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Distribution and fauna characteristics of Zeuzerinae (Lepidoptera, Cossidae) in the New World

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Abstract

The New World fauna of Zeuzerinae remains insufficiently studied in faunistic and biogeographical terms, despite the economic importance of some species and the broad distribution of the subfamily. It currently comprises 45 valid species in 10 genera, including the introduced species *Zeuzera pyrina*. The present study is based on museum material, literature data, and verified publicly available occurrence records. Using these data, we characterise the geographical distribution of the subfamily in the New World, identify the principal distribution patterns of its species, evaluate taxonomic diversity across major biogeographical units, countries, and biomes, identify the main centres of endemism, compare faunal similarity among regions, and assess the distinctiveness of the New World fauna in relation to other parts of the world.

Keywords

America, Biodiversity, Carpenter moths, fauna, Nearctic, Neotropics

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Introduction

Zeuzerinae is a widely distributed subfamily of Cossidae (Lepidoptera, Cossoidea), comprising 433 species in 55 genera. It occurs almost worldwide, except in the subarctic regions of the Holarctic, the southernmost part of South America, and Antarctica. Representatives of this subfamily are characterised by a broad range of adult sizes (from 20 to 280 mm in wingspan) and considerable variation in wing pattern, ranging from faint markings to well-developed reticulate, striate, or spotted patterns, sometimes with bright orange areas. Despite the fact that many zeuzerine species are serious pests of agriculture and forestry, the group remains insufficiently studied in both faunistic and taxonomic respects, a situation that is particularly evident among the Zeuzerinae of the Neotropical and Nearctic regions.

The study of the distribution of Zeuzerinae in the New World developed gradually. Initially, knowledge of the geographical range of this group did not arise from targeted chorological studies, but rather accumulated through records of individual species and information on their type localities in descriptive works published from the late eighteenth to the early twentieth century (Cramer 1779; Percheron and Guérin-Méneville 1838; Herrich-Schäffer [1853–1858]; Walker 1856; Grote 1866; Felder 1874; Burmeister 1878; Dognin 1891, 1911, 1916; Hampson 1898, 1904).

One of the earliest attempts not only to revise the taxonomy of the group but also to interpret its geographical distribution was the work of Houlbert (1916), in which the broad and heterogeneous genus *Xyleutes* was divided into a series of narrower taxa placed in the tribe Xyleutini; the author also proposed his own hypothesis of the faunal genesis of this group. Considering Australia as the presumed centre of origin, Houlbert emphasised the relative paucity of American *Xyleutes*-like forms, despite the presence of endemic taxa in the New World. In the first half of the twentieth century, alongside predominantly descriptive studies (Schaus 1894, 1901, 1911, 1921, 1934; Dyar 1906, 1910, 1914, 1918, 1925; Turner 1918; Lindsey 1926), a more detailed understanding of the regional distribution of American Zeuzerinae also began to emerge, as reflected in specialised faunistic and taxonomic syntheses of the Cossidae of North and tropical America (Barnes and McDunnough 1910, 1911; Dyar 1940).

A major contribution to the systematisation of distributional data was made by Schoorl (1990), whose monograph, in addition to recording type localities, incorporated additional collection material that allowed the distributions of a number of taxa to be refined. Subsequently, the redescription of the genus *Morpheis* (Donahue 1980), the compilation of Neotropical Cossidae with information on type localities and faunal composition (Donahue 1995), and later faunistic publications clarifying the distribution of individual species in the countries and islands of the New World (Becker and Miller 2002; Aguila and Cañamero 2012; Miller et al. 2012) were of particular importance for refining species ranges and assigning species to particular parts of the Nearctic and Neotropical regions.

Since the mid-2010s, the authors have been conducting a taxonomic revision of Zeuzerinae in the Neotropical and Nearctic regions, the results of which have been presented in a series of publications (Penco et al. 2015; Yakovlev et al. 2016, 2017, 2019a, 2019b, 2020a, 2020b, 2020c, 2021; Naydenov et al. 2019, 2021a, 2021b, 2021c, 2024, 2025). These data, together with the material available to the authors, allow an analysis of the distribution of Zeuzerinae in the New World.

Materials and methods

The study was based on 1,605 specimens of Zeuzerinae, including type material, deposited in 6 private collections and 16 state and public museums in Argentina, the USA, France, the United Kingdom, the Netherlands, Germany, Norway, and Russia. In addition, 1,474 occurrence records from GBIF (2025a, 2025b) and 243 observations suitable for reliable species-level identification from the iNaturalist project "New World Zeuzerinae Observations" (iNaturalist 2025) were used to refine distributional data.

The biogeographical regionalisation of the world followed Morrone (2015a), whereas the internal subdivision of the Neotropical, Andean, and Nearctic regions followed Morrone (2014, 2015b) and Escalante et al. (2021). Distributional analyses were conducted in accordance with the classification of ecoregions and biomes proposed by Olson et al. (2001). A comparative analysis of faunal similarity among biogeographical areas was performed using the Jaccard index (Jaccard 1902). The dendrogram based on faunal similarity was constructed using the single-linkage clustering method in Statistica 12.0. The map was produced using the open-source software SimpleMappr (https://www.simplemappr.net/).

The following collection abbreviations are used in Fig. 1: MNHN (Muséum National d'Histoire Naturelle, Paris, France); MWM (Museum Witt Munich, Munich, Germany); NHMUK (The Natural History Museum, London, UK); USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA); ZISP (Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia).

Results

I. Taxonomic composition and species list

At present, the subfamily Zeuzerinae in the New World comprises 45 valid species belonging to 10 genera, including the species *Zeuzera pyrina*, introduced into North America (Fig. 1).

1. *Zeuzera pyrina* (Linnaeus, 1761)
2. *Psychonoctua albogrisea* (Dognin, 1916)

3. *Psychonoctua atra* (Barnes & McDunnough, 1910)
4. *Psychonoctua chaska* (Yakovlev, Penco & Witt, 2017)
5. *Psychonoctua diiorioi* Yakovlev, Penco & Naydenov, 2020
6. *Psychonoctua gilensis* (Barnes & McDunnough, 1910)
7. *Psychonoctua itys* (Druce, 1911)
8. *Psychonoctua klagesi* (Yakovlev, Naydenov & Penco, 2021)
9. *Psychonoctua kon* (Yakovlev, Penco & Witt, 2017)
10. *Psychonoctua lineaeplena* (Dognin, 1911)
11. *Psychonoctua personalis* Grote, [1866]
    a. *Psychonoctua personalis personalis* Grote, [1866]
    b. *Psychonoctua personalis benestriata* (Hampson, 1904)
    c. *Psychonoctua personalis cracens* Yakovlev, Penco & Naydenov, 2020
    d. *Psychonoctua personalis jamaicensis* Schaus, 1901
    e. *Psychonoctua personalis lillianae* Lindsey, 1926
    f. *Psychonoctua personalis muricolora* (Dyar, 1940)
    g. *Psychonoctua personalis ravida* Yakovlev, Penco & Naydenov, 2020
12. *Psychonoctua thonyi* (Yakovlev, Penco & Witt, 2017)
13. *Psychonoctua unilinea* Dyar, 1925
14. *Psychonoctua xuna* (Dyar, 1940)
15. *Schreiteriana pectinicornis* (Dyar, 1940)
16. *Carohamilia masoni* (Schaus, 1894)
17. *Carohamilia ophelia* (Schaus, 1921)
18. *Carohamilia poam* (Dyar, 1918)
19. *Carohamilia terrafirma* (Schaus, 1911)
20. *Allocryptobia musae* (Herrich-Schäffer, [1854])
21. *Ceuroma mucorea* (Herrich-Schäffer, [1853])
22. *Listrada sulbaiana* Naydenov, Yakovlev, Penco & Witt, 2019
23. *Morpheis clenchi* Donahue, 1980
24. *Morpheis cognatus* (Walker, 1856)
25. *Morpheis comisteus* (Schaus,1911)
26. *Morpheis humboldti* Naydenov, Yakovlev & Penco, 2021
27. *Morpheis impeditus* (Wallengren, 1860)
28. *Morpheis mathani* (Schaus, 1901)
29. *Morpheis melanoleucus* (Burmeister, 1878)
30. *Morpheis putridus* (Percheron, 1838)
31. *Morpheis pyracmon* (Cramer, [1780])
32. *Morpheis votani* (Schaus, 1934)
33. *Morpheis xylotribus* (Herrich-Schäffer, [1853])
34. *Brypoctia aeetes* (Druce, 1901)
35. *Brypoctia desdemona* (Dyar, 1940)
36. *Brypoctia eqaqo* Yakovlev, Penco & Witt, 2019
37. *Brypoctia greifensteini* Yakovlev, Penco & Witt, 2019
38. *Brypoctia itzamna* Yakovlev, Penco & Witt, 2019

39. *Brypoctia kurupi* Yakovlev, Penco & Witt, 2019
40. *Brypoctia monai* Yakovlev, Penco & Witt, 2019
41. *Brypoctia punctifer* (Hampson, 1898)
42. *Brypoctia ramosa* (Schaus, 1892)
43. *Brypoctia ramuscula* (Dyar, 1906)
44. *Brypoctia strigifer* (Dyar, 1910)
45. *Klagesiana amazoniensis* Yakovlev, Naydenov & Penco, 2020

Because the species boundaries between *Morpheis putridus* and *M. pyracmon* remain unclear, their distribution was not considered in the species-level analyses, but was taken into account at the genus level and above.

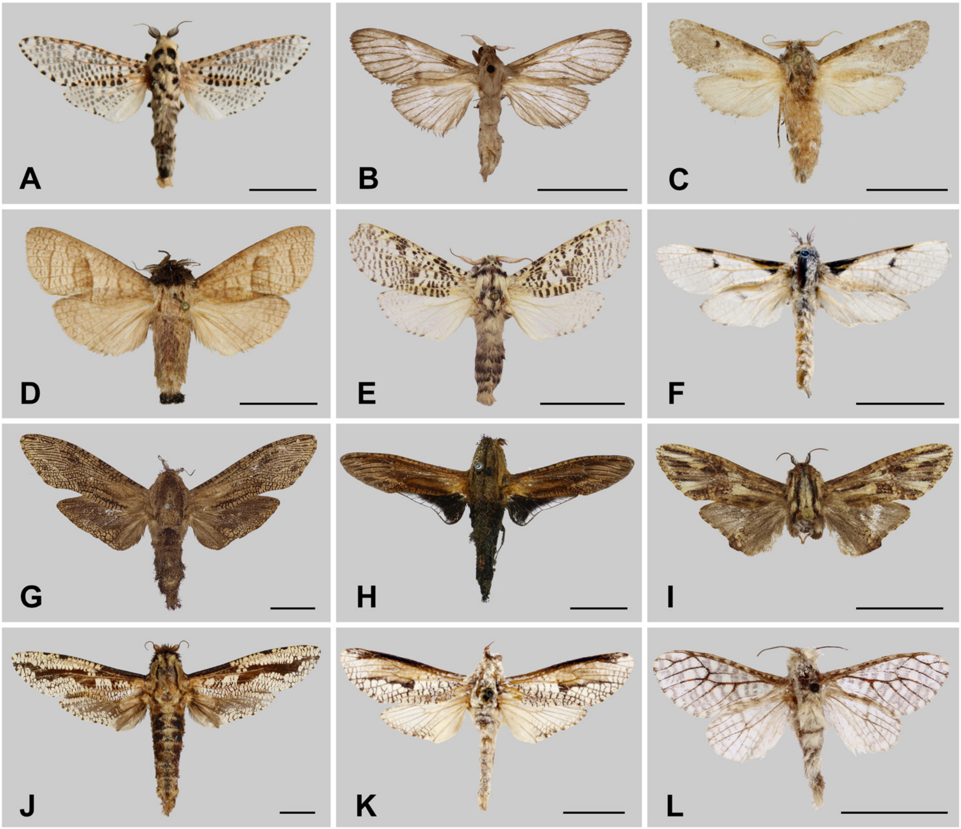

Figure 1. Species of genera of New World Zeuzerinae (adult male specimens): **A.** *Zeuzera pyrina*, USA, Colorado (MNHN); **B.** *Psychonoctua klagesi*, paratype, Brazil, Amazonas (NHMUK); **C.** *P. personalis*, Cuba, Holguin (MWM); **D.** *P. thonyi*, Peru, Huánuco (MWM); **E.** *Schreiteriana pectinicornis*, Argentina, Misiones (MWM); **F.** *Carohamilia ophelia*, holotype, Guatemala, Cayuga (USNM); **G.** *Allocryptobia musae*, paralectotype (ZISP); **H.** *Ceuroma mucorea*, Venezuela, Valencia (NHMUK); **I.** *Listrada sulbaiana*, holotype, Brazil, Bahia (MWM); **J.** *Morpheis pyracmon*, Venezuela, Yaracuy (MWM); **K.** *Brypoctia ramosa*, holotype, [Brazil], Rio [de] Janeiro (USNM); **L.** *Klagesiana amazoniensis*, [Brazil], Amazonas, Fonte Boa (NHMUK).

II. General characteristics and limits of geographical distribution

Based on the examined material and distributional records from GBIF and iNaturalist used in the analysis, a point-occurrence map of Zeuzerinae in the New World was compiled (Fig. 2). The natural range of the group extends across large parts of two continents, from the Mojave and Sonoran deserts of southern California and Arizona, USA, in the north to the Monte Desert in Río Negro Province, Argentina, in the south. It encompasses a broad range of ecoregions in North, Central, and South America, but excludes the high-elevation areas of the Andes. Biogeographically, the range of Zeuzerinae in the New World lies predominantly within the Neotropical Region; only five species extend into the southern Nearctic Region, and three species have been recorded in the South American Transition Zone, which forms a transitional biogeographical area between the Neotropical and Andean regions.

In latitudinal terms, the natural range of the subfamily is confined to the subtropical zone in both the northern and southern hemispheres. The northernmost record is of *Psychonoctua gilensis* at 35°16'N, whereas the southernmost record is of *Morpheis votani* at 39°00'S.

Altitudinally, all species of Zeuzerinae in North and South America have been recorded up to the upper forest limit. The highest-elevation record is that of *Brypoctia aeetes*, based on a specimen collected at 3,400 m above sea level in Colombia, within the Magdalena Valley montane forests. *Morpheis mathani* was described from material collected in a mountain valley near Huambo, Peru, at approximately 3,300 m above sea level, and a specimen of *Morpheis xylotribus* was collected at 3,060 m in the Bolivian Yungas. All highest-elevation records refer to relatively widespread species that have also been recorded in the lowland and coastal parts of South America. Thus, in altitudinal terms, the range of Zeuzerinae in the New World is limited to the *Tierra fría* belt, i.e. the upper forest belt of the Andean mountain system.

The range of the introduced species *Zeuzera pyrina* lies well to the north of the natural range of Zeuzerinae in North America. The first reliable published record of the species dates from 1882 and refers to a record from Hoboken, New Jersey, USA (Doll 1882; Britton and Cromie 1911). At present, the species is distributed mainly in the north-eastern USA and south-eastern Canada.

III. Range types of New World Zeuzerinae

The classification of species ranges is an important component of the zoogeographical analysis of any animal group. However, the absence of a well-developed system for classifying ranges in North and South America, together with the relatively small number of species analysed, did not allow the species to be grouped unambiguously according to shared distribution patterns. For the purposes of the present study, the species were therefore provisionally divided into six groups. Within these groups, species may form subgroups to varying degrees and on the basis of different features, or may exhibit unique distribution patterns that do not correspond to the limits of individual biogeographical areas.

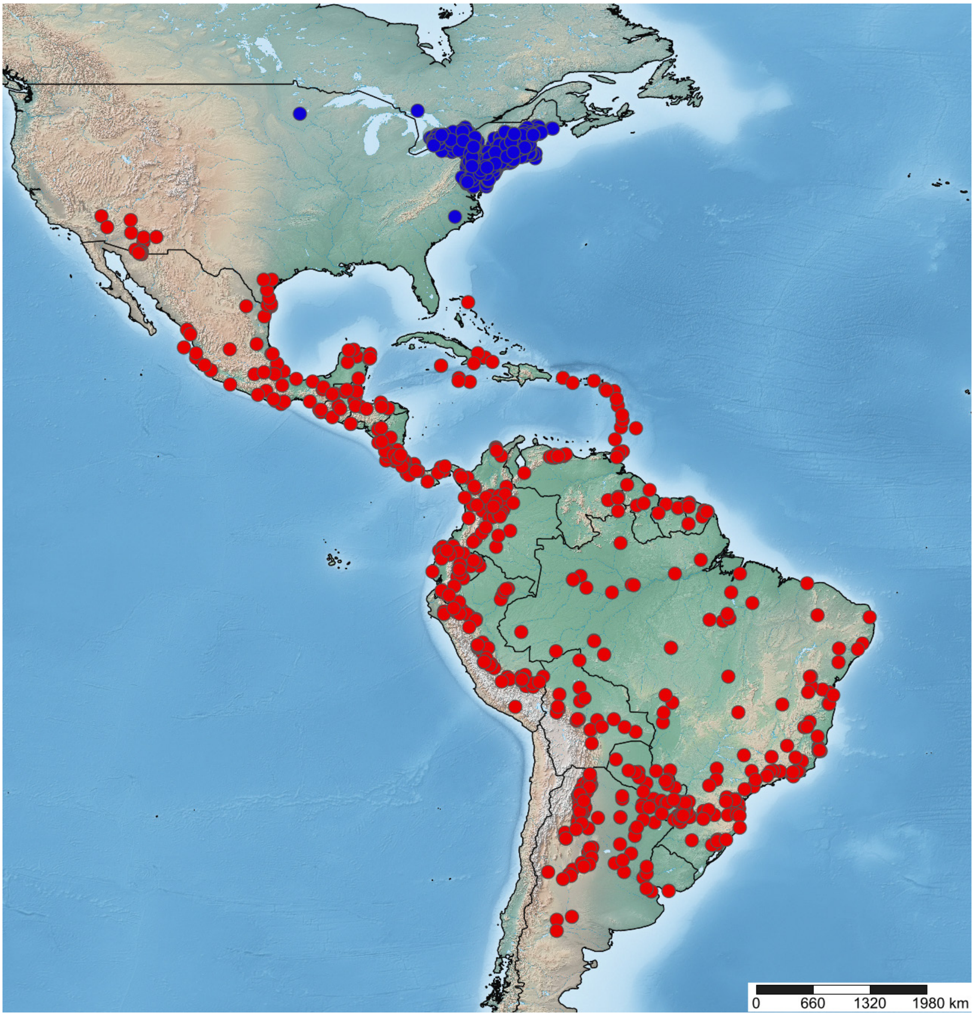

Figure 2. Distributional records of the subfamily Zeuzerinae in the New World. The natural distribution is shown in red. The distribution of the non-native species *Zeuzera pyrina* is shown in blue.

1. Southern Nearctic species

Four zeuzerine species occur exclusively in the Nearctic Region: *Psychonoctua atra*, *P. gilensis*, *Morpheis clenchi*, and *Brypoctia ramuscula*. Their ranges are relatively restricted and are confined mainly to the deserts and xeric shrublands of the southern USA and northern Mexico.

2. Nearctic–Neotropical species

Carohamilia masoni also occurs in the Nearctic Region and has a transboundary range extending into the Neotropical Region. Its southern limit reaches Central America, placing this species in both the Nearctic and Neotropical faunas.

3. West Indian species

The Antillean biogeographical subregion, including the Antilles and the Bahamian Islands, is inhabited by only two species: *Psychonoctua personalis* and *Brypoctia punctifer*. The ranges of both species are confined to the West Indies. Whereas *P. personalis* is widely distributed, from the Bahamas to Grenada, the range of *B. punctifer* is restricted to the Lesser Antilles. It should be noted that the widespread *P. personalis* is represented by a number of well-differentiated subspecies: *P. personalis personalis* (Cuba); *P. personalis benestriata* (Bahamas: Abaco); *P. personalis cracens* (Cayman Islands: Cayman Brac); *P. personalis jamaicensis* (Jamaica); *P. personalis lillianae* (Leeward Islands: Antigua, St Kitts, Nevis); *P. personalis muricolora* (Puerto Rico); *P. personalis ravida* (Barbados).

4. North-western Neotropical species

The Brazilian subregion, occupying the north-western part of the Neotropical Region, is the most species-rich, harbouring 31 species. However, only 22 species have ranges confined entirely to this subregion.

For the purposes of the present study, Central America is understood as extending from the northern boundary of the Neotropical Region to the Isthmus of Panama. Six species are endemic to this area: *Psychonoctua unilinea*, *P. xuna*, *Carohamilia ophelia*, *C. poam*, *Morpheis cognatus*, and *Brypoctia itzamna*. Some species that also occur in Central America extend much farther south. Thus, the southern limits of the ranges of *Carohamilia terrafirma*, *Allocryptobia musae*, and *Brypoctia strigifer* extend to the continental part of the Pacific biogeographical dominion, whereas the range of *Morpheis comisteus* extends to the Peruvian Yungas and Brazilian Amazonia (South Brazilian biogeographical dominion), also covering northern South America.

Psychonoctua itys, *P. kon*, and *Brypoctia greifensteini* occur exclusively in the north-western part of South America, and their ranges do not extend beyond the Pacific dominion. *Brypoctia aeetes* is also characteristic of this biogeographical area, but additionally occurs in the Boreal Brazilian biogeographical dominion, whereas *Psychonoctua albogrisea*, in addition to the above-mentioned dominions, extends farther south to central Amazonia (South Brazilian dominion).

A more southerly range is shown by *Psychonoctua lineaeplena*, which occurs in the Guianan moist forests, central Amazonia, and the Peruvian Yungas (Boreal Brazilian and South Brazilian dominions). One of the largest range groups, however, is formed by species occurring exclusively within the South Brazilian dominion. This group includes six species: *Psychonoctua chaska*, *P. klagesi*, *P. thonyi*, *Morpheis humboldti*, *Brypoctia eqaqo*, and *Klagesiana amazoniensis*.

Among the north-western Neotropical species, *Morpheis mathani* has the broadest range, occurring in the Brazilian subregion (Boreal Brazilian, South Brazilian, and Pacific dominions, including the Ecuadorian province), the Chacoan subregion (South-eastern Amazonian dominion), and the South American Transition Zone (Huambo, Peru, on the border between the Sechura Desert and the Tumbes–Piura dry forests).

5. South-eastern Neotropical species

The Chacoan subregion, occupying the south-eastern part of the Neotropical Region, includes 13 species. However, only five species are endemic to this subregion. Of these, four have been recorded exclusively in the humid tropical forests of the Paraná dominion: *Listrada sulbaiana*, *Brypoctia desdemona*, *B. kurupi*, and *B. monai*. The remaining species, Brypoctia ramosa, occurs not only in Paraná but also in drier ecoregions such as the Cerrado and Chaco of the Chacoan dominion.

Five species whose ranges are centred mainly in the Chacoan subregion extend into the Brazilian subregion. Despite differences in their distributions within the Chacoan subregion, all of these species have also been recorded from the Yungas province, which belongs to the Brazilian subregion. Thus, *Psychonoctua diiorioi* has been recorded from Chaco and Yungas; *Schreiteriana pectinicornis* from Paraná, Chaco, and Yungas; *Morpheis melanoleucus* from Pampa, Chaco, and Yungas; *Morpheis impeditus* from Monte, Chaco, Pampa, Paraná, Rondônia, and Yungas; and *Morpheis votani* from Monte, Chaco, Pampa, and Yungas. Particularly noteworthy is the southern distributional limit of the last two species, namely the Monte Desert, which belongs to the South American Transition Zone; this makes *M. impeditus* and *M. votani* the southernmost representatives of Zeuzerinae in the New World.

6. Widespread Neotropical species

Among New World Zeuzerinae, *Morpheis xylotribus* has the broadest range, extending from southern Mexico (Central American pine–oak forests) to northern Argentina (Pampean province). The species has been recorded from all continental biogeographical subregions and dominions of the Neotropical Region.

Ceuroma mucorea also has a relatively broad range. The few records of this rare species from different parts of South America, including northern Venezuela, the montane humid tropical forests of Peru, the Chaco of Paraguay, and the humid Atlantic forests of coastal Brazil, indicate an extensive, albeit still poorly studied, range across much of the continent.

The broad ranges of these species are probably associated with the breadth of their trophic associations, which remain very poorly studied in the Neotropics.

IV. Assessment of species and generic diversity across biogeographical areas

The highest species and generic diversity of Zeuzerinae in the New World is found in the Neotropical Region, whose fauna comprises 40 species in nine genera. The Nearctic Region contains five species in four genera, excluding the introduced species *Zeuzera pyrina*. The transition zones are the most species-poor areas in terms of zeuzerine species composition: the South American Transition Zone supports three species in a single genus, whereas only one species, belonging to the *Morpheis putridus–M. pyracmon* complex, has been recorded from the Mexican Transition Zone. No Zeuzerinae have been recorded from the Andean Region.

A finer-scale assessment of taxonomic diversity at the level of biogeographical subregions and dominions (Fig. 3) showed that the highest species and generic diversity occurs in the South Brazilian dominion, where 17 species in six genera have been recorded. The Pacific dominion contains the same number of genera, although its species richness is somewhat lower (15 species). The Mesoamerican dominion contains 11 species in five genera. The Chacoan and Paraná dominions contain nine and eight species, respectively, each represented by five genera. The lowest taxonomic diversity occurs in the Boreal Brazilian dominion, where six species in three genera have been recorded. Two species in two genera have been recorded from the Antillean subregion, whereas the South-eastern Amazonian dominion contains two species in a single genus.

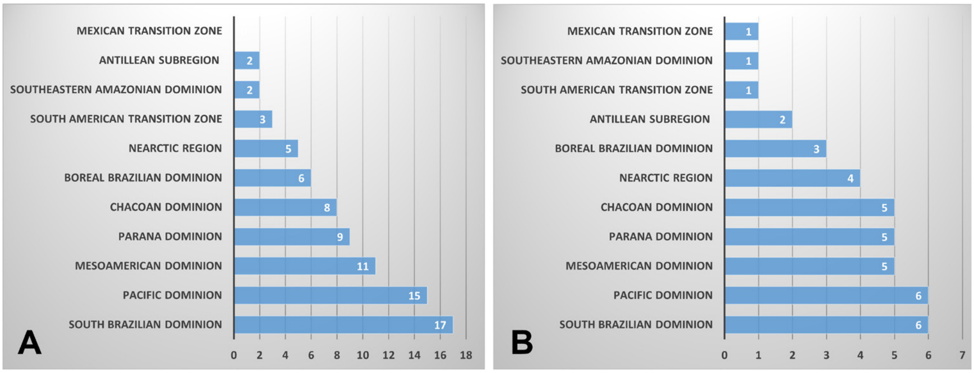

Figure 3. Number of species (**A**) and genera (**B**) of Zeuzerinae in biogeographic regions, subregions, transition zones and dominions of the New World.

The distribution of Zeuzerinae species across the biogeographical provinces of the New World is presented in Tables 1 and 2.

Table 1. Distribution of Zeuzerinae species in biogeographic provinces of the New World (part 1)

	Desert province	Monte province	Xingu-Tapajós province	Caatinga province	Cerrado province	Chaco province	Pampean province	Atlantic province	Parana province	Araucaria Forest province	Pacific Lowlands province	Balsas Basin province	Veracruzan province	Yucatán Peninsula province	Mosquito province	Guatuso-Talamanca province	Puntarenas-Chiriquí province	Chocó-Darién province	Guajira province	Venezuelan province	Trinidad province	Magdalena province	Sabana province	Cauca province
Psychonoctua albogrisea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Psychonoctua atra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua chaska	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua diiorioi	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua gilensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua itys	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	+
Psychonoctua klagesi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua kon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua lineaeplena	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua personalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua thonyi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua unilinea	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua xuna	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Schreiteriana pectinicornis	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia masoni	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	-	-
Carohamilia ophelia	-	-	-	-	-	-	-	-	-	-	+	-	-	+	+	-	-	-	-	-	-	-	-	-
Carohamilia poam	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-

	Desert province	**Monte province**	**Xingu-Tapajós province**	**Caatinga province**	**Cerrado province**	**Chaco province**	**Pampean province**	**Atlantic province**	**Parana province**	**Araucaria Forest province**	**Pacific Lowlands province**	**Balsas Basin province**	**Veracruzan province**	**Yucatán Peninsula province**	**Mosquito province**	**Guatuso-Talamanca province**	**Puntarenas-Chiriquí province**	**Chocó-Darién province**	**Guajira province**	**Venezuelan province**	**Trinidad province**	**Magdalena province**	**Sabana province**	**Cauca province**
Carohamilia terrafirma	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	+	+	-	-	-	-	-	+
Allocryptobia musae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	+	-	+	-	+
Ceuroma mucorea	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Listrada sulbaiana	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis clenchi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis cognatus	-	-	-	-	-	-	-	-	-	-	+	+	+	-	+	-	+	-	-	-	-	-	-	-
Morpheis comisteus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-	-	-	+
Morpheis humboldti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis impeditus	-	+	-	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis mathani	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis melanoleucus	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis votani	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis xylotribus	-	-	+	+	+	+	+	+	+	+	-	-	+	-	-	+	+	-	-	+	-	+	-	+
Brypoctia aeetes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	+	+	-	+
Brypoctia desdemona	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia eqaqo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia greifensteini	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-
Brypoctia itzamna	-	-	-	-	-	-	-	-	-	-	+	-	+	+	+	-	+	-	-	-	-	-	-	-
Brypoctia kurupi	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	Desert province	Monte province	Xingu-Tapajós province	Caatinga province	Cerrado province	Chaco province	Pampean province	Atlantic province	Parana province	Araucaria Forest province	Pacific Lowlands province	Balsas Basin province	Veracruzan province	Yucatán Peninsula province	Mosquito province	Guatuso-Talamanca province	Puntarenas-Chiriquí province	Chocó-Darién province	Guajira province	Venezuelan province	Trinidad province	Magdalena province	Sabana province	Cauca province
Brypoctia monai	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia punctifer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia ramosa	-	-	-	-	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia ramuscula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia strigifer	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	+	+	-	-	-	-	-	-	+
Klagesiana amazoniensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 2. Distribution of Zeuzerinae species in biogeographic provinces of the New World (part 2)

	Western Ecuador province	Ecuadorian province	Napo province	Imerí province	Pantepui province	Guianan Lowlands province	Roraima province	Pará province	Ucayali province	Madeira province	Rondônia province	Yungas province	Bahama province	Cuban province	Cayman Islands province	Jamaica province	Puerto Rico province	Lesser Antilles province	Mohavian	Navahonian	Sonora	Chihuahuan	Texan	Tamaulipan
Psychonoctua albogrisea	-	-	-	-	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua atra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Psychonoctua chaska	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-

	Western Ecuador province	Ecuadorian province	Napo province	Imerí province	Pantepui province	Guianan Lowlands province	Roraima province	Pará province	Ucayali province	Madeira province	Rondônia province	Yungas province	Bahama province	Cuban province	Cayman Islands province	Jamaica province	Puerto Rico province	Lesser Antilles province	Mohavian	Navahonian	Sonora	Chihuahuan	Texan	Tamaulipan
Psychonoctua diiorioi	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua gilensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-
Psychonoctua itys	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua klagesi	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua kon	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua lineaeplena	-	-	-	-	-	+	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua personalis	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+	-	-	-	-	-	-
Psychonoctua thonyi	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua unilinea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua xuna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schreiteriana pectinicornis	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia masoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Carohamilia ophelia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia poam	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia terrafirma	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Allocryptobia musae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ceuroma mucorea	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Listrada sulbaiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis clenchi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-

	Western Ecuador province	Ecuadorian province	Napo province	Imerí province	Pantepui province	Guianan Lowlands province	Roraima province	Pará province	Ucayali province	Madeira province	Rondônia province	Yungas province	Bahama province	Cuban province	Cayman Islands province	Jamaica province	Puerto Rico province	Lesser Antilles province	Mohavian	Navahonian	Sonora	Chihuahuan	Texan	Tamaulipan
Morpheis cognatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis comisteus	-	-	-	-	+	+	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis humboldti	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis impeditus	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis mathani	-	+	+	-	-	+	-	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis melanoleucus	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis votani	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis xylotribus	-	+	-	-	+	+	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia aeetes	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia desdemona	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia eqaqo	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia greifensteini	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia itzamna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia kurupi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia monai	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia punctifer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Brypoctia ramosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia ramuscula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Brypoctia strigifer	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Klagesiana amazoniensis	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Thus, the Yungas Province, part of the South Brazilian dominion, can be regarded as the area with the highest taxonomic diversity. This narrow, elongated zone along the eastern slopes of the Andes in Peru, Bolivia, and northern Argentina has the highest zeuzerine species richness and also one of the highest levels of generic richness. This pattern is explained both by the pronounced altitudinal zonation of the region and by its position at the junction of three major biogeographical complexes: the Central Andes, Amazonia, and the Gran Chaco. In addition, the Yungas Province, together with the Cauca Province, which has the same maximum number of genera and a relatively high number of species, forms part of the Tropical Andes, one of the world's biodiversity hotspots (Myers 1988; Myers et al. 2000), which is consistent with the present results.

Relatively high taxonomic diversity, although without a pronounced concentration in particular provinces, is also characteristic of the Pacific dominion (predominantly humid equatorial and subequatorial montane forests), the Mesoamerican dominion (humid tropical forests of the Atlantic coast and dry tropical forests of the Pacific coast), the central Amazonian forests of the Madeira Province, the humid tropical forests of Paraná and the Brazilian Atlantic coast, and the tropical forests and woodlands of the Gran Chaco.

V. Assessment of taxonomic diversity across countries of the New World

Data on the occurrence of Zeuzerinae species in New World countries are presented in Tables 3 and 4.

The highest species and generic richness is found in Brazil, where 15 species belonging to six genera have been recorded. This high level of taxonomic diversity is explained by the country's large area and pronounced ecological heterogeneity, encompassing a wide range of biomes, from savannas and tropical woodlands to humid Atlantic forests and Amazonian rainforests.

The high diversity of Zeuzerinae in Mexico (12 species in four genera) is explained by the combination of arid lowlands, humid tropical forests, and mountain regions, together with the country's transitional position at the junction of the Neotropical and Nearctic regions. Costa Rica, one of the best-studied countries in the region, has 10 species in four genera; this is likewise explained by its transitional position, in this case between the Central American and South American faunas. Peru also has 10 species in four genera, which may be explained by the heterogeneity of its ecoregions, including Amazonian rainforests, dry coastal forests, and the Yungas, a centre of species diversity for Zeuzerinae. Argentina has nine species in four genera, most of them occurring in the northern and north-western parts of the country, particularly in the Yungas and Chaco zones. In Ecuador, eight species belonging to five genera have been recorded. Despite the country's relatively small area, its comparatively high faunal richness, as in Peru, is explained by the combination of Pacific ecoregions, the vertical zonation of the Northern Andes, and western Amazonia.

Table 3. Distribution of Zeuzerinae species by country in the New World (part 1)

	United States	Mexico	Belize	Guatemala	Honduras	Costa Rica	Nicaragua	Panama	El Salvador	Antigua and Barbuda	The Bahamas	Barbados	Grenada	Dominica	Cuba	Saint Vincent and the Grenadines	Saint Kitts and Nevis	Saint Lucia
Psychonoctua albogrisea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua atra	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua chaska	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua diiorioi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua gilensis	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua itys	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua klagesi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua kon	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua lineaeplena	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua personalis	-	-	-	-	-	-	-	-	-	+	+	+	-	-	+	-	+	-
Psychonoctua thonyi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua unilinea	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua xuna	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schreiteriana pectinicornis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia masoni	+	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia ophelia	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia poam	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia terrafirma	-	+	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
Allocryptobia musae	-	-	-	-	+	+	-	+	-	-	-	-	-	-	-	-	-	-
Ceuroma mucorea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Listrada sulbaiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis clenchi	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis cognatus	-	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-
Morpheis comisteus	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
Morpheis humboldti	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis impeditus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis mathani	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis melanoleucus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

	United States	Mexico	Belize	Guatemala	Honduras	Costa Rica	Nicaragua	Panama	El Salvador	Antigua and Barbuda	The Bahamas	Barbados	Grenada	Dominica	Cuba	Saint Vincent and the Grenadines	Saint Kitts and Nevis	Saint Lucia
Morpheis votani	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis xylotribus	-	+	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia aeetes	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia desdemona	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia eqaqo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia greifensteini	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia itzamna	-	+	+	+	+	+	-	-	+	-	-	-	-	-	-	-	-	-
Brypoctia kurupi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia monai	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia punctifer	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	+	+
Brypoctia ramosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia ramuscula	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia strigifer	-	+	+	+	+	+	+	+	-	-	-	-	-	-	-	-	-	-
Klagesiana amazoniensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 4. Distribution of Zeuzerinae species by country in the New World (part 2)

	Trinidad and Tobago	Jamaica	Guadeloupe	Cayman Islands	Martinique	Puerto Rico	Argentina	Bolivia	Brazil	Venezuela	Guyana	Colombia	Paraguay	Peru	Suriname	Uruguay	Ecuador	French Guiana
Psychonoctua albogrisea	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	+
Psychonoctua atra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua chaska	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Psychonoctua diiorioi	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua gilensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua itys	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-
Psychonoctua klagesi	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-

	Trinidad and Tobago	**Jamaica**	**Guadeloupe**	**Cayman Islands**	**Martinique**	**Puerto Rico**	**Argentina**	**Bolivia**	**Brazil**	**Venezuela**	**Guyana**	**Colombia**	**Paraguay**	**Peru**	**Suriname**	**Uruguay**	**Ecuador**	**French Guiana**
Psychonoctua kon	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Psychonoctua lineaeplena	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+
Psychonoctua personalis	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua thonyi	-	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-
Psychonoctua unilinea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Psychonoctua xuna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schreiteriana pectinicornis	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-
Carohamilia masoni	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia ophelia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia poam	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carohamilia terrafirma	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-
Allocryptobia musae	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	+	-
Ceuroma mucorea	-	-	-	-	-	-	-	-	+	+	-	-	+	+	-	-	-	-
Listrada sulbaiana	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Morpheis clenchi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis cognatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Morpheis comisteus	-	-	-	-	-	-	-	-	+	+	-	-	-	+	+	-	+	-
Morpheis humboldti	-	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	-
Morpheis impeditus	-	-	-	-	-	-	+	+	+	-	-	-	+	-	-	+	-	-
Morpheis mathani	-	-	-	-	-	-	-	+	+	-	+	-	-	+	-	-	+	+
Morpheis melanoleucus	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Morpheis votani	-	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-
Morpheis xylotribus	-	-	-	-	-	-	+	+	+	+	-	+	+	+	+	+	+	-
Brypoctia aeetes	+	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	+	+
Brypoctia desdemona	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-
Brypoctia eqaqo	-	-	-	-	-	-	+	+	-	-	-	-	-	+	-	-	-	-
Brypoctia greifensteini	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-
Brypoctia itzamna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia kurupi	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Brypoctia monai	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Brypoctia punctifer	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia ramosa	-	-	-	-	-	-	+	-	+	-	-	-	+	-	-	-	-	-

	Trinidad and Tobago	**Jamaica**	**Guadeloupe**	**Cayman Islands**	**Martinique**	**Puerto Rico**	**Argentina**	**Bolivia**	**Brazil**	**Venezuela**	**Guyana**	**Colombia**	**Paraguay**	**Peru**	**Suriname**	**Uruguay**	**Ecuador**	**French Guiana**
Brypoctia ramuscula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brypoctia strigifer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Klagesiana amazoniensis	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-

Moderate species richness is found in Colombia (seven species in five genera), Venezuela (six species in four genera), Paraguay (six species in four genera), and the USA (five species in four genera), as well as in Bolivia, Guatemala, and Belize (five species in three genera each), Panama (four species in four genera), and Honduras and French Guiana (four species in three genera each). Nicaragua and Saint Kitts and Nevis each contain two species in two genera. Only two species belonging to a single genus have been recorded from Suriname and Uruguay.

In a number of countries and island territories, only one species of Zeuzerinae has been recorded. These include Guyana, El Salvador, Antigua and Barbuda, the Bahamas, Barbados, Grenada, Dominica, Cuba, Saint Vincent and the Grenadines, Saint Lucia, Trinidad and Tobago, Jamaica, Guadeloupe, the Cayman Islands, Martinique, and Puerto Rico. This apparent faunal poverty is probably explained by a combination of small area, insularity, and insufficient study of the Lepidoptera fauna. The same is likely true for several island states from which Zeuzerinae have not yet been recorded and from which entomological material is either absent or extremely poorly represented.

VI. Analysis of species richness across biomes

The highest zeuzerine species richness is found in Tropical and Subtropical Moist Broadleaf Forests, where 35 species have been recorded. In Tropical and Subtropical Dry Broadleaf Forests, despite the more seasonal pattern of precipitation and less stable environmental conditions, 11 species have been recorded. The same number of species (11) occurs in Tropical and Subtropical Grasslands, Savannas and Shrublands. Temperate Grasslands, Savannas and Shrublands (4 species) and Deserts and Xeric Shrublands (4 species) are characterised by markedly lower species richness.

Thus, the highest species richness of Zeuzerinae is associated with more humid biomes with high plant productivity and diverse woody communities. Arid ecosystems are characterised by a marked decline in species richness within the subfamily.

VII. Comparison of Zeuzerinae faunas among biogeographical areas of the New World

The results of the analysis of Zeuzerinae faunas across different biogeographical areas of North and South America are illustrated in a dendrogram of species-composition similarity (Fig. 4). The Antillean subregion (the Antilles and the Bahamian Islands) was excluded from this analysis because its fauna is entirely unique at the species level.

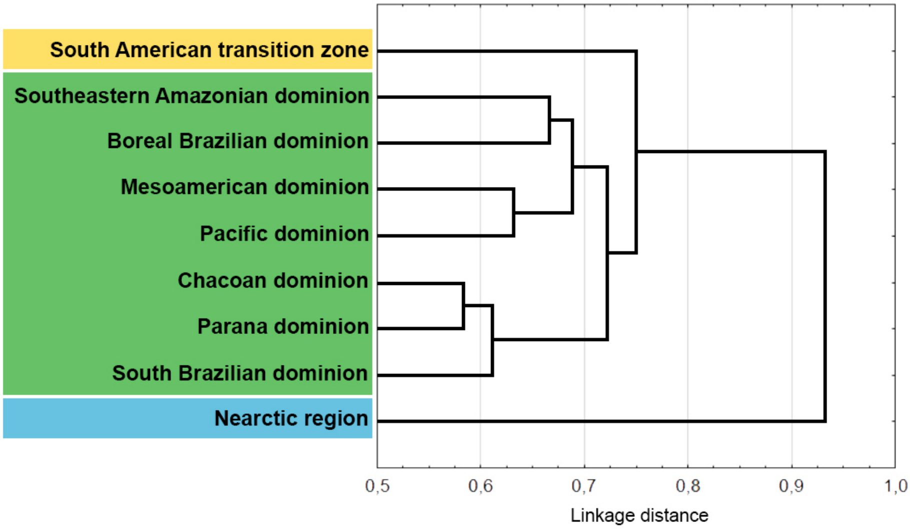

Figure 4. Tree diagram of similarity of Zeuzerinae species composition in the different areas of the New World. The green color indicates the dominions of the Neotropical region. Single-linkage clustering, Jaccard index.

All biogeographical units representing continental dominions of the Neotropical Region form a single cluster. Within this cluster, two subclusters may be recognised, corresponding broadly to the northern and southern parts of the Neotropics. The "northern subcluster" includes two paired groups: the Pacific and Mesoamerican dominions, and the Boreal Brazilian and South-eastern Amazonian dominions. The "southern subcluster" includes the most similar pair, the Paraná and Chacoan dominions, together with the adjacent South Brazilian dominion. The grouping of the South Brazilian dominion with the Paraná and Chacoan dominions contradicts the arrangement of biogeographical dominions into subregions proposed by Morrone (2014). This result is associated with the distribution patterns of a number of species (*Psychonoctua diiorioi*, *Schreiteriana pectinicornis*, *Morpheis melanoleucus*, *M. impeditus*, *M. votani*), whose ranges cover the Paraná and Chacoan dominions and whose western limits also include the Yungas Province, particularly its southern

Andean part, which is assigned to the South Brazilian dominion within the Brazilian subregion. This once again highlights the unique status of the Yungas Province as a faunal link between northern and southern Neotropical faunas. The placement of the South-eastern Amazonian dominion in the "northern subcluster" also contradicts the biogeographical system proposed by Morrone (2014). This is evidently related to *Morpheis mathani*, whose range extends broadly across Amazonia, a region divided among several biogeographical dominions. At the same time, the still insufficiently known Zeuzerinae fauna of the South-eastern Amazonian dominion, from which only two species have so far been recorded, does not allow this dominion to be assigned unambiguously to the "northern subcluster".

The results are broadly consistent with the biogeographical division of the New World, as reflected in the relative isolation of the South American Transition Zone from the Neotropical dominions and the even greater isolation of the Nearctic Region from all other biogeographical areas included in the comparison.

VIII. Analysis of endemism

An analysis of the distribution of endemic species and genera of the subfamily Zeuzerinae in the New World reveals several principal centres of endemism. These are listed below in descending order.

The South Brazilian dominion contains six endemic species and one endemic genus and therefore represents both a centre of endemism and the principal centre of species diversity of Zeuzerinae in the New World.

The Paraná dominion contains four endemic species and one endemic genus.

The Mesoamerican dominion contains four endemic species.

The arid southern provinces of the Nearctic Region (Mohavian, Sonoran, and Chihuahuan) contain three endemic species.

The Pacific dominion and the Antillean subregion each contain two endemic species.

Thus, the results indicate the presence of continental centres of endemism within the Neotropical Region, namely the South Brazilian, Paraná, Mesoamerican, and Pacific dominions, which also coincide with areas of high species and generic diversity; insular centres, represented by the West Indies, which broadly conform to general patterns of island endemism; and peripheral centres, represented by the southern Nearctic deserts at the northern limit of the natural range of Zeuzerinae in the New World, which are probably associated with adaptation to the distinctive conditions of the arid subtropical ecosystems of southern North America.

IX. Distinctiveness of the New World Zeuzerinae fauna and its relationships with other regions

At the species and genus levels, the Zeuzerinae fauna of the New World may be regarded as unique, with the sole exception of *Zeuzera pyrina*, which was introduced into North America. The only way to establish possible links between the faunas of the world's biogeographical regions is therefore through the recognition of suprageneric groupings within the subfamily. This is complicated, however, by the relative simplicity of genital morphology, the general uniformity of wing venation in most taxa, and the evident convergent similarity of a number of characters in the genital structures, wing pattern, and wing shape. These difficulties, together with the poor knowledge of female genital morphology in many genera, currently preclude the construction of a comprehensive phylogeny of the subfamily and a robust phylogeographical reconstruction based on morphology alone.

Suprageneric groupings within Zeuzerinae, as currently circumscribed, were first recognised by Houlbert (1916), who distinguished the tribe Xyleutinæ (= Xyleutini). Most of the species now assigned to the genus *Morpheis* were placed in the Neotropical subgenus *Neocossus* Houlbert, 1916, whereas *Xyleutes xylotriba* (Herrich-Schäffer, [1853]) (now *Morpheis xylotribus*), owing to its presumed resemblance to the African species *Xyleutes crassa* (Drury, 1782), was assigned by Houlbert to the subgenus *Strigocossus* Houlbert, 1916. The monophyly of the Neotropical genus *Morpheis* appears evident, as does its close relationship with another Neotropical genus, *Brypoctia* Schoorl, 1990. Species of these genera are characterised by distinctive genital features, including gnathos arms broadening into sclerotised, unfused plates and the presence of a papilliform harpe on the ventral side of the valve. Although the circumscription and limits of the tribe Xyleutini remain ambiguous, we are inclined to regard the Neotropical genera *Morpheis* and *Brypoctia*, together with *Allocryptobia*, *Ceuroma*, and *Listrada*, as belonging to a large assemblage of genera that also includes taxa from the Old World and the Australian Region: *Chalcidica* Hübner, [1820]; *Xyleutes* Hübner, [1820]; *Endoxyla* Herrich-Schäffer, [1854]; *Duomitus* Butler, 1880; *Strigocossus* Houlbert, 1916; *Alophonotus* Schoorl, 1990; *Catoxophylla* Turner, 1945; *Bergaris* Schoorl, 1990; *Eburgemellus* Schoorl, 1990; *Panau* Schoorl, 1990; *Paralophonotus* Schoorl, 1990; and *Pseudozeuzera* Schoorl, 1990. Representatives of all these genera are usually medium-sized to large moths and are generally characterised by antennae with a well-developed pectinate basal portion and a long distal serrate-filiform portion, as well as by the characteristic shape of the male wings. In most of them, the male forewing is narrow, with a well-developed apex and tornal angle and a slightly concave dorsal margin; the hindwing is only rarely rounded and more often has a distinct apex and a straight, more rarely concave, outer margin. Nevertheless, the lack of reliable morphological characters in the Zeuzerinae considered here does not currently allow the relationships between particular New World genera and genera from other biogeographical regions to be established with confidence.

A similar situation applies to such New World genera as *Psychonoctua*, *Schreiteriana*, and *Carohamilia*. On the basis of several characters, including a long, slender uncus, thin gnathos arms, and an elongate ovipositor, representatives of these taxa resemble numerous genera widely distributed in the Old World: *Azygophleps* Hampson, 1892; *Oreocossus* Aurivillius, 1910; *Phragmacossia* Schawerda, 1924;

Sympycnodes Turner, 1932; *Aethalopteryx* Schoorl, 1990; *Skeletophyllon* Schoorl, 1990; *Rapdalus* Schoorl, 1990; *Trismelasmos* Schoorl, 1990; *Sinjaeviella* Yakovlev, 2009; and *Acosma* Yakovlev, 2011. However, the lack of sufficiently informative diagnostic characters, combined with the independent acquisition of certain genital features, namely a papilliform harpe on the ventral side of the valve (in Schreiteriana, some species of *Skeletophyllon*, and *Acosma*) and narrowing and elongation of the phallus accompanied by enlargement of the saccus (in *Carohamilia* and some species of *Skeletophyllon*), currently precludes the recognition of natural suprageneric groups.

The most informative taxa for characterising the distinctiveness of the New World Zeuzerinae fauna are the morphologically most isolated genera of the subfamily. One such example is the monotypic genus *Klagesiana* Yakovlev, Naydenov & Penco, 2020, which is morphologically highly distinctive. Although *K. amazoniensis* externally resembles the *Zeuzera sensu lato* group in having white semi-translucent wings with a dark streaky pattern, the peculiarities of its wing venation and wing shape, the reduced pectination of the antennae, and the presence of a papilliform harpe on the ventral side of the valve do not allow this genus to be confidently associated with any known taxon of Zeuzerinae.

It should also be noted that a number of groups occurring in the Old World and the Australian Region are not represented in the Americas. For example, representatives of the tribe Cecryphalini, comprising two genera (*Cecryphalus* Schoorl, 1990 and *Tarsozeuzera* Schoorl, 1990), occur in the Old World and in the northern part of the Australian biogeographical region. Another fairly large assemblage absent from the New World includes the genera *Phragmataecia* Newman, 1950; *Relluna* Schoorl, 1990; *Sansara* Yakovlev, 2004; *Roerichiora* Yakovlev & Witt, 2009; and *Davidlivingstonia* Yakovlev, 2020. Females of these genera, where studied, have a short ovipositor and a relatively small bursa. On the basis of such general characters as relatively long and narrow valves, a broad and usually non-elongate uncus, weakly developed gnathos arms, and characteristic antennal structure, this assemblage may also include *Zeuzeropecten* Gaede, 1929; *Butaya* Yakovlev, 2004; *Lakshmia* Yakovlev, 2004; and *Wittoecia* Yakovlev, 2020. All representatives of these genera occur exclusively in the Palaearctic, Oriental, and Ethiopian regions. The *Zeuzera* group of genera is likewise absent from the New World. Its representatives are characterised by a typical external appearance, namely whitish, more or less semi-translucent wings with rows of black dots between the veins, sometimes passing into a striate or streaky pattern of varying intensity. This group includes the genera *Zeuzera* Latreille, 1804; *Neurozerra* Yakovlev, 2011; *Orientozeuzera* Yakovlev, 2011; *Polyphagozerra* Yakovlev, 2011; *Schoorlea* Yakovlev, 2011; *Zeuroepkia* Yakovlev, 2011; and *Zeurrora* Yakovlev, 2011, distributed in the Palaearctic, Oriental, and Australian regions. Also absent from the New World is the group of genera including *Eulophonotus* Felder, 1874 and *Rugigegat* Schoorl, 1990, whose representatives occur in the Ethiopian and Oriental regions. Males of species in these genera are characterised by relatively small body size, hyaline wings, a small hindwing, and a relatively broad forewing.

Overall, the Zeuzerinae fauna of the New World is characterised by relatively low taxonomic diversity. Whereas 45 species in 10 genera have been recorded from North and South America, 389 species in 46 genera are known from the Old World and the Australian Region. This low diversity is also reflected in the absence from the New World fauna of several generic groups, such as *Zeuzera*, *Eulophonotus*, and *Phragmataecia*, as well as the tribe Cecryphalini. At the same time, the distinctiveness of the New World fauna is enhanced by the presence of the morphologically isolated genus *Klagesiana* and by a number of unique morphological characters found in some Neotropical genera, which nevertheless appear to show affinities with the faunas of the Ethiopian, Oriental, Australian, and Palaearctic regions. At present, however, it is not possible to establish closer relationships between the New World Zeuzerinae fauna and the faunas of other continents, such as Africa or Australia. In theory, such relationships might be reflected in clearly delimited supra-generic groups and explained by palaeogeographical circumstances, including the prolonged connection between South America and Africa prior to their separation, as well as the existence of an Antarctic land bridge towards Australia. The morphological evidence currently available is insufficient for this purpose: on the one hand, the informative value of the characters is limited by the general simplicity of genital morphology; on the other, many characters show convergence, especially in size, wing shape, and wing pattern.

It should be emphasised that the principal stages in the formation of the modern Zeuzerinae fauna of the New World were associated primarily with the Neotropical Region, above all South America. This is indirectly indicated, on the one hand, by the markedly greater species richness of Zeuzerinae in South America than in North America and, on the other, by the overall concentration of diversity in the southern biogeographical regions (Ethiopian, Oriental, and Australian). Taken together, these observations are consistent with the hypothesis of a "southern" (provisionally Gondwanan) component in the early history of the group, although they do not in themselves allow the centre of origin to be localised with confidence and require testing on the basis of phylogenetic data. The present occurrence of Zeuzerinae in Central America and southern North America most probably reflects northward dispersal of Neotropical lineages towards the Nearctic, a process that may have intensified considerably with the formation of the Panamanian land corridor in the Late Pliocene. A similar interpretation of the northward expansion of South American lineages was previously proposed, in particular, for representatives of the tribe Xyleutini (Houlbert 1916).

Conclusion

The Zeuzerinae fauna of the New World currently comprises 45 valid species in 10 genera, including the introduced species *Zeuzera pyrina*. Analysis of distributional data allowed the range of the subfamily to be delimited, its natural distribution being confined to the subtropical deserts of North and South America and the *Tierra fría* belt of the Andes. On the basis of distributional data for each species, six provisional range groups were distinguished and characterised in the context of the accepted biogeographical regionalisation.

The analysis of taxonomic diversity also permitted an assessment of species and generic composition across the biogeographical units of the New World. The highest taxonomic diversity was recorded in the Yungas Province of the South Brazilian biogeographical dominion, with 14 species belonging to five genera. The South Brazilian dominion itself is the most species-rich of all biogeographical units examined, supporting 17 species in six genera. A similar analysis carried out at the country level showed that the highest species and generic diversity occurs in Brazil, where 15 species belonging to six genera have been recorded.

Analysis of Zeuzerinae species richness across the biomes of North and South America showed that representatives of the subfamily occur in five biomes, although the highest species richness (35 species) is found in Tropical and Subtropical Moist Broadleaf Forests. The principal centres of endemism were likewise identified. The most important of these lies within the South Brazilian dominion, which contains six endemic species and one endemic genus.

Assessment of similarity among the Zeuzerinae faunas of the biogeographical areas of the New World using the Jaccard index showed that the resulting dendrogram is broadly consistent with current concepts of zoogeographical regionalisation, except for the unique species composition of the Antillean subregion and the strong faunal affinity of the Yungas Province with the Paraná and Chacoan dominions.

The Zeuzerinae fauna of the New World is characterised by relatively low species and generic diversity compared with the faunas of the Old World and the Australian Region, while at the same time showing marked distinctiveness. The principal stages in the formation of the modern Zeuzerinae fauna of the New World appear to have taken place primarily in the Neotropical Region, above all in South America. This is consistent with the highest species richness of the group on that continent and supports the hypothesis of a “southern” (provisionally Gondwanan) component in its early history, whereas the occurrence of Zeuzerinae in Central America and the southern Nearctic is most probably associated with the dispersal of Neotropical lineages following the formation of the Panamanian land corridor in the Late Pliocene.

Nevertheless, the Neotropical Region remains one of the least studied regions of the world with respect to biodiversity. Given the faunistic richness of most Neotropical ecoregions, combined with the extremely limited geographic representation of entomological material in the world’s collections, numerous additional faunistic records are likely to be discovered, leading to substantial revision of current knowledge of species ranges, while many new taxa also remain to be described.

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