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THE STAPHYLINID FAUNA OF PANGUANA, PERU – DIVERSITY AND ZOOGEOGRAPHIC ASPECTS

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Abstract. The present study aimed to add Staphylinidae to the known faunal composition of the Panguana area, a hotspot of biodiversity world-wide. The investigation is based mainly on the material collected by W. Hanagarth and M. Verhaagh but it also includes species described from the area and collected by other scientists. From the total of 1470 specimens, 178 were identified to species level. According to the Chao-1 method, approximately 700 – 1300 species can be expected for the soil surface staphylinid fauna of the study region. Species diversity ranged between 2.3 and 4.6 ln H(s) with highest values in the rainforest and lowest in agricultural fields. The same relation is true for number of species and evenness. The comparison of the 11 different habitats identified by the Detrended Correspondence Analysis showed that the main axes correlate with environmental parameter inundation frequency and human impact. The zoogeographic analysis revealed 41 species that are likely endemic for the region, which corresponds to 23% of the identified species. Weak relations exist to the geographic regions of the Atlantic rainforest and to the Amazon lowland rainforest by combining common species. Habitats with human impact have the lowest percentage of endemic species and the highest of widely distributed Neotropical species, whereas near-natural habitats reveal the inverse relation.

Keywords: *Coleoptera, Staphylinidae, Neotropics, zoogeography, biodiversity*

INTRODUCTION

The Biological Station Panguana, Huanuco, Peru, was founded in 1968 by the German biologists Maria and Hans-Wilhelm Koepke. It is located in one of the world's biodiversity hotspots (Myers et al. 2000) in the Tropical Andes region with 6.7 % endemic plants and 5.7 % endemic vertebrates. It has been assigned high conservation priority and is today the property of the private Panguana foundation (Niessner et al. 2020). This regional composition with outstanding biodiversity and the characteristic land-use for the pre-Andean regions was the reason for M. and H.-W. Koepke to found the station in the region and to open it for biological and ecological research. Since 1968 numerous biological investigations have been performed, beginning with birds and mammals (Hutterer 1995, Patterson et al. 1998, Servat et al. 2012), arthropods (Verhaagh et al. 1991) or molluscs (Wendebourg & Hausdorf 2019). General ecological habitat-orientated studies have also been carried out e.g., by Hanagarth (1981). A short overview of research facilities at Panguna is given in Niessner et al. (2020).

The beetle family Staphylinidae is one of the largest beetle families and is characterised by its megadiverse species richness, having 66,928 species world-wide (Newton 2022). In the Neotropics at present 11,675 species are known (Asenjo et al. 2019). For Peru, 1018 staphylinid species belonging to 246 genera are recorded (Asenjo et al. 2019). These data also include the subfamilies Scydmaeninae, Pselaphinae, and Scaphidinae which were still separate coleopteran families at the start of my research and were not considered in the present study. Even without these, Staphylinidae are still well qualified to answer biodiversity questions regarding zoogeographic relations across large areas and regionally in the interactions between species and habitats. The present study is mainly based on the material collected by W. Hanagarth and M. Verhaagh in the Panguana region. Here, I focus on zoogeographic questions to determine (1) the species inventory of the poorly investigated rove beetles in the Pre-Andean region, (2) assess whether there are biodiversity parameters that explain local species distribution (e.g. habitats) and land use impacts, and (3) compare the zoogeographic relations

of the Panguana staphylinid species with those found in neighbouring regions to find the origin of the species involved in the regional ecological processes.

METHODS

Study area and habitat notes

The investigated region is in the Peruvian province Huanuco. The Biological Station Panguana (9.62°S 74.93°W) is approximately 200 km south of the city of Pucallpa and located at the margins of the Rio Yuyapichis, which through drainage of the Rio Pachitea and then into the Rio Ucayali becomes one of the headwaters of the Rio Amazonas. The studied material originates from the near-Panguana area up to the 30 km northern village of Puerto Inca. The region is situated at the eastern slope of the Andes on the West and the Sira mountain range on the East. The site is at approximately 250 m a.s.l., therefore about 200 m higher than the 2000 km distant Central Amazonas. The climate is characterised by annual even high temperatures between 24°C and 26°C. However, distinct rainy and dry seasons exist with high rainfall in December/January and low rainfall in June/July. Annual mean rainfall was 1475 mm in the years 1974/75 (Hanagarth 1981).

Beside the terra-firme rainforests (primary and secondary), samples also originated from floodplain forests, so-called matorrales between the riverbanks and the inundation forest consisting of bushy and shrubby vegetation with caña-brava vegetation (*Gynericum sagittatum*, Poaceae) and tropical kudzu (*Neustanthus phaseoloides*, Fagaceae), and riverbanks at the margins of Rio Yuyapichis. Furthermore, anthropogenic habitats such as banana plantations and agricultural fields (e.g., manioc plantations of different ages), pastures with grass and pastures with tropical kudzu and clear-cut areas were included. At so-called cochas, bayous separated from the main river, matorrales are covered by more vegetation in the undergrowth. The vegetation-poor river margins, matorrales and the floodplain forests, were non-periodically inundated in seasonally changing frequency. The number of flooding events increased from floodplain forests to matorrales and riverbanks. During the fieldwork of W. Hanagarth, matorrales at the cocha with five to six flooding events per year were more frequently inundated than the matorrales more distant from the riverside with two to three flooding events per year. More detailed information about the climate and ecological situation of the different habitats is available in Hanagarth (1981). The vegetation of the Panguana region is described in more detail by Seidenschwarz (1986). Habitat comparisons and the biodiversity calculations are based only on the material collected by W. Hanagarth and M. Verhaagh who sampled in diverse habitats.

Collecting methods and identification

The material was mainly sampled by pitfall traps targeting fauna active at the soil surface by W. Hanagarth from January 1974 to February 1975 and M. Verhaagh from January 1984 to January 1985. The used pitfall traps had an opening of 6.8 cm circumference at the soil surface, filled with 4% formaldehyde, and covered by a plastic roof against rainfall approximately 10 cm distant from the soil surface. W. Hanagarth also used the Kerosin-method from 500 cm³ litter, as well as a smaller amount of active hand-sampling. Additional material from different years of other scientists was also included to complete the species list. This material, however, consists of only a few species and specimens. At the time the material was collected, knowledge of Neotropical Staphylinidae was very poor. In the meantime, it has increased tremendously (Asenjo et al. 2019). Therefore, today it is possible to identify many specimens to species level. The number of publications is very large; thus, it is not possible to list here all the publications used for the identification of species, and only the following few are cited: Piestinae (Caron et al. 2011), Osoriinae (Irmler 2009, 2014), Staphylininae (Chani-Posse et al. 2018; Irmler 2017, 2021), Steninae (Puthz 2006), Aleocharinae (Pace 2008). Therefore, identified Staphylinidae are divided into those identified to species level and those only identified to genus level and subsequently numbered. For the zoogeographic analysis, only the species

identified to species level were used. The known distribution of species was used as documented in the author's database (Irmler & Asenjo 2018) considering the following types of distribution: (P) pantropic: Neotropics and other tropical countries in the world; (N) neotropic: total Neotropics from Mexico to northern Argentina; (SA) South American: only in tropical South American countries from Venezuela to northern Argentina; (SN) southern Neotropics: regions south of the Amazon basin from Bolivia/Peru via Paraguay to south-east Brazil and northern Argentina; (Am) Amazon basin: lowland Amazon rainforest in Brazil, Columbia, Ecuador, and Peru; (EA) eastern slopes of the Andes: east Andean slopes from Costa Rica to Bolivia; (E) endemic: known only from the eastern Andean slopes of Peru or southern Ecuador.

Statistical analysis

For the statistical analyses of diversity, the investigated and separated habitats by Hanagarth (1981) were used. The program PAST 3 was used (Hammer et al. 2012) for the calculation of diversity: Shannon index ln (Hs) considers the number of species and specimens, and evenness indicates the dominance of species. Total species richness was estimated by Chao-1 and individual rarefaction. The similarity between the differentiated habitats was tested by the

Detrended Correspondence Analysis (DCA) and the Simpson ordination. DCA avoids implemented errors resulting from the older CA analysis. The first axis reflects the axis with the highest differentiation. Thus, only the first two axes are considered. According to ter Braak (1986) habitats are sufficiently differentiated by an eigenvalue of 0.5. Simpson ordination was used to group the habitats ordered by the DCA with adjustments: unpair group as algorithm and Simpson as similarity index.

RESULTS

Regional species richness and diversity

A total of 178 species were identified to species level out of 795 specimens (Table 1). If the specimens only identified to genus level are also included in the species count, a total number of 416 species out of 1470 specimens were identified (Tables 3 and 4). While the well-studied subfamilies Osoriinae, Piestinae and Steninae could all be identified to species level, Aleocharinae and Paederinae could mostly be identified to genus level only. Nevertheless, these two subfamilies had the highest species richness in the Panguana region. In total, 123 genera were identifed. A total of 53 newly described species were identified out of the 795 specimens collected in the Panguana region (e.g., Irmler 1981, 1994, 2014, 2017). The genera with highest number of species were *Atheta* Thomson, 1858 and *Apalonia* Casey, 1906 (Aleocharinae) with 14 species each. From the Tachyporinae subfamily the genus *Coproporus* Kraatz, 1857 also presented 14 species. Among the Paederinae, the genus *Scopaeus* has the highest species richness with 13 species.
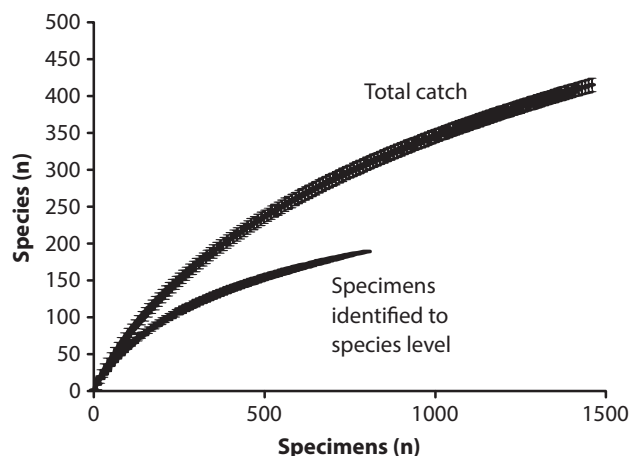

Figure 1. Results of the rarefaction analysis for specimens identified to species level and total number of specimens including also those identified only to genus level.

According to the Chao-1 analysis, total species richness was estimated at 709 (percentiles: 510, 602). Allowing for the imprecision of the method, total species richness of the soil surface might range between 500 and 1200 species in the region. The evenness of approximately 0.5 indicates a relatively even dominance between the species.

The most frequent species were *Thoracophorus guadalupensis* with 14.8 % of all individuals, followed by *Nacaeus claviger* with 5.9% and *Hoplandria inca* with 3.2%. Most species were only rarely found. Out of the total number of 416 species, 194 species were only found with 1 specimen; this corresponds to 46.6% of the total number of species caught. The low status of species collection is also documented by the rarefaction analysis (Fig. 1). Both curves

Table 1. Species richness for subfamilies and diversity indices

Subfamilies	Species level		Total	
	Species	Specimens	Species	Specimens
Aleocharinae	31	169	110	380
Omaliinae	-	-	2	2
Osoriinae	62	340	62	340
Oxytelinae	3	15	41	128
Paederinae	31	88	106	306
Piestinae	7	25	7	25
Staphylininae	33	127	60	165
Steninae	9	27	9	27
Tachyporinae	1	4	20	97
Sum	**178**	**795**	**405**	**1470**
Individuals	795		1470	
Shannon_H	4.45		5.45	
Evenness	0.46		0.56	
Chao-1	302		709	

show that the number of species has not reached a saturated state and will increase continuously if more specimens are caught, even if only the soil surface fauna is considered.

Habitat diversity and composition

Out of the total number of specimens, 1300 were assigned to specific habitats (Table 2). On average, the lowest diversities were calculated for habitats impacted by humans e.g., agricultural fields, clear cutting areas, whereas the highest diversities were found in natural habitats e.g., river margins, cochas or rainforests. However, diversity is correlated with the number of specimens per habitat ($p = 0.03$), which suggests that the investigation effort is involved in the diversity results. Agricultural fields are characterised by the lowest diversity and evenness of the eleven habitats, which indicates the dominance of few species, whereas rainforests have the highest values. This indicates that agricultural fields are characterised by few but frequent species, while rainforests have a higher number of species with more even dominances. Unfortunately, specimen numbers are too low in several habitats to execute a habitat specific rarefaction analysis. Only for maniok, cochas and rainforest rarefaction analyses were possible that result in 26, 17, and 32 species, respectively, for a number of 50 specimens.

Characteristic species of habitats with agricultural impacts are *Acrotona loreticola* Pace, 2008 and *Diochus verhaaghi* Irmler, 2017. *Nacaeus claviger* (Cameron, 1913) is the most euryoecious species (Table 3) being found in nine of the eleven habitats. Several species, e.g., *Diochus hanagarthi* Irmler, 2017, *Diochus perplexus* Cameron, 1922, *Diochus tarsalis* Sharp, 1876, and *Thoracophorus guadalupensis*
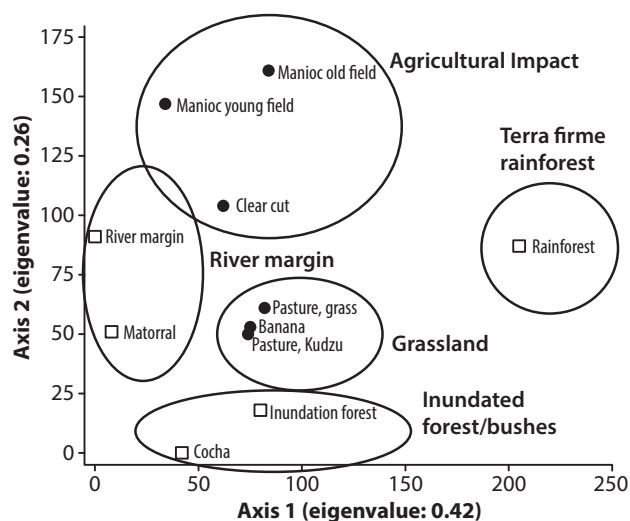

Figure 2. Results of the Detrended Correspondence Analysis with eigenvalues of the first two axes (natural habitats marked by square symbols. habitats with human impact by circular symbols).

Cameron, 1913 reached high abundances in agricultural fields but also occur in the riverine habitats. *Macrogerodonia foveaventer* Pace, 2009 was only found in rainforests. Typical species for the inundated habitats are: *Hoplandria inca* Pace, 1990 and *Hoplandria mochicorum* Pace, 1990.

The present ordination results in an eigenvalue of 0.42 of the 1st axis and is, thus, slightly lower than ter Braak's (1986) recommended value of 0.5, which shows comparatively weak differentiation of assemblages (Fig. 2). Nevertheless, the ordination reveals a distinct trend from rainforests to river margins. which certainly reflects the soil wetness and inundation frequency in natural habitats along the first axis. In contrast, the second axis seems to

Table 2. Number of species, specimens, and diversity indices for the eleven different habitats identified.

Habitat	Species level		Total species		Diversity	Evenness
	Species	Specimens	Species	Specimens		
Agricultural field	11	92	27	149	2.3	0.37
Forest clearing	10	36	26	55	2.4	0.41
Matoral	14	21	27	64	3.0	0.71
Tropical grassland	14	17	25	30	3.1	0.92
Banana plantation	12	22	29	51	3.2	0.82
Floodplain forest	21	44	37	72	3.3	0.76
Pasture	25	43	44	71	3.6	0.80
Manioc plantation	31	89	70	186	3.9	0.70
River margin	20	30	78	151	4.0	0.67
Cocha	39	126	95	244	4.1	0.62
Rainforest	50	109	124	227	4.6	0.81
Mean (species); Sum (specimens)	22.5	629	52.9	1300	3.4	0.69

Table 3. Species identified to species level with records in the five identified assemblages and zoogeographic classification
Subfamily: Aleoch.: Aleocharinae, Staphylin.: Staphylininae; Zoogeo.: Zoogeography; Am: Amazonas (Brazilian Amazonas and adjacent regions), E: endemic, EA: East Andean (Costa Rica - Peru), N: Neotropics (South and Central America), P: pantropic, SA: South America, SN: Southern Neotropics (South Brazil, Paraguay, Peru), - no information on habitat available

Species	Subfamily	Habitat type					Zoogeo.
		Agric. impact	Grass-land	River margin	Inun. forest/ bushes	Rain-forest	
Acrotona loreticola Pace, 2008	Aleoch.	5	3	0	0	0	EA
Adinopsis myllenoides Kraatz, 1857	Aleoch.	0	0	1	0	1	N
Allotrochus minor Irmler, 2000	Osoriinae	-	-	-	-	-	EA
Aneucamptus crassus (Sharp, 1876)	Osoriinae	-	-	-	-	-	N
Aneucamptus geroi Irmler, 2001	Osoriinae	0	1	0	0	0	E
Anotylus insignitus (Gravenhorst, 1806)	Oxytelinae	1	1	0	0	1	N
Apalonia clavicornis Pace, 2008	Aleoch.	2	0	0	1	6	EA
Apalonia cuzcoensis (Pace, 1986)	Aleoch.	0	0	0	3	0	E
Apalonia minor Pace, 2008	Aleoch.	0	0	0	0	1	EA
Apalonia sigchosensis Pace, 2008	Aleoch.	0	0	0	0	2	EA
Apocellus laevis Sharp, 1876	Oxytelinae	8	0	0	2	0	SA
Astenus serpens (Sharp, 1876)	Paederinae	0	0	1	0	0	SA
Atanygnathus nasutus (Sharp, 1876)	Staphylin.	2	0	0	2	0	SA
Belonuchus prasinipennis Bernhauer, 1917	Staphylin.	-	-	-	-	-	EA
Belonuchus xanthopterus (Nordmann, 1837)	Staphylin.	0	0	0	2	0	SA
Caloderella humboldti Pace, 1996	Aleoch.	-	-	-	-	-	EA
Clavilispinus exiguus (Erichson, 1840)	Osoriinae	1	3	0	5	0	P
Clavilispinus junkii Irmler, 2003	Osoriinae	-	-	-	-	-	N
Clavilispinus megacephalus (Fauvel, 1865)	Osoriinae	0	0	1	0	2	N
Clavilispinus minutus (Sharp, 1887)	Osoriinae	-	-	-	-	-	N
Clavilispinus politus (Sharp, 1887)	Osoriinae	0	0	0	1	0	N
Coproporus ignavus Sharp, 1876	Tachypor.	0	0	1	0	0	N
Dacnochilus laetus LeConte, 1863	Paederinae	0	4	0	0	0	N
Dacnochilus pagana (Sharp, 1876)	Paederinae	0	1	0	0	0	SA
Diochus hanagarthi Irmler, 2017	Staphylin.	11	0	1	0	0	SA
Diochus perplexus Cameron, 1922	Staphylin.	2	3	1	0	0	N
Diochus tarsalis Sharp, 1876	Staphylin.	4	6	2	4	0	Am
Diochus verhaaghi Irmler, 2017	Staphylin.	7	1	0	0	0	N
Echiaster fumatus Sharp, 1876	Paederinae	2	3	0	0	0	SA
Echiaster longicollis Erichson, 1840	Paederinae	-	-	-	-	-	SA
Echiaster schadei Scheerpeltz, 1968	Paederinae	0	0	0	2	0	SN
Ectionides volans Assing, 2012	Paederinae	-	-	-	-	-	E
Edaphus bryanti Puthz, 1973	Steninae	0	1	0	0	0	SN
Edaphus depressus Puthz, 1973	Steninae	0	1	0	0	0	SA
Eleusis nigerrima (Fauvel, 1865)	Osoriinae	-	-	-	-	-	N
Espeson titschacki Bernhauer, 1941	Steninae	3	0	0	2	0	N
Eudera napofluminis Pace, 2008	Aleoch.	1	0	0	3	0	E
Euthorax longicornis Wasmann, 1893	Aleoch.	3	0	0	0	0	SN
Gastrisus viridicollis (Bernhauer, 1908)	Staphylin.	0	0	0	2	0	SN

Table 3. (Continued)

Species	Subfamily	Habitat type					Zoogeo.
		Agric. impact	Grass-land	River margin	Inun. forest/ bushes	Rain-forest	
Geomitopsis amazonensis Irmler, 2016	Osoriinae	1	1	0	0	0	Am
Geotrochopsis pubescens Irmler, 2016	Osoriinae	0	0	0	0	2	N
Glyptoma lescheni Irmler, 2015	Osoriinae	-	-	-	-	-	EA
Glyptoma nitidum (Bernhauer, 1908)	Osoriinae	1	3	0	0	0	N
Holotrochopsis pubescens (Sharp, 1876)	Osoriinae	-	-	-	-	-	Am
Holotrochopsis setifera (Irmler, 2010)	Osoriinae	-	-	-	-	-	Am
Holotrochus hanagarthi Irmler, 1981	Osoriinae	0	0	0	1	0	EA
Holotrochus lineatus Irmler, 1981	Osoriinae	0	0	0	3	0	E
Holotrochus milleri Irmler, 1981	Osoriinae	0	1	0	0	0	N
Holotrochus neotropicus Irmler, 1981	Osoriinae	-	-	-	-	-	E
Holotrochus poundi Blackwelder, 1943	Osoriinae	2	1	0	0	0	N
Holotrochus pumilius Irmler, 1981	Osoriinae	-	-	-	-	-	SA
Holotrochus syntheticus Sharp, 1876	Osoriinae	1	1	0	0	1	SA
Homaeotarsus opacifrons (Sharp, 1876)	Paederinae	0	0	3	0	0	Am
Hoplandria ecuadoriensis Pace, 1990	Aleoch.	0	4	2	13	2	EA
Hoplandria inca Pace, 1990	Aleoch.	0	0	2	23	0	E
Hoplandria mochicorum Pace, 1990	Aleoch.	0	0	0	11	0	EA
Hoplandria umbrina Kraatz, 1857	Aleoch.	0	3	0	0	0	EA
Hypotelus laevis (Solsky, 1872)	Piestinae	0	0	0	2	0	EA
Hypotelus micans Sharp, 1876	Piestinae	0	0	0	1	1	N
Leptonia athaualapai Pace, 1986	Aleoch.	1	0	0	0	1	E
Leptonia klimaszewskii Pace, 2008	Aleoch.	0	0	4	4	0	EA
Leptonia nobilis Pace, 2009	Aleoch.	2	1	1	0	2	E
Lispinus attenuatus Erichson, 1840	Osoriinae	-	-	-	-	-	SA
Lispinus bolivianus Bernhauer, 1929	Osoriinae	0	0	0	0	1	N
Lispinus catena Sharp, 1876	Osoriinae	-	-	-	-	-	N
Lispinus fungicola Irmler, 2001	Osoriinae	1	0	0	0	0	EA
Lispinus laeviusculus Bernhauer & Schubert, 1910	Osoriinae	-	-	-	-	-	SA
Lispinus linearis Erichson, 1840	Osoriinae	-	-	-	-	-	N
Lispinus listenbarthi Irmler, 1994	Osoriinae	-	-	-	-	-	EA
Lithocharodes bicornis Irmler, 2021	Paederinae	0	0	0	2	0	E
Lithocharodes brooksi Irmler, 2021	Staphylin.	-	-	-	-	-	E
Lithocharodes hanagarthi Irmler, 2021	Paederinae	0	1	0	2	0	E
Lithocharodes verhaagi Irmler, 2021	Staphylin.	-	-	-	-	-	Am
Lobrathium deletum (Sharp, 1876)	Paederinae	0	0	0	3	0	SA
Macrogerodonia colombiana Pace, 1997	Aleoch.	0	0	0	0	1	EA
Macrogerodonia foveaventer Pace, 2009	Aleoch.	0	0	0	0	6	E
Macrogerodonia magnicollis (Bernhauer, 1908)	Aleoch.	0	0	0	3	0	SA
Macrogerodonia magnioculata Pace, 1986	Aleoch.	4	0	0	2	6	EA
Macrogerodonia peruviana (Bernhauer, 1908)	Aleoch.	0	0	0	0	5	EA
Macrogerodonia rougemonti Pace, 2008	Aleoch.	0	2	0	1	0	E

Table 3. (Continued)

| Species | Subfamily | Habitat type | | | | | Zoogeo. |
		Agric. impact	Grass-land	River margin	Inun. forest/ bushes	Rain-forest	
Mimogionia antennata Irmler, 1981	Osoriinae	-	-	-	-	-	Am
Mimogonia brunnea Irmler, 1981	Osoriinae	0	0	0	2	0	E
Mimogonia hanagarthi Irmler, 2007	Osoriinae	1	0	0	0	0	E
Mimogonia pumilia Irmler, 1981	Osoriinae	0	0	0	0	0	E
Mimogonia subopaca Irmler, 1981	Osoriinae	-	-	-	-	-	E
Molosoma bicolor (Irmler, 2014)	Osoriinae	0	0	0	8	0	E
Molosoma bicornis (Irmler, 2014)	Osoriinae	0	0	1	0	0	E
Molosoma boliviensis (Irmler, 2014)	Osoriinae	-	-	-	-	-	E
Molosoma fumarius (Irmler, 2014)	Osoriinae	0	0	0	1	0	E
Molosoma hanagarthi (Irmler, 2014)	Osoriinae	0	1	3	6	0	SA
Molosoma luteus (Irmler, 2014)	Osoriinae	1	0	1	0	2	SA
Molosoma sticticus (Irmler, 2014)	Osoriinae	0	0	0	0	1	EA
Molosoma verhaaghi (Irmler, 2014)	Osoriinae	0	2	0	5	8	EA
Molosoma weberi (Blackwelder, 1943)	Osoriinae	1	0	0	0	0	SA
Monista longula Sharp, 1876	Paederinae	0	1	0	0	0	SN
Nacaeus claviger (Cameron, 1913)	Osoriinae	13	5	4	15	5	N
Nacaeus cordiger Irmler, 2003	Osoriinae	0	0	0	0	1	Am
Nacaeus peruvianus Irmler, 2003	Osoriinae	-	-	-	-	-	SA
Nacaeus planellus (Sharp, 1887)	Osoriinae	0	1	0	0	2	P
Neobisnius ludicrus (Erichson, 1840)	Staphylin.	0	0	0	2	0	N
Neobisnius simplex (Sharp, 1885)	Staphylin.	-	-	-	-	-	N
Mesoplandria loreticola Pace, 2008	Aleoch.	0	0	1	0	0	EA
Neolara angulipennis Pace, 1990	Aleoch.	4	0	0	0	0	SA
Neolindus amazonicus Irmler, 1981	Paederinae	0	1	0	0	0	E
Neolindus hanagarthi Irmler, 1981	Paederinae	0	0	0	0	1	E
Neolindus luciamans Assing, 2012	Paederinae	-	-	-	-	-	E
Neolindus peruvianus Irmler, 1981	Paederinae	0	1	0	0	0	E
Neolindus punctiventris Irmler, 1981	Paederinae	-	-	-	-	-	E
Neolindus retusus Herman, 1991	Paederinae	0	0	0	1	0	EA
Neolindus verhaaghi Irmler, 2011	Paederinae	0	0	0	0	1	E
Nordus antennatus (Sharp, 1876)	Staphylin.	-	-	-	-	-	SA
Nordus nigroscutellatus (Bernhauer, 1905)	Staphylin.	0	0	0	4	0	EA
Ochthephilum fuscipenne (Sharp, 1876)	Paederinae	2	6	0	0	0	Am
Ochthephilum megacephalum (Bernhauer, 1911)	Paederinae	0	1	0	0	0	SN
Ochthephilum opacifrons (Sharp, 1876)	Paederinae	0	0	0	3	0	SN
Oligota ecuadoriensis Pace, 2008	Aleoch.	0	0	0	1	0	EA
Oligotergus fasciatus (Nordmann, 1837)	Staphylin.	0	0	0	2	0	N
Oligotergus luridipes (Erichson, 1840)	Staphylin.	0	0	1	0	0	EA
Ophites raphidioides Erichson, 1840	Paederinae	0	0	0	2	0	EA
Orphnebius iquitoensis Pace, 2008	Aleoch.	0	0	1	0	0	EA
Orphnebius napoensis Pace, 2008	Aleoch.	0	2	0	0	4	EA

Table 3. (Continued)

Species	Subfamily	Agric. impact	Grass-land	River margin	Inun. forest/ bushes	Rain-forest	Zoogeo.
Orphnebius peruvianus Pace, 1986	Aleoch.	2	0	0	3	2	E
Orphnebius tarapotensis Pace, 2009	Aleoch.	1	0	0	0	2	E
Orphnebius vesicularis Pace, 1997	Aleoch.	1	2	0	0	0	EA
Oryssoma schwarzi Notman, 1925	Osoriinae	0	0	0	0	1	N
Osoriosetus hanagarthi Irmler, 2015	Osoriinae	0	0	2	3	0	E
Osorius pusillus Irmler, 2010	Osoriinae	0	0	0	0	3	E
Osorius verhaaghi Irmler, 2010	Osoriinae	0	0	0	0	1	E
Ouloglene barberi Notman, 1925	Osoriinae	-	-	-	-	-	N
Paederomimus abactus (Sharp, 1876)	Staphylin.	0	1	0	0	0	Am
Paederomimus aeneiceps (Sharp, 1876)	Staphylin.	0	0	0	1	0	Am
Paederomimus conformis (Sharp, 1876)	Staphylin.	0	0	0	1	0	N
Philonthus flavolimbatus Erichson, 1840	Staphylin.	6	1	0	0	0	SA
Philonthus hepaticus Erichson, 1840	Staphylin.	-	-	-	-	-	N
Philothalpus antennaria (Bernhauer, 1907)	Staphylin.	0	0	1	0	0	SN
Philothalpus brooksi Chatzimanolis & Ashe, 2005	Staphylin.	0	0	0	1	1	N
Piestus bicornis (Olivier, 1811)	Piestinae	0	0	2	0	0	N
Piestus pygmaeus Laporte, 1834	Piestinae	0	0	0	0	0	N
Piestus spinosus (Fabricius, 1801)	Piestinae	-	-	-	-	-	SA
Piestus sulcatus Gravenhorst, 1806)	Piestinae	1	1	0	0	3	N
Piestus validus Sharp, 1876	Piestinae	0	0	1	0	0	SA
Platydracus bolivianus (Bernhauer, 1908)	Staphylin.	0	0	0	0	3	E
Platydracus emeritus (Herman, 2001)	Staphylin.	0	0	0	0	3	Am
Probrachida dimidiaticornis (Pace, 2008)	Aleoch.	0	1	0	0	0	EA
Pseudastenus plaumanni (Bierig, 1939)	Paederinae	1	0	0	0	0	SN
Renda brevipennis Marquez, 2010	Staphylin.	0	0	0	0	1	E
Renda fasciata Marquez, 2010	Staphylin.	0	0	0	0	1	EA
Renda minor (Sharp, 1876)	Staphylin.	0	0	1	0	0	SA
Rugilus amazonicus (Sharp, 1876)	Paederinae	0	0	0	1	0	Am
Rugilus peruvianus (Bernhauer, 1921)	Paederinae	1	0	2	0	0	EA
Sciocharis boopina (Bernhauer, 1921)	Paederinae	1	0	0	0	0	EA
Sciocharis egena (Sharp, 1876)	Paederinae	2	0	1	0	0	EA
Sciocharis exilis (Erichson, 1840)	Paederinae	3	1	0	0	0	N
Somoleptus elongatus Irmler, 2022	Staphylin.	0	0	0	1	1	E
Stenaesthetus castaneus Orousset, 1990	Steninae	1	0	0	3	4	SA
Stenaesthetus immarginatus (Erichson, 1840)	Steninae	-	-	-	-	-	SA
Stenaesthetus praestans Orousset, 1990	Steninae	0	1	0	2	1	SN
Stenus hromadkaianus Puthz, 1993	Steninae	0	0	3	0	0	Am
Stenus inti Puthz, 1988	Steninae	0	0	2	0	0	E
Stenus nusta Puthz, 2005	Steninae	-	-	-	-	-	E
Stenus obductus Sharp, 1876	Steninae	0	1	0	0	0	SA
Stereocephalus seriatipennis Lynch, 1884	Paederinae	1	1	1	1	1	Am

Table 3. (Continued)

Species	Subfamily	Habitat type					Zoogeo.
		Agric. impact	Grass-land	River margin	Inun. forest/ bushes	Rain-forest	
Suniotrichus sordidus Sharp, 1886	Paederinae	0	1	0	0	0	N
Tannea amazonica Irmler, 2003	Osoriinae	0	0	0	0	1	Am
Tannea leticiae Irmler, 2005	Osoriinae	0	0	0	0	1	SA
Thoracophorus denticollis (Erichson, 1840)	Osoriinae	-	-	-	-	-	N
Thoracophorus distinguendus Irmler, 2005	Osoriinae	0	0	0	0	1	EA
Thoracophorus guadalupensis Cameron, 1913	Osoriinae	108	0	3	1	0	N
Thoracophorus sallaei Sharp, 1887	Osoriinae	-	-	-	-	-	N
Thoracophorus sculptilis (Erichson, 1840)	Osoriinae	0	0	0	0	1	N
Thoracophorus verhaaghi Irmler	Osoriinae	0	0	0	0	1	E
Trogactus godmani Sharp, 1887	Oxytelinae	1	1	0	0	0	N
Tumboecus verhaaghi Irmler, 2015	Osoriinae	1	1	0	0	6	E
Vatesus goianus Borgmeier, 1961	Staphylin.	0	1	0	0	0	SN
Verhaaghiella becki (Irmler, 2001)	Osoriinae	0	1	0	0	0	E
Xanthopygus nigripes Sharp, 1876	Staphylin.	0	0	0	0	1	SA
Xenopygus analis (Erichson, 1840)	Staphylin.	0	0	0	0	1	N
Xenopygus bicolor (Laporte, 1835)	Staphylin.	0	0	0	0	2	N

reflect the human impact with manioc and other agricultural fields on the one hand and grassland and pastures on the other. Overall, the cluster analysis differentiated five assemblages, with rainforest and river margins as the habitats with the most specific species compositions.

Zoogeographic relations of the region
Among the 178 species identified to species level, 41 species were regarded to be endemic in the region because they are known only from Panguana and the adjacent

regions (Table 3, Fig. 3). This corresponds to 23% of the considered species richness. If the East Andean species are included as extended endemics, 36 species (20%) must be added, which amount to a total of 43% of the species restricted to the East Andean region. Only two species are regarded as pantropic and 42 species are known from the total Neotropical region, which amounts to a total of 24% of all species identified to species level that have a wide geographical distribution. However, the number of species regarded as limited to the Amazon basin is low, with
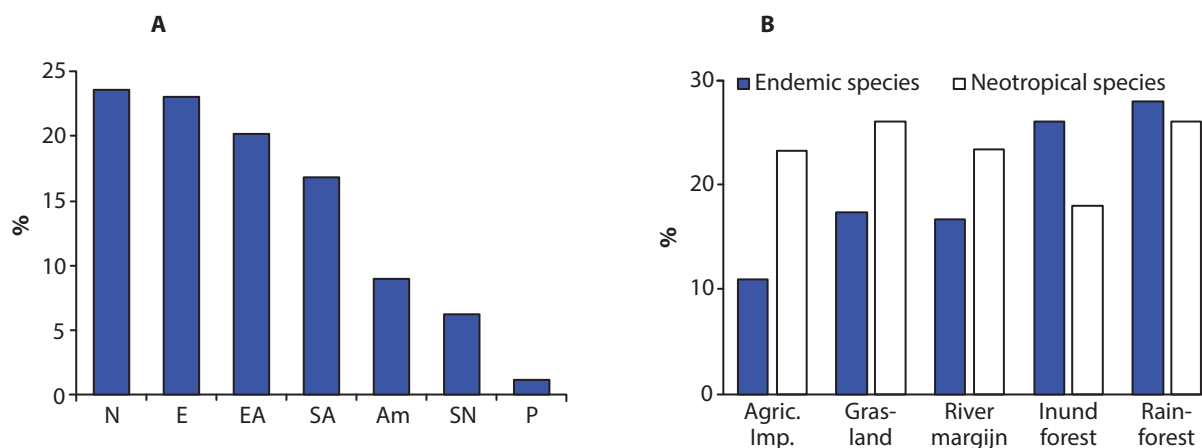

Figure 3. Percent relations of the differentiated zoogeographic regions (A) and percent of endemic and Neotropical species numbers for the differentiated habitat types (B). For abbreviations of the regions see Table 2.

Table 4. List of genera per subfamily and number of morphospecies per genus

Subfamily Genera	# of morpho-species	Subfamily Genera	# of morpho-species	Subfamily Genera	# of morpho-species	Subfamily Genera	# of morpho-species
Aleocharinae		**Aleocharinae** (cont.)		**Paederinae**		**Paederinae** (cont.)	
Acrotona	3	*Orphnebius*	4	*Aderocharis*	1	*Stamnoderus*	1
Aleodorus	1	*Parasilusa*	1	*Araeocerus*	1	*Stilomedon*	1
Apalonia	10	*Phanerota*	1	*Astenus*	1	*Sunicharis*	1
Atheta (Datomicra)	3	*Plesiomalota*	1	*Biocrypta*	4	indet. genus 4	1
Atheta	12	indet. genus 1	2	*Echiaster*	4		
Caloderella	1	indet. genus 2	1	*Eustilicus*	6	**Staphylininae**	
Falagria	1	indet. genus 3	1	*Homaeotarsus*	10	*Acylophorus*	4
Gansia	1			*Lathrobium*	2	*Atanygnathus*	3
Geitonusa	1	**Omaliinae**		*Leptobium*	2	*Heterotops*	3
Homalota	2	*Phloeonomus*	2	*Lobrathium*	3	*Lissohypnus*	5
Hoplandria	5			*Medon*	4	*Neohypnus*	3
Hydrosmecta	1	**Oxytelinae**		*Monista*	1	*Paederomimus*	3
Hygronoma	5	*Anotylus*	9	*Ochthephilum*	5	*Philonthus*	1
Leptonia	2	*Bledius*	11	*Palaminus*	2	*Quedius*	1
Macrogerodonia	1	*Carpelimus*	9	*Pinophilus*	3		
Meronera	3	*Sciotrogus*	1	*Ronetus*	3	**Tachyporinae**	
Neolara	2	*Thinobius*	5	*Sciocharis*	5	*Bryoporus*	3
Oligota	7	*Thinodromus*	1	*Scopaeus*	13	*Coproporus*	13
Ophioglossa	2			*Sphaeronum*	1	*Sepedophilus*	1

16 species (9%), and only slightly higher than the 11 species restricted to the southern Neotropics which connect Peru with south-east Brazil. If the habitat types are considered separately, inundation forests and rainforests have distinctly higher percentages of endemic species in comparison to the two habitats with human impact, agricultural fields and grassland (Fig. 3). The numbers of endemic species in the near-natural habitats are higher than those with neotropical distribution. In contrast to these near-natural habitats, the habitats with human impact have relatively higher numbers of the widely distributed neotropical species. The river margins show an intermediate relation between endemic and Neotropical species with five endemic and seven Neotropical species.

DISCUSSION

Densities of Staphylinidae seem to be lower in similar habitats of tropical South America than in temperate zones. According to Irmler and Lipkow (2018) densities in tropical South America range between 5 and 74 ind. m^{-2}.

The observed values are consistent with the densities of 20-70 ind. m^{-2} found by Hanagarth (1983) with the highest densities at the river margins (Hanagarth 1983). In contrast, densities in similar habitats of temperate zones are much higher, ranging between 30 and 700 ind. m^{-2} (Irmler & Lipkow 2018). These relations suggest that Staphylinidae in the studied region are of lower importance for the ecosystems than in temperate zones. Nevertheless, due to their megadiverse species richness Staphylindae may be valuable for evaluating the ecological conditions of habitats. Unfortunately, ecological studies on staphylinids are rare in South America due to the difficulties with identification. Similar studies like those in the Panguana region were carried out in Central Amazonian inundation forests (Irmler 1978). The number of species in the inundation forests was 192, which is distinctly lower than the 416 found in the Panguana region. However, in the Panguana region habitat diversity was higher because agricultural habitats and rainforests were included. If only those habitats are considered which are subject to inundations, 190 species were found in the Panguana region, which is on the same level

as in Central Amazonia. A study including a fragmented landscape in Pernambuco, Brazil, resulted in only 14 species during the dry season using 240 pitfall traps, which, however, is unfavourable for Staphylinidae (Salomão et al. 2019). In agricultural and fragmented forests of São Paulo, Brazil, only 32 species were recorded using 48 pitfall traps (Martins et al. 2009). These values correspond with the 27 species found in agricultural fields of the Panguana region. In riverine habitats of Colombia, 63 species were found in inhomogeneous sampling methods in 46 sites, which is nearly on the same level as the 78 species recorded in the Panguana region (Gutiérez-Chacon et al. 2009). In lettuce and tomato plantations only 27 staphylinid species were recorded using 66 pitfall traps (Rouaux et al. 2020). Thus, the habitat-specific number of species seems to be approximately similar throughout South America. The high species richness in the Panguana region is, therefore, also an effect of the multiple number of habitats there. As species richness depends on the sampling effort and number of habitat types, species richness values are hardly comparable between different studies. Moreover, the true species richness must be much higher in the forested sites than the value estimated by the Chao-1 method because species living in the canopy or specific microhabitats were not caught. This is certainly true not only for the Panguana study but also for any study in such habitats.

Evenness reflects a more valuable index of the community structure than do diversity indices. In the present study, higher evenness values were found in the near-natural habitats such as rainforests than in the agricultural fields. In the Central Amazonian inundation forests evenness was on the same level (0.84–0.90) as in the Panguana rainforest or grassland (0.81–0.90) (Irmler 1978). Agriculturally used habitats such as agricultural fields, manioc or banana plantations revealed values between 0.37 and 0.82, which are like the values found in the agrarian landscape in São Paulo with 0.40 to 0.77 (Martins et al. 2009). Hanagarth (1981) analysed diversity as ln H(s) for carabid beetles from the same material as used here and found values ranging between 0.5 and 3.0 without any relationship to human impact. For Staphylinidae these values are (1) much higher at 2.3 and 4.6 and (2) show a distinct increase from strongly impacted systems, e.g. agricultural fields, to natural systems such as rainforests. In the Central Amazon inundation forests (Irmler 1978), values were published as ld H(s) and revealed no significant difference between Carabidae and Staphylinidae. Diversity indices between different studies are hard to compare because several studies used the log or the ld basis and not the ln basis.

Regarding Carabidae in the Paguana region, Hanagarth (1983) found only few species that could be considered as euryoecious, which corresponds to the results from inundation forests in Central Amazonia where 12% of species were recorded from all forests studied (Irmler 1978). In contrast to Carabidae in the Panguana region where species numbers in the rainforests were low, Staphylinidae showed the highest species richness there. Agricultural fields had a high percentage of euryoecious species, together with species originating from the inundated habitats (Hanagarth 1981). Overall, Hanagarth (1981) emphasised that carabid species were highly habitat specific. Agricultural habitats had the lowest number of specific species. These results correspond to the results found for Staphylinidae. In ants, too, high differences were found between anthropogenic habitats and the natural rainforests (Verhaagh 1991). According to the DCA, the habitats with human impact were more similar to riverine habitats than to rainforests, which indicates that their fauna is mainly influenced by the wet and inundated habitats. The inundation gradient seems to be one of the most important ecological factors in the studied region. The composition of Panguana snail fauna assemblages was significantly affected by elevation, which corresponds to inundation frequency, and additionally by distance from the forest edge, canopy cover and human impact (Wendebourg & Hausdorf 2019). Specific species for agricultural habitats exist in all three groups (Carabidae, Staphylinidae, Gastropoda). According to MacArthur (1965), the low similarity between habitats in the tropics and the high total species richness can be explained by the 'between habitat' diversity. Staphylinidae assemblages were not strongly differentiated in terms of species composition, which means that there was a high similarity among the assemblages. This may be a result of the low numbers of species that reach high dominance in specific habitats. Therefore, soil moisture combined with inundation frequency seems to be the most important factor influencing the species composition of the natural habitats. As these habitats are intermediate between river margins and rainforests, it can be assumed that assemblages of the agriculturally impacted sites are more influenced by wet sites from the Cochas and inundation forests than by rainforest. In the Panguana agricultural sites the number of dominant species was distinctly higher than in the forested sites. In the Argentinian lettuce and tomato plantation *Apocellus obscurus* was most frequent with 32% dominance (Rouaux et al. 2020). In the Panguana field sites *Thoracophorus guadalupensis* reached similar dominance with 28%. For all other species dominance was below 10%.

According to Morrone (2014), the Panguana region located in the Ucayali and Yungas provinces is part of the South Brazilian biogeographic dominion. Both provinces are located on the central eastern slopes of the Andes in

eastern Peru, northern Bolivia and western Brazil. Müller (1973) assigned this region as part of the montane dispersal centre on the eastern Andean slopes (Yungas centre) and the lowland rainforest centre. For the Ucayali and Yungas provinces 16 and 30 endemic species, respectively, are listed in Morrone (2014). The present study found 41 endemic species of Staphylinidae. Although the distribution of Staphylinidae is less well studied than some other coleopteran families, e.g., Cerambycidae, the endemic status is likely for the species supposed as endemic here, e.g., *Aneucamptus geroi* Irmler, 2001 with five records only from the region. The two other *Aneucamptus* species with 97 and 137 known records are distributed throughout the Neotropics. The same is true for the other Osoriinae endemic species and *Somoleptus elongatus* Irmler, 2022, *Lithocharodes bicornis* Irmler, 2021, and *Lithocharodes hanagarthi* Irmler, 2021. Even endemic genera are known and newly described only from Panguna region, e.g., *Osoriosetus* Irmler 2015 and *Verhaghiella* Irmler, 2001. The high number of endemic species is conspicuous compared to vertebrates and plants both ranging between 5.7% to 6.7% (Myers, et al. 2000). Even if we suppose that the distribution of species is poorly known, it can be assumed that in the region the number of endemic species among Staphylinidae is high. This may be supported by the high affinity to the soil based habitats among staphylinids. The endemic species mostly have reduced hindwings and, thus, may have a low dispersal power. The low dispersal power of such species combined with their affinity to soil crevices may explain the high number of endemic species. The connection to the Amazon lowland rainforest is documented by the occurrence of the *Holotrochopsis* and the *Mimogonia* species. Species of both genera are restricted to the Amazonian lowland rainforest (Irmler & Asenjo 2018). But the zoogeographic relation to the lowland rainforest is low with 9% compared to the relations to the pre-Andean region. There are also connections to the Atlantic province (Serra do Mar dispersal centre of Müller 1973), e.g., the occurrence of *Pseudastenus plaumanni* (Bierig 1939) in both provinces (Busanello et al. 2020). Overall, the Panguana region has a high proportion of endemic species and is mainly characterised by a specific species composition of the eastern Andean slope and only low connections to the lowland Amazon area. Considering the amount of endemic and widely distributed neotropical species among the studied habitats, a higher number of endemic species in the near-natural habitats compared to habitats with human impact can be noticed. In the two habitats with human impact dominate the widely distributed neotropical species, whereas in the near-natural habitats the relation is vice versa. Thus, near-natural habitats

are the most important ecosystems to preserve the regionally specific species and are, therefore, most important for the overall species diversity not only for the region but also generally for the total Neotropics.

CONFLICT OF INTEREST

The author declares that he has no conflict of interest.

REFERENCES

Asenjo A, Irmler U, Klimaszewski J, Chandler DS, Fierros-López HE, Vieira JS (2019) Staphylinidae (Insecta: Coleoptera) in Latin America: synopsis, annotated catalog, diversity and distribution. Zootaxa 4621:1-406.

Busabnello D, Irmler U, Caron E (2020) Revision of *Pseudastenus* Bernhauer, synonym with Xenastenus Newton and six new species (Coleoptera, Staphylinidae, Paederinae). Zootaxa 4755:139-154.

Caron E, Ribeiro-Costa C, Newton A (2011) Cladistic analysis and revision of *Piestus* Gravenhorst with remarks on related genera (Coleoptera: Staphylinidae: Piestinae). Invertebrate Systematics 25:490-585.

Chani-Posse M, Newton A, Kappel-Hansen A, Solodivnikov A (2018) Checklist and taxonomic changes for Central and South American Philonthina (Coleoptera: Staphylinidae). Zootaxa 4449:1-95.

Gutiérez-Chacon C, Zúnica M, van Bodegom PM, Cará J, Giraldo LP (2009) Rove beetles (Coleoptera: Staphylinidae) in Neotropical riverine landscapes: characterising their distribution. Insect Conservation and Diversity 2:106-115.

Hammer Ø, Harper D, Ryan P (2012) PAST: paleontological statistics software. Palaeontologia Electronica 4.

Hanagarth W (1981) Vergleichend-ökologische Untersuchungen an epigäischen Arthropoden aus Naturbiotopen und Kulturland im tropischen Regenwald Perus. Ein Beitrag zur Agrarökologie der Tropen. PhD thesis, University of Hamburg, Hamburg.

Hanagarth W (1983) Überschwemmungsgebiete im peruanischen Amazonasgebiet als Quellfauna für Agrargebiete. Amazoniana 8:111-128.

Herman L (1991) Revision of the subtribe Cylindroxystina (Coleoptera: Staphylinidae: Paederinae). Bulletin of the American Museum of Natural History 203:1-84.

Hutterer R. (1995) An inventory of mammals observed at Panguana station, Amazonia Peru. Ecotropica 1:3-20.

Irmler U (1981) Desciption of new neotropical *Holotrochus* and a key to the species of the genus (Coleoptera: Staphylinidae). Coleopterist's Bulletin 379-397.

Irmler U (1994) Taxonomie und Verbreitung neotropischer *Lispinus* Er. (Coleoptera, Staphylinidae). Contributions to Entomology 44:53-82.

Irmler U (1978) Die Struktur der Carabiden- und Staphylinidengesellschaften in zentralamazonischen Überschwemmungswäldern. Amazoniana 6:301-326.

Irmler U (2009) New species and records of the genus *Lispinus* with a key to rthe species from Peru (Coleoptera: Stapghylinidae: Osoriinae). Zootaxa 2263:42-58.

Irmler U (2014) The Neotropical species of the genus *Osoriellus* Fagel, 1959 (Coleoptera: Staphylinidae: Osoriinae). Contributions to Entomology 64:231-354.

Irmler U (2017) A review of the Neotropical genus *Diochus* Erichson, 1840 (Coleoptera: Staphylinidae: Staphylininae). Contributions to Entomology 67:1-62.

Irmler U (2021) The Neotropical species of the genus *Lithocharodes* SHARP, 1876 (Coleoptera: Staphylinidae: Staphylininae: Xantholinini). Contributions to Entomology 71:29-85.

Irmler U, Asenjo A (2018) Biodiversity and geographic patterns of Neotropical Staphylinidae. In: Betz O, Irmler U, Klimaszewski J (eds) Biology of rove beetles (Staphylinidae). Springer, Stuttgart, pp 47-65.

Irmler U, Lipkow E (2018) Effect of environmental conditions on distribution patterns of rove beetles. In: Betz O, Irmler U, Klimaszewski J (eds) Biology of rove beetles. Springer, Stuttgart, pp 117-144.

MacArthur R (1965) Patterns of species diversity. Biological Reviews 40:510-533.

Martins ICF, Cividanes FJ, Barbosa JC, de Souza Araújo E, Haddad GQ (2009) Análise de fauna e flutuação populacional de Carabidae e Staphylinidae (Coleoptera) em sistemas de plantio direto e convencional. Revista Brasiliera de Entomologia 53:432-443.

Morrone J (2014) Biogeographical regionalisation of the Neotropical region. Zootaxa 3782:1-110.

Müller P (1973) The dispersal centres of terrestrial vertebrates in the Neotropical realm. Biogeographica 2:1-243.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853-858.

Newton, A. (2022). StaphBase. In O. Bánki, Y. Roskov, M. Döring, G. Ower, D. R. Hernández Robles, C. A. Plata Corredor, T. Stjernegaard Jeppesen, A. Örn, L. Vandepitte, D. Hobern, P. Schalk, R. E. DeWalt, K. Ma, J. Miller, T. Orrell, R. Aalbu, J. Abbott, R. Adlard, E. M. Adriaenssens, et al., Catalogue of Life Checklist (Aug 2022). https://doi.org/10.48580/dfsr-3gk

Niessner A, Monzón J, Gerlach G, Diller J (2020) Biological research station and private conservation area Panguana. Ecotropica 22:1-5.

Pace R (2008) New records of Aleocharina from Ecuador and Peru, with description of new species, new subgenera and new genera (Coleoptera, Staphylinidae). Biodiversity of South America, I. Memoirs on Biodiversity 1:225-398.

Patterson B, Stotz D, Solari S, Fitzpatrick J (1998) Contrasting patterns of elevational zonation for birds and mammals in the southeastern Peru. Journal of Biogeography 25:593-607.

Puthz V (2006) Revision der neotropischen *Stenus* (*Tesnus*) Arten (Coleoptera: Staphylinidae). 288. Beitrag zue Kenntnis der Steninen. Revue Suisse de Zoologie 88:617-674.

Rouaux J, Cabrerea N, Martínez AS, Posse M-C, Luna MG (2020) Diversity and phenology of epigeal Coleoptera assemblages in lettuce and tomato crops in Northern Buenos Aires province, Argentina. Anais da Academia Brasileira de Ciencias 92 (Suppl):2-16.

Salomão RP, Brito LC, Iannuzzi L, Lira AFA, Albuquerque CMR (2019) Effects of environmental parameters on beetle assemblages in a fragmented tropical rainforest of South America. Journal of Insect Conservation 23:111-121.

Seidenschwarz F (1986 Vergleich von Flußuferkrautgesellschaften mit Wildkrautvegetation im tropischen Tiefland von Peru. Amazonina 10:79-111.

Servat G, Franke I, Terborgh J, (2012) Maria Koepke and her contribution to Peru and Neotropical ornithology. Ornithologia Neotropical 23:399-404.

Newton, A. (2022). StaphBase. In O. Bánki, Y. Roskov, M. Döring, G. Ower, D. R. Hernández Robles, C. A. Plata Corredor, T. Stjernegaard Jeppesen, A. Örn, L. Vandepitte, D. Hobern, P. Schalk, R. E. DeWalt, K. Ma, J. Miller, T. Orrell, R. Aalbu, J. Abbott, R. Adlard, E. M. Adriaenssens, et al., Catalogue of Life Checklist (Aug 2022). https://doi.org/10.48580/dfsr-3gk

ter Braak C (1986) Canonical correspondence analysis: a new eigenvector technique for multivarite direct gradient analysis. Ecology 67:1167-1179.

Verhaagh M, Veeresh GK, Mallik B, Viraktamath CA (1991) The Formicidae of the rain forest in Panguana, Peru: the most diverse local ant fauna ever recorded. Social insects and the environment: Proceedings of the 11th International Congress of IUSSI: 217-218.

Wendebourg B, Hausdorf B (2019) The land snail fauna of a South American rainforest biodiversity hotspot: the Panguana conservation area in the Peruvian Amazon. Journal of Molluscan Studies 85:311-318.