Revista Mexicana de Biodiversidad

Revista Mexicana de Biodiversidad 93 (2022): e933848

Conservation

Species richness and abundance of leaf litter weevils (Coleoptera: Curculionidae) in oak forests under different disturbance regimes in Central Mexico

Riqueza y abundancia de picudos en hojarasca (Coleoptera: Curculionidae) en bosques de encino bajo diferentes regímenes de disturbio en el centro de México

Robert W. Jones *, Yolanda Bizuet-Flores, Jesús Luna-Cozar

Universidad Autónoma de Querétaro, Facultad de Ciencias Naturales, Avenida de las Ciencias s/n, 76230 Juriquilla, Querétaro, Mexico

*Corresponding author: rjones@uaq.mx (R.W. Jones)

Received: 4 December 2020; accepted: 25 June 2021

Abstract

The objectives of the study were to determine and compare species richness and abundance of weevils (Coleoptera: Curculionidae) from leaf litter of oak forests from 3 isolated mountain ranges with different disturbance regimes in the state of Querétaro, Mexico. A total of 1,099 weevils were collected from 639 litter samples with total weevil densities averaging 1.72 ± 1.31 individuals per 0.5 m^2. Nineteen genera and 49 species were recorded with an estimated richness of 69.23 (Chao 1). All but 2 weevil genera have been previously reported from cloud forests of southern Mexico, and most species (88%) represented undescribed taxa. Fewer than 25% of the species were shared among the 3 sites. The differences in species richness and abundance between paired plots with different disturbance regimes were most marked in the least disturbed sites in Pinal de Amoles and San Joaquín. Results indicate that leaf litter weevil communities in oak forests of central Mexico are similar in taxonomic composition and richness to cloud forests from southern Mexico and that even small, moderately disturbed fragments may be sufficient to maintain their populations.

Keywords: Temperate forests; Beetles; Conservation; Deforestation; Mountains

Resumen

Los objetivos del estudio fueron comparar y determinar la abundancia y riqueza de especies de picudos (Coleoptera: Curculionidae) de la hojarasca de bosques de encinos de 3 sistemas montanos con diferentes regímenes de disturbio en el estado de Querétaro, México. Un total de 1,099 picudos fueron recolectados de 639 muestras de hojarasca con densidades promedio totales de 1.72 ± 1.31 individuos por 0.5 m^2. Diecinueve géneros y 49 especies fueron registradas con una riqueza estimada de 69.23 (Chao 1). Todos los géneros de picudos, con la excepción de 2, han sido previamente

ISSN versión electrónica: 2007-8706; Universidad Nacional Autónoma de México, Instituto de Biología. https://doi.org/10.22201/ib.20078706e.2022.93.3848

reportados de bosques mesófilos en el sur de México y muchas especies (88%) representan taxones no descritos. Menos del 25% de las especies fueron compartidas entre los 3 sitios. Las diferencias en la abundancia y riqueza de especies entre las parcelas con diferentes regímenes de disturbio fueron más marcadas en los sitios menos perturbados, Pinal de Amoles y San Joaquín. Los resultados indican que las comunidades de picudos de la hojarasca en bosques de encinos del centro de México, son similares en composición taxonómica y riqueza a los bosques mesófilos del sur de México y que fragmentos pequeños moderadamente alterados, pueden ser suficientes para mantener sus poblaciones.

Palabras clave: Bosques templados; Escarabajos; Conservación; Deforestación; Montañas

Introduction

The temperate forests of Mexico are considered among the 200 most important ecoregions of the world (Olson & Dinerstein, 1998). These forests include temperate humid forests (cloud forests) and subhumid temperate forests that include primarily conifer and oak forests (Challenger & Soberón, 2008). Besides providing important timber species, temperate forests are essential for capture and storage of water within the most important watersheds of Mexico, as well as providing control of soil erosion on mountainous slopes and are important in the capture of carbon (Challenger, 1998; Spracklen & Righelato, 2014). An additional ecosystem service provided by the temperate forests in tropical latitudes is the maintenance of a diverse and highly endemic biodiversity (Anderson & Ashe, 2000; Challenger & Soberón, 2008; Peterson et al., 1993; Rzedowski, 1996; Williams-Linera et al., 1996).

The biodiversity of Mexican temperate forests is especially high in taxa such as mosses, ferns, birds, amphibians, bats, and selected invertebrates (Anderson & Ashe, 2000; Jones et al., 2008; Peterson et al., 1993; Pineda et al., 2005; Ramírez-Barahona et al., 2011; Sánchez-Cordero, 2001). These groups often have high beta diversity with marked differences in diversity and composition among different temperate forest sites. This is especially the case for invertebrates inhabiting leaf litter where there is high diversity, high endemism, and the majority of the species are undescribed. For example, Anderson and Ashe (2000) reported more than 500 undescribed species of 2 beetle families, Staphylinidae and Curculionidae, in leaf litter from 13 protected cloud forests in Honduras. In a single cloud forest site in Chiapas, Mexico, Jones et al. (2008) reported a total of 56 species of weevils (Curculionidae) also in leaf litter, of which 95% were undescribed.

The genera of leaf litter weevil in montane forests of Mexico and Central America are notably similar but hyperdiverse at the species level. Representative genera include *Heptarthrum* (Cossoninae); *Eurhoptus*, *Tylodinus* (Cryptorhynchinae); *Sciomias*, *Trachyphloeomimus* (Entiminae); *Anchonus*, *Lepilius*, *Dioptrophorus,* and *Theognete* (Molytinae) (Anderson & O'Brien, 1996). Although species in most of these genera remain undescribed, recent works have begun to describe some of this diversity. Anderson (2010) described 92 new species of the genus *Theognete* from montane forests of Central America and Mexico, Luna-Cozar et al. (2014) described 32 species of the genus *Tylodinus* (Curculionidae), found in leaf litter from cloud forests of the state of Chiapas, and Barrios-Izás et al. (2016) described the new genus *Plumolepilius* and 9 of its species from leaf litter cloud forests in Guatemala and Chiapas, Mexico.

Coleoptera inhabiting leaf litter have been utilized for comparing the diversity and the general conservation status of temperate forests in Mexico and Central America (Anderson & Ashe, 2000; Cano & Schuster, 2009; Dolson et al., 2021; Jones et al., 2008; Negrete-Yankelevich et al., 2007). Advantages in using these leaf litter taxa is their high endemism and diversity, the relative ease of sampling, and the possibility of well-defined sample units based on litter volume or area sampled permitting quantitative analysis. Although weevils and other macroinvertebrate groups in leaf litter have been studied in montane forests of southern Mexico, there are no comparative studies from the montane forests of central and northern Mexico (Anderson & Ashe, 2000; Jones et al., 2008; Luna-Cozar et al., 2014; Negrete-Yankelevich et al., 2007).

In the present study we had 2 principal objectives. The first was to determine the species richness and abundance of leaf litter weevils (Coleoptera: Curculionidae) among 3 montane oak forests in the central Mexican state of Querétaro, Mexico and compare these communities with those reported from cloud forests of southern Mexico, and Central America. The second was to analyze the effect of different disturbance regimes on the richness and abundance of leaf litter between paired plots within each of the 3 study sites.

Materials and methods

Three study sites, all classified as oak forests or oak-conifer forests, were selected where 2 comparable plots with different levels of disturbance were sampled (INEGI, 2015; Zamudio et al., 1992; Fig. 1). Mean annual temperature and precipitation for the general region of each site was 16.7 ºC and 1,025 mm, 14.5 ºC and 777 mm, and 15.6 ºC and 809 mm, respectively for Pinal de Amoles, Amealco, and San Joaquín (Anonymous, 2021). At each sample site, the characteristics of the vegetation of the 2 paired plots were recorded once within 3 to 6 samples of 100 m^2 depending on the size of the plot. Data recorded in these samples included the following: *1)* number and diameter at breast height (DAP) of trees > 3.0 cm, *2)* genus of trees > 3.0 cm, *3)* number of stumps, and *4)* coverage of leaf canopy using 15 measurements with a spherical densitometer (Strickler, 1959). The first site was in the municipality of Pinal de Amoles, Querétaro, 1 km SW above the town of Pinal de Amoles in a humid oak forest with an approximately 30º slope and on the edge of a 2.6 km^2 polygon of steep, forested terrain. The first plot within the area was forested and at 21º08'08'' N, 99º38'03'' W, and at 2,442 m. Mean tree density was 0.09/m^2, mean tree diameter (DAP) was 24.0 ± 16.4, 76% of the trees were oaks, fewer than 5% were stumps, and mean canopy coverage was 78.5%. The second plot was an abandoned, deforested plot, approximately 400 m^2, surrounded by forest at 21º08'09'' N, 99º38'07''W and at 2,393 m. Mean tree density was 0.07/m^2, mean tree diameter was 17.3 ± 17.4, 45% of the trees were oaks, fewer than 5% were stumps, and mean canopy coverage was 51.1%. These 2 plots were separated by 0.2 km. The second study site was in the municipality of Amealco, and part of an oak montane forest fragment of approximately 26 km^2 within a heavily modified agricultural plain. The first plot was a forested ridge at 20º15'15'' N, 100º15'05'' W and at 2,706 m under private ownership presently being held for housing lots. This plot had a mean tree density of 0.13/m^2, mean tree diameter was 14.9 ± 10.3, 90% of the trees were oaks, fewer than 5% were stumps, and mean canopy coverage was 72.3%. The second plot of this site was located 1.8 km NE along the same ridge, but was under ejidal ownership and modified primarily through continual extraction for firewood by locals with moderate cattle grazing. This plot had a mean tree density of 0.05/m^2, mean tree diameter was 9.1 ± 8.6, 95% of the trees were oaks of which 66% were stumps, and mean canopy coverage was 53.1%. The third study site was in the municipality of San Joaquín within a mosaic of forested areas, with scattered pastures and apple orchards. The first plot here was a relatively old (> 70 yrs.) forested area located on a ridge 1.5 km W of San Joaquín, 20º54'49'' N, 99º34'45''W and at 2,512 m. Mean tree density was 0.03/m^2, mean tree diameter was 47.5 ± 16.4, 94% of the trees were oaks, and mean canopy coverage was 69.0%. The second plot here was a secondary oak forest located on the same ridge as the forested plot, 1.8 km N of the town of San Joaquín, 20º55'38'' N, 99º33'54'' W and at 2,402 m. Mean tree density was 0.29/m^2, mean tree diameter was

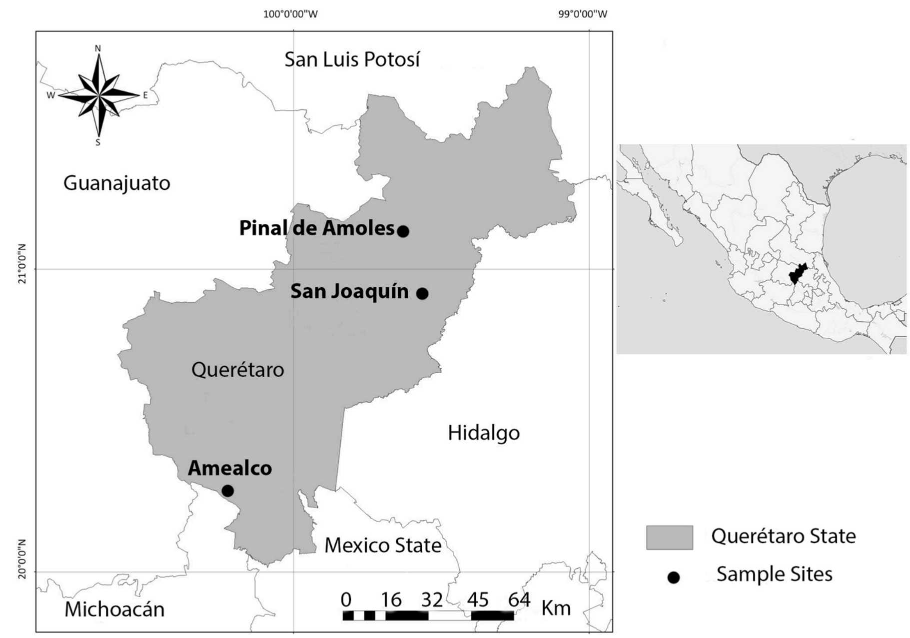

Figure 1. Sample sites of leaf litter samples from Querétaro, Mexico.

12.3 ± 5.1, 15.7% of the trees were oaks, and mean canopy coverage was 76.4%.

Weevil Sampling Methodology. A total of 639 leaf litter samples were taken within the study sites with from 95 to 118 samples from each of the 6 plots. The sample unit consisted of all organic debris (leaves, twigs, fungi, wood debris, etc.) down to, but not including, the soil within the 0.5 m^2 circle, which was collected and placed in a litter reducer (Martin, 1977). The reduced debris was transferred to labelled cloth bags and transported to the laboratory. Samples were initially collected in a line of 12 during (2007 to 2008) and all later samples were arranged within a cross of 8 samples in a 4 by 4 sample cross each separated by 2 m. Sample crosses were separated by a minimum of 5 m when larger numbers of samples were collected.

In the laboratory, leaf litter samples in cloth bags were placed on wire mesh in metal Berlese funnels (1 sample per funnel) under 60-watt light bulbs for 3 days. Weevils escaping the light and heat were collected in 80% ethyl alcohol. Samples were observed under a stereo microscope and weevils separated and then mounted on points and labelled as to sample number, site, and date of collection. Weevil species known not to be leaf litter inhabitants ("tourists"), for example Apionidae, were excluded from analysis. Once pinned and labelled, all weevil samples were sorted to morpho-species. First, samples were sorted to genera and then split into distinct morpho-species. Species were identified when possible based on comparison with identified material in the collection the Universidad Autónoma de Querétaro and from published descriptions and keys of the genera (Anderson, 2010, 2012; Anderson & Caterino, 2018; Cortés-Hernández & Morrone, 2020; Champion, 1903; 1910; Gibson, 1964; Luna-Cozar et al., 2014; O'Brien, 1972). Difficult morpho-species such as *Eurhoptus* were separated by comparison of male genitalia when possible.

Diversity measures and statistical analysis. The numbers of individuals for each species were recorded along with data of each sample, plot and sample site. These data were used to estimate total weevil richness, richness in all study sites, and mean number of weevils per site and plot. Species accumulation curves and the richness estimator Chao 1 (Chao, 1984) were calculated using the EstimateS 9.1.0 for Windows computer program (Colwell, 2013). Chao 1 was calculated for the total sampled diversity and for each study site and plot.

Comparison of the mean number of weevils per sample (0.5 m^2 leaf litter) among study plots was tested using GLM procedures for quasi-Poisson transformations and Null deviance test with 'multicomp' and included the use of the 'sandwich' procedure (Hothorn & Westfall, 2019; Zeileis et al., 2019). This transformation was chosen because data were not normal and were unbalanced, with heterogeneous variances and overdispersion (Herberich et al., 2010; Rader et al., 2011; Zuur et al., 2010). Jaccard's Similarity Index was calculated and presented in a dendrogram comparing the 3 study sites and the 6 paired study plots using PAST statistics software (Hammer et al., 2001).

Results

A total of 1,099 weevils from 639 samples of leaf litter were found from the 3 study sites in the state of Querétaro, Mexico. Weevil individuals were represented by 19 genera (Table 1) and were separated into 49 species (representatives in Fig. 2). The richness estimator, Chao 1, predicted a combined richness total of 69.23 ± 20.17 species.

Only 6 of the taxa could be identified to described species: *Conotrachelus scoparius* Champion, *Isodacrys brevirostre* Howden, *Theognete tuberosa* Anderson (Fig. 2), *Theognete laurentae* Anderson, *Trachyphloeomimus spurcus* Champion (Fig. 2), and *Sciomias subtilis* Sharp. Based on our morphological analysis, the remaining (88%) individuals collected in the present study represent undescribed taxa. A species of the genus *Eurhoptus* (sp. 6) was the most frequently collected species with 182 individuals and *Theognete tubersosa* was the second most numerous with 158.

The species composition among the 3 study sites were notably different, sharing fewer than 26% of species between Amealco and San Joaquín and fewer than 16% when comparing these sites to Pinal de Amoles (Fig. 3). Between paired plots from the same study sites, differences between plots were less than 65%, 59%, and 41% in Amealco, San Joaquín, and Pinal de Amoles, respectively (Fig. 3). Only 1 species was found at all sites, *Trachyphloeomimus spurcus* Champion, with a combined total of 96 individuals. Of the rare species, there were 9 singletons (18%) and 2 doubletons (4%). At the genus level, 5 genera were found at all 3 sites: *Trachyphloeomimus, Eurhoptus, Dioptrophorus, Tylodinus*, and *Conotrachelus*, of which *Eurhoptus* was the most abundant (Table 1). These 5 genera accounted for 64% of the total individuals. Only 2 genera were shared at 2 sites, whereas 12 genera were found at only 1 site. Of these, 7 were recorded from the most species rich site, Pinal de Amoles, 1 from Amealco, and 3 from San Joaquín (Table 1).

Comparison of forest disturbance with the richness and densities of leaf litter weevils. Weevil species richness was greatest in the forested Pinal de Amoles plot when compared to all plots of the 3 study sites. Additionally, this was the only site where there were significant differences in species richness between the forested and deforested paired plots (Table 2). Chao 1 predictions suggested that sampling completeness was relatively high at these 2 plots, indicating that 82.3% and 85.4% of the species were sampled at the forested and deforested sites, respectively. The driest study site of Amealco had the lowest species richness for both plots, and richness predictions indicated 71.2% and 97.7% of the species were registered for the forested and managed plots, respectively (Table 2). The San Joaquín plots had equal species richness (15) but also had the lowest predicted completeness of species sampling, with only 65.3% and 55.5% of predicted richness for forested and secondary plots, respectively.

Of all sites, the 2 plots with the largest trees in the least disturbed forested plots of Pinal de Amoles and San Joaquín had significantly higher weevil densities than all

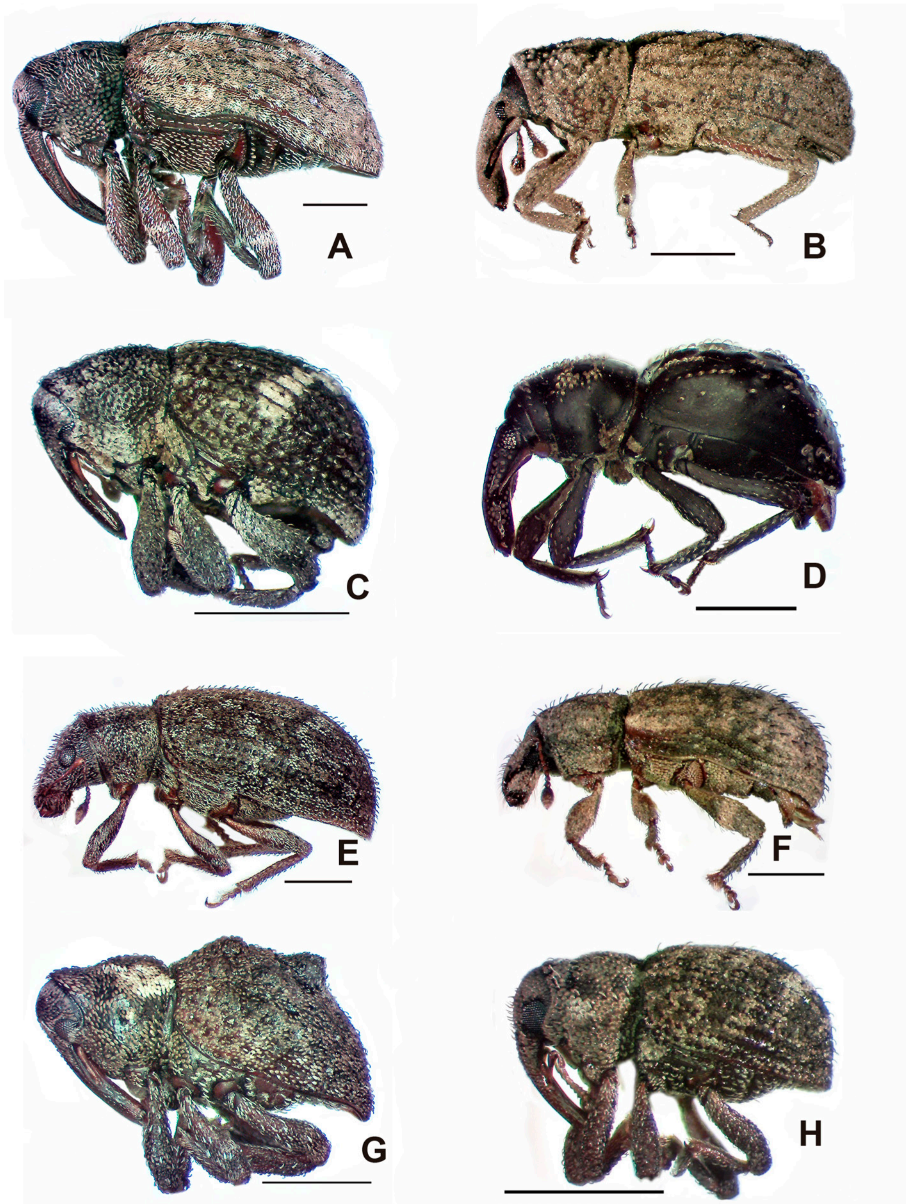

Figure 2. Representative genera of leaf litter weevils (Curculionidae) from 3 sites (municipalities) in Querétaro, central Mexico. A, *Conotrachelus posticatus* Boheman, Pinal de Amoles; B, *Dioptrophorus* sp. 2, Pinal de Amoles; C, *Eurhoptus* sp. 4, San Joaquín; D, *Theognete tuberosa* Anderson, Pinal de Amoles; E, *Sciomius* sp. 8, Amealco; F, *Trachyphloeomimus spurcus* Champion; G, *Tylodinus* sp. 2, Pinal de Amoles; H, *Lepilius* sp. 1, San Joaquín.

other plots (Table 2), and thus, these sites had significantly greater densities than their respective disturbed paired plots. Weevil densities in the plot of secondary vegetation in San Joaquín had the lowest densities, which also represented the greatest difference (6-fold) between paired plots (Table 2). The paired plots in the Amealco study site had relatively low and similar densities with less than 1.0 weevil/0.5 m^2, similar to densities at the other disturbed sites in Pinal de Amoles and San Joaquín (Table 2).

Discussion

All but 2 of the identified genera of weevils found from the 3 oak forests in the present study of central Mexico have been previously reported from other leaf litter studies of Curculionidae from cloud forest sites in southern Mexico and Central America (Anderson & Ashe, 2000; Jones et al., 2008). These included the distinctive leaf litter genera: *Eurhoptus*, *Tylodinus*, *Dioptrophorus*, *Theognete*, *Sciomias*, and *Lepilius*. Although localities from northern Mexico are cited in some individual taxonomic studies, our work confirms that these species also occur in similar communities in the relatively dry and more seasonal oak forests on the western edge of the Sierra Madre Oriental and even in the isolated forest peak in the Mexican Altiplano at the Amealco site. There were differences in the relative proportions of individuals and species from previous studies, however. For example, *Trachyphloeomimus* was one of the most common genera (96 individuals) and found in all sites of the present study (Table 1) but only 10 individuals were reported from a cloud forest study (Jones et al., 2008). Also, several of the leaf litter genera were not present in all of the study areas: *Theognete* and *Anchonus* were only found in Pinal de Amoles, *Sciomias* was only found in Amealco, and *Lepilius* was only found in San Joaquín. The site most similar to the weevil communities of the more southern cloud forests was Pinal de Amoles, which although classified as an oak forest, has slightly more annual precipitation than the other sites and probably more cloud cover based on greater presence of epiphytes

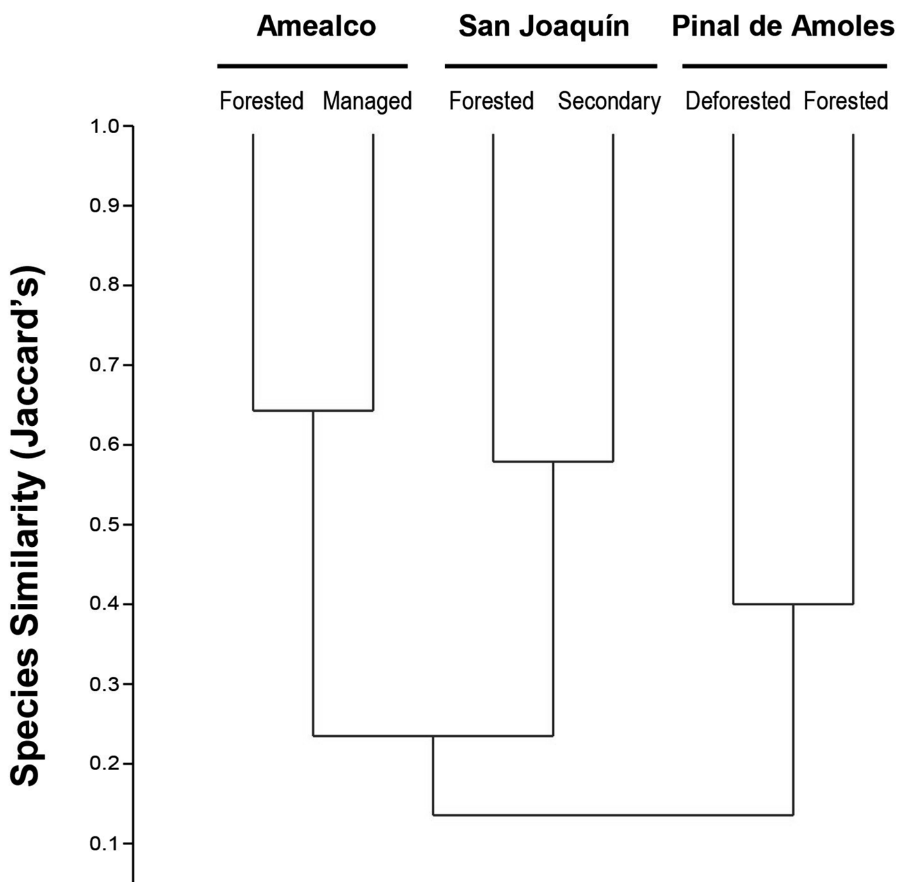

Figure 3. Similarity of shared species of leaf litter weevils using Jaccard's Similarity Index from 3 study sites and 6 paired study plots of differing disturbance regimes in the state of Querétaro, Mexico.

https://doi.org/10.22201/ib.20078706e.2022.93.3848

Table 1

Comparison of presence and abundance of leaf litter weevil genera (Curculionidae) among 3 sites in montane oak forests of Querétaro, Mexico.

Genera	Number of species	Abundance	Pinal de Amoles		Amealco		San Joaquín	
			Forested	Deforested	Forested	Managed	Forested	Secondary
Curculioninae								
Otidocephalini								
Oopterinus [2]	1	1	1	0	0	0	0	0
Cossoninae								
Rhyncholini								
Heptarthrum [1,2]	2	7	4	0	0	0	3	0
Baridinae								
Crostis sp. nov	1	1	0	1	0	0	0	0
Cryptorhynchinae Cryptorhynchini								
Eurhoptus [1,2]	6	385	181	12	38	23	107	24
Tylodinus [1,2]	5	94	51	8	1	0	22	12
Genus nov. 1	1	13	12	1	0	0	0	0
Genus nov. 2	1	13	13	0	0	0	0	0
Genus nov. 3	1	1	1	0	0	0	0	0
Genus nov. 4	4	25	23	1	0	0	1	0
Entiminae Sciaphilini								
Sciomias [1,2]	3	44	0	0	33	11	0	0
Trachyphloeini								
Trachyphloeomimus [1,2]	2	96	2	6	5	38	43	2
Tanymecini								
Isodacrys	1	7	0	0	0	0	0	7
Molytinae Anchonini								
Anchonus [1,2]	2	29	16	13	0	0	0	0
Conotrachelini								
Conotrachelus [1,2]	3	74	29	0	11	6	25	3
Lepilius [1,2]	1	68	0	0	0	0	62	6
Microhyus [1,2]	1	3	3	0	0	0	0	0
Lymantini								
Dioptrophorus [1,2]	8	53	12	21	10	1	8	1
Theognete [1,2]	2	181	143	38	0	0	0	0
Raymondioniminae								
Genus Nov. 1	2	4	0	0	0	0	0	4

1/ Previously cited in faunal studies for Honduras, Central America by Anderson and Ashe (2000).

2/ Previously cited in faunal studies in Chiapas, Mexico by Jones et al. (2008).

Table 2

Species richness and abundance of individuals of Curculionidae at 3 study sites, each with plots of different disturbance levels in montane oak forests in the state of Querétaro, Mexico.

	Richness			Abundance individuals	
Study plots	N	Number of species	Chao 1 Estimate	Total Sum	Mean density + Stderr/ 0.5 m^2 of leaf litter **
			Pinal de Amoles		
Forested	102	29*	35.24	491	4.81 + 4.26 d
Deforested	104	13*	15.23	101	0.96 + 0.57 b
			Amealco		
Forested	116	11	15.46	101	0.87 + 0.61 ab
Ejidal Managment	95	12	12.26	86	0.91 + 0.40 b
			San Joaquín		
Forested	102	15	22.97	268	2.63 + 1.86 c
Secondary Vegetation	119	15	27.01	52	0.44 + 0.17 a

* Number of species significantly different between paired plots per site based on 95% confidence intervals using rarefaction curve of species accumulation (Colewell et al., 2012).

** Mean density of total number of weevils per site with the same letter not significantly different (General Linear Model quasi-Poisson test, $F_{(5, 628)} = 2996$, $p = < 0.0001$; mean separation using Tukey's test).

and mosses (INEGI, 2015; Zamudio et al., 1992). The 2 genera not cited in previous studies were *Isodacrys* and *Crostis* (Anderson & Ashe, 2000; Jones et al., 2008). The former genus has only been collected in montane leaf litter and other habitats of central Mexico (Howden, 1961). The distinctive genus *Crostis* is only reported from South America with no known information of its biology (Alonso-Zarazaga & Lyal, 1999).

The genera of the majority of the characteristic leaf litter weevils have distributions that fit well within the Montane Mesoamerican cenocron (Halffter & Morrone, 2017; Morrone, 2010; O'Brien & Wibmer, 1982), in that they all occur in tropical montane habitats with high diversity in southern Mexico and Central America. The taxa of this cenocron apparently have their origins in the Oligocene, before the connection between North and South America (Morrone, 2010). This suggests that the weevil communities of the leaf litter of temperate oak forests of central Mexico including the Sierra Madre Oriental have a similar North and Central American origin and probably form comparable ecological communities as those of the moister cloud forests to the south. Further research is needed of the phylogenies of these taxa to clarify patterns in geographical diversification and chronology, as well as investigations of their basic biology.

The 3 oak forests shared relatively few species among sites (Fig. 3), as reported from more southern cloud forests (Anderson, 2010; Anderson & Ashe, 2000; Luna-Cozar 2014). Fewer than 26% of the species were shared among the 3 forests, and fewer than 16% for the 2 sites separated by only 24 km (Pinal de Amoles and San Joaquín). This high beta diversity is a general pattern in fauna of montane temperate forests of Mexico, and for leaf litter invertebrates, in particular (Anderson & Ashe, 2000; Dolson et al., 2021; Luna-Cozar et al., 2014; Peterson et al., 1993). For leaf litter weevils, this low similarity pattern is partially explained by the low dispersal powers of the majority of the species because they are apterous (Anderson & Ashe, 2000; Jones et al., 2008). Of the species reported here, 93% were apterous. This condition, combined with the archipelago configuration ("sky island") of cloud forests and many temperate forests of Mexico, apparently promotes vicariant evolution within separate mountain ranges. Additional processes have been proposed in which glacial cycles cause elevational shifts of temperate adapted species. These cycles are purported to result in periodic dispersal of similar species during cool periods at low elevations followed by subsequent and repeated separations at higher elevations driven by warmer periods, resulting in further vicariant speciation (Adams, 1977; Hazzi et al., 2018; Ramírez-Barahona & Eguiarte, 2013). Patterns of genetic diversity of these weevils may further elucidate the evolutionary processes involved in promoting high endemism diversity patterns of organisms in montane forests of Mexico, such as the models proposed by Ramírez-Barahona and Eguiarte (2013).

The leaf litter fauna in temperate oak forests of Querétaro was apparently relatively resilient to moderate disturbance. Of the paired comparisons within the 3 areas studied, only the site with substantial deforestation in Pinal de Amoles had significantly reduced weevil richness (Table 2). This was despite the proximity of relatively intact forest around the deforested plot and the presence of small trees that provided some canopy coverage and maintained a layer of leaf litter. The other 2 disturbed sites had similar richness to their forested counterparts. At the Amealco sites, richness and densities were almost identical although the effects of firewood extraction and tree removal by ejido members at the disturbed site was evidenced by the large number of stumps and significantly reduced canopy coverage. The differences between the sites in San Jaoquín were also similar in species richness, but the densities of weevils in the site of secondary vegetation was significantly lower (6-fold) than the forested site. This suggests although the secondary vegetation can maintain the same number of species, overall weevil densities were less and thus perhaps would be more vulnerable to extirpation. However, not enough is known about the biology of these insects to predict vulnerability, although simple extrapolation of calculated abundance for the majority of the species suggests densities of greater than 1,000 individuals/ha. Such densities may be sufficient to maintain viable populations in small forest fragments, based on studies from other organisms (Traill et al., 2007).

The beetles of the leaf litter of cloud and temperate forests of Mexico and Central America represent a virtually undescribed fauna (Anderson & Ashe, 2000; Dolson et al., 2021; Negrete-Yankelevich et al., 2007). Leaf litter weevils, as for other leaf litter inhabitants of these forests, are poorly collected with many undescribed species and with apparently, highly endemic distributions. The present study also suggests that small, oak forest fragments with moderate disturbance may still retain viable population densities of a portion of their original leaf litter weevil fauna, and they also may retain other associated, highly diverse, and undescribed arthropods. This highlights the importance of conserving even small, moderately disturbed, temperate forests fragments of Mexico that although they may have lost larger fauna, they may still be of sufficient size and ecological integrity to maintain populations of these highly diverse arthropods.

Acknowledgement

To Viviana Martínez Mandujano, Gabriel Sencial, Irma Aviles Carrillo, and Noé Omar Mendoza Villa. This study was partially funded by the internal research program of the Universidad Autónoma de Querétaro of the "Fondo para el Fortalecimiento de la Investigación UAQ-2018", FNB-2018-12, which provided scholarships for the technical help to Itzel Mendoza Montes, Teresa de Jesús Saucedo Moreno, and Sofía Martínez Sánchez.

References

Adams, M. J. (1977). Trapped in a Colombian Sierra. *Geographical Magazine*, *49*, 250–254.

Alonso-Zarazaga, M. A., & Lyal, C. H. C. (1999). *A World Catalogue of families and genera of Curculionoidea (Insecta: Coleoptera), (Excepting Scolytidae and Platypodidiae)*. Barcelona: Entomopraxis.

Anderson, R. S. (2010). A taxonomic monograph of the Middle American leaf-litter inhabiting weevil genus *Theognete* Champion (Coleoptera: Curculionidae; Molytinae; Lymantini). *Zootaxa*, *2458*, 1–127. https://doi:10.11646/zootaxa.2458.1.1

Anderson, R. S. (2012). The genus *Lepilius* Champion (Coleoptera: Curculionidae: Molytinae: Conotrachelini) in North America, with description of a new species, *Lepilius chisosensis* Anderson, from Big Bend National Park, Texas, USA. The *Coleopterists Bulletin*, *66*, 67–69. https://doi.org/10.1649/072.066.0122

Anderson, R. S., & Ashe, J. S. (2000). Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae). *Biodiversity & Conservation*, *9*, 617–653. https://doi.org/10.1023/A:1008937017058

Anderson, R. S., & Caterino, M. S. (2018). A revision of the genus *Eurhoptus* LeConte, 1876 (Curculionidae, Cryptorhynchinae) of America, north of Mexico. *Zookeys 787*, 37. https://doi:10.3897/zookeys.787.26948

Anderson, R. S., & O'Brien, C. W. (1996). Curculionidae. In J. E. Llorente-Bousquets, A. N. García-Aldrete, & E. González-Soriano (Eds.), *Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento* (329–351), México D.F.: UNAM.

Anonymous. (2021). Querétaro clima: En.climate-data.org Available at: https://es.climate-data.org/america-del-norte/mexico/queretaro-23/ [Accessed 25 March 2021].

Barrios-Izás, M. A., Anderson, R. S., & Morrone, J. J. (2016). A taxonomic monograph of the leaf-litter inhabiting weevil genus *Plumolepilius* new genus (Coleoptera: Curculionidae: Molytinae: Conotrachelini) from Mexico, Guatemala, and El Salvador. *Zootaxa*, *4168*, 061–091 https://doi.org/10.11646/zootaxa.4168.1.3

Cano, E. B., & Schuster, J. C. (2009). Beetles as indicators for forest conservation in Central America. In K. Del Claro, P. S. Oliveira, & V. Rico-Gray, in *Tropical Biology and Conservation Management-XI* (pp. 99–124), Oxford, UK: Eolss Publishers.

Colwell, R. K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: June, 2020: http://purl.oclc.org/estimates

Cortés-Hernández, K. A., & Morrone, J. J. (2020). Systematic revision of the genus *Isodacrys* Sharp, 1911 (Coleoptera: Curculionidae: Entiminae: Tanymecini). *PeerJ*, *8*, e10191. https://doi.org/10.7717/peerj.10191

Challenger, A. (1998). *Utilización y conservación de los ecosistemas terrestres de México. Pasado, presente y futuro*. México D.F.: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Challenger, A., & Soberón, J. (2008). Los ecosistemas terrestres. In *Capital Natural de México, vol. I. Conocimiento actual de la biodiversidad (*pp. 87–108). México D.F.: Conabio.

Champion, G. C. (1903). Biologia Centrali-Americana. Insecta, Coleoptera. Rhynchophora. Curculionidae. Curculioninae (concluded) and Calandrinae¸ vol. 4, pt. 4.

Champion, G. C. (1910). Biologia Centrali-Americana. Insecta, Coleoptera. Rhynchophora. Curculion. Curculioninae (concluded) and Calandrinae¸ vol. 4, pt. 7.

Chao, A. (1984). Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, *11*, 265–270

Dolson, S. J., Loewen, E., Jones, K., Jacobs, S. R., Solis, A., Hallwachs, W. et al. (2021). Diversity and phylogenetic community structure across elevation during climate change in a family of hyperdiverse neotropical beetles (Staphylinidae). *Ecography*, *44*, 1–13. https://doi.org/10.1111/ecog.05427

Gibson, L. P. (1964). Biology and life history of acorn-infesting weevils of the genus *Conotrachelus* (Coleoptera: Curculionidae). *Annals of the Entomological Society of America*, *57*, 521–526. https://doi.org/10.1093/aesa/57.5.521

Halffter, G., & Morrone, J. J. (2017). An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. *Zootaxa*, *4226*, 1. https://doi:10.11646/zootaxa.4226.1.1

Hammer, Ø., Harper, D. A., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, *4*, 1–9.

Hazzi, N. A., Moreno, J. S., Ortiz-Movliav, C., & Palacio, R. D. (2018). Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences*, *115*, 7985–7990. https://doi.org/10.1073/pnas.1803908115

Herberich, E., Sikorski, J., & Hothorn, T. (2010). A robust procedure for comparing multiple means under heteroscedasticity in unbalanced designs. *Plos One*, *5*, e9788. https://doi.org/10.1371/journal.pone.0009788

Hothorn T., & Westfall P. (2019). multcomp: Simultaneous Inference for General Linear Hypotheses. Version 1.4.10, R Foundation for Statistical Computing. URL: http://CRAN.R-project.org/package=multcomp

Howden, A. T. (1961). A revision of the genus *Isodacrys* Sharp (Curculionidae, Tanymecini). *The Coleopterists' Bulletin*, *15*, 75–95.

INEGI (Instituto Nacional de Estadística y Geografía). (2015). Guía para la interpretación de cartografía: uso del suelo y vegetación: escala 1:250, 000: serie V/ Instituto Nacional de Estadística y Geografía, México: INEGI, c2014.

Jones, R. W., O'Brien, C. W., Ruiz-Montoya, L., & Gómez-Gómez, B. (2008). Insect diversity of tropical montane forests: diversity and spatial distribution of weevils (Coleoptera: Curculionidae) inhabiting leaf litter in southern Mexico. *Annals of the Entomological Society of America*, *101*, 128–139. https://doi.org/10.1603/0013-8746(2008)101[128:IDOTMF]2.0.CO;2

Luna-Cozar, J., Anderson, R. S., Jones, R. W., & León-Cortéz, J. L. (2014). A taxonomic monograph of the genus *Tylodinus* Champion (Coleoptera: Curculionidae: Cryptorhynchinae: Tylodina) of Chiapas, Mexico. *Zootaxa*, *3788*, 1–63. https://doi.org/10.11646/zootaxa.3788.1.1

Martin, J. H. (1977). *Collecting, preparing, and preserving insects, mites, and spiders. The insects and arachnids of Canada. Part 1*. Ottawa, ON: Agriculture Canada.

Morrone, J. J. (2010). Fundamental biogeographic patterns across the Mexican Transition Zone: an evolutionary approach. *Ecography*, *33*, 355–361. https://doi.org/10.1111/j.1600-0587.2010.06266.x

Negrete-Yankelevich, S., Fragoso, C., Newton, A. C., & Heal, O. W. (2007). Successional changes in soil, litter and macroinvertebrate parameters following selective logging in a Mexican Cloud Forest. *Applied Soil Ecology*, *35*, 340–355. https://doi.org/10.1016/j.apsoil.2006.07.006

O'Brien, C. W. (1972). A review of the Mexican and Central American genus *Trachyphloeomimus*, with new species and new synonymy (Coleoptera: Curculionidae, Otiorhynchinae). The *Coleopterists' Bulletin*, *26*, 165–178.

O'Brien, C. W., & Wibmer, G. J. (1982). Annotated checklist of the weevils (Curculionidae sensu lato) of North America, Central America, and the West Indies (Coleoptera: Curculionidae). *Memoirs American Entomological Institute*. *34*, 1–382.

Olson, D. M., & Dinerstein, E. (1998). The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology*, *12*, 502–515. https://doi.org/10.1046/j.1523-1739.1998.012003502.x

Peterson, A. T., Flores-Villela, O. A., León-Paniagua, L. S., Llorente-Bousquets, J. E., Luis-Martínez, M. A., Navarro-Siguenza, A. G. et al. (1993). Conservation priorities in Mexico: moving up in the world. *Biodiversity Letters*, *1*, 33–38. https://doi.org/10.2307/2999648

Pineda, E., Moreno, C., Escobar, F., & Halffter, G. (2005). Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. *Conservation Biology*, *19*, 400–410. https://doi.org/10.1111/j.1523-1739.2005.00531.x

Rader, R., Edwards, W., Westcott, D. A., Cunningham, S. A., & Howlett, B. G. (2011). Pollen transport differs among bees and flies in a human-modified landscape. *Diversity and Distributions*, *17*, 519–529. https://doi.org/10.1111/j.1472-4642.2011.00757.x

Ramírez-Barahona, S., & Eguiarte, L. E. (2013). The role of glacial cycles in promoting genetic diversity in the Neotropics: the case of cloud forests during the Last Glacial Maximum. *Ecology and Evolution*, *3*, 725–738. https://doi.org/10.1002/ece3.483

Ramírez-Barahona, S., Luna-Vega, I., & Tejero-Díez, D. (2011). Species richness, endemism, and conservation of American tree ferns (Cyatheales). *Biodiversity and Conservation*, *20*, 59–72. https://doi.org/10.1007/s10531-010-9946-2

Rzedowski, J. (1996). Análisis preliminar de la flora vascular de los bosques mesófilos de montaña de México. *Acta Botanica Mexicana*, *35*, 25–44.

Sánchez-Cordero, V. (2001). Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. *Global Ecology and Biogeography*, *10*, 63–76. https://doi.org/10.1046/j.1466-822x.2001.00235.x

Spracklen, D. V., & Righelato, R. (2014). Tropical montane forests are a larger than expected global carbon source. *Biogeosciences*, *11*, 2741–2754. https://doi.org/10.5194/bg-11-2741-2014

Strickler, G. S. (1959). Use of the densiometer to estimate density of forest canopy on permanent sample plots. *PNW Old Series Research Notes*, *180*, 1–5.

Traill, L. W., Bradshaw, C. J., & Brook, B. W. (2007). Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biological Conservation*, *139*,159–166.

Williams-Linera, G., Tolome, J., Forest, C., & Forest, L. M. (1996). Litterfall, temperate and tropical dominant trees, and climate in a Mexican lower montane forest. *Biotropica*, *28*, 649–656. https://doi.org/10.2307/2389051

Zamudio, S., Rzedowski, J., Carranza, E., & Calderón, G. (1992). *La vegetación de Querétaro*. Pátzcuaro, Michoacán: Consejo para la Ciencia y Tecnología del Estado de Querétaro/ Instituto de Ecología/ Centro regional del Bajío.

Zeileis, A., Lumley, T., Berger, S., & Graham, N. (2019). Sandwich: robust covariance matrix estimators. Version 2.5.1, R Foundation for Statistical Computing. URL: http://CRAN.R-project.org/package=sandwich

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2010). *Mixed effects models and extensions in ecology with R, Statistics for Biology and Health*. New York: Springer.