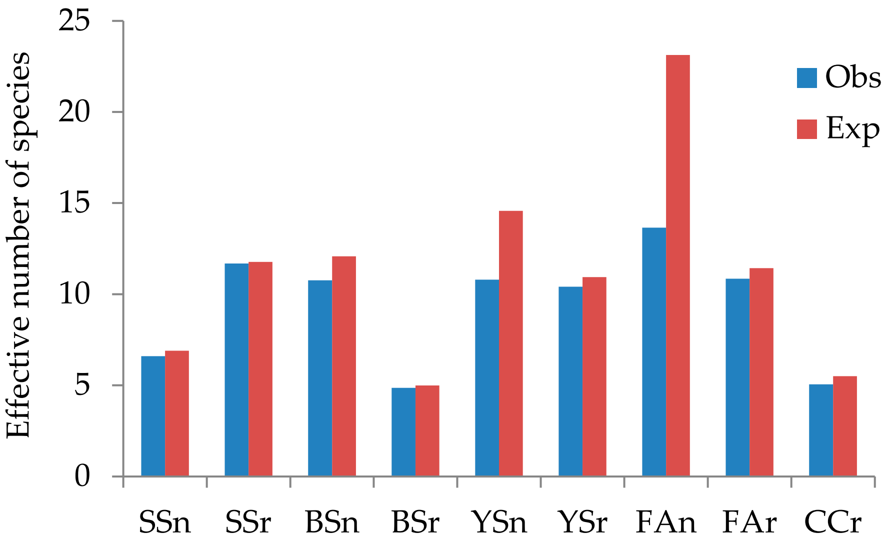

Figure 5. Temporal variation in observed and expected true diversity of Trichoptera in the Sierra de Juárez, Oaxaca, Mexico.

Beta diversity significantly increased with altitude (r^2 = 0.99, $p < 0.005$). The mean β_{cc} values varied between 83% (BS and YS) and 94% (FA). The inverse relationship between taxonomic richness and altitude is characterized by the replacement of species (β_{-3}). Dissimilarity percentages between assemblages ranged from 65% to 100%, while nesting explained between 3% (SS) and 13% (YS) of the total beta diversity. The most dissimilar assemblages were SS and BS relative to CC (Table 6).

Table 6. Global beta diversity values (β_{cc}), species turnover (β_{-3}), and differences in richness (β_{rich}) among the Trichoptera assemblages from the Sierra de Juárez, Oaxaca, Mexico.

		BS	**YS**	**FA**	**CC**	**Mean**
SS	β_{cc}	0.72	0.85	0.92	1.00	0.87
	β_{-3}	0.59	0.78	0.86	1.00	0.81
	β_{rich}	0.13	0.07	0.07	0.00	0.07
BS	β_{cc}		0.65	0.87	0.98	0.83
	β_{-3}		0.63	0.83	0.93	0.80
	β_{rich}		0.01	0.04	0.05	0.03
YS	β_{cc}			0.72	0.93	0.83
	β_{-3}			0.63	0.77	0.70
	β_{rich}			0.09	0.17	0.13
FA	β_{cc}				0.94	0.94
	β_{-3}				0.86	0.86
	β_{rich}				0.08	0.08

Altitudinally closer assemblages were more similar; however, a significant replacement of species was recorded mainly between the CC and the rest of the assemblages in both seasons (Table 7).

The mean alpha diversity was 8.57 effective species, and beta diversity was 2.01 effective communities; thus, the gamma diversity of caddisflies in the Sierra de Juárez was 17.22 effective species.

The two-way ANOVA showed a significant effect of the site and the collection season on total caddisfly richness and abundance, and on the abundance of dominant species (Table 8). The season showed a positive correlation with species richness, total abundance, and abundances of the dominant species, while the site showed a negative correlation with all of the above variables (Table 9).

Table 7. Values of total beta diversity between Trichoptera assemblages and between "nortes" and rainy seasons in the Sierra de Juárez, Oaxaca, Mexico.

	SSn	**BSn**	**YSn**	**FAn**	**CCn**	**SSr**	**BSr**	**YSr**	**FAr**	**CCr**
SSn	0.00	0.93	0.99	0.99	1.00	0.72	0.93	0.98	0.99	1.00
BSn		0.00	0.93	0.89	1.00	0.91	0.93	0.78	0.87	0.99
YSn			0.00	0.32	1.00	1.00	0.99	0.67	0.74	0.99
FAn				0.00	1.00	1.00	0.98	0.61	0.52	0.95
CCn					0.00	1.00	1.00	1.00	1.00	1.00
SSr						0.00	0.41	0.88	0.99	1.00
BSr							0.00	0.90	0.97	1.00
YSr								0.00	0.22	0.99
FAr									0.00	0.99
CCr										0.00

Table 8. Values of F for two-way ANOVA test to evaluate season, site, and interaction (season X site) effects on total richness, total abundance of Trichoptera, and on the two dominant species, in the Sierra de Juárez, Oaxaca, Mexico. * $p < 0.001$; gl season = 1, gl site = 4, gl interaction = 4.

	Total Richness	**Total Abundance**	***Nectopsyche gemmoides***	***Smicridea radula***
Season	256.40 *	147.65 *	37.39 *	70.74 *
Site	127.55 *	74.55 *	132.08 *	38.84 *
Interaction	16.79 *	24.11 *	33.26 *	27.97 *

Table 9. Multiple correlation coefficients between season, site, total richness, total abundance of Trichoptera, and the two dominant species, in the Sierra de Juárez, Oaxaca, Mexico. gl = degrees free, * significative differences.

	Total Richness	**Total Abundance**	***Nectopsyche gemmoides***	***Smicridea radula***
Season	$r^2 = 0.47$ * $gl = 2.32$ $p = 0.00$	$r^2 = 0.42$ * $gl = 2.32$ $p = 0.00$	$r^2 = 0.19$ * $gl = 2.32$ $p = 0.00$	$r^2 = 0.33$ * $gl = 2.32$ $p = 0.00$
Site	$r^2 = -0.43$ * $gl = 2.32$ $p = 0.00$	$r^2 = -0.43$ * $gl = 2.32$ $p = 0.00$	$r^2 = -0.52$ * $gl = 2.32$ $p = 0.00$	$r^2 = -0.44$ * $gl = 2.32$ $p = 0.00$

The discriminant analyses performed on families, genera, and species in relation to environmental variables and seasonality showed a clear differentiation between sites mainly determined by temperature (Figure 6). In the "nortes" season, the assemblages of families (Figure 6a), genera (Figure 6c), and species (Figure 6e) in CC are separated from the groups YS + FA and SS + BS. In the rainy season, assemblages are divided into two groups, CC + FA (sites at the highest altitudes) and SS + BS + YS (Figure 6b,d,f). For assemblages of families and genera in the "nortes" season, temperature was more strongly correlated with axis 1 (90.24% of the variance, eigenvalue = 29.90, and 86.26% of the variance, eigenvalue = 32.39, respectively), while relative humidity showed a stronger correlation with axis 2 (5.16% of the variance, eigenvalue = 1.71 and 6.47% of the variance, eigenvalue = 2.43, respectively). In contrast, for the species assemblage in the "nortes" season and for all assemblages in the rainy season, both temperature and relative humidity were more strongly correlated with axis 1, explaining between 74.28% (genera in the rainy season) and 88.64% (species in the "nortes" season) of the variance.

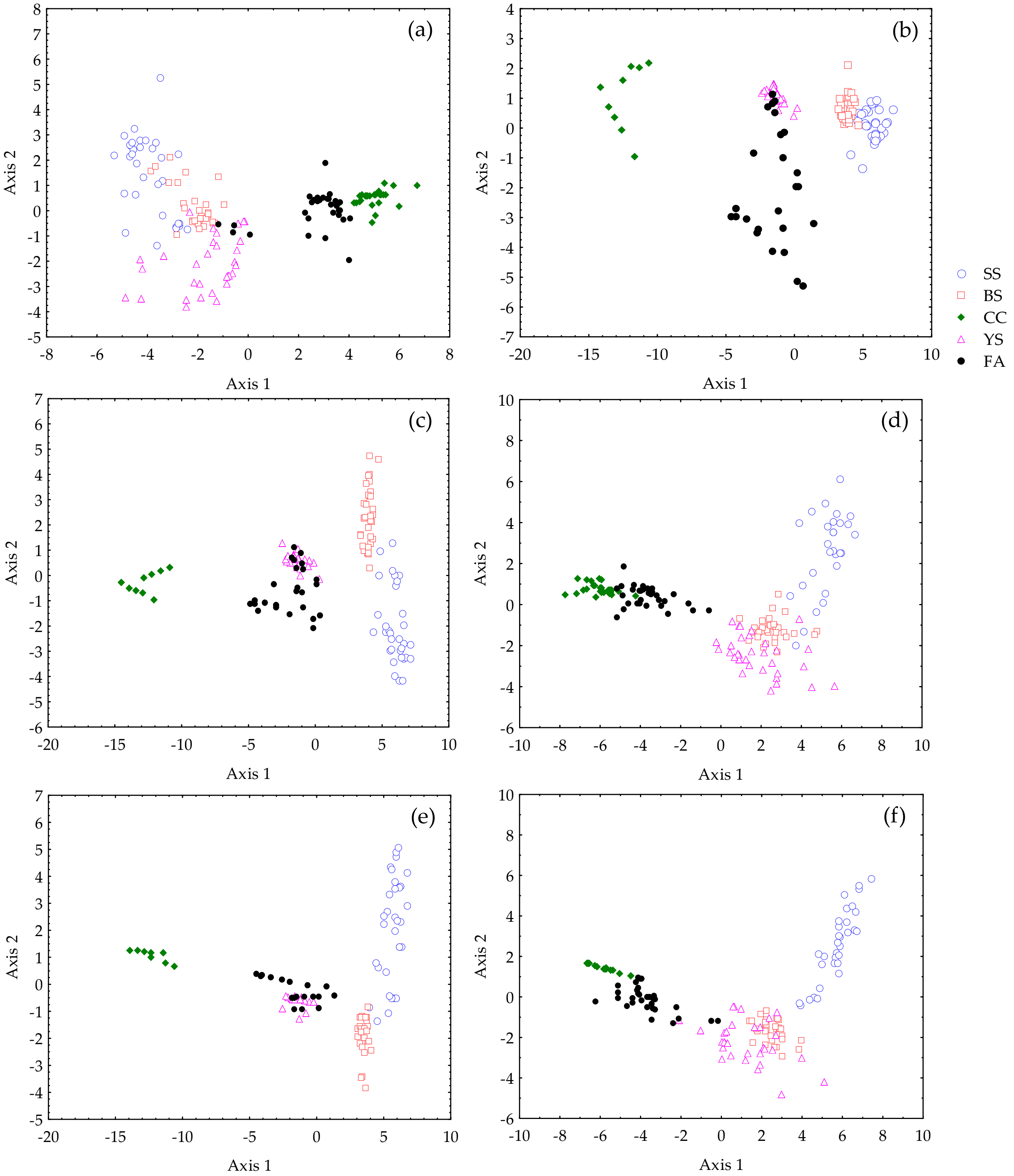

Figure 6. Discriminant analysis based on the abundance of different taxa and different seasons in relation to the temperature and relative humidity in the Sierra de Juárez, Oaxaca, Mexico. Axes 1 and 2. (**a**) families "nortes", (**b**) families rains, (**c**) genera "nortes", (**d**) genera rains, (**e**) species "nortes", (**f**) species rains.

4. Discussion

This study evaluated the alpha, beta, and gamma components of male caddisfly diversity in relation to air temperature and relative humidity along an altitudinal gradient in Sierra de Juárez, Oaxaca. As far as we know, this is the first study of its kind conducted in Mexico and provides evidence to elucidate the ecological factors that shape caddisfly assemblages in mountain streams.

As expected, air temperature and relative humidity varied with altitude. Our results showed that temperature decreases and relative humidity increases with altitude [13,15].

These results suggest that caddisfly richness and diversity in Sierra de Juárez are high, as the 121 species reported here represent 20.86% of caddisfly diversity in Mexico and 58.17% in Oaxaca [46–49]. It should be noted that we collected 51 species (33.11%) that had not previously been reported for the state. Regarding estimates of richness by site, the results suggest that between 9.11% and 55.5% of the Trichoptera remains to be discovered, and a more extensive sampling in such a heterogeneous region as the Sierra de Juárez may significantly increase the number of species recorded. Other taxa in the area for which high richness has been reported are papilionid lepidopterans [50], some angiosperm groups [51], Crassulaceae of the genus *Sedum* [52], and mosses [53]. The above demonstrates the high species richness of caddisflies in Mexico and the desirability for further studies focused on various aspects of this group.

Hydropsychidae and Leptoceridae were dominant taxa, confirming that these are the most abundant families in tropical regions [15,54]. The observed changes in sex ratio may reflect the sex ratio of larvae in streams or may be due to the sex selectivity of the blacklight trap [55]. This study did not record data on larvae, so we cannot determine the cause.

The results showed a clear variation of caddisfly assemblages related to the altitudinal gradient, thus supporting our first hypothesis that Trichoptera richness would decrease with increasing altitude [13,18,22]; our results are in contrast with the findings of Malicky and Chantaramongkol [10] and Kučinić et al. [12], who recorded a higher richness concentrated in intermediate sites along the altitudinal range. Similarly, the dendrogram showed that the assemblages studied, although segregated according to altitude, were not structured along the spatial gradient, which may be due to the fact that other factors, such as the dispersal capacity, might have a greater influence on the structuring of assemblages [56]. In addition, the similarity analysis by Wigger et al. [13] showed the segregation of sites with significant differences, which was not observed here.

In contrast to the second hypothesis, alpha diversity showed an oscillatory trend, with the highest diversity in FA (Figure 3), one of the highest-altitude sites (1967 m a.s.l.). With regards to temporal variation, it was observed that alpha diversity increased with altitude in the “nortes” season, except for CC, where a single specimen was collected. In contrast, alpha diversity was higher at intermediate altitudes in the rainy season, as reported for a Thai stream running across an altitudinal gradient similar to the one studied here [10]. Species-rich assemblages such as SS, BS, and YS ($J' = 0.18$, $J' = 0.16$, and $J' = 0.28$, respectively) had lower diversity values—mainly driven by the presence of highly dominant species—than FA, which showed a lower richness and a more even distribution of species abundances ($J' = 0.44$). The best example of the first case was SS, where 38.64% of the individuals collected corresponded to the species *Nectopsyche gemmoides* and *Smicridea radula*.

The assemblages observed at the lowest elevations were shaped similarly to the SS assemblage. The CC assemblage showed a low richness, but it is highly important for the regional fauna because most of its species are not shared with the other assemblages studied and are most likely endemic to Mexico. This locality is situated in the highest part of the subbasin, forming part of a stream head. Despite its low alpha diversity, CC is critical to regional diversity because of its unique spatial characteristics [57]. In several works carried out on stream headwaters [58–61], up to 50% of all the taxa are unique to a particular site, as also observed in this study.

As for beta diversity, the results are also consistent with those reported by Jacobsen [62] and Castro et al. [18], where beta diversity increases with altitude in terms of greater species turnover between the lower and the higher sites of the gradient. The greatest contribution of beta diversity to the regional diversity of the Sierra de Juárez represents an addition of species to the community as a result of the environmental variation between sites, a pattern recorded in other tropical mountains [16,18,62] and vascular plant assemblages [63]. Differences in vegetation along the altitudinal gradient may translate into habitat complexity since the structure of streams is more complex at lower altitudes, allowing for the presence of more diverse assemblages [64]. Similarly, the higher diversity observed during the rainy season can be explained by the greater availability of resources at that time.

Beta diversity significantly contributed to gamma diversity, maybe due to the limited dispersal capacity of caddisflies [65,66], so the distance between study sites may have caused the variation in assemblage composition and a high level of endemism [19]. The overall beta diversity values (β_{cc}) significantly contributed to the replacement of species (β_{-3}), which, at the same time, is an expression of the number of unique species of a site. In contrast, the dissimilarity due to the species richness in each assemblage had a smaller contribution relative to species replacement. The pattern mentioned above is not new, as Hernández-Rodríguez and Aguirre-Hidalgo [53], when studying bryophyte assemblages in Santiago Comaltepec, reported similar contributions for the β_{-3} and β_{rich} elements of beta diversity. Other studies have theorized that the high beta diversity at high-altitude sites may be a consequence of the lower dispersal capacity of insects caused by ecological and historical factors, including cold weather, wind, or impassable topographic barriers [57,62,65]; also, beta diversity increases as we approach the tropics [9].

Our results indicate that temperature is a driver of the spatial distribution of caddisfly assemblages, since the discriminant analysis showed that this parameter has a strong influence on them, regardless of the taxonomic level; furthermore, it explains a large percentage of the observed variance (more than 75.25% in all cases). In this sense, it has been argued that high temperatures favor high mutation rates and shorter generations, thus fostering evolution and the speciation process [23,67]. This pattern is dissimilar between seasons, probably because the factors associated with temperature that have the greatest influence on assemblages differ in each season; however, the segregation of sites according to temperature and altitude is evident. These results are consistent with several studies showing the preponderance of temperature over other parameters, such as the composition of the vegetation cover, the percentage of shade, and organic matter content in deep sediments, among others, in structuring caddisflies assemblages [13,68,69].

Additional important aspects shaping assemblages are historical factors. Of these, biogeographical history apparently has great influence because the Sierra de Juárez is located in the Zona de Transición Mexicana (Mexican Transition Zone), which in turn is located in the transition between the biogeographical provinces of Sierra Madre del Sur, Veracruzana, and Cuenca del Balsas [70]. A reflection of its biogeographical complexity are the eight generalized tracks crossing the region [71] and integrating species from different biotic components. The location of Sierra de Juárez enhances the expansion of the distribution ranges of species and promotes speciation events [72], which explains to some extent the high beta diversity recorded.

To improve the current knowledge of Trichoptera diversity in the Sierra de Juárez and the factors that shape its assemblages, it will be necessary to explore other habitats within the region and incorporate additional environmental factors into the analysis, such as water conditions and physicochemical parameters in relation to immature stage assemblages, which may be directly or indirectly defining diversity patterns at different scales, as suggested by other studies [8,18]. The diversity of adult caddisfly assemblages should also be analyzed in the dry season, as well as the diversity of juvenile assemblages. Nevertheless, the results reported here provide a solid argument for promoting protection and management actions that support the conservation of the streams in the Sierra de Juárez and their enormous biodiversity.

Trichoptera is one of the most diverse orders of aquatic insects and is widely distributed in both tropical and temperate environments. However, its diversity patterns have not been studied in depth in Mexico, and little is known about its geographic distribution patterns and ecology. The results reported here highlight the importance of these studies, not only for contributing to the species inventory of the Sierra de Juárez, but also for the information they provide about the importance of conserving the aquatic ecosystems in the region. Furthermore, in order to understand the actual diversity of caddisflies at the species level, considerable taxonomic research is needed to associate and describe the females and larvae of species currently only identified as males.

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