

Current status of dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) diversity and conservation in Natural Protected Areas in Chiapas (Mexico)

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Abstract

Natural Protected Areas (NPAs) are considered adequate tools for biodiversity conservation. Currently in Mexico there are 182 federal NPAs classified according to their management objectives. Chiapas is the Mexican state with the highest number of decreed NPAs and also allocates one of the largest territorial extensions for its protection. Unlike other taxa, and despite their proven ability to respond to ecosystem changes, the study of dung beetles within Mexican NPAs has been underestimated, as they are not considered as a priority group within their management and conservation programs. Based on the review of information available in publications and database on dung beetles, a list of 112 species and seven subspecies recorded in 16 of the 19 federal NPAs established in Chiapas is presented. The species recorded by each NPA show a significant correlation with the number of publications, but a

low percentage of them correspond to studies with systematic samplings and most of the species reported in several of the NPAs come from sporadic records, which prevents the study of several basic and applied aspects of dung beetles in the region. Therefore, studies that extensively analyze the communities of arthropod groups, such as the Scarabaeinae, are necessary to understand their response to changes in the ecosystem at local and regional scale. It is advisable that these insects be included in the previous justifying studies for the designation or establishment of NPAs and, in turn, considered in the biological monitoring programs of these areas for their capacity as a bioindicator group.

Keywords

bioindicator, biological monitoring, corridor, Faunistic complex, management, NPAs

Introduction

Natural Protected Areas (NPAs) are considered the main tool for the conservation of biological diversity worldwide (Bezaury-Creel and Gutiérrez Carbonell 2009). These are defined as areas that have been designated and regulated to achieve specific objectives of conservation, protection and maintenance of biological diversity, as well as associated natural and cultural resources (Dudley and Stolton 2008; Gillespie 2009). Mexican legislation conceptualizes NPAs as areas where the original environments have not been significantly altered by human activities, which need to be preserved or restored and are subject to the protection regime of the General Law of Ecological Balance and Environmental Protection (LGEEPA in Spanish) (SEMARNAT 2018).

The federal NPAs are those that are not restricted to a geopolitical limit within the Mexican territory and are managed by the National Commission of Natural Protected Areas (CONANP 2016). Currently, Mexico has a total of 182 federal NPAs that occupy about 13% of the national territory and are grouped into six different categories according to their management objectives and by the type of zoning that they may be subject to (Table 1) (Íñiguez et al. 2014; CONANP 2016). For now, Chiapas is the Mexican state with the highest number of decreed NPAs ($n = 19$) being the one that assigns one of the largest territorial extensions for its protection, as it is located in one of the zones richest in biodiversity and natural resources from the country (CONANP 2016).

The dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae) are a group of insects with a wide global distribution, finding representatives on all continents (except Antarctica), but whose diversity is mainly concentrated in the tropical and subtropical regions (Scholtz et al. 2009). The ecological functions in which these beetles are involved provide valuable ecosystem services, such as secondary seed dispersal, nutrient cycle and biological control of pests, among others (Nichols et al. 2008). Moreover, different authors have indicated that these arthropods are organisms sensitive to structural changes in habitats caused by disturbances, exhibiting drastic permutations in their development and distribution in the modified landscapes (Halffter and Favila 1993; Halffter and Arellano 2002; Arellano and Halffter 2003; Reyes-Novelo et al. 2007; Otavo et al. 2013; Mannu et al. 2018).

Table 1. Categories and main characteristics of the Mexican Natural Protected Areas, including their representativeness in Chiapas.

Categories	Mexico		Chiapas		Characteristics
	N	Extension in ha	n	Extension in ha (%)	
Flora and Fauna Protection Area	40	6,996,864.1	4	24,980.7 (0.36)	Its focus is towards the species conservation. The objective is to conserve the habitats where wild flora and fauna live, develop and evolve.
Natural Resources Protected Area	8	4,503,345.2	2	198,551.5 (4.41)	Areas dedicated to the preservation and protection of soils, watersheds and natural resources of forestlands. It includes protection areas of national water bodies, especially when they are used to supply human populations.
Natural Monument	5	16,269.1	2	6,978.7 (42.90)	Specific sites that contain natural elements with an exceptional value of aesthetic, historical or scientific type. Extractive type exploitation is banned.
National Park	67	16,220,099.3	3	29,583.4 (0.18)	They are sites with ecosystems that have mainly scenic beauty, historical, scientific, educational and recreational value, that preserve special flora and fauna and that present, above all, aptitude for tourism development.
Biosphere Reserve	44	62,952,750.5	7	932,095.8 (1.48)	They are established in places that represent the diversity of the country's ecosystems. Representativeness is also taken into account in terms of biological diversity and the presence of endemic, threatened or endangered species.
Sanctuary	18	150,193.3	1	212.5 (0.14)	They stand out for maintaining a high species richness or species of restricted distribution in delimited sites. This includes ravines, relicts, caves, cenotes, caletas and other specific geographical units
Total	182	90,839,521.5	19	1,192,402.6 (1.3)	

In order to understand the links between ecological functions and ecosystem services they offer, some authors have proposed the subfamily Scarabaeinae as a focus group for applied research in biodiversity conservation (Spector 2006; Nichols and Gardner 2011), categorizing it as a bioindicator that allows adequate monitoring of the impact of anthropic alterations in tropical forests (Halffter and Favila 1993; Favila and Halffter 1997; Spector 2006; Nichols et al. 2007). Despite the bioindicator potential offered by this group of insects, their study in the Mexican protected areas has been underestimated and, unlike other taxa (e.g. mammals and birds), they are not considered within their management and conservation programs. This work aims to provide an overview of the distribution of the Scarabaeinae species in the federal NPAs of the state of Chiapas in order to create a reference point for future biodiversity projects and their monitoring in these territories.

Materials and methods

Data source

Published studies on dung beetles species occurring in the federal NPAs of Chiapas (see Table 2) were checked in the academic databases Google Scholar (www.scholar.google.com), SciELO (www.scielo.org), Web of Science (www.isiwebofknowledge.com) and Scopus (www.scopus.com). This search was performed using commonly

Table 2. Characteristics of the 19 federal Natural Protected Areas decreed in Chiapas¹.

Categories	Name	Acronym	Year of decree	Extension (ha)	Main vegetation types*
Flora and Fauna Protected Area	Aqua Azul	APFFAA	1980	2,580	TRF
	Chan-Kin	APFFCK	1992	12,184.98	TRF, MRF, SV, HV
	Metzabok	APFFM	1998	3,841.47	TRF, ECF, OF, SV
	Nahá	APFFN	1998	3,368.36	TRF, MRF, ECF
Natural Resources Protected Area	La Frailescana	APRNF	1997	177,546.17	TDF, TRF, MRF
	Villa Allende	APRNVA	1939	21,005.27	TDF, ECF, MRF, OF
Natural Monument	Yaxchilán	MNY	1992	2,621.25	TRF
	Bonampak	MNB	1992	4,357.42	TRF, MRF, ECF
National Park	Cañón del Sumidero	PNCS	1980	21,789.42	TDF, MRF, XV, SV
	Lagunas de Montebello	PNLM	1959	6,022	OF, ECF, SV
	Palenque	PNP	1981	1,772	TRF, G
Biosphere Reserve	Lacan-Tun	REBILA	1992	61,873.96	TRF, HV
	Selva El Ocote	REBISO	1982	101,288.15	TRF, MRF, SV
	El Triunfo	REBITRI	1990	119,177.29	ECF, TRF
	La Encrucijada	REBIEN	1995	144,868.16	M, MRF, TDF, CD
	La Sepultura	REBISE	1995	167,309.86	OF, PF, OFP, MRF, SV
	Montes Azules	REBIMA	1978	331,200	TRF, MRF, POF, ECF
	Volcán Tacaná	REBIVTA	2003	6,378.37	ECF, MRF
	Playa de Puerto Arista	SPPA	1986	212.48	CD, M, HV, TDF

TRF: tropical rainforest; MRF: mountain rainforest; TDF: tropical deciduous forest; ECF: evergreen cloud forest; PF: pine forest; POF: pine-oak forest; OFP: oak-pine forest; SV: secondary vegetation; XV: xerophytic vegetation; HV: hydrophilic vegetation; M: mangrove; CD: coastal dunes; G: grassland. ¹CONANP (2016). *According Breedlove (1981).

used keywords to name the species of the subfamily Scarabaeinae, as well as terms related to the designations of the NPAs of Chiapas and any possible combination between them (and equivalent terms in Spanish): “dung beetles”, “Scarabaeinae”, coprophagous”, “necrophilous”, “copronecrophagous”, “Chiapas”, “National Park”, “Biosphere Reserve”, “protected area”, “rain forest”, “cloud forest”, “deciduous forest”, “Lacandonia rainforest”. Subsequently, a manual search of publications that potentially contained data on dung beetles was carried out to avoid the exclusion of information not contained in the academic databases (i.e. printed papers not available online), but bypassing literature that does not conform adequately to the bibliographic control standards (e.g. thesis or technical reports). According to the studies approach, the selected publications were classified into three general topics: 1) Taxonomic (works containing supra-specific monographic reviews and description of new species), 2) ecological/faunistic (systematic sampling with lists of species and analysis of assemblages of a specific region or location) and, 3) geographical distribution (works that include geographic range extension data). In addition, records were obtained from the Global Biodiversity Information Facility database (GBIF 2019).

Institutional acronyms

The records obtained from the GBIF database come from the following entomological collections:

CACH Colección Entomológica, Facultad de Ciencias Agronómicas, Universidad Autónoma de Chiapas, Chiapas, México;

CADR	Colección Alfonso Díaz Rojas, Xalapa, Veracruz, México;
CEUA	Colección Entomológica Universidad de Alicante, Alicante, España;
CDNG	Colección Darío Navarrete Gutiérrez, San Cristóbal de Las Casas, Chiapas, México;
CMNEN	Canadian Museum of Nature Insect Collection, Ontario, Canada;
CNCI	Canadian National Collection of Insects, Ontario, Canada;
CNIABM	Colección Nacional de Insectos Dr. Alfredo Barrera Marín, México;
CNIN	Colección Nacional de Insectos, Universidad Nacional Autónoma de México, Ciudad de México, México;
CZRN	Colección Entomológica, Instituto de Historia Natural y Ecología, Chiapas, México;
ECO-SC-E	Colección Entomológica, El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México;
ECO-TAP-E	Colección Entomológica, El Colegio de la Frontera Sur, Tapachula, Chiapas, México;
ERCVC	Colección Eduardo Rafael Chamé Vázquez, Tapachula, Chiapas, México;
FVMC	Fernando Zagury Vaz de Mello Collection, Cuiabá, Brazil;
GHAC	Colección Gonzalo Halffter, Xalapa, Veracruz, México;
IAvH-E	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia;
IEXA	Colección Entomológica Instituto de Ecología, Xalapa, Veracruz, México;
MXAL	Colección Miguel Ángel Morón, Xalapa, Veracruz, México;
SEMC	Snow Entomological Museum Collection, University of Kansas, Kansas, United States of America;
SMCC	Scott McCleve Collection, Arizona, United States of America;
TAMU	Texas A&M University Insect Collection, Texas, United States of America;
UAIC	University of Arizona Insect Collection, Arizona, United States of America.

The list of species obtained was reviewed and updated according to the supra-generic designation proposed by Bouchard et al. (2011) and although there are 11 recognized tribes, only seven are found in Mexico. Supra-specific revisions of the genera *Canthon* (Rivera-Cervantes and Halffter 1999), *Coprophanaeus* (Edmonds and Zídek 2010), *Deltochilum* (Génier 2012; González-Alvarado and Vaz-de-Mello 2014; Silva et al. 2015), *Dichotomius* (López-Guerrero 2005), *Martinezidium* (Vaz-de-Mello 2008) and *Phanaeus* (Edmonds and Zídek 2012), were also taken into account because they include changes of status for several species on the list. Some species were omitted from the list and those records were considered erroneous or corresponded to incorrect geographic records (see discussion). Finally, a review of the red list of threatened species of the International Union for the Conservation of Nature (IUCN 2018) was carried out to include the status in which the species on the list could be considered.

Data analysis

We use simple linear regressions to determine the influence of the number of publications in each NPA and its area size (has) with the number of species that each one recorded. This analysis was performed in the R software (R Core Team 2019) and using the ggplot2 package (Wickham 2020). To determine any similarities in the species composition between NPAs, a cluster analysis was performed using the unweighted pair group method (UPGMA), calculated with the Simpson index in the software PAST v.3.26 (Hammer et al. 2001). To avoid bias due to faunistic disproportion and aggregation by inclusion, NPAs with a record equal to or less than five species were omitted from the similarity analysis.

Results

A total of 112 species and seven subspecies belonging to 23 genera, seven tribes and four subtribes of the subfamily Scarabaeinae were found (Table 3). Tribe Deltochilini included the largest number of genera and species (six genera, 27 spp), followed by Ateuchini at the generic level (five genera) and Onthophagini for their number of species (25 spp). Sisyphini is the least representative tribe with only one species. *Onthophagus* and *Canthon* are the most diversified genera, with 24 and 15 species, respectively, which together represent 34.82% of the total species, while eight genera are represented by only one species (Fig. 1).

A total of 47 publications provided records of 104 species, of which 48.9% ($n = 23$) corresponded to taxonomic studies, 31.9% ($n = 15$) were ecological/faunistic works and only 19.2% ($n = 9$) presented geographic distribution data. For its part, the GBIF database presented records that corresponded to 94 species. *Canthon indigaceus chevrolati* (Harold, 1868), *Eurysternus plebejus* Harold, 1880, *Onthophagus championi* Bates, 1887, *O. corrosus* (Bates, 1887), *O. guatemalensis* Bates, 1887, *O. marginicollis* Harold, 1880, *O. nasicornis* Harold, 1869 and *O. sharpi* Harold, 1875, were not registered in any of the publications, so they were exclusive records from this database (Table 3).

Of the 19 NPAs analyzed, 16 presented records of Scarabaeinae (84.2%), except APFFAA, APFFCK and REBILA (Fig. 2). The species reported showed a significant relation with the number of publications that registered them in each NPA ($R^2 = 0.80$, $F = 56.47$, $P = 0.0001$, Fig. 3A) but not with the area size of each one of them ($R^2 = 0.069$, $F = 1.039$, $P = 0.325$, Fig. 3B). REBIMA and REBISO highlighted for presenting the largest number of registered species, both with 61, while APFFM, REBIEN and SPPA presented records of only one species (Fig. 4). At least 20 taxa (species and subspecies) have been described from organisms collected in ten of the NPAs studied. According to the IUCN red list of threatened species, 13 species are found in two low-risk categories, 12 in the least concern category and only one as near threatened (Table 3).

A high specificity of species was found for the NPAs, with 33 species (29.5%) registered in a protected area alone: REBIMA ($n = 7$), REBISO ($n = 6$), APRNVA

Table 3. List of the dung beetle species registered in the Natural Protected Areas of Chiapas, Mexico.

Species	NPAs	Resources
Ateuchini, Ateuchina		
<i>Ateuchus candezei</i> (Harold, 1868)	PNLM, PNP, REBIMA	Kohlmann 1984, 1997, 2000; Morón et al. 1985; Navarrete and Halffter 2008a; Delgado et al. 2012; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Ateuchus chrysopyge</i> (Bates, 1887)	PNLM, REBIMA, REBISO	Kohlmann 2000; Navarrete and Halffter 2008a, b; Sánchez-de-Jesús et al. 2016; GBIF 2019
¹ <i>Ateuchus guatemalensis</i> (Bates, 1887)	REBIVTA	Kohlmann 2000
<i>Ateuchus illaesum</i> (Harold, 1868)	PNLM, REBIMA, REBIVTA	Kohlmann 1984; Coutiño et al. 2005; Santos-Heredia et al. 2018; GBIF 2019
* <i>Ateuchus laetitia</i> Kohlmann, 1981	REBIMA	Kohlmann 1981, 1984
* <i>Ateuchus perezvelai</i> Kohlmann, 2000	REBISO	Gómez et al. 2017; Sánchez-Hernández et al. 2018
<i>Ateuchus rodriguezi</i> (Preudhomme de Borre, 1886)	REBISO, REBIVTA, APRNVA	Kohlmann 1984, 1997; Arellano et al. 2008, 2009, 2013; Cancino-López et al. 2014; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Bdelyropsis bowditchi</i> Paulian, 1939	REBIMA, MNB, MNY	Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018
* ² <i>Bdelyropsis newtoni</i> Howden, 1971	PNP	Howden 1971
<i>Uroxys boneti</i> Pereira & Halffter, 1961	MNB, PNP, REBIMA, REBISO	Halffter et al. 1992; Delgado and Kohlmann 2007; GBIF 2019
* <i>Uroxys deavilai</i> Delgado & Kohlmann, 2007	PNCS, REBISO, APRNVA	Delgado and Kohlmann 2007; Arellano et al. 2008, 2009, 2013; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Uroxys microcularis</i> Howden & Young, 1981	MNB, MNY, REBIMA, REBISO	Delgado and Kohlmann 2007; Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; Gómez et al. 2017; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Uroxys micros</i> Bates, 1887	PNP, REBIMA, MNY	Delgado and Kohlmann 2007; Sánchez-de-Jesús et al. 2016; GBIF 2019
<i>Uroxys platypyga</i> Howden & Young, 1981	MNB, REBIMA	Delgado and Kohlmann 2007; Navarrete and Halffter 2008a, b; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
* <i>Uroxys tacanensis</i> Delgado & Kohlmann, 2007	REBIVTA	Delgado and Kohlmann 2007
Ateuchini, Scatimina		
* <i>Martinezidium maya</i> (Vaz-de-Mello, Halffter & Halffter, 2004)	PNCS, APRNVA	Vaz-de-Mello et al. 2004; Vaz-de-Mello 2008; Arellano et al. 2009, 2013; GBIF 2019
<i>Scatimus ovatus</i> Harold, 1862	MNB, PNLM, PNCS, REBIMA, REBISE, REBISO, APRNVA	Génier and Kohlmann 2003; Arellano et al. 2008; Navarrete and Halffter 2008a; Arellano et al. 2009, 2013; Sánchez-de-Jesús et al. 2016; Gómez et al. 2017; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
Coprin		
<i>Canthidium ardens</i> Bates, 1887	REBIMA, REBIVTA, APRNVA	Arellano et al. 2008; Navarrete and Halffter 2008a; Cancino-López et al. 2014; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Canthidium centrale</i> Boucomont, 1928	MNB, REBIMA, REBISE, REBISO, MNY	Palacios-Ríos et al. 1990; Morón et al. 1985; Kohlmann and Solís 2006; Navarrete and Halffter 2008; Blas and Gómez 2009; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Canthidium laetum</i> Harold, 1867	APRNVA	Arellano et al. 2009, 2013; GBIF 2019
* <i>Canthidium moroni</i> Kohlmann & Solís, 2006	APFFN, REBIMA, REBISO	Kohlmann and Solís 2006; Gómez et al. 2017
* <i>Canthidium pseudoperceptibile</i> Kohlmann & Solís, 2006	MNB, APFFN, APRNVA, REBIMA, REBISO	Kohlmann and Solís 2006; Sánchez-Hernández et al. 2018; GBIF 2019
* <i>Canthidium pseudopuncticolle</i> Solís & Kohlmann, 2004	REBISO	Kohlmann and Solís 2006; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Canthidium vespertinum</i> Howden & Young, 1981	REBIMA	Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; GBIF 2019
* <i>Copris costaricensis dolichocerus</i> Matthews, 1961	REBIVTA	Matthews 1961; Coutiño et al. 2005; Cancino-López et al. 2014; GBIF 2019

Species	NPAs	Resources
<i>Copris incertus</i> Say, 1835	APRNVA, REBIVTA, PNCS	Arellano et al. 2009, 2013; GBIF 2019
<i>Copris laeviceps</i> Harold, 1862	PNP, REBIMA, REBISO, MNY, APRNVA, PNCS	Morón et al. 1985; Palacios-Ríos et al. 1990; Arellano et al. 2008; Navarrete and Halfpter 2008a; Arellano et al. 2009, 2013; Sánchez-de-Jesús et al. 2016; Gómez et al. 2017; Darling and Génier 2018; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Copris lugubris</i> Boheman, 1858	APRN, PNLM, REBISO, REBISE, APFFN, REBIMA, REBITRI, MNY, REBIVTA, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Arellano et al. 2008, 2009; Blas and Gómez 2009; Navarrete and Halfpter 2008a; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Darling and Génier 2018; Santos-Heredia et al. 2018; GBIF 2019
* ¹ <i>Copris matthewsi matthewsi</i> Delgado & Kohlmann, 2001	PNLM	Delgado and Kohlmann 2001
* ¹ <i>Copris matthewsi pacificus</i> Delgado & Kohlmann, 2001	REBITRI, REBIVTA	Delgado and Kohlmann 2001; Coutiño et al. 2005; Cancino-López et al. 2014
<i>Dichotomius amplicollis</i> (Harold, 1869)	PNLM, PNP, PNCS, REBIMA, REBISO, APRNF, REBITRI, APRNAVA,	Morón et al. 1985; Halfpter et al. 1992; Arellano et al. 2008, 2009; Blas and Gómez 2009; Navarrete and Halfpter 2008a; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Dichotomius annae</i> Kohlmann & Solís, 1997	REBIMA, REBISE, REBITRI, REBIVTA	Coutiño et al. 2005; Navarrete and Halfpter 2008; Sánchez-de-Jesús et al. 2016; GBIF 2019
<i>Dichotomius colonicus</i> Say, 1835	PNLM, PNCS, PNP, REBIMA, APRNF, REBISE, APRNVA, REBISO, REBITRI, REBIVTA	Arellano et al. 2008, 2009; Delgado et al. 2012; Arellano et al. 2013, Gómez et al. 2017; GBIF 2019
¹ <i>Dichotomius maya</i> Peraza & Deloya, 2006	REBISO	Sánchez-Hernández et al. 2019
<i>Dichotomius satanas</i> Harold, 1867	APRNVA, PNLM, PNP, REBIMA, REBISO, MNY	Morón et al. 1985; Palacios-Ríos et al. 1990; Halfpter et al. 1992; Navarrete and Halfpter 2008; Blas and Gómez 2009; Delgado et al. 2012; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
¹ <i>Ontherus azteca</i> Harold, 1869	REBIMA, REBISO	Génier 1996; Navarrete and Halfpter 2008a; GBIF 2019
* <i>Ontherus mexicanus</i> Harold, 1868	PNLM, REBISO	Génier 1996; Gómez et al. 2017
Deltochilini		
<i>Agamopus lampros</i> Bates, 1887	APRNVA	Arellano et al. 2008, 2009, 2013
<i>Canthon angustatus</i> Harold, 1867	PNP, REBIMA	Chamé-Vázquez and Gómez 2005; Navarrete and Halfpter 2008a; Halfpter and Halfpter 2009; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Canthon championi</i> Bates, 1887	REBISO, REBITRI	Blas and Gómez 2009; GBIF 2019
<i>Canthon cyanellus</i> LeConte, 1859	REBISO, PNCS, PNP, REBIMA, REBIVTA, MNY, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Halfpter et al. 1992; Arellano et al. 2008, 2009; Navarrete and Halfpter 2008a; Blas and Gómez 2009; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Canthon delgadoi</i> Rivera-Cervantes & Halfpter, 1999	APRNVA	Arellano et al. 2008, 2009; Halfpter and Halfpter 2009; Arellano et al. 2013; GBIF 2019
<i>Canthon euryscelis</i> Bates, 1887	MNB, PNP, MNY, REBISO, REBIMA	Morón et al. 1985; Rivera-Cervantes and Halfpter 1999; Navarrete and Halfpter 2008a; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Canthon femoralis</i> (Chevrolat, 1834)	PNCS, REBIMA, PNP, REBISO, REBISE, MNY, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Rivera-Cervantes and Halfpter 1999; Navarrete and Halfpter 2008a; Arellano et al. 2009, 2013; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Canthon humectus incisus</i> Robinson, 1948	PNLM, APRNVA, PNCS	Delgado et al. 2012; GBIF 2019
<i>Canthon humectus sayi</i> Robinson, 1948	APRNVA, PNCS	Arellano et al. 2008, 2009, 2013; GBIF 2019
¹ <i>Canthon indigaceus chevrolati</i> Harold, 1868	PNCS, REBIEN	GBIF 2019

Species	NPAs	Resources
<i>Canthon indigaceus chiapas</i> Robinson, 1948	APRNVA, PNCS, PNLM, REBISE, REBISO	Arellano et al. 2008, 2009; Blas and Gómez 2009; Arellano et al. 2013; GBIF 2019
<i>Canthon leechi</i> (Martínez, Halffter & Halffter, 1964)	PNCS, PNLM, PNP, REBIMA, REBISE, REBISO	Halffter et al. 1992; Rivera-Cervantes and Halffter 1999; Navarrete and Halffter 2008; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Canthon lituratus</i> (Germar, 1813)	REBIMA	Navarrete and Halffter 2008a, b; GBIF 2019
* <i>Canthon lucreciae</i> Halffter & Halffter, 2009	APRNVA	Halffter and Halffter 2009; Arellano et al. 2013
<i>Canthon meridionalis</i> (Martínez, Halffter & Halffter, 1964)	REBISO	Gómez et al. 2017
<i>Canthon morsei</i> Howden, 1966	MNY, PNP, REBIMA, REBISO	Palacios-Ríos et al. 1990; Navarrete and Halffter 2008a; Halffter and Halffter 2009; Sánchez-de-Jesús et al. 2016; GBIF 2019
<i>Canthon subhyalinus subhyalinus</i> Harold, 1867	MNB, MNY, PNP, REBIMA, REBISO	Palacios-Ríos et al. 1990; Halffter et al. 1992; Rivera-Cervantes and Halffter 1999; Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Canthon vazquezae</i> (Martínez, Halffter & Halffter, 1964)	MNB, MNY, PNCS, PNP, REBIMA, REBISE, REBISO, APRNVA	Palacios-Ríos et al. 1990; Rivera-Cervantes and Halffter 1999; Arellano et al. 2008; Blas and Gómez 2009; Sánchez-Hernández et al. 2018; GBIF 2019
* <i>Cryptocanthon montebello</i> Cook, 2002	PNLM	Cook 2002; GBIF 2019
<i>Deltochilum acropyge</i> Bates, 1887	REBISO, MNY	Cano 1998; Blas and Gómez 2009; GBIF 2019
* <i>Deltochilum carilloi</i> González-Alvarado & Vaz-de-Mello, 2014	REBISO, REBIMA, APRNVA	González-Alvarado and Vaz-de-Mello 2014
<i>Deltochilum densepunctatum</i> Balthasar, 1939	REBISO	González-Alvarado and Vaz-de-Mello 2014
<i>Deltochilum lobipes</i> Bates, 1887	REBIMA, APRNVA	Arellano et al. 2008, 2009; Navarrete and Halffter 2008a; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Deltochilum mexicanum</i> Burmeister, 1848	PNLM, REBISO, REBITRI, REBIVTA	Coutiño et al. 2005; Blas and Gómez 2009; Delgado et al. 2012; Cancino-López et al. 2014; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Deltochilum pseudoparile</i> Paulian, 1938	PNP, REBIMA, REBISO, MNB, MNY, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Navarrete and Halffter 2008a; Blas and Gómez 2009; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Deltochilum scabriuscum</i> Bates, 1887	PNCS, PNLM, PNP, REBIMA, REBISE, REBISO, REBITRI, MNY, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Arellano et al. 2008, 2009; Navarrete and Halffter 2008a; Génier 2012; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Deltochilum sublaeve</i> Bates, 1887	PNLM, PNP, MNY, APRNVA, REBIMA, REBISO, REBITRI, REBIVTA	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Navarrete and Halffter 2008; Arellano et al. 2009; Blas and Gómez 2009; Arellano et al. 2013; Cancino-López et al. 2014; González-Alvarado and Vaz-de-Mello 2014; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Megathoposoma candezei</i> Harold, 1873	MNY, PNP, REBIMA	Morón et al. 1985; Halffter et al. 1992; Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Pseudocanthon perplexus</i> (LeConte, 1847)	APRNVA, PNCS, PNP	Arellano et al. 2008; GBIF 2019
Oniticellini, Eurysternina		
<i>Eurysternus angustulus</i> Harold, 1869	APFFM, MNB, PNP, REBIMA, REBISO, MNY	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Navarrete and Halffter 2008a; Génier 2009; Sánchez-de-Jesús et al. 2016; Gómez et al. 2017; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Eurysternus caribaeus</i> Herbst, 1789	MNB, PNLM, PNP, REBIMA, REBISO, MNY	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Navarrete and Halffter 2008a; Blas and Gómez 2009; Génier 2009; Delgado et al. 2012; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019

Species	NPAs	Resources
<i>Eurysternus foedus</i> Guérin, 1844	REBIMA, REBISO,	Morón et al. 1985; Navarrete and Halffter 2008a; Génier 2009; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Eurysternus magnus</i> Castelnau, 1840	APRN, PNLM, PNCS, PNP, REBIMA, REBISE, REBISO, REBIVTA	Coutiño et al. 2005; Génier 2009; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; GBIF 2019
* <i>Eurysternus maya</i> Génier, 2009	MNB	Génier 2009
<i>Eurysternus mexicanus</i> Harold, 1869	MNB, PNLM, PNP, REBIMA, REBISO, APRNVA, MNY	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Navarrete and Halffter 2008a; Arellano et al. 2009; Génier 2009; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Eurysternus plebejus</i> Harold, 1880	REBIMA	GBIF 2019
<i>Eurysternus velutinus</i> Bates, 1887	REBIMA	Morón et al. 1985
Oniticellini, Oniticellina		
* <i>Euoniticellus intermedius</i> (Reiche, 1849)	REBISE, REBISO, REBITRI, APRNVA, REBIVTA	Morales et al. 2004; Coutiño et al. 2005; Arellano et al. 2008, 2009, 2013; GBIF 2019
Onthophagini		
* <i>Digitonthophagus gazella</i> (Fabricius, 1757)	REBISO, REBITRI, SPPA, PNP, APRNVA, APRNF	Morales et al. 2004; Arellano et al. 2008; GBIF 2019
<i>Onthophagus acuminatus</i> Harold, 1880	REBIMA, APRNVA	Delgado 1997; Navarrete and Halffter 2008a; Arellano et al. 2009, 2013; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Onthophagus anthracinus</i> Harold, 1873	REBISO, REBIVTA	Coutiño et al. 2005; Cancino-López et al. 2014; Gómez et al. 2017; GBIF 2019
<i>Onthophagus batesi</i> Howden & Cartwright, 1963	PNLM, PNCS, REBIMA, REBISE, REBISO, REBITRI, PNP, MNY, APRNVA	Palacios-Ríos et al. 1990; Halffter et al. 1992; Arellano et al. 2008; Navarrete and Halffter 2008a; Delgado et al. 2012; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Gómez et al. 2017; Santos-Heredia et al. 2018; GBIF 2019
<i>Onthophagus belorhinus</i> Bates, 1887	REBISE	GBIF 2019
* <i>Onthophagus carpophilus</i> Pereira & Halffter, 1961	APFFN, REBIMA, REBISO, MNY, PNP	Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Onthophagus championi</i> Bates 1887	REBISE	GBIF 2019
* <i>Onthophagus chiapanecus</i> Zunino & Halffter, 1988	REBISE, REBITRI	Zunino and Halffter 1988; GBIF 2019
<i>Onthophagus coscineus</i> Bates, 1887	REBIMA	Delgado 1997; Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; Santos-Heredia et al. 2018; GBIF 2019
<i>Onthophagus corrosus</i> Bates, 1887	PNP	GBIF 2019
<i>Onthophagus crinitus</i> Harold, 1869	PNP, REBIMA, REBISO, MNY, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Arellano et al. 2008; Navarrete and Halffter 2008a; Blas and Gómez 2009; Arellano et al. 2013; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Onthophagus cyanellus</i> Bates, 1887	PNLM, REBISE, REBITRI, REBIVTA	Coutiño et al. 2005; Delgado et al. 2012; Cancino-López et al. 2014; GBIF 2019
<i>Onthophagus cyclographus</i> Bates, 1887	PNLM, REBIMA, REBISO	Navarrete and Halffter 2008a; Sánchez-Hernández et al. 2018
<i>Onthophagus guatemalensis</i> Bates, 1887	REBISE, REBITRI, PNP	GBIF 2019
<i>Onthophagus igualensis</i> Bates, 1887	APRNVA, PNCS, PNP, REBISE, REBITRI	Arellano et al. 2008, 2013; GBIF 2019
<i>Onthophagus incensus</i> Say, 1835	REBIMA, REBISO, REBIVTA, PNP, MNY	Coutiño et al. 2005; Navarrete and Halffter 2008a; Cancino-López et al. 2014; Gómez et al. 2017; Sánchez-Hernández et al. 2018; GBIF 2019

Species	NPAs	Resources
<i>Onthophagus landolti</i> Harold, 1880	PNP, REBISO, APRNVA	Halffter et al. 1992; Kohlmann and Solís 2001; Arellano et al. 2009, 2013; Gómez et al. 2017; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Onthophagus longimanus</i> Bates, 1887	REBISO	Sánchez-Hernández et al. 2017; Sánchez-Hernández et al. 2018
<i>Onthophagus marginicollis</i> Harold, 1880	PNP	GBIF 2019
* <i>Onthophagus maya</i> Zunino, 1981	REBIMA, REBISE, REBISO, MNY, PNP	Morón et al. 1985; Palacios-Ríos et al. 1990; Blas and Gómez 2009; Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Onthophagus nasicornis</i> Harold, 1869	REBIMA, PNP	GBIF 2019
<i>Onthophagus rhinolophus</i> Harold, 1869	PNLM, PNP, REBIMA, REBISO, MNY	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Navarrete and Halffter 2008a; Blas and Gómez 2009; Delgado et al. 2012; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Onthophagus sharpi</i> Harold, 1875	PNP	GBIF 2019
<i>Onthophagus violetae</i> Zunino & Halffter, 1997	APRNVA, APFFN	Arellano et al. 2009, 2013; GBIF 2019
<i>Onthophagus yucatanus</i> Delgado, Peraza & Deloya, 2006	REBIMA, REBISO	Navarrete and Halffter 2008a, b; Sánchez-de-Jesús et al. 2016; Gómez et al. 2017; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018
Phanaeini		
¹ <i>Coprophanaeus corythus</i> Harold, 1863	MNB, PNP, REBIVTA, REBIMA, REBISO, MNY, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Coutiño et al. 2005; Arellano et al. 2008, 2009; Navarrete and Halffter 2008a; Blas and Gómez 2009; Edmonds and Zidek 2010; Arellano et al. 2013; Cancino-López et al. 2014; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Coprophanaeus gilli</i> Arnaud, 1997	MNB, REBIMA, REBISO, PNP	Navarrete and Halffter 2008a, Edmonds and Zidek 2010; Sánchez-Hernández et al. 2018; GBIF 2019
<i>Coprophanaeus pluto</i> Harold, 1863	REBITRI	Edmonds and Zidek 2010; GBIF 2019
<i>Phanaeus amethystinus</i> Harold, 1863	MNY, PNLM, REBISE, REBITRI	Edmonds 1994; GBIF 2019
<i>Phanaeus demon</i> Castelnau, 1840	REBISE, APRNVA, PNCS	Edmonds 1994; Arellano et al. 2009, 2013; GBIF 2019
<i>Phanaeus endymion</i> Harold, 1863	MNB, PNCS, PNLM, PNP, REBIMA, REBISO, REBIVTA, MNY, APRNVA	Morón et al. 1985; Palacios-Ríos et al. 1990; Halffter et al. 1992; Edmonds 1994; Navarrete and Halffter 2008a; Blas and Gómez 2009; Arellano et al. 2013; Cancino-López et al. 2014; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
<i>Phanaeus guatemalensis</i> Harold, 1871	REBIVTA	Coutiño et al. 2005; Cancino-López et al. 2014; GBIF 2019
<i>Phanaeus melampus</i> Harold, 1863	REBIMA	Navarrete and Edmonds 2006; Navarrete and Halffter 2008a; GBIF 2019
<i>Phanaeus pilatei</i> Harold, 1863	MNY	Palacios-Ríos et al. 1990
¹ <i>Phanaeus pyrois</i> Bates, 1887	REBISO, REBIVTA, APRNVA	Delgado 1997; Arellano et al. 2008, 2009; Blas and Gómez 2009; GBIF 2019
<i>Phanaeus sallei</i> Harold, 1866	MNB, MNY, PNP, PNLM REBIMA, REBISO	Morón et al. 1985; Halffter et al. 1992; Edmonds 1994; Navarrete and Halffter 2008a; Palacios-Ríos et al. 1990; Sánchez-de-Jesús et al. 2016; Sánchez-Hernández et al. 2018; Santos-Heredia et al. 2018; GBIF 2019
¹ <i>Phanaeus tridens</i> Laporte-Castelnau, 1840	REBISE, REBISO, REBITRI, PNCS, APRNVA	Edmonds 1994; Arellano et al. 2009, 2013; GBIF 2019
<i>Phanaeus wagneri</i> Harold, 1873	PNLM, PNCS, APRNVA	Edmonds 1994; Arellano et al. 2008, 2009, 2013
<i>Sulcophanaeus chryseicollis</i> (Harold, 1863)	MNB, REBIMA, REBISO, PNP	Halffter et al. 1992; Edmonds 2000; Navarrete and Halffter 2008a; Sánchez-de-Jesús et al. 2016; GBIF 2019
Sisyphini		
<i>Sisyphus mexicanus</i> Harold, 1863	REBITRI	Gómez and Chamé-Vázquez 2003; GBIF 2019

*Species/subspecies described from organisms collected in Natural Protected Areas of Chiapas. ¹Invasive species. ²Least concern and ³Near threatened in the IUCN Red List.

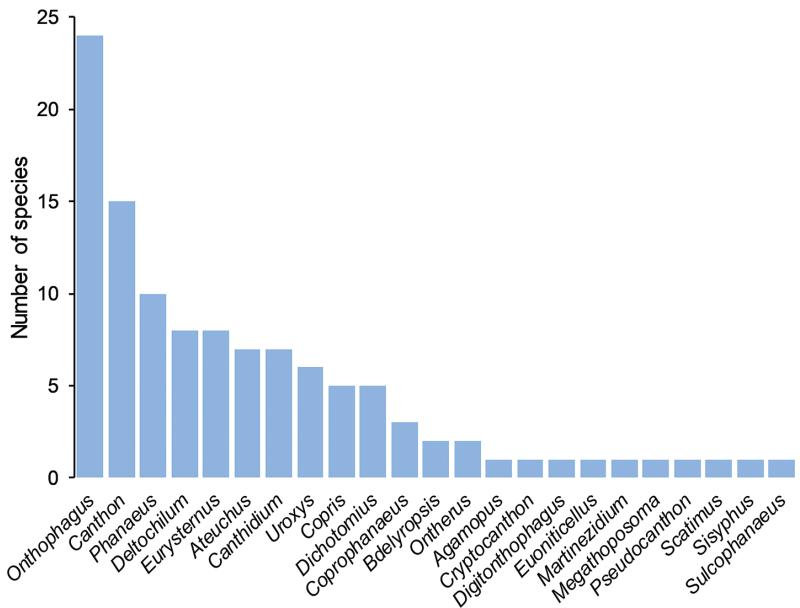


Figure 1. Number of species registered by genus in the Natural Protected Areas of Chiapas.

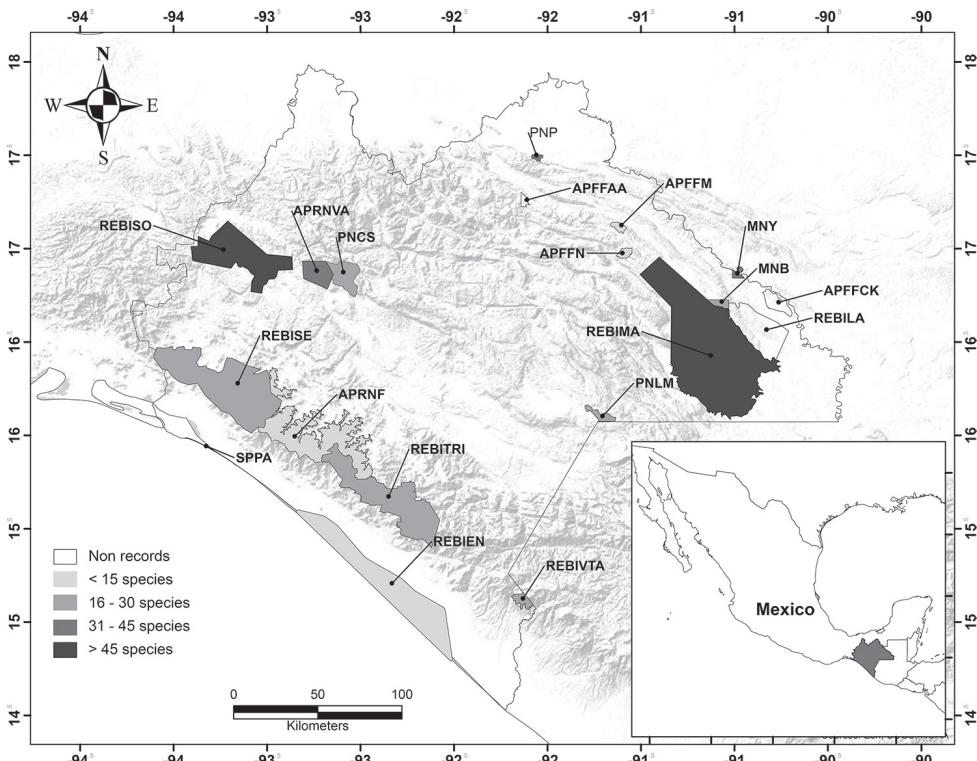


Figure 2. Natural Protected Areas of Chiapas grouped into five categories according to the number of species they register. See acronym in Table 2.

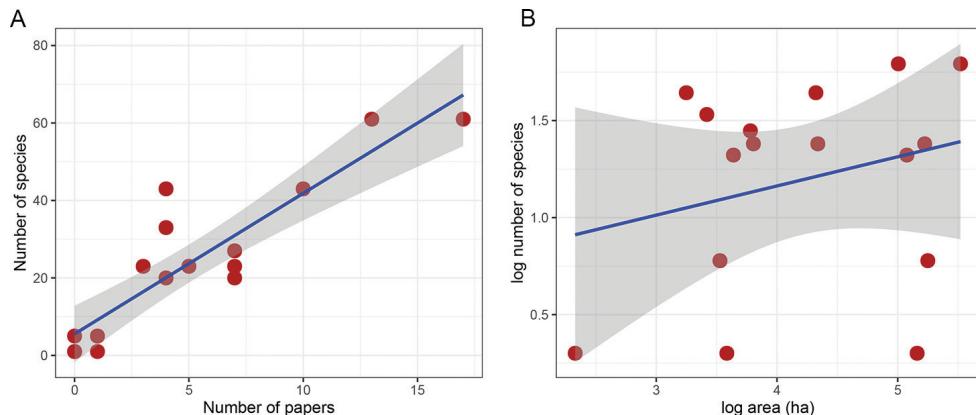


Figure 3. Simple linear regression analysis between the (A) species recorded and the publications that register them; and (B) with the area size of each natural protected areas.

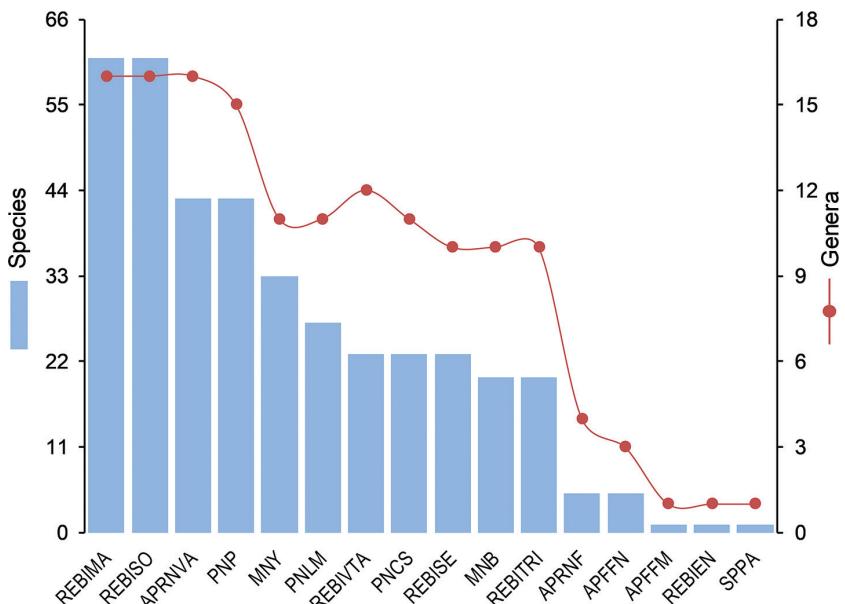


Figure 4. Number of species and genera of Scarabaeinae registered by Natural Protected Area in Chiapas.

($n = 4$), PNP ($n = 4$), REBIVTA ($n = 4$), PNLM ($n = 2$), REBISE ($n = 2$), REBITRI ($n = 2$), MNB ($n = 1$) and MNY ($n = 1$). The similarity analysis indicated the formation of three large groups of reserves with faunistic similarities (Fig. 5). One of them is formed by the reserves in the Sierra Madre de Chiapas, where montane forests predominate (REBISE and REBITRI) with approximately 87% similarity; another group corresponding to tropical rain forests consisted of five reserves (MNB, MNY, PNP, REBIMA and REBISO) with about 73% similarity; and the last was composed of two NPAs of deciduous forests (APRNVA and PNCS) with 60% similarity. PNLM

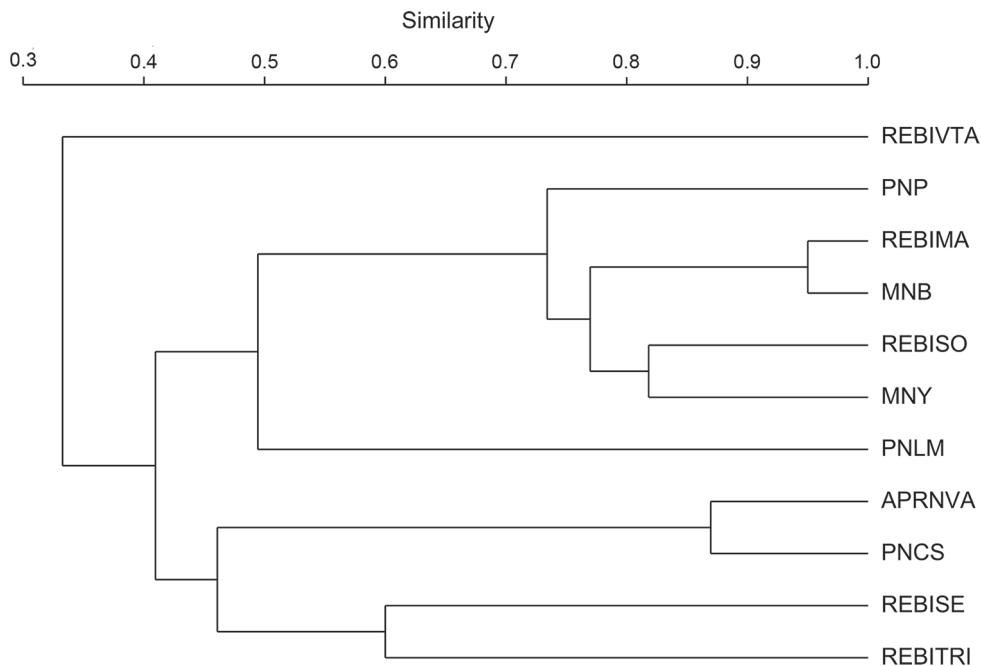


Figure 5. Faunistic similarity analysis of dung beetles between the Natural Protected Areas of Chiapas. Only NPAs with more than five registered species were included.

was more related to the rain forests and shared 50% of its fauna with this group, but with typical elements of montane forests that separated it from the group; while REBIVTA was isolated from the rest of the reserves, sharing a low percentage of its fauna with all of them.

Discussion

Biodiversity of Scarabaeinae in the NPAs of Chiapas

The 112 species reported in the federal natural protected areas correspond to 91% of the Scarabaeinae fauna of Chiapas and 38.1% of the 294 species estimated for Mexico (Sánchez-Hernández and Gómez 2018; Sánchez-Hernández et al. 2019). While the numbers reported here are high, knowledge about dung beetles in Chiapas is far from complete. Of the total publications revised, there were few studies that correspond to inventory works with systematic sampling (32.6%), restricted to only seven of the protected areas (APRNVA, MNY, REBIMA, REBISO, REBIVTA, PNLM and PNP). The NPAs with the highest number of registered species (i.e. REBIMA and REBISO) were, in the same way, the ones that present the greatest number of studies, while most of them lacked studies that extensively analyze the Scarabaeinae communities. This greatly prevents the study of several basic and applied aspects

of dung beetles, from diversity and distribution to conservation. The above also shows evidence that a greater sampling effort focused on the least studied reserves would increase the possibility of discovering unregistered or described species and, thereby, broadening the knowledge of the dung beetle diversity in Chiapas, regardless of the area size of the NPAs.

REBIVTA, the reserve with the lowest faunistic affinity in the study, is located in an area with Central American influence that emerged during the volcanism in the Pliocene (Halffter 2003). This reserve is located at a point of confluence of three tectonic plates (Cocos, North American and Caribbean) and is limited by the trench of Central America and the Motagua-Polochic fault system (García-Palomo et al. 2006). Cano et al. (2018) consider its geology as a biogeographic barrier that separates the Passalidae (Coleoptera) faunas between Central America (including the Tacaná volcano) and southeastern Mexico. Similarly, they recognize that the Motagua-Cuilco dry valleys system and the Motozintla-Comaltitlán suture zones represent barriers involved in beetles vicariance processes, including other genera of Passalidae (Schuster 1993; Schuster et al. 2003), Scarabaeidae (Micó et al. 2006), and Carabidae (Sokolov and Kavanaugh 2014). This would explain the isolation of the fauna found in the REBIVTA against the other Chiapas reserves, because its function as a biogeographic barrier that prevents Central American elements from crossing northwards on the Pacific slope.

PNP, REBISO, MNY, REBIMA and MNB, formed a faunistic complex of rain forests located on the gulf slope with a high percentage of similarity (above 70%). They became a group of reserves clearly different from the other group formed by the interaction of two areas (PNCS and APRNVA) characterized by dry forests. Both NPAs groups are made up of fauna with neotropical affinity that is distributed over the biogeographic province of the Gulf of Mexico (Morrone 2006), but which diverge by the type of vegetation they present. Finally, the PNLM is a reserve that presents transition characteristics between the rain forests (Gulf of Mexico province) and the temperate forests (Chiapas province) formed by species with Central American and central Mexico origin (Delgado 2011), thereby separating it from the Gulf of Mexico NPAs groups.

Species with doubtful distribution in Chiapas

We consider that seven species cited by some of the reviewed works do not have a presence in Chiapas, or that their distribution needs to be confirmed in some of the reserves studied. The reports of *Dichotomius centralis* (Harold, 1869) in the works of Morón et al. (1985), Palacios-Ríos et al. (1990) and Halffter et al. (1992) correspond to *D. amplicollis* (Harold, 1869). The overlap area of these species is in Guatemala and *D. centralis* is likely to be marginally on the Pacific slope, however its presence in Chiapas has not been confirmed (López-Guerrero 2005).

Gomez et al. (2017) reported to *Dichotomius carolinus* (Linnaeus, 1767) and *Dichotomius amicitiae* Kohlmann & Solís, 1997, but none of these species has been

corroborated in Mexico. *Dichotomius carolinus* is distributed exclusively in the United States and the individuals rather correspond to *D. colonicus*, a species with which it relates and is widely distributed in Mexico. On the other hand, *D. amicitiae* is a species whose distribution is restricted to Costa Rica and Panama (Kohlmann and Solís 1997), hence this record was confused with *D. annae*, a closely related Mexican species (Peraza and Deloya 2006).

Similarly, Morón et al. (1985) cited *Onthophagus nasicornis* Harold, 1869 but the species is only known in central Mexico and, this record has not been corroborated in Chiapas. *Onthophagus nitidior* Bates, 1887 is distributed in the low deciduous and subdeciduous forests of the Mexican Central Pacific slope (Hernández and Navarrete-Heredia 2018), so that, the report by Palacios-Ríos et al. (1990) on the Gulf of Mexico slope, is possibly incorrect record and corresponds to other species of the same group (*hirculus* species group) reported in Chiapas.

We also consider that *Onthophagus rhinophyllus* Harold, 1868, a species that is distributed only in Venezuela and Colombia (Delgado et al. 2006), constitutes an erroneous record of Halffter et al. (1992). *Onthophagus atrosericeus* Boucomont, 1932, is another species erroneously cited in Mexico. The distribution of this species is restricted to mountains of elevation greater than 1,700 m in Costa Rica and Panama (Kohlmann and Solís 2001), while the record of Halffter et al. (1992) is in a locality at ~100 m altitude, approximately 1,000 km from its nearest record in Costa Rica.

Monitoring and conservation

Biodiversity monitoring in natural protected areas represents an integral component to assess its performance and provide the information necessary for effective management (Halffter et al. 2015). In this sense, Schuster et al. (2000) mention that the use of a group that meets the bioindicator requirements can save time and money in conservation strategies and, at the same time, give objective and reliable criteria for the prioritization of areas, especially when the change in land use is accelerated and the need for conservation is urgent. One of the key reasons to conserve and monitor invertebrates in these areas is to ensure adequate protection of rare and threatened species and communities. Furthermore, many of them are appropriate and highly effective and informative indicators of other elements of biodiversity, ecosystem health and associated threats (McGeoch et al. 2011; Gerlach et al. 2013).

Due to the great variety of ecological functions in which they intervene (Nichols et al. 2008), their ability to respond in the short term to forest fragmentation (Nichols et al. 2007), its developed correlation and direct dependence on the presence of mammals in the ecosystem (Nichols et al. 2009; Bogoni et al. 2016; Mannu et al. 2018), the inclusion of the subfamily Scarabaeinae in these types of studies has been widely justified. They are well defined from a taxonomic and functional viewpoint, and methods for their sampling has been standardized (Spector 2006; Nichols and Gardner 2011). In addition, the analysis of their communities allows different and more detailed results which can be obtained in relation to works based only

on the study of vertebrates and plants (Kohlmann et al. 2007). So that, inventories and monitoring of Scarabaeinae communities can be useful during several stages of NPAs management, but statistically rigorous estimates of species richness, information on their spatial and temporal distribution are required, or their design should target to threatened and rare species or to identify possible indicator and/or invasive species (Engelbretch 2010). However, despite its characteristics as a bioindicator group, in Mexico the dung beetles are not included among the priority groups within the monitoring programs that support the management of NPAs, underestimating their results compared to those that produce studies on vertebrates and plants.

On the other hand, conservation efforts through NPAs would be much more relevant and effective when they are linked at a landscape or ecosystem scale (Moctezuma et al. 2018), because the resulting connectivity is essential for the biological diversity of the areas included, as it allows genetic and energy exchange through a greater geographical extent (Roy et al. 2010). For Scarabaeinae, these ecosystem complexes can promote the dispersion and survival of populations of certain common species in conserved areas of the region and, at the same time, maintain the optimal conditions for species with a restricted range of distribution. For instance, although the 13 species indicated on the IUCN red list of threatened species (see Table 3) do not meet the criteria to be considered in some type of immediate risk, most of these species present isolated populations in habitats with a high degree of vulnerability and reduced geographical range, some of them, known only from the material used for its description. Due to these characteristics, these species could be considered rare and indicators of conservation, which makes it necessary to consider adaptation measures to guarantee the survival of their populations. However, at present, there are no conservation strategies for any of them (IUCN 2018). Likewise, it would be important to establish strategies for monitoring the populations of *D. gazella* and *E. intermedius*, two invasive alien species widely distributed in Mexico that have been reported in several NPAs of Chiapas and that have probably been established in other contiguous reserves, since they have a high dispersal capacity, and can negatively affect the abundance of most native species, favoring the local extinction of species with similar nesting behavior (Montes de Oca and Halfpter 1998; Filho et al. 2018).

In Chiapas, the ecosystem-scale conservation approach through corridors that link protected areas has recently emerged. An example of this is the “Complejo Selva Zoque of Natural Protected Areas”, whose objective is to enable the connectivity and conservation of biodiversity between five protected areas, three federal NPAs (REBISO, APRNVA and PNCS) and two state-protected areas (La Pera and Cerro Meyapac) (RAC 2015). This can be taken as a reference to establish connectivity strategies that allow the genetic flow between NPAs from other regions with similar characteristics. For example, in the Lacandona rainforest, a region that has been seriously affected by the accelerated change in land use, mainly due to the rapid expansion of oil palm crops, replacing large areas of forest in Chiapas (Castellanos-Navarrete and Jansen 2018). Unlike other tree crops, oil palm is a particularly poor

substitute for either primary or degraded forests and especially damaging to biodiversity (Fitzherbert et al. 2008), including the functional (Edwards et al. 2014) and taxonomic diversity of dung beetles (Gray et al. 2014; Harada et al. 2020).

Data presented in this work can be used as a reference to monitor dung beetle communities in the NPAs of Chiapas, both to conduct research in areas that have not been investigated and to continue monitoring in the NPAs explored, and thus analyze the dynamics of the communities over time. These studies can help to understand their response to ecosystem alterations, since indirectly reducing the beetles' diversity through different factors of anthropic origin puts ecosystems at risk and promotes the loss of biodiversity. These changes will have significant negative impacts on the functional and ecological services that this insect group provide. Therefore, it is recommended that groups of arthropods such as the Scarabaeinae should be included in the previous justifying studies for the designation or establishment of NPAs and in turn considered in the biological monitoring programs of these reserves since they meet the characteristics of an efficient bioindicator group.

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