UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE CIENCIAS

SISTEMÁTICA

PATRÓN DE DIVERSIDAD DE CURCULIONIDAE EN UN GRADIENTE ALTITUDINAL EN LA RESERVA DE LA BIÓSFERA EL CIELO, TAMAULIPAS, MÉXICO

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

LEAF LITTER WEEVIL RICHNESS INCREASES WITH ALTITUDE IN A TROPICAL-TEMPERATE TRANSITIONAL FOREST IN EL CIELO BIOSPHERE RESERVE, NORTHEASTERN MEXICO

QUE PARA OPTAR POR EL GRADO DE:

MAESTRO EN CIENCIAS BIOLÓGICAS

PRESENTA:

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Ciudad Universitaria, CD. MX. **agosto 2023**

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Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **24 de abril de 2023** se aprobó el siguiente jurado para el examen de grado de **MAESTRO EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Sistemática** del (la) alumno(a) **VILLASEÑOR AMADOR LUIS DAMIÁN** con número de cuenta **522461352** por la modalidad de graduación de **tesis por artículo científico** titulado: **“LEAF LITTER WEEVEL RICHNESS INCREASES WITH ALTITUDE IN A TROPICAL-TEMPERATE TRANSITIONAL FOREST IN EL CIELO BIOSPHERE RESERVE, NOETHEASTERN MEXICO”,** que es producto del proyecto realizado en la maestría que lleva por título “**Patrón de diversidad de Curculionidae en un gradiente altitudinal en la Reserva de la Biósfera El Cielo, Tamaulipas, México**” ambos realizados bajo la dirección del **DR. JUAN JOSE MORRONE**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
“POR MI RAZA HABLARÁ EL ESPÍRITU”
Ciudad Universitaria, Cd. Mx., a 08 de junio de 2023

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RESUMEN

Se estudiaron comunidades de gorgojos de la hojarasca a lo largo de un gradiente altitudinal de 2000 m en la Reserva de la Biósfera El Cielo, en el noreste de México, dentro de la Zona de Transición Mexicana, un área en la que se superponen las biotas Neártica y Neotropical. Se obtuvo una completitud del inventario alta (cobertura de muestreo del sitio igual a 0.922). La riqueza global (diversidad alfa) consistió en 81 morfoespecies, de las cuales 55 corresponden a gorgojos de la hojarasca. La estructura de la comunidad (diversidad beta) mostró altos valores de disimilitud, estos fueron explicados más por el recambio de especies que por el anidamiento. La diversidad de gorgojos en la hojarasca aumentó con la elevación a lo largo del gradiente altitudinal. La interacción entre la estructura del bosque (medida como la mediana del DAP) y la precipitación estacional, explicó más del 20% de la variación en la riqueza de especies de gorgojos: los gorgojos estaban asociados positivamente con una estatura de árbol reducida y una baja variación estacional, características del bosque tropical mesófilo de montaña. Las afinidades biogeográficas fueron seleccionadas a partir del conocimiento taxonómico y la distribución de los taxones estudiados. La riqueza máxima de los gorgojos de la hojarasca fue a los 1,600 m, mientras que otros insectos de la hojarasca como las hormigas, alcanzan su riqueza máxima en elevaciones inferiores a 1,000 m.

Palabras clave: Curculionidae, gradiente ambiental, pico de elevación media, mesofauna del suelo, distribución de especies, Tamaulipas, bosque de niebla, montaña tropical.

ABSTRACT

We studied communities of leaf litter weevils along a 2000 m elevation gradient in El Cielo Biosphere Reserve, northeastern Mexico, within the Mexican Transition Zone, an area where Nearctic and Neotropical biotas overlap. We achieved high inventory completeness (0.922 site sample coverage). The overall richness (alpha-diversity) consisted of 81 morphospecies, of which 55 correspond to leaf litter inhabitants. Community structure (beta-diversity) showed more dissimilarity explained by species turnover rather than by nestedness. The diversity of leaf litter weevils increased with elevation across the elevational gradient. The interaction between forest structure (measured as median DBH) and precipitation seasonality explained more than 20% of the variation in weevil species richness: weevils were positively associated with reduced tree stature and low seasonal variation, characteristics of tropical montane cloud forests. Leaf litter weevil richness peaked at 1,600 m, whereas other Mesoamerican leaf litter insects, like ants, peak at elevations lower than 1,000 m.

Keywords: Curculionidae, environmental gradient, mid-elevation peak, soil mesofauna, species distribution, Tamaulipas, tropical montane cloud forest, tropical mountain.

INTRODUCCIÓN GENERAL

Las montañas son entornos ideales para el estudio de la distribución de las especies (Körner, 2007) porque permiten explorar las preferencias ambientales de los organismos en escalas espaciales pequeñas. Los hábitats montañosos albergan una extraordinaria riqueza de especies: 87 % de los anfibios, aves y mamíferos del mundo y al menos un tercio de las plantas terrestres (Barthlott et al., 1996) se encuentran en solo el 25 % de las montañas de nuestro planeta (Rahbek et al., 2019). Las montañas en las zonas de transición son de particular interés, ya que pueden actuar como rutas que permiten la dispersión de biotas de diferentes orígenes (Ferro & Morrone, 2014; Morrone, 2020). Este es el caso de la Zona de Transición Mexicana (ZTM), donde se superponen biotas de diferentes orígenes (Halffter, 1987).

Los modelos utilizados para explicar la composición de la biota montañosa de la ZTM son la colonización horizontal por linajes que habitan en altitudes más elevadas, así como la colonización vertical por linajes de las tierras bajas circundantes (Lobo & Halffter, 2000; Escobar et al., 2007). Cuando domina la colonización vertical, se espera una disminución en la riqueza de especies conforme aumente la altitud. Cuando predomina la colonización horizontal, se observa una reemplazo de linajes de tierras bajas tropicales por linajes de tierras altas templadas (Lobo & Halffter, 2000; Halffter & Morrone, 2017; Joaqui et al., 2021). Se han documentado patrones de pico de elevación media para las hormigas de la hojarasca en la ZTM (Pérez-Toledo et al., 2021) y en toda el área mesoamericana (Longino y Branstetter, 2019). Los cambios en la diversidad de las hormigas a través de los gradientes altitudinales en todo México y Centroamérica son constantes: un aumento en la riqueza de especies que alcanza un máximo a 400 m, seguido de una disminución exponencial (Longino & Branstetter, 2019). Ambos escenarios (es decir, la disminución de la riqueza con la altitud y una riqueza máxima en elevaciones medias) son patrones comunes a lo largo de los gradientes altitudinales (McCain, 2009). Solo en raras ocasiones, la riqueza de especies aumenta con la elevación (McCain, 2009; Maioglio et al., 2022), como en el caso de las salamandras Mesoamericanas (Rovito et al., 2013).

Un grupo poco representado en estudios de la ZTM han sido los gorgojos (Coleoptera: Curculionidae), a pesar de ser una familia abundante con más de 3,000 especies en el país (Morrone, 2014) y al menos 51,000 estimadas para todo el mundo (Oberprieler et al., 2007). Los gorgojos de la hojarasca son de especial interés porque juegan un papel importante en la descomposición de la hojarasca (Anderson & Ashe, 2002). La mayoría no están descritos y parecen tener altos índices de diversidad y endemismo a nivel mundial (Jones et al., 2008, 2022). Los Curculionidae que habitan en los bosques tropicales se encuentran entre los taxones numéricamente más dominantes en la comunidad de la hojarasca (Anderson & Ashe, 2000). Tal es el caso de los miembros de Cryptorhynchini, un clado de gorgojos con muchos representantes de la hojarasca cuya diversidad global supera las 15,000 especies no descritas (Riedel et al., 2016; Letsch et al., 2020), siendo la mayoría de sus especies descritas (>6,000) Neotropicales (Riedel et al., 2016). A pesar de su diversidad, Cryptorhynchini y otros grupos de gorgojos de la hojarasca siguen siendo poco conocidos, permaneciendo subrepresentados en los estudios del Neotrópico (Anderson & Ashe, 2002; Jones et al., 2008, 2022; Maioglio et al., 2022). Sin embargo, gracias a la facilidad de muestreo en hojarasca y a unidades de muestreo bien definidas basadas en el área o el volumen de la hojarasca (Jones et al., 2022), se pueden realizar muestreos reproducibles y estandarizables (Maioglio et al., 2022). Además, se puede llevar a cabo un análisis cuantitativo robusto utilizando morfoespecies de gorgojos de la hojarasca, ya que debido a su abundancia y baja movilidad se pueden recolectar suficientes datos (Maioglio et al., 2022). Debido a que muchos gorgojos de la hojarasca son especies no descritas, una clasificación tradicional en especies requeriría un extenso trabajo preliminar descriptivo (Jones et al., 2008; 2022; Maioglio et al., 2022).

En este estudio se evaluaron los patrones de riqueza y composición de gorgojos de la hojarasca a lo largo de un gradiente altitudinal en uno de los bosques de transición tropicales-templados más septentrionales de América. Con base en los procesos de colonización de montañas de Lobo y Halffter (2000), se hipotetizó una disminución en la riqueza de especies conforme aumentara la elevación. Se espera encontrar patrones de diversidad explicados por diferencias en el reemplazo, ganancia y pérdida de especies, así como por factores ambientales que determinan la riqueza de especies a lo largo de gradientes altitudinales (ej. temperatura y humedad) (Pérez-Toledo et al., 2021) y variables de hábitat que moldean la composición de la hojarasca (ej. estructura del bosque, profundidad de la hojarasca y humedad de la hojarasca) (Maioglio et al., 2022). Los objetivos son: (a) determinar la diversidad y la composición de la comunidad de gorgojos de la hojarasca en un bosque tropical-templado de transición en el noreste de México; (b) evaluar los factores ambientales que conforman las comunidades de gorgojos de la hojarasca a lo largo de un gradiente altitudinal.

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Leaf litter weevil richness increases with altitude in a tropical-temperate transitional forest in El Cielo Biosphere Reserve, northeastern Mexico

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Leaf litter weevil richness increases with altitude in a tropical-temperate transitional forest in El Cielo Biosphere Reserve, northeastern Mexico

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1. INTRODUCTION

Mountains are ideal environments for the study of species distributions (Körner, 2007), because they allow the exploration of environmental preferences of organisms at relatively short spatial scales. Montane habitats harbor extraordinary species richness: 87% of the world's amphibians, birds, and mammals, up to 40% of which are endemic (Rahbek et al., 2019) and at least one-third of terrestrial plants (Barthlott et al., 1996) are found across only 25% of the Earth's mountain land mass (Rahbek et al., 2019). Mountains in transition zones are of particular interest, because they can act as routes that allow biotas of different origin to disperse (Ferro & Morrone, 2014; Morrone, 2020). Such is the case of the Mexican Transition Zone (MTZ), where biotas of different origin overlap (Halffter, 1987).

Models used to explain the composition of the MTZ mountain biota are horizontal colonization, by lineages inhabiting higher elevations, and vertical colonization by lineages from surrounding lowlands (Lobo & Halffter, 2000; Escobar et al., 2007). When vertical colonization dominates, a sharp decrease in species richness with elevation is predicted. When horizontal colonization prevails, a replacement of tropical lowland lineages by temperate highland lineages will take place (Lobo & Halffter, 2000; Halffter & Morrone, 2017; Joaqui et al., 2021). Mid-elevation peak patterns, or hump-shaped patterns, have been also documented for leaf litter ants in the MTZ (Pérez-Toledo et al., 2021) and across the Mesoamerican area (Longino & Branstetter, 2019). Ant diversity changes across elevational gradients throughout Mexico and Central America are remarkably constant: an increase in species richness peaking at 400 m, followed by an exponential decrease (Longino & Branstetter, 2019). Both scenarios (i.e., richness decrease and a mid-elevation richness peak) are common patterns along elevational gradients (McCain, 2009). Only in rare instances, species richness increases with elevation (McCain, 2009; Maioglio et al., 2022), like Mesoamerican salamanders (Rovito et al., 2013).

An underrepresented group in MTZ studies has been the weevils (Coleoptera: Curculionidae), despite being an abundant family with over 3,000 described species in the country (Morrone, 2014) and at least 51,000 estimated worldwide (Oberprieler et al., 2007). Leaf litter weevils are of particular interest because play a huge role in litter decomposition (Anderson & Ashe, 2002). Most weevil species are undescribed and appear to have high rates of worldwide diversity and endemism (Jones et al., 2008, 2022). Curculionidae inhabiting tropical forests are among the most numerically dominant taxa in the leaf litter community (Anderson & Ashe, 2000; Maioglio et al., 2022). Such is the case for members of Cryptorhynchini, a weevil clade with many leaf litter representatives whose global diversity may well be above 15,000 undescribed species (Riedel et al., 2016; Letsch et al., 2020), with the bulk of their described species (>6,000) being Neotropical (Riedel et al., 2016). Despite their diversity, Cryptorhynchini and other leaf litter weevil groups are still poorly understood, remaining underrepresented in studies from the Neotropics (Anderson & Ashe, 2000; Jones et al., 2008, 2022; Maioglio et al., 2022) and other tropical regions of the world (Riedel et al., 2016; Letsch et al., 2020). However, leaf litter sampling has well-defined sample units based on litter area or volume (Jones et al., 2022), making the sampling of this habitat reproducible and easily standardized (Maioglio et al., 2022). Additionally, robust quantitative analysis can be made using leaf litter weevil morphospecies as study model, due to their high frequency and low mobility, allowing for enough data to be collected (Maioglio et al., 2022). The morphospecies approach (grouping of specimens into morphologically uniform taxa based on external characters) has been used in the past by authors studying leaf litter weevil diversity (Maioglio et al., 2022). Because many litter weevils remain undescribed species (Maioglio et al., 2022) a traditional classification into species would require a lengthy preliminary descriptive work (Jones et al., 2008; 2022; Maioglio et al., 2022).

Here, we studied the patterns of leaf litter weevil richness and composition along an elevational gradient in one of the northernmost tropical-temperate transitional forests in the Americas. Based on Lobo & Halffter's (2000) mountain colonization processes, we hypothesize a decrease in species richness with increasing elevation. We expect to find diversity patterns driven by differences in species replacement and species gains and losses, as well as driven by environmental factors that determine species richness along elevational gradients (i.e. temperature and humidity) (Pérez-Toledo et al., 2021) and habitat variables that shape litter composition (i.e. forest structure, litter depth and litter humidity) (Maioglio et al., 2022). We aim: (a) to determine the diversity and community composition of leaf litter weevils in a tropical-temperate transitional forest in northeastern Mexico and (b) to assess the environmental factors shaping the leaf litter weevil assemblage along an elevational gradient.

2. METHODS

2.1. Study area

El Cielo Biosphere Reserve is located in the Sierra Madre Oriental biogeographic province (Morrone, 2020), in northeastern Mexico (23.25N, -99.833W). It is part of the MTZ, covering an area of 1,445.3 km^2, with a maximum elevation of 2,320 m a.s.l (Sánchez-Ramos et al., 2005) (Figure S1). Vegetation includes deciduous and semideciduous tropical forests at 150-800 m, cloud forests at 800-1,500 m, oak-pine forests at 1,200-1,900 m and pine forests at 1,800-2,200 m (González-Medrano, 2005).

2.2. Study design

Two elevational transects were established in 2019 and 2020 (hereafter transect one and transect two) in the municipalities of Gómez Farías and Jaumave, Tamaulipas, Mexico. Both transects were oriented in an east-west direction (transect one from 23.036889N, -99.131611W to 23.041389N, -99.267139W, while transect two from 23.098444N, -99.158806W to 23.185056N, -99.245333W). Leaf litter samples were collected from July 8 to October 21, 2019 (transect one), and from September 29 to October 31, 2020 (transect two), from 200 to 2,000 m a.s.l. within the reserve. Samples were taken at 10 successive elevations corresponding to 200 m of elevation from 200 to 2,000 m, the distance between elevations depended on the terrain steepness. At each elevation we sampled two plots of 20 m^2, in which 1 m^2 leaf litter samples were taken at 5 m intervals, for a total of 25 samples per plot, accounting for 50 samples per elevation level and 500 samples per transect. In total, 1,000 samples were collected. Due to time constraints, 300 samples representative of the entire sampling protocol were processed. All organic debris (i.e., leaves, twigs, fungi, and wood debris) down to, but excluding the soil, were processed using Winkler extraction sieving. After sieving the litter of each 1 m^2, it was hung in mini-Winkler traps and left to dry for at least three days. The 98% alcohol saturated flasks with the insects were labelled with date and collection site and brought to the laboratory. Adult weevils were separated into morphospecies by visual inspection using a 45x stereoscopic microscope (AmScope®, T1A). At least one weevil specimen per morphospecies per plot was mounted and labelled. The remaining weevils were stored in freezers in absolute ethanol in 2 ml microtubes, sorted in Zip-Lock® bags by morphospecies, sample, plot and transect. Weevils were identified using descriptions and taxonomic keys (Morrone, 2000; Anderson, 2002) or by M. Barrios-Izás, R. W. Jones, L. Chamorro, B. Anderson, J. J. Morrone, F. Armendariz and L. Kirkendall.

The following environmental variables were recorded for each plot: elevation, temperature, relative humidity, tree abundance and species richness, median tree diameter at breast height (median DBH), leaf litter depth and leaf litter humidity. Temperature and relative humidity were recorded by a Kestrel® 4000 weather meter at the time each 20 m^2 plot was sampled. Litter depth was measured with a millimetric ruler and litter humidity was classified into five categories (0 = dry, 1 = barely moist, 2 = moist, 3 = very moist, 4 = wet) according to Jones et al. (2008). As a proxy to evaluate vegetation affinity effects, the relative abundance of two genera of boreal trees (*Pinus* and *Quercus*) and one tropical tree (*Ternstroemia*) were estimated. For the analyses we also included WorldClim's 19 'BIO' current climate variables (Fick & Hijmans, 2017).

Weevils not considered by M. Barrios-Izás, R. W. Jones, F. Armendariz and L. Kirkendall as part of leaf litter fauna, but occasionally present in leaf litter samples, were excluded from the analyses to avoid overestimating richness. Species not normally associated with the habitat sampled are called "tourists" (Jones et al., 2008). In our case, tourist litter weevils were winged, macrophthalmic and colorful specimens (Anderson & Ashe, 2002; Maioglio et al., 2022), belonging to subfamilies Baridinae, Curculioninae and Conoderinae. Despite being winged, *Conotrachelus* was included in the analysis, because previous leaf litter weevil studies have included the genus (Jones et al., 2008; 2022). Bark beetles (Scolytinae) were also excluded from the analysis because most species do not reproduce in leaf litter (F. Armendariz & L. Kirkendall, per. com.).

2.3. Statistical analyses

2.3.1. Weevil diversity and community composition

To assess the inventory completeness, we calculated sample coverage (Chao & Jost, 2012) and species richness estimators Chao 2 and first-order Jackknife (Jack 1), because they have shown good performance with arthropod data (Jones et al., 2012). An abundance matrix was constructed by pooling morphospecies abundances of each of the 10 elevational floors. Site sample coverage ranged from 0.922 (200 m plot) to 0.994 (1800 m). Because the minimum sample coverage was above 0.9 (0.922 in 200 m plot), richness was not standardized for later analyses. All sample coverage calculations were performed in R statistical software v.4.1.0 (R Core Team, 2019) with the *iNEXT* v.2.0.20 package (Hsieh et al., 2016). Richness estimators were calculated with the package *vegan* v.2.5.7 (Oksanen et al., 2020).

To assess the elevation and richness relationship for litter weevils we used linear, quadratic, cubic, exponential, and null models and compared those that fitted the data best (Joaqui et al., 2021). As a response variable, richness per plot per transect was used (n=20). The model with the smallest Akaike Information Criterion for small samples (ΔAICc) was chosen as the best fit (Richards, 2015). Variation explained by the model was obtained with the *model.avg* function of the R package *MuMIn* v.1.43.17 (Barton, 2020). To plot litter weevil richness along the elevational gradient, we used the R package *ggplot2* v.3.3.5 (Wickham, 2016).

The variation of β-diversity in species composition along the elevational gradient was evaluated following Baselga's dissimilarity measures for multiple site incidence-based (Baselga, 2010; Baselga & Orme, 2012) and abundance-based (Baselga, 2017). Multiple site beta diversity offers information on the spatial heterogeneity of community assemblages (Baselga & Orme, 2012) and can be partitioned into multiple site turnover and multiple site nestedness. To analyze whether leaf litter weevil community heterogeneity was dissimilar among transects, we simulated 1,000 multiple site β-diversity values from one randomly chosen half of all elevational floors (n=5). We used both incidence and abundance-based data: for incidence data we chose the Jaccard and Sørensen indices, and for abundance-based data we chose the Bray-Curtis index. Based on the Bray-Curtis index we computed turnover with balanced variation and nestedness with abundance gradient measurements (Baselga, 2017). We compared the resulting distributions for each transect with the package *mded* (Aizaki, 2014), which allows the quantification of the difference between two empirical distributions (Poe et al., 1997, 2005). Additionally, we evaluated the elevational β-diversity among elevation floors of leaf litter weevil species using all three indices. Total dissimilarity, turnover and nestedness were computed through pairwise comparisons between all ten elevational floors and plotted with heat maps representing β-diversity between elevations. The β-diversity calculations were made with the *betapart* package v.1.5.4 (Baselga & Orme, 2012) in the R statistical software v.4.1.0 (R Core Team, 2019).

2.3.2 Environmental factors shaping weevil assemblage

We carried out Generalized Linear Models (GLMs) using environmental variables as explanatory variables, and leaf litter weevil richness and mean total dissimilarity (mean βsør) as response variables for the elevational sites of transects one and two (n=20). Mean βsør was determined as the average pairwise βsør dissimilarity values for each elevational floor per transect. Only the effect of simple and two-way interactions between explanatory variables were examined. Environmental variables included WorldClim's 19 'BIO' current climate variables (see Fick & Hijmans, 2017), variables measured in the plots (elevation, temperature, relative humidity, leaf litter depth, leaf litter humidity, tree species richness, tree abundance and median DBH) and the relative abundance of *Pinus, Quercus* and *Ternstroemia* per plot. All environmental variables were tested for multicollinearity with the *chart.Correlation* function in the R package *PerformanceAnalytics* v.2.0.4 (Peterson & Carl, 2020). Only those with a Spearman correlation coefficient $P > 0.05$ and a VIF < 1.5 (Zuur et al., 2009) were chosen. Selected variables were elevation, litter depth, median DBH, tree richness and WorldClim 'BIO15' (precipitation seasonality). Explanatory variables were standardized by subtracting the mean and dividing by one standard deviation, but because standardized and non-standardized models had a non-significant difference (χ^2=-4.969, df = 5, P=0.419), analyses were run with non-standardized explanatory variables. The minimum model was selected using stepwise backwards model simplification (Crawley, 2013). We assumed a Poisson distribution error for species richness and Binomial distribution for mean total dissimilarity.

To further disentangle the effect of environmental variables (elevation, litter depth, median DBH, tree richness per plot, precipitation seasonality) on the litter weevil community, we carried out ordination analyses. Because we wanted to test vegetation affinity effects, we included the proportion of *Pinus*, *Quercus* and *Ternstroemia*. We did not characterize the habitat in terms of tree distribution in the space or tree age structure, because not being the main objective of the work we deemed it sufficient to measure tree size (median DBH) and dominant tree species (relative proportion of *Pinus*, *Quercus,* and *Ternstroemia*).We performed a Detrended Correspondence Analysis (DCA) to estimate the gradient lengths of the axes in SD units to choose between linear (Redundancy Analysis, RDA) or unimodal (Canonical Correspondence Analysis, CCA) unconstrained ordination methods (Lepš & Šmilauer, 2014). The length of the first DCA axis was 4.559 SD units, indicating a heterogenous dataset on which unimodal unconstrained ordination methods (CCA) should be used (Lepš & Šmilauer, 2014). Before running the CCA, rare species (singletons and doubletons) were removed from the dataset (Borcard et al., 2018). Forward selection ($P < 0.05$, 999 permutations) was used to test for the significance of each explanatory variable. We used variation partitioning to assess the relative contribution to the explained variance of each significant environmental predictor. Ordination analyses were carried out with the *vegan* package v.2.5.7 (Oksanen et al., 2020), with functions *decorana* and *cca* for DCA and CCA, respectively.

3. RESULTS

3.1. Weevil diversity and community composition

In total 4,004 leaf litter weevils were recovered from 291 samples of 1 m^2 from El Cielo Biosphere Reserve. The remaining nine samples did not have any Curculionidae. Leaf litter weevils were sorted into 55 morphospecies, representing 26 genera. Only six morphospecies could be assigned to species level despite thorough revisions by expert taxonomists (Table S1). At least seven morphospecies represent undescribed taxa (Table S1). An undescribed *Eurhoptus* species (*Eurhotpus* sp. 1) had the most individuals (1,113), followed by *Trachyphloeomimus mexicanus* (760 individuals) and *Dioptrophorus* sp. 1 (378 individuals). There were eight singletons and five doubletons (Table S1). The most abundant subfamily was Molytinae with 3,235 individuals (79%, 50 morphospecies), followed by Entiminae with 762 individuals (19%, three species), Brachycerinae with 14 individuals (0.3%, one species) and Cossoninae with seven individuals (0.2%, two species). Non-leaf litter weevils (tourist species) collectively had 98 individuals and 25 morphospecies. Tourist species belonged to Baridinae, Conoderinae, Curculioninae, and Scolytinae. Here we treated Cryptorhynchini as a tribe of Molytinae (Lyal, 2014).

Total weevil richness and density per 1 m^2 of leaf litter averaged 3.63 ± 3.02 (X ± SE) species and 13.76 ± 16.38 individuals, respectively. Our number of morphospecies collected (55) was 75-82% of the predicted richness calculated by Chao 2 (73 ± 28) and Jackknife 1 (67 ± 7) estimators. The number of expected species increased at a rate similar to the actual randomized species accumulation curve (Figure S2). The relationship between richness and elevation was better explained by a quadratic model (Table S2), showing a mid-peak pattern around 1,600 m (Figure 1). Abundance showed a similar trend (Figure 1). Most of the 26 genera were present above 1,000 m (Figure 2).

Leaf litter weevil species dissimilarity was high along El Cielo elevational gradient (mean βsør = 0.78), with turnover having a greater contribution ($\beta_{SIM} = 0.59$) than nestedness ($\beta_{SNE} = 0.19$). Community heterogeneity across the gradient did not change significantly between transects, as shown by the multiple sites' abundance-based β-diversity curves ($P>0.05$, Figure 3). Jaccard, Sørensen and Bray-Curtis dissimilarity indices showed greater values as differences in elevation increased (Figure 4). Incidence-based indices (Jaccard and Sørensen) and the abundance-based index (Bray-Curtis) lead to the same pattern. Turnover explained more dissimilarity than nestedness (Figure 4).

3.2. Environmental factors shaping weevil assemblage

The best fit GLM for weevil richness included five environmental variables and five interactions (Table 1). Elevation and the interaction between median DBH and precipitation seasonality explained over 80% of species richness variation. Elevation and weevil richness are positively correlated. When explaining dissimilarity (mean βsør), the best fit was the null model, meaning that none of the chosen environmental predictors explained any significant dissimilarity variation.

Canonical correspondence analysis explained over 30% variance in the composition of the litter weevil community (adjusted $R^2 = 0.321$) (Figure 5) with respect to environmental variables. The efficiency of the variability possible to explain by any predictors in the CCA was up to 58% for the first canonical axis and 38% for the second. Significant explanatory variables were elevation, median DBH and *Quercus* proportion (Table 2), which accounted for 25.7% of all variation in weevil communities across the elevational gradient. The variables litter depth, tree richness per plot, precipitation seasonality, the proportion of *Pinus* and the proportion of *Ternstroemia* lacked statistical support ($P > 0.05$). In general, the first canonical axis corresponded to the elevational gradient, as the highest elevation plots (1,800 – 2,000 m) were separated from the other elevation sites; some species of *Tylodinus*, *Theognete*, *Trachyphloeomimus* and *Epibaenus* were associated with these high-elevation sites. Axis two also separated mostly low-elevation plots (200 – 800 m) from high-elevation ones, and several species of genera *Eurhoptus* and *Conotrachelus* were associated with these sites (Figure 5). Many weevils were associated with deeper leaf litter and a diverse tree community (high tree richness) at lower elevations, with smaller trees (low median DBH). One *Trachyphloeomimus*, one *Tylodinus* and one Cryptorhynchini were associated with vegetation dominated by *Quercus*.

4. DISCUSSION

Leaf litter weevil studies for the Neotropics are scarce (Anderson & Ashe, 2000; Jones et al., 2008, 2022; Maioglio et al., 2022), and only two so far evaluated ground-dwelling Curculionidae diversity pattern along an elevational gradient (Olson, 1994; Maioglio et al., 2022). No previous study examined the elevation distribution pattern of leaf litter weevils in a northern tropical-temperate transitional forest of the MTZ. Genera with broad elevation ranges in our study (*Eurhoptus* and other Cryptorhynchini, *Dioptrophorus*, *Trachyphloeomimus*, *Tylodinus*, and *Theognete*) (Figure 2) were also predominant in other studies of Mexican fauna (Jones et al., 2022). Molytinae (including Cryptorhynchini) was the subfamily with the highest species number in El Cielo, Tamaulipas (79%, 50 morphospecies), as it was in Cerro Huitepec, Chiapas (87.7%, 50 morphospecies) (Jones et al., 2008). Molytinae also dominated in the tropical montane cloud forest of Otonga Reserve, Ecuador (Maioglio et al., 2022), but the most represented tribe was Anchonini, not Cryptorhynchini (Maioglio et al., 2022). A further comparison with the Ecuadorian litter weevil diversity showed that El Cielo had a higher specimen density (five specimens per 1 m^2 in Otonga, Ecuador vs. 13 specimens per 1 m^2 in El Cielo, Mexico) but only half its richness (100 species of 24 genera in Otonga, Ecuador vs. 55 species of 26 genera in El Cielo, Mexico).

Our results show a mid-peak increase in species richness along the elevational gradient. This is because our maximum species diversity (33 ± 3.412 95% CI) at 1,600 m is over 25% more (McCain, 2009) than the species richness at the base (7 ± 2.605, 200 m) and top (22 ± 3.183, 2000 m) of our elevational gradient. Even though the elevational variation of El Cielo weevil community does not follow a monotonical increase, like those of salamanders in Mexico (Rovito et al., 2013), it shows an opposite trend to most of other Mesoamerican insects, where species richness decreases as elevation increases (Longino & Branstetter, 2019; Joaqui et al., 2021). In a recent study (Maioglio et al., 2022), leaf litter weevils in tropical forests in Otongachi and Otonga in Ecuador had more species as elevation increased. Ecuadorian litter weevils had a more marked richness increase from 1,800 m and above, in a gradient spanning from 800 – 2,300 m (Maioglio et al., 2022); it is important to mention that the gradient was incomplete, lacking samples at intermediate elevations (1,100 – 1,700 m) (Maioglio et al., 2022). In our study, the highest richness was found at 1,600 m (Figure 1), while in a previous study in Panama (Olson, 1994) it was reported that ground-dwelling Curculionidae peaked at 1750 m. Olson (1994), however, reported a high elevational variation throughout the gradient (250 – 2,000 m). Like our study, Olson (1994) found a higher abundance of Curculionidae at higher elevations. Olson (1994) did not attempt to explain the elevation trend for weevils but argued that for Carabidae collected in the same samples, a more uniform distribution was found in upper montane forests due to uniform moisture conditions and a lack of prey, favoring generalist species. Although leaf litter weevil diet is unknown, it has been suggested that they may eat dead plant material (Jones et al., 2008) or fungus-infested plant debris (Luna-Cozar et al., 2014; Anderson & Caterino, 2018), decaying organic matter and small branches and roots (Maioglio et al., 2022), but until future works test it out, the effect of diet on the richness-elevation relationship will remain uncertain.

El Cielo Biosphere Reserve reaches a maximum elevation of 2,320 m a.s.l. (Sánchez-Ramos et al., 2005), with the majority of the highest parts located between 1,900-2,050 m. We found leaf litter weevils up to 2,000 m in El Cielo. In central and southern Mexico, the same genera community composition (but with different species) was found in study sites of 2,230-2,710 m (Pinal de Amoles, San Joaquín and Amealco, Querétaro, Jones et al., 2022) and 2,393-2,512 m (Cerro Huitepec Biosphere Reserve, Chiapas, Jones et al., 2008), respectively. Having the same weevil genera assemblages from north to south of the MTZ increases the chances of their ancestors dispersing from a tropical area of origin. Therefore, the vertical colonization model best fits our results rather than horizontal colonization.

A dung beetle study in the MTZ performed on the highest Mexican mountain (5,600 m, Joaqui et al., 2021), found a mid-plateau pattern with a decrease of species richness as elevation increased: the highest dung beetle richness was below 1,000 m. In our study, weevil richness peaked at 1,600 m. Because El Cielo does not have the same elevation as other mountains in the MTZ, it is possible to consider our study site as a truncated gradient; however, gradient truncation occurs when only a portion of the mountain is sampled (McCain & Grytnes, 2010). In our study, we covered the entirety of El Cielo elevational gradient. Additionally, our gradient ends in the forest, while other mountains end in alpine shrubs and herbs. Similarly, the Otonga elevational gradient in Ecuador is comprised of primary forest, and its leaf litter weevil fauna also increased with elevation, peaking at their highest sampling plot (32 species at 2,238 m). Sam et al. (2020) argued that above 2,200 m a.s.l. insect diversity and abundance decline due to low temperatures. In our study, this limiting factor is never reached since in El Cielo does not have an alpine zone and most of the forest habitat reaches elevations of around 2,000 m. El Cielo is the northernmost Biosphere Reserve located in the MTZ (Morrone, 2020). This Mexican Sierra is not further connected up north, therefore colonization from southern species is more likely.

The spatial structure of leaf litter weevil assemblages did not change between transects, as shown by an overlap in the distributions of multiple sites abundance-based β-diversity of transects one and two (Figure 3). The litter weevil communities across the two transects are not taxonomically dissimilar (MβD Bray *P*=0.69), nor do they have significant differences in turnover (MβD Bray balanced variation *P*=0.626) or nestedness (MβD Bray abundance gradient *P*=0.451) rates. However, when taking El Cielo as a single elevational gradient, dissimilarity was high (0.78), with turnover being predominant over nestedness, which indicates almost no weevil species and even genera were shared between the base and the top of the mountain (Figure 4). The community structure in the lowlands (>1,000 m) and highlands (<1,000 m) are unique (they are not subsets of each other); therefore, even though the highest taxonomical richness (α-diversity) was at 1,600 m (Figure 1), the whole gradient should be included for an adequate understanding of the leaf litter weevil diversity of the region.

Njovu et al. (2021) found that for phytophagous weevils along an elevational gradient in Mt. Kilimanjaro, current climate variables were the best predictors driving an increase in richness and abundance with elevation. We only included precipitation seasonality as a climate predictor, because all other current climate variables (Fick & Hijmans, 2017), as well as vegetation variables (i.e. leaf litter humidity, proportion of *Pinus*, *Quercus* and *Ternstroemia*), were colinear with a VIF > 1.5 + Spearman correlation coefficient $P > 0.05$ Nevertheless, comparisons between El Cielo litter weevils and Mt. Kilimanjaro phytophagous weevils can be only partial as the African gradient is considerably longer (866 – 4,550 m), with richness and abundance peaking above 3,000 m. González-Megías et al. (2008) reported that beetle litter communities between 2,000 and 3,000 m in Sierra Nevada National Park, Spain, had over 50% of their diversity explained by plant diversity and shrub cover. In our study, tree diversity explained only 0.2% of weevil diversity, while the interaction between tree size (measured as DBH) and precipitation seasonality explained up to 20.7% of weevil richness across the gradient (Table 1). Over 50% of the beetles sampled by González-Megías et al. (2008) were leaf beetles (Coleoptera: Chrysomelidae), which probably explains why plant diversity and shrub cover were important factors in their study. Furthermore, weevils sampled in Sierra Nevada National Park belonged to different subfamilies (ej. Cyclominae, Conoderinae) (González-Megías et al., 2008) than the dominant one in the leaf litter of El Cielo (Molytinae). For the weevils sampled in the Otonga Reserve, Ecuador, most were Molytinae (Maioglio et al., 2022) and microhabitat characteristics (i.e. presence of decaying wood, moss, litter humidity and canopy coverage) were non-significant when analyzed together with elevation (Maioglio et al., 2022).

According to the CCA analysis, neither tree diversity nor precipitation seasonality was significant in explaining the variance given by environmental predictors in weevil community composition. Elevation, relative abundance of *Quercus* and tree size (measured as median DBH) were the main factors affecting leaf litter weevil abundance and distribution (Table 2). Surprisingly, leaf litter depth had no significant effect on weevil species richness (GLM, Table 1) nor weevil abundance (CCA, Table 2). A previous study assessing ant community composition on slopes of Mt. Wilhelm, Papua New Guinea, has shown that deeper leaf litter has a negative effect on ant abundance and ant richness above 700 m, but is positively correlated with species richness below 700 m (Moses et al., 2021). For the weevils sampled in the Otonga Reserve, Ecuador, most were Molytinae (Maioglio et al., 2022) and microhabitat characteristics (i.e. presence of decaying wood, moss, litter humidity and canopy coverage) were non-significant when analyzed together with elevation (Maioglio et al., 2022). In our study, CCA axes mostly separated weevil species by elevation, highlighting elevation as being more important than tree proportion or tree size (Table 2) when determining the diversity pattern of these taxa. In comparison, Jones et al. (2008) concluded that the spatial distribution patterns of leaf litter weevils in tropical montane forests in southern Mexico, are given by vegetation composition, seasonality, habitat type, and dispersion indices. Wingless weevils such as *Eurhoptus* and other low-dispersing genera, like *Tylodinus*, *Anchonus* and *Theognete*, were associated to moist primary forests without herbaceous vegetation. Winged leaf litter weevils like *Conotrachelus* were more common in early successional forests, and species of Entiminae (*Trachyphloeomimus*) were found in herbaceous vegetation and bushes. Finally, species of *Anchonus* (Molytinae) were the only ones found during the wet season (Jones et al., 2008).

Leaf litter weevil richness decreased as tree size (measured as DBH) increased. It is known that litter Curculionidae thrives in tropical montane cloud forests (Anderson & Ashe, 2002; Jones et al., 2008), which include trees of reduced stature (Webster, 1995) in comparison with lowland tropical forests. The positive association with El Cielo litter weevils with slim trees, is possibly a consequence of the association with the tropical montane cloud forest present at the site in elevations above 1,200 m. Cloud forests are known to be less seasonally variable than other montane forests (Jarvis & Mulligan, 2011), which is reflected in the association we found between weevil richness and low precipitation seasonality. Leaf litter composition of cloud forests could have more readily available food resources for weevils, which would explain their higher diversity rates in this ecosystem, but further studies are needed to understand the dietary habits of these insects. Furthermore, now that we have probably found an association between leaf litter weevil communities and tropical montane cloud forests, future works could perform a finer habitat characterization to strengthen or challenge this hypothesis.

Since Curculionidae are largely understudied and lack species and genus-level phylogenies for most Nearctic and Neotropical lineages, we could not infer the origin of El Cielo species by an appropriate historical biogeographic analysis, which would consist in sorting the Neotropical taxa into at least three different cenocrons: Mexican Plateau, Mountain Mesoamerican and Typical Neotropical (Halffter & Morrone, 2017; Morrone, 2020). It has been argued that typical leaf litter genera have distributions well fitted within the Mountain Mesoamerican cenocron (Halffter & Morrone, 2017), because they occur in tropical montane habitats with high diversity in southern Mexico and Central America (Jones et al., 2022). Even though no formal definition of the Typical Neotropical and Mountain Mesoamerican litter weevil lineages has been presented for the MTZ; in El Cielo, Mountain Mesoamerican weevils might be predominant over Typical Neotropical ones, explaining the increasing richness pattern along the gradient. Before any conclusion is reached regarding this topic, phylogenetic analyses and dating of the lineages are critically needed to infer the biogeographical origin.

In summary, contrary to our expectations but in line with previous works (Olson, 1994; Anderson & Ashe, 2002; Maioglio et al., 2022), weevil species richness increased with elevation, peaking at 1,600 m. The elevational variation of the community was best explained by a mid-peak pattern, as the maximum species richness was found above 300 m and at its peak was more than 25% that found at the base and top of the elevational gradient. The most important environmental predictor of community structure was an interaction between tree size and precipitation seasonality, which probably reflects a positive association between weevils and tropical montane cloud forest habitats. As leaf litter weevils are highly diverse and with high turnover rates they can serve as important bioindicators in conservation planning, providing information about changes in the condition of tropical forests due to fragmentation and degradation. Further phylogenetic work is needed to reconstruct the origin of American tropical leaf litter weevils, as well as to analyze their diet, in order to determine how these factors influence their elevational distribution.

TABLES

Table 1. Effects predicted by the simplest generalized linear model in leaf litter richness.

Model McFadden pseudo-R^2 = 0.874.

Source	**McFadden pseudo-R^2**	***P***
Elevation	0.602	0.003
Leaf litter depth	0.029	0.012
Precipitation seasonality (BIO15)	0.009	0.091
Tree richness	0.009	0.004
DBH (median)	0.003	0.003
DBH x BIO15	0.209	0.003
DBH x tree richness	0.03	0.003
Leaf litter depth x BIO15	0.003	0.014
Leaf litter depth x DBH	0.001	0.005
Elevation x DBH	0.002	0.008

Table 2. Results of most parsimonious canonical correspondence analysis (CCA) on the significant explanatory variables (forward-selected at $P<0.05$ with 999 permutations) of all plots explaining weevil species composition across El Cielo elevational gradient. The explanatory variables shown accounted for 25.7% of total adjusted variance.

Explanatory factor	**% of all variation (R^2 adj)**	**pseudo-F**	***P***
Elevation	11.7	4.3255	0.001
Quercus proportion	9.8	3.5872	0.001
DBH (median)	4.2	2.0222	0.023

Table S1. Leaf litter weevil species found across an elevational gradient in El Cielo Biosphere Reserve, Tamaulipas, Mexico.

Taxa	**200**	**400**	**600**	**800**	**1000**	**1200**	**1400**	**1600**	**1800**	**2000**	**Total abundance**
COSSONINAE											
Cossonini											
Cossonus sp. 1	0	0	0	0	0	0	0	0	6	0	6
Heptarthrum sp. 1	0	0	0	0	0	0	0	1	0	0	1
ENTIMINAE											
Anypotactini											
Polydacrys sp. 1	0	0	0	0	0	0	1	0	0	0	1
Geonemini											
Claeoteges granulosa	0	0	0	0	1	0	0	0	0	0	1
Trachyphloeini											
Trachyphloeomimus mexicanus	0	0	0	0	22	99	111	35	134	359	760
MOLYTINAE											
Anchonini											
Anchonus sp. 1	0	0	1	0	18	13	13	37	8	6	96
Anchonus sp. 2	0	0	0	0	2	0	0	4	2	0	8
Anchonus sp. 3	0	0	0	0	22	12	23	11	3	1	72
Anchonus sp. 4	0	0	0	0	3	0	0	0	1	0	4
Conotrachelini											

Aeatus ebeninus	0	0	1	0	4	0	0	0	0	0	5
Genus nov. 1 sp. nov. 1	0	0	0	0	0	0	12	29	16	4	61
Conotrachelus sp. 1	0	1	0	0	11	3	6	8	4	10	43
Conotrachelus sp. 2	0	1	3	0	5	0	0	0	0	0	9
Conotrachelus sp. 3	0	4	1	0	0	1	0	0	0	0	6
Enomides sp. 1	0	0	0	0	0	0	0	1	0	1	2
Lepilius sp. 1	0	0	0	0	0	1	1	5	21	5	33
Microhyus sp. 1	0	0	0	0	0	0	0	1	0	0	1
Microhyus sp. 2	0	0	0	0	0	0	0	1	0	0	1
Microhyus sp. 3	0	0	0	0	0	0	0	0	1	0	1
Cryptorhynchini											
Acalles sp. 1	0	0	0	0	0	0	0	1	0	0	1
Acalles sp. 2	0	0	0	0	0	1	2	2	0	0	5
Acalles sp. 3	0	0	0	0	0	0	2	2	0	0	4
Acalles sp. 4	0	0	0	0	0	1	1	3	8	2	15
Canistes sp. 1	0	3	5	0	2	0	0	0	0	0	10
Genus nov. 1 sp. nov. 1	0	0	0	0	18	41	50	71	62	25	267
Genus nov. 2 sp. nov. 1	0	0	1	0	1	0	0	15	47	99	163
Genus nov. 3 sp.	0	1	3	0	4	0	0	0	0	0	8

nov. 1											
Genus nov. 3 sp. nov. 2	1	9	4	0	0	0	0	0	0	0	14
Genus nov. 3 sp. nov. 3	1	3	1	2	3	0	0	0	0	0	10
Genus nov. 3 sp. nov. 4	0	0	1	0	1	0	0	0	0	0	2
Genus nov. 4 sp. nov. 1	20	18	35	3	3	0	0	0	0	0	79
Genus nov. 4 sp. nov. 2	1	0	0	0	0	0	0	0	0	0	1
Cryptorhynchus sp. 1	0	0	0	0	0	0	2	0	0	0	2
Eurhoptus sp. 1	0	0	0	0	49	48	273	402	147	194	1113
Eurhoptus sp. 2	0	0	0	0	0	0	0	4	6	4	14
Eurhoptus sp. 3	10	7	55	12	40	4	22	107	65	18	340
Eurhoptus sp. 4	1	3	12	3	32	10	3	2	0	0	66
Eurhoptus sp. 5	0	0	1	1	2	0	0	0	0	0	4
Eurhoptus sp. 6	0	0	0	0	0	0	0	0	1	1	2
Eurhoptus sp. 7	0	0	0	0	0	0	2	2	1	7	12
Tylodinus sp. 1	0	0	0	0	2	0	10	22	3	6	43
Tylodinus sp. 2	0	0	0	0	0	0	0	2	0	1	3
Tylodinus sp. 3	0	0	0	0	0	0	1	1	4	0	6
Tylodinus sp. 4	0	0	0	0	0	0	2	1	0	2	5
Tylodinus sp. 5	0	0	0	0	0	0	0	3	1	2	6

Ulosomimus sp. 1	0	0	0	2	0	0	0	0	0	0	2
Lymantini											
Dioptrophorus sp. 1	0	0	0	0	39	89	14	124	75	37	378
Epibaenus exaratus	0	0	0	0	0	0	0	3	0	0	3
Epibaenus sp. 1	4	4	2	0	10	2	2	0	0	0	24
Genus nov. 1 sp. nov. 1	0	0	0	0	0	0	1	6	0	0	7
Theognete echinata	0	0	0	0	0	1	2	22	165	30	220
Theognete sp. 1	0	0	0	0	0	0	0	6	0	0	6
Theognete sp. 2	0	0	0	0	0	0	0	0	7	0	7
Theognete sp. 3	0	0	0	0	0	0	1	0	2	0	3
Theognete striatifemur	0	0	0	0	4	12	0	32	0	0	48

Table S2. Regression models for leaf litter weevil species richness using all sampled plots (n = 20), along the elevational gradient of El Cielo Biosphere Reserve. Null, linear, exponential, quadratic and cubic models were tested against each other. The chosen model had the lowest ΔAICc value and a normal distribution of residuals (Shapiro–Wilk test, $P > 0.05$). ωAIC indicates the relative weight of each model.

		Coefficients					
Model	**Intercept**	**Linear**	**Quadratic**	**Cubic**	**ΔAICc**	**ωAIC**	***P*-Shapiro**
Quadratic	0.8322	0.0024	-6.46×10^{-9}		0	0.61	0.5046
Cubic	1.4679	-4.47×10^{-5}	1.72×10^{-6}	-6.75×10^{-10}	1.24	0.33	0.2735
Linear	1.5985	0.0008			4.76	0.06	0.3929
Exponential	2.0455		2.95×10^{-7}		14.27	0	0.5464
Null	2.5764				53.96	0	0.851

FIGURES

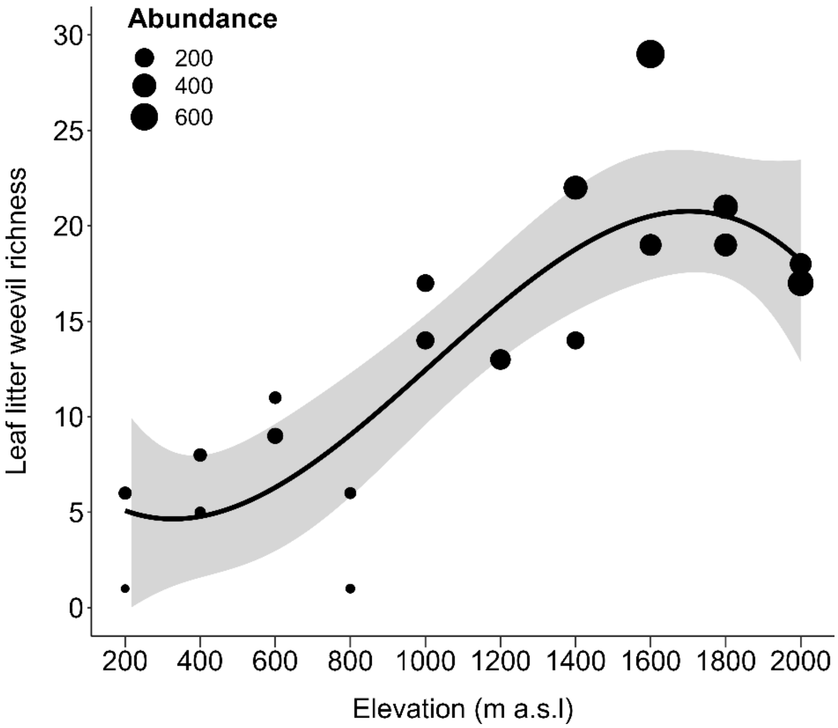

FIGURE 1. Leaf litter weevil observed richness given elevation with a fitted quadratic model, notice the highest richness at 1,600 m.

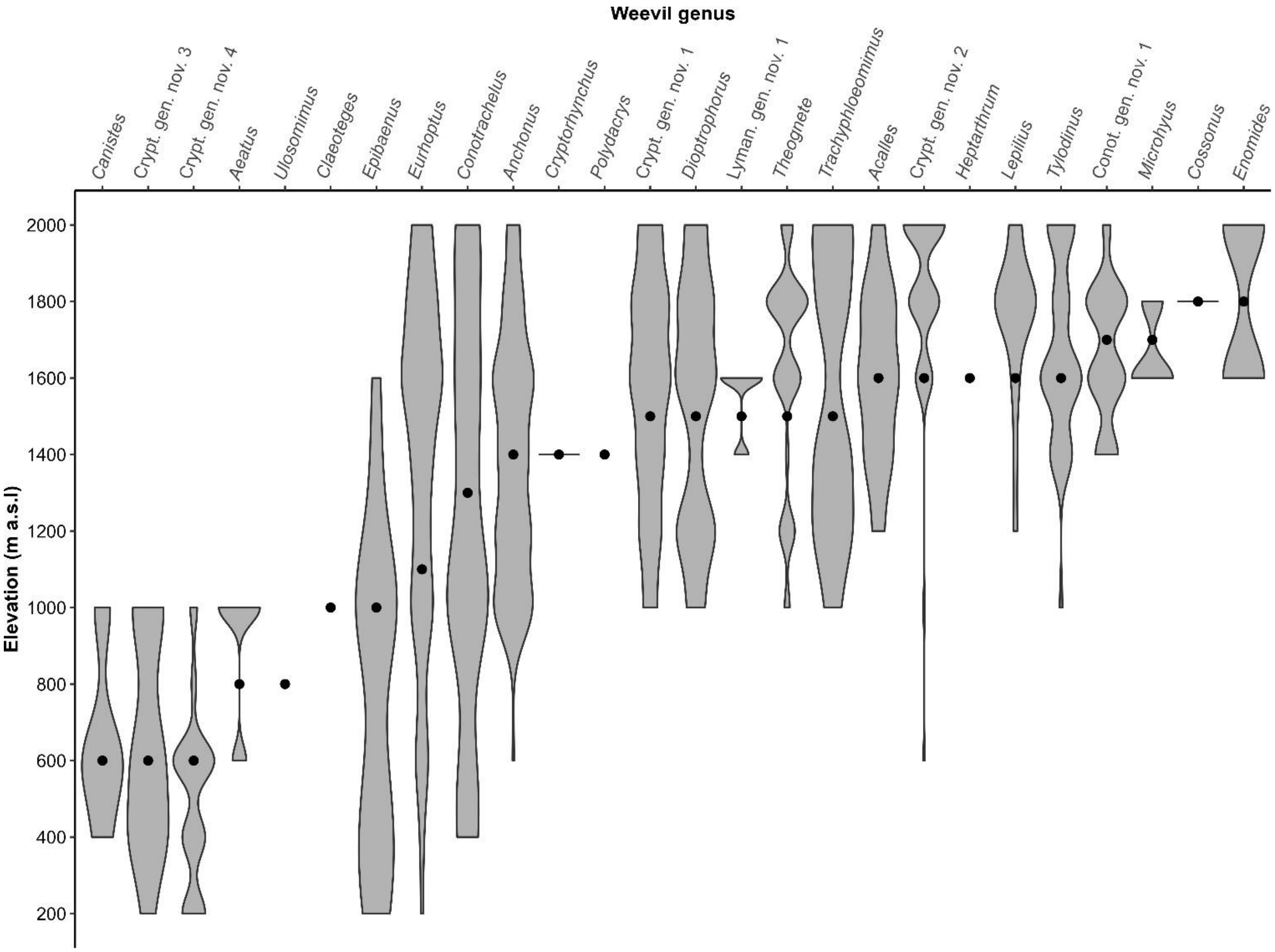

FIGURE 2. Elevation ranges for the 26 leaf litter weevil genera of El Cielo in 20 plots (10 elevational floors in each of two transects) from 200 to 2,000 m. Genera names are on the X-axis. The plot shows the rank of each genus, assuming continuous ranges between minimum and maximum recorded elevations. Genus are ordered by median elevation.

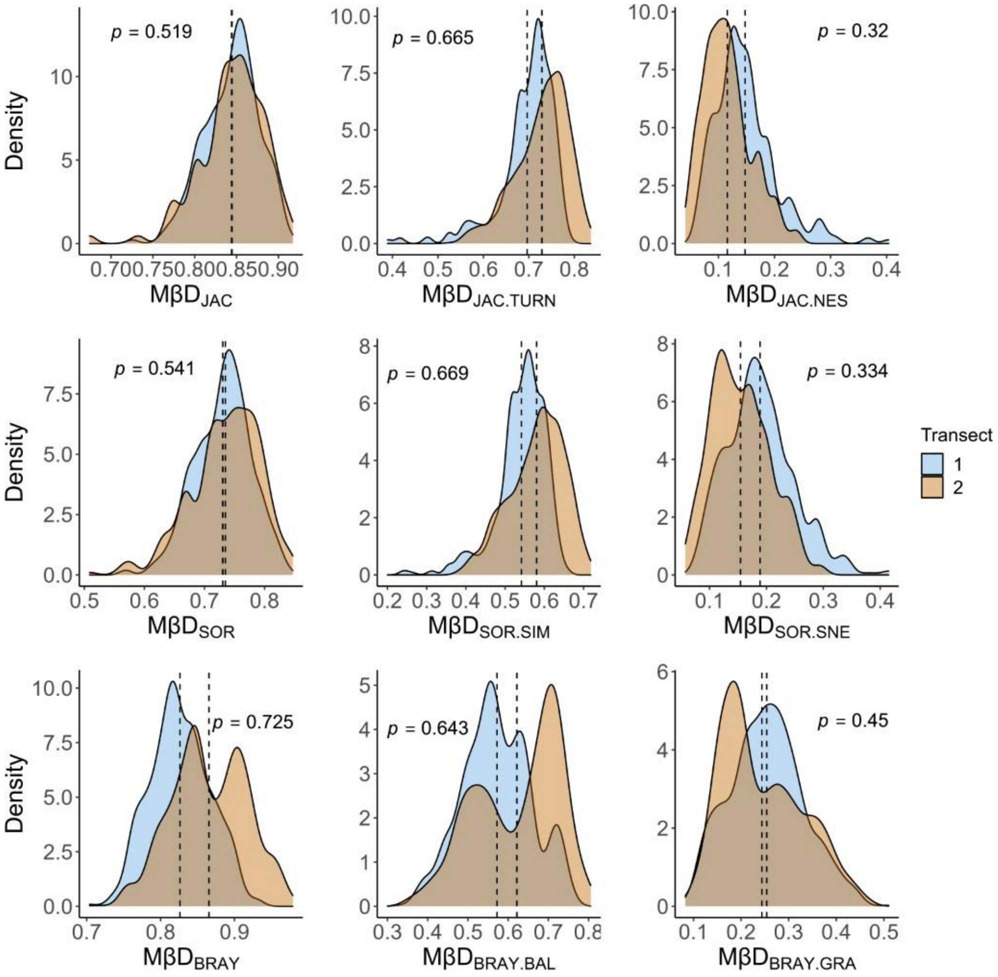

FIGURE 3. Density plots showing the partition of multiple-β-diversity (MβD) with Jaccard, Sørensen and Bray-Curtis indices into total dissimilarity ($M\beta D_{JAC}$, $M\beta D_{SOR}$, $M\beta D_{BRAY}$), turnover ($M\beta D_{JAC.TURN}$, $M\beta D_{SOR.SIM}$, $M\beta D_{BRAY.BAL}$) and nestedness ($M\beta D_{JAC.NES}$, $M\beta D_{SOR.SNE}$, $M\beta D_{BRAY.GRA}$) for transect one and transect two. Dashed lines show the mean value of the metric across the sampled distribution of 1000 values from five random elevational floors, with *P*-values of empirical tests shown. For all instances, no significant differences were found.

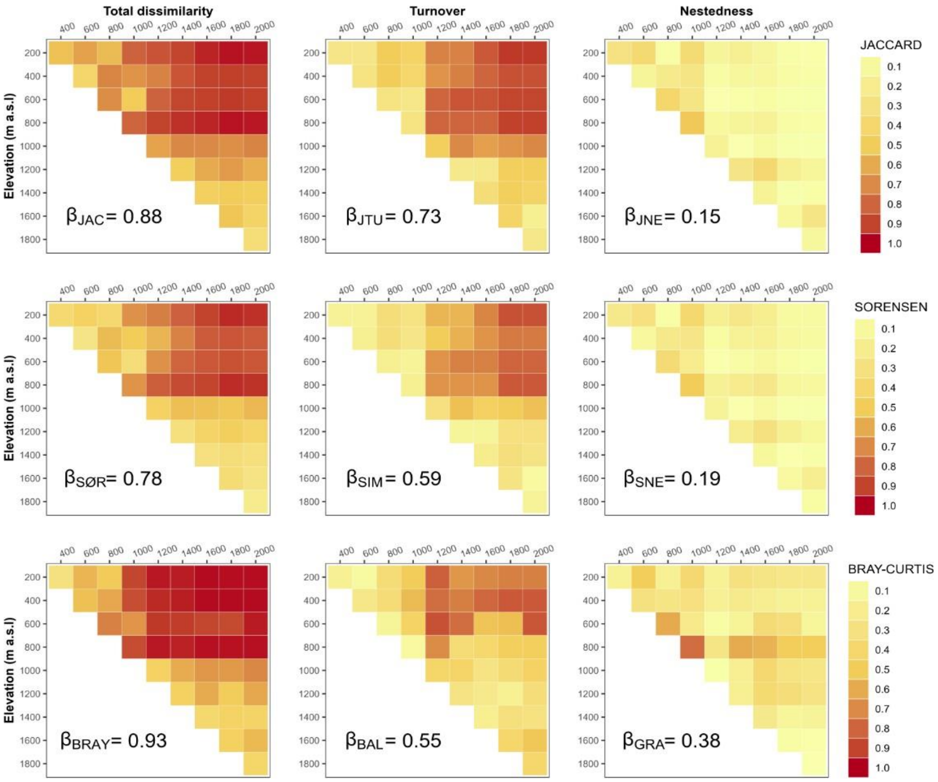

FIGURE 4. Heat maps displaying β-diversity along El Cielo gradient within plots between elevational floors. Top and middle rows represent leaf litter weevil morphospecies presence-absence data measured with Jaccard and Sørensen indices, respectively. Bottom row shows genera abundance data measured with Bray-Curtis index. For all indices β-diversity has been partitioned into turnover (middle column) and nestedness (right column). β- diversity (0→1) near 1 means weevil assemblages have different genera (or different dominant genera for Bray–Curtis) between the compared elevations, while 0 means having the same genera. Turnover (0→1) close to 1 means the dissimilarity is driven only by the replacement of genera along the elevational gradient (i.e. without changes in richness). Conversely, nestedness close to 1 means the dissimilarity is driven only by differences in richness (i.e. poorest communities hosting a subset of the genera present in the richest one).

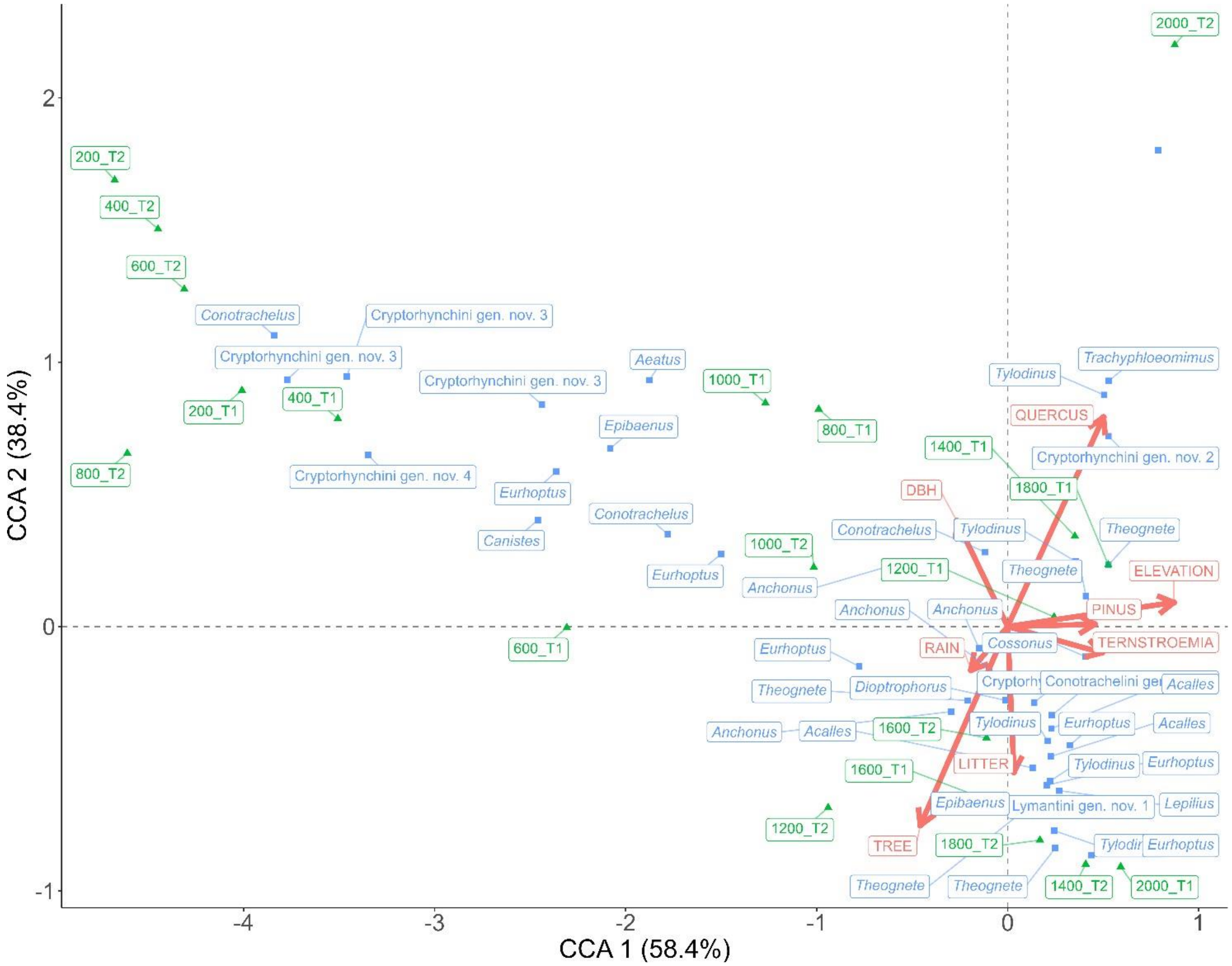

FIGURE 5. Ordination plot of the first two canonical axes of CCA, explaining variation in weevil community composition by elevation, litter depth (LITTER), median DBH (DBH), tree richness per plot (TREE), precipitation seasonality (RAIN), proportion of *Pinus*, *Ternstroemia* and *Quercus*. Study plots are represented in green and weevil morphospecies in blue (weevil labels show genera names).

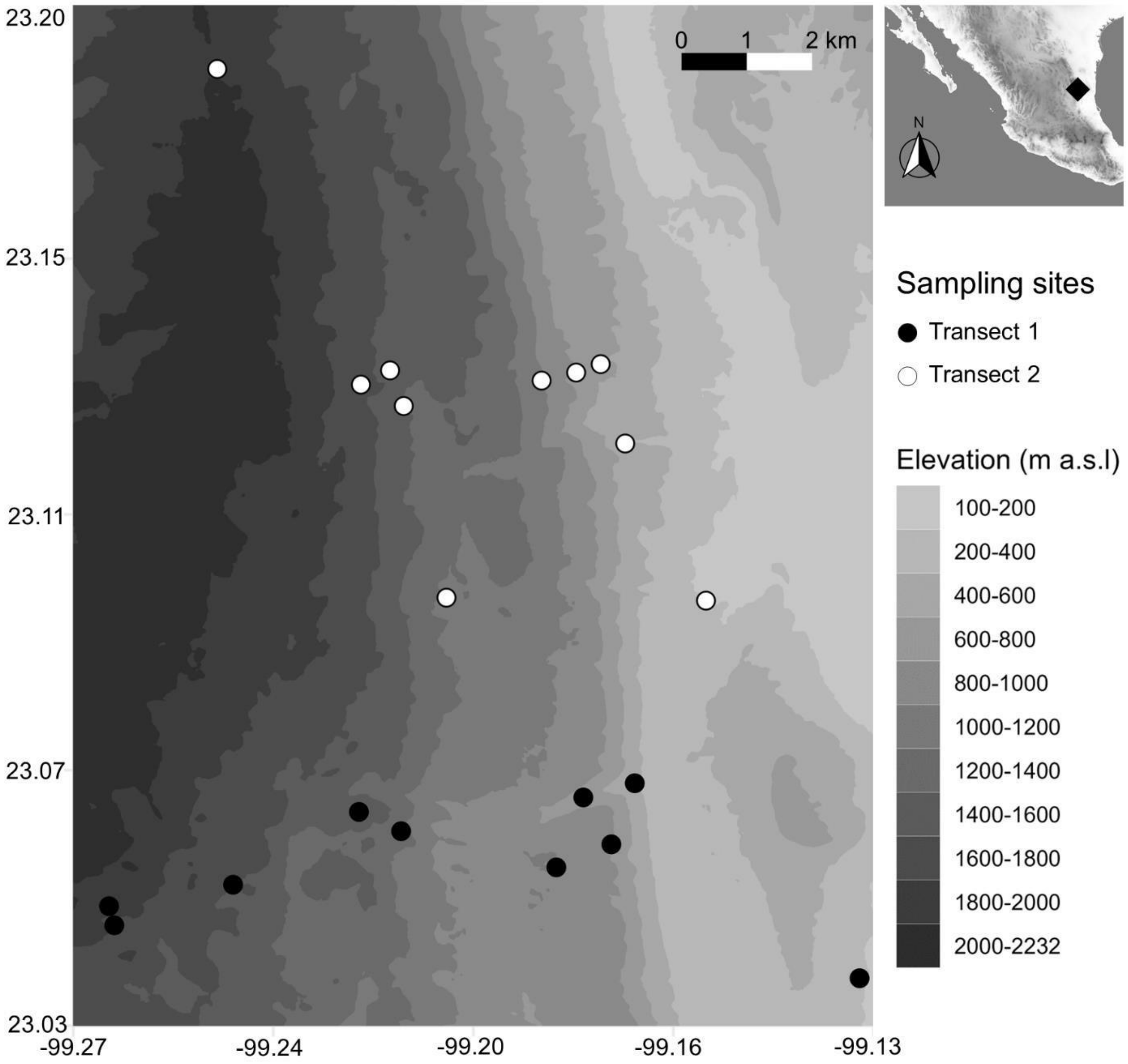

Figure S1. Map of sampling sites spaced by approximately 200 m a.s.l along the El Cielo Biosphere Reserve elevational gradient, Tamaulipas, Mexico. Elevation is shown as a gray scale gradient.

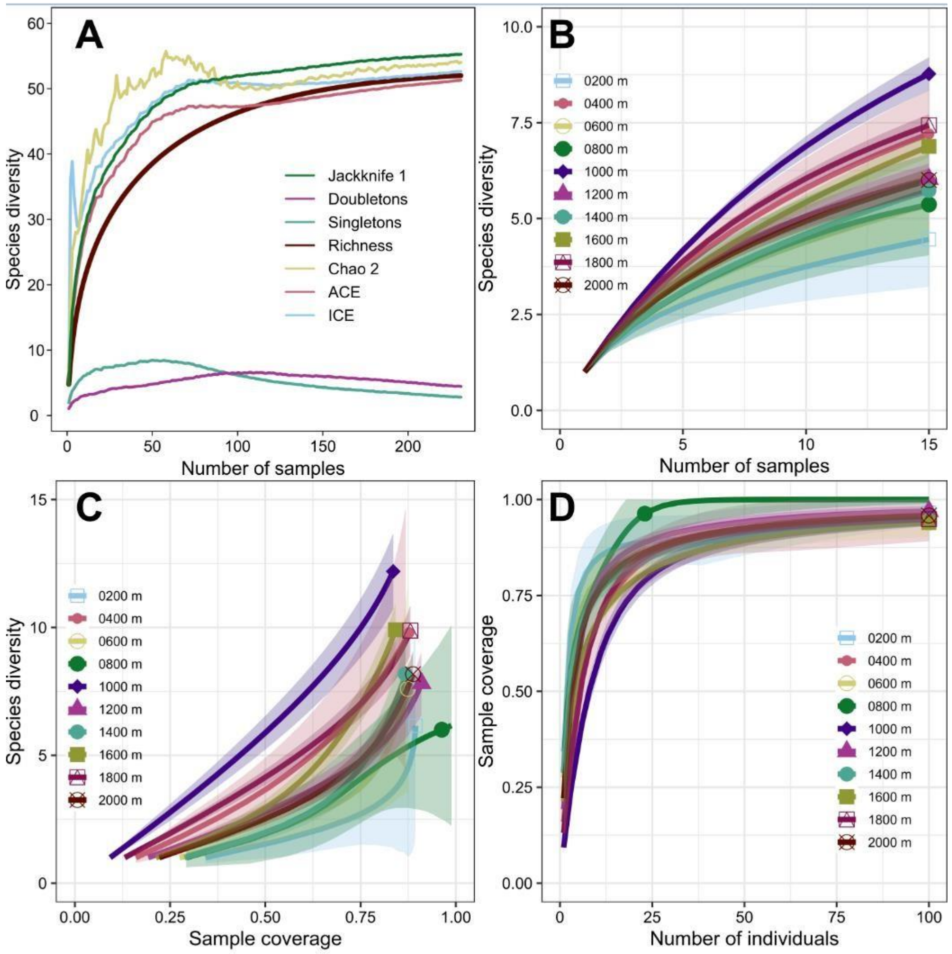

Figure S2. (a) Accumulation curves of number of weevil species with increasing number of samples processed for the whole El Cielo elevational gradient (n = 291). (b) Accumulation curves of weevil species for each of the locations (ten elevational floors spaced by 200 m a.s.l, Figure S1). Curves were generated using abundance data. Solid lines are interpolation with 95% confidence intervals (shaded areas), and the points represent observed total species richness values. (c) Coverage-based rarefaction curves of weevil species with 95% confidence intervals (shaded areas) for ten elevational floors in El Cielo gradient. (d) Sample-completeness rarefaction curves with respect to sample size (number of individual weevil specimens collected) for ten elevational floors in El Cielo gradient.

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AUTHOR CONTRIBUTION

FMSB, MRM and MJ carried out data collection. DVA, MJ, MRM and JJM designed the project and MJ ad MRM provided the funding. DVA and FMSB performed the statistical analyses. DVA, MJ and JJM wrote the manuscript.

COMPETING INTERESTS

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the GitHub repository at https://github.com/Damian-VA/El_Cielo_leaf_litter_weevils

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DISCUSIÓN GENERAL Y CONCLUSIONES

Los estudios sobre gorgojos de la hojarasca para el Neotrópico son escasos (Anderson & Ashe, 2000; Jones et al., 2008, 2022; Maioglio et al., 2022), y sólo dos hasta ahora han evaluado el patrón de diversidad de Curculionidae que viven en el suelo a lo largo de un gradiente altitudinal (Olson, 1994; Maioglio et al., 2022). Ningún estudio anterior examinó el patrón de distribución de los gorgojos de la hojarasca en un bosque de transición tropical-templado en la ZTM. Los géneros con amplios rangos de elevación en nuestro estudio (*Eurhoptus* y otros Cryptorhinchini, *Dioptrophorus*, *Trachyphloeomimus*, *Tylodinus* y *Theognethe*) también fueron predominantes en otros estudios de la fauna mexicana (Jones et al., 2022). Molytinae (incluyendo Cryptorhynchini) fue la subfamilia con el mayor número de especies en El Cielo, Tamaulipas (79%, 50 morfoespecies), al igual que en Cerro Huitepec, Chiapas (87.7% 50 morfoespecies) (Jones et al., 2008). Molytinae también dominó en el bosque mesófilo de la Reserva Otonga, Ecuador (Maioglio et al., 2022), pero la tribu más representada fue Anchonini, no Cryptorhynchini (Maioglio et al., 2022). Una comparación adicional con la diversidad de gorgojos de la hojarasca ecuatorianos mostró que El Cielo tiene una mayor densidad de especímenes (cinco especímenes por cada metro cuadrado en Otonga, Ecuador vs. 13 especímenes en El Cielo, México), pero solo la mitad de su riqueza (100 especies de 24 géneros en Otonga, Ecuador vs. 55 especies de 26 géneros en El Cielo, México).

Los resultados muestran un aumento de la riqueza de especies a lo largo del gradiente altitudinal. Aunque la variación altitudinal de la comunidad de gorgojos de El Cielo no sigue un incremento monotónico, como los de las salamandras en México (Rovito et al., 2013), muestra una tendencia opuesta a la mayoría de otros insectos Mesoamericanos, donde la riqueza de especies disminuye a medida que aumenta la elevación (Longino & Branstetter, 2019; Joaqui et al., 2021). En un estudio reciente (Maioglio et al., 2022), los gorgojos del mantillo en bosques tropicales en Otongachi y Otonga en Ecuador tuvieron más especies a medida que aumentaba la elevación. Los gorgojos del mantillo ecuatorianos tuvieron un aumento de riqueza más marcado a partir de los 1,800 m y por encima, en un gradiente que abarcó desde los 800 a los 2,300 m (Maioglio et al., 2022); es importante mencionar que el gradiente fue incompleto, ya que faltaban muestras en elevaciones intermedias (1,100 – 1,700 m) (Maioglio et al., 2022). En este estudio, la mayor riqueza se encontró a 1,600 m, mientras que en un estudio anterior en Panamá (Olson, 1994) se reportó que Curculionidae del suelo alcanzaban su máxima riqueza a 1,750 m. Sin embargo, Olson (1994) informó de una gran variación altitudinal a lo largo del gradiente (250 - 2,000 m). Al igual que en nuestro estudio, Olson (1994) encontró una mayor abundancia de Curculionidae a mayor altura. Olson (1994) no intentó explicar la tendencia de elevación para los gorgojos, pero argumentó que para los Carabidae recolectados en las mismas muestras, se encontró una distribución más uniforme en los bosques montanos superiores debido a las condiciones uniformes de humedad y a la falta de presas, favoreciendo a las especies generalistas. Aunque se desconoce la dieta de los gorgojos de la hojarasca, se ha sugerido que pueden comer material vegetal muerto (Jones et al., 2008) o restos vegetales infestados de hongos (Luna-Cozar et al., 2014; Anderson & Caterino, 2018), materia orgánica en descomposición y pequeñas ramas y raíces (Maioglio et al., 2022), pero hasta que futuros trabajos lo comprueben, el efecto de la dieta en la relación riqueza-elevación seguirá siendo incierto.

La Reserva de la Biosfera del Cielo alcanza una elevación máxima de 2,320 m.s.n.m. (Sánchez-Ramos et al., 2005), con la mayoría de las partes más altas ubicadas entre 1,900-2,050 m. En el presente estudio se encontraron gorgojos de hojarasca hasta los 2,000 m de altitud. En el centro y sur de México, se encontró una composición de comunidad de los mismos géneros (pero con diferentes especies) en sitios de estudio de 2,230-2,710 m (Pinal de Amoles, San Joaquín y Amealco, Querétaro, Jones et al., 2022) y 2,393-2,512 m (Reserva de la Biosfera Cerro Huitepec, Chiapas, Jones et al., 2008), respectivamente. El hecho de tener las mismas agrupaciones de géneros de gorgojos de norte a sur de la zona de transición altitudinal aumenta las posibilidades de que sus ancestros se hayan dispersado desde un área tropical de origen. Por lo tanto, el modelo de colonización vertical se ajusta mejor a nuestros resultados que la colonización horizontal.

Un estudio de escarabajos peloteros en la ZTM, realizada en la montaña más alta de México (5,600 m, Joaqui et al., 2021), encontró un patrón de riqueza con una meseta en altitudes medias, seguida de una disminución a medida que aumentó la elevación: la mayoría de las especies de escarabajos estercoleros estaban por debajo de los 1,000 m. En el presente estudio, la riqueza de gorgojos alcanzó su máximo a los 1,600 m. Debido a que El Cielo no tiene la misma altitud que otras montañas más altas de la ZTM, es tentador considerar al presente sitio de estudio como un gradiente truncado; sin embargo, esto ocurre cuando sólo se muestrea una parte de la montaña (McCain & Grytnes, 2010). En el presente estudio se muestreó la totalidad del gradiente altitudinal de El Cielo. Este gradiente termina en bosque, mientras que otras montañas terminan en arbustos y hierbas alpinas. De manera similar, el gradiente de elevación de Otonga en Ecuador está compuesto por bosque primario, y su fauna de gorgojos de hojarasca también aumentó con la elevación, alcanzando su punto máximo en el sitio de muestreo más alto (32 especies a 2,238 m). Sam et al. (2020) argumentaron que por encima de los 2,200 m la diversidad y abundancia de insectos disminuye debido a las bajas temperaturas. En el presente trabajo, este factor limitante nunca se alcanza ya que en El Cielo no existe una zona alpina y la mayor parte del bosque alcanza elevaciones de 2,000 m. El Cielo es la Reserva de la Biósfera más septentrional ubicada en la ZTM (Morrone, 2020). Esta sierra mexicana no está conectada más al noreste, por lo que es más probable la colonización por especies sureñas.

La estructura espacial de las comunidades de gorgojos de la hojarasca no cambió entre los transectos, como se muestra por una superposición en las distribuciones de la β-diversidad de los transectos uno y dos. Las comunidades de gorgojos de la hojarasca en los dos transectos no son disímiles desde el punto de vista taxonómico (MβD Bray *P*=0.69), ni presentan diferencias significativas en las tasas de recambio (variación equilibrada MβD Bray *P*=0.626) o de anidamiento (gradiente de abundancia MβD Bray *P*=0.451). Sin embargo, al tomar El Cielo como un único gradiente altitudinal, la disimilitud fue alta (0.78), donde predomina el recambio sobre la anidación, lo que indica que casi ninguna especie (o género) de gorgojo fueron compartidos entre la base y la cima de la montaña. La estructura de la comunidad en las tierras bajas (>1,000 m) y en las altas (<1,000 m) es única (no son subconjuntos entre sí); por lo tanto, aunque la mayor riqueza taxonómica (diversidad α) se dio a 1,600 m, todo el gradiente debe ser incluido para una adecuada comprensión de la diversidad de gorgojos de la hojarasca de la región.

Njovu et al. (2021) encontraron que las variables climáticas actuales son los mejores predictores del aumento de la riqueza y la abundancia de gorgojos fitófagos a lo largo del gradiente altitudinal en el Monte Kilimanjaro. En el presente estudio, sólo se incluyó la precipitación estacional como predictor climático porque todas las demás variables climáticas actuales (Fick & Hijmans, 2017), así como las variables de vegetación (humedad de la hojarasca, la proporción de *Pinus*, *Quercus* y *Ternstroemia*), fueron colineales con un VIF > 1,5 + un coeficiente de correlación de Spearman $P > 0.05$. No obstante, las comparaciones entre los gorgojos de la hojarasca de El Cielo y los escarabajos fitófagos del Monte Kilimanjaro son parciales, ya que el gradiente del estudio en Kilimanjaro es considerablemente más largo (866 – 4,550 m), con una riqueza y abundancia máximas por encima de los 3,000 m. González-Megías et al. (2008) informaron que las comunidades de escarabajos de la hojarasca entre 2,000 y 3,000 m en el Parque Nacional de Sierra Nevada, España, tenían más del 50 % de su diversidad explicada por la diversidad de plantas y la cobertura de arbustos. En El Cielo, la diversidad de árboles explicó sólo el 0.2 % de la diversidad de gorgojos, mientras que la interacción entre el tamaño del árbol (medido como DAP) y la precipitación estacional explicó hasta el 20.7 % de la riqueza de gorgojos a lo largo del gradiente. Más del 50 % de los escarabajos muestreados por González-Megías et al. (2008) fueron escarabajos de las hojas (Coleoptera: Chrysomelidae), lo que probablemente explica por qué la diversidad de plantas y la cobertura de arbustos fueron factores importantes en su estudio. Además, los gorgojos muestreados en el Parque Nacional de Sierra Nevada pertenecían a subfamilias diferentes (ej. Cyclominae, Conoderinae) (González-Megías et al., 2008) que la dominante en la hojarasca de El Cielo (Molytinae). Para los gorgojos muestreados en la Reserva Otonga, Ecuador, la mayoría eran Molytinae (Maioglio et al., 2022) y las características del microhábitat (por ejemplo, la presencia de madera en descomposición, musgo, humedad de la hojarasca y cobertura del dosel) no fueron significativas cuando se analizaron junto con la altitud (Maioglio et al., 2022).

Según el análisis CCA, ni la diversidad de árboles ni la precipitación estacional fueron significativos al momento de explicar la variación, dada por los predictores ambientales, en la composición de la comunidad de gorgojos de la hojarasca. La altitud, la abundancia relativa de *Quercus* y el tamaño de los árboles (medido como la mediana del DAP) fueron los principales factores que afectaron la abundancia y distribución de los gorgojos de la hojarasca. Para los gorgojos muestreados en la Reserva Otonga, Ecuador, la mayoría pertenecían a la subfamilia Molytinae (Maioglio et al., 2022) y las características del microhábitat (es decir, la presencia de madera en descomposición, musgo, humedad de la hojarasca y cobertura del dosel) no fueron significativas cuando se analizaron junto con la elevación (Maioglio et al., 2022). En el presente estudio, el CCA separó la mayoría de las especies de gorgojos por elevación, indicando que la altitud resultó más importante que la proporción de árboles, o el tamaño de estos, a la hora de determinar el patrón de diversidad de estos taxones. En comparación, Jones et al. (2008) concluyeron que los patrones de distribución espacial de los gorgojos de la hojarasca en los bosques tropicales montanos del sur de México están dados por la composición de la vegetación, la estacionalidad, el tipo de hábitat y los índices de dispersión. Los gorgojos sin alas como *Eurhoptus* y otros géneros de baja dispersión como *Tylodinus*, *Anchonus* y *Theognete*, prefieren los bosques primarios húmedos sin vegetación herbácea. Los gorgojos alados de la hojarasca, como *Conotrachelus*, eran más comunes en los bosques de sucesión temprana, y las especies de Entiminae (como *Trachyphloeomimus*) se encontraban en la vegetación herbácea y los arbustos. Por último, las especies de *Anchonus* (Molytinae) fueron las únicas que se encontraron durante la estación húmeda (Jones et al., 2008).

Se observó una disminución en la riqueza de gorgojos de la hojarasca a medida que aumentaba el tamaño de los árboles. Se sabe que los Curculionidae de la hojarasca prosperan en los bosques nublados tropicales de montaña (Anderson y Ashe, 2002; Jones et al., 2008), que incluyen árboles de menor estatura (Webster, 1995) en comparación con los bosques tropicales de tierras bajas. La asociación positiva de los gorgojos de la hojarasca de El Cielo con árboles delgados posiblemente se deba a la asociación con el bosque nublado tropical de montaña, el cual está presente en el sitio a elevaciones por encima de los 1,200 m. Se sabe que los bosques mesófilos tienen menos variación estacional que otros bosques de montaña (Jarvis y Mulligan, 2011), lo que se refleja en la asociación encontrada entre la riqueza de gorgojos y la baja precipitación estacional. La composición de la hojarasca de los bosques mesófilos podría tener alimento más fácilmente disponible para los gorgojos, lo que explicaría la alta diversidad en este ecosistema, sin embargo se necesitan estudios adicionales para evaluar los hábitos alimenticios de estos insectos. Además, ahora que se ha encontrado una probable asociación entre las comunidades de gorgojos de la hojarasca y los bosques nublados tropicales de montaña, futuros trabajos podrían realizar una caracterización más fina del hábitat para corroborar o cuestionar esta hipótesis.

Dado que Curculionidae es una familia taxonómica poco estudiada que carece de filogenias para la mayoría de los linajes Neotropicales, no se pudo inferir el origen de las especies de El Cielo mediante un análisis biogeográfico. Un estudio biogeográfico apropiado consistiría en clasificar los taxones Neotropicales en al menos tres cenocrones distintos: Meseta Mexicana, Mesoamericano de Montaña y Neotropical Típico (Halffter y Morrone, 2017; Morrone, 2020). Se ha argumentado que los géneros típicos de la hojarasca tienen distribuciones bien ajustadas dentro del cenocrón Mesoamericano de Montaña (Halffter y Morrone, 2017), porque se encuentran en hábitats tropicales de montaña con alta diversidad en el sur de México y América Central (Jones et al., 2022). Aunque no se ha presentado una definición formal de los linajes de gorgojos de hojarasca Neotropical Típico y Mesoamericano de Montaña para la ZTM; en El Cielo, los gorgojos Mesoamericanos de Montaña podrían ser predominantes sobre los Neotropicales Típicos, lo que explicaría el patrón de incremento en riqueza a lo largo del gradiente. Pero antes de llegar a cualquier conclusión sobre este tema, se necesitan análisis filogenéticos y para inferir el origen biogeográfico.

En resumen, contario a lo hipotetizado, pero en línea con trabajos previos (Olson, 1994; Anderson y Ashe, 2002; Maioglio et al., 2022), la riqueza de especies de gorgojos aumentó con la elevación, alcanzando un máximo a los 1,600 m. La variación altitudinal de la comunidad se explicó mejor por un patrón de riqueza máxima en elevaciones medias. El predictor ambiental más importante de la estructura de la comunidad fue una interacción entre el tamaño de los árboles y la precipitación estacional, lo que probablemente refleja una asociación positiva entre los gorgojos y los hábitats de bosques tropicales mesófilos de montaña. Dado que los gorgojos de hojarasca son altamente diversos y con altas tasas de recambio, pueden servir como importantes bioindicadores en la planificación de la conservación, proporcionando información sobre los cambios en la condición de los bosques tropicales debido a la fragmentación y degradación. Se necesitan trabajos filogenéticos para reconstruir el origen de los gorgojos de la hojarasca tropicales americanos, así como para analizar su dieta, a fin de determinar cómo estos factores influyen en su distribución altitudinal.

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