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Touching the Sky: Coccinellids (Coleoptera: Coccinellidae) at High Altitudes in South America

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Abstract
Records of extreme altitudes where several coccinellid species from South America inhabit the Andes of Argentina, Bolivia, Chile, Colombia, Ecuador, and Peru are provided. After an intensive review of several entomological collections and literature, records for 35 species with at least one location over 3500-m elevation were obtained, including the genera *Cycloneda* (ten species), *Eriopis* (15 species and one subspecies), *Harmonia* (one species), *Hippodamia* (two species), *Mimoscymnus* (two species), *Psyllobora* (one species), and *Stenadalia* (four species). In total, 184 location records are listed, of which 119 were from between 3000 and 4000 m, 57 between 4000 and 4900 m and eight above 4900 m, with the highest altitude record at 5250 m for *Eriopis minima* Hofmann. All records above 4000 m were obtained in the Puna biogeographic province within the Paramo Puneña biogeographic subregion. These records are the highest altitudes observed for the American continent and by far surpass others known for coccinellids worldwide. Several species of coccinellids living in sympatry at these high altitudes were verified, and in some cases, in situ development was inferred by the presence of immature stages. These findings are important to foresee the future effects of global warming that will affect especially the biological communities of extreme altitudes.

Introduction

Insects living at high altitudes have been the object of many studies, most of them oriented to physiological aspects and their relationship with environmental factors (temperature, air density, relative humidity), or behavior such as flight or the formation of aggregations in high areas (Güven *et al* 2015). Examples are the classic studies of Mani (1968) and Mani & Giddins (1980) of the old world fauna. Only isolated records are known of coccinellid fauna at high altitudes. Even current books on the biology and ecology of coccinellids do not include a synthesis of this aspect (see Hodek *et al* 2012 and Majerus *et al* 2016). Canepari (1997) studied the fauna of Coccinellidae of Nepal in the Himalayas, finding specimens of *Priscibrumus disjunctus* Canepari at altitudes of 3800 to 4150 m, *Hippodamia variegata* (Goeze) at 3650 to 4000 m, and *Coccinella septempunctata* L. at 4100 to 4500 m. Subsequent studies of the fauna of Nepal did not provide records at higher altitudes (Canepari 2003, 2012). Mani (1968) indicated the presence of aggregations of *C. septempunctata* at 4200 m in the Himalayas. In Oceania, Englund *et al* (2010) established the presence of *Hippodamia convergens* (Guerin-Meneville) and *C. septempunctata* at 4226 m in Hawaii, but they considered that these specimens could have been brought to this altitude by wind or migration and thus would not be established at that altitude. Regarding this possibility, Jeffries *et al* (2013), through the analysis of radar data, found in England that *Harmonia axyridis* (Pallas) and *C. septempunctata* could travel in flight up to 1100 m above ground level at speeds of up to 60 km/h, dispersing up to 120 km in a single flight.

Studies on the biogeography of South American coccinellids, and particularly on species at high altitudes, are scarce, scattered, and very specific. Gordon (1975) studied the zoogeography of the tribe Epilachnini in South America (as subfamily Epilachninae), recognizing four groups according to geographical distribution, the most important of which is concentrated in the highlands of the Andes. Gordon (1977) analyzed the distribution of the family Sticholoditinae (currently Sticholotidini + Microweisinae), recognizing its basically archaic (ancient) and pantropical character, while Gordon (1994) studied the Coccidulini tribe, enhancing its almost exclusive association with the temperate forests of *Nothofagus* from southern Chile and Argentina. Finally, González (2014b), in a study of the fauna of the Argentinian coccinellids, recognized two biogeographical groups in the coccinellid fauna of the Andean region, one of which is associated with *Nothofagus* forests and very rich in the Coccidulinae subfamily, with some genera, especially *Stenadalia*, penetrating into Peru and Bolivia through the mountains; the other biogeographical group of high Andean origin is characterized by the high richness of the genus *Eriopis*. Thus, the Andes has been an important factor in the biogeographic origin and spread of genera of this family.

This South American mountain range represents one of the largest mountain masses on the planet, being surpassed in altitude only by the Himalayas in Asia. Most of the high areas of the Andes belong to the Andean biogeographic region, subregion Paramo Puneña. Following Morrone (2001), these areas correspond to the biogeographical provinces of the Paramo Norandino in Colombia and Ecuador, the Puna province from eastern Peru, and western Bolivia to northern Argentina and Chile, where it reaches down to Copiapó, including the area known as the highlands (Altiplano). The Prepuna province extends to the south in this area towards central Argentina and Chile (to Talca) (Fig 1). These biogeographic provinces are characterized by their own flora and fauna, providing stable ecosystems that have allowed the presence of numerous species of plants and animals that reproduce and thrive in them (Morrone 2001). For altitudinal characterization, Villagrán *et al* (1982) established the Puneño zone (3000 to 4000 m), the Altoandino zone (4000 to 4900 m), and the Subnival zone (4900 to 5200 m). The Puneño zone includes shrub steppes relatively rich in species and vegetation cover; the Altoandino zone is characterized by the presence of low scrubs, high-altitude wetlands, and cushion plants, whereas the Subnival zone is considered a sub-desert ecosystem (Moreira-Muñoz *et al* 2016).

Although there have been efforts to characterize the South American fauna of insects from extreme altitudes, there is little information; data are scattered in multiple taxonomic and biological studies or on local lists, which in many cases do not include records with precise altitudes (e.g., Peña 1959). Among these studies, Sømme *et al* (1996) studied the adaptation of Carabidae to the heights on the Chimborazo volcano in Ecuador, including records of up to 4800 m, and Despland (2014) described butterflies of high altitudes in the Atacama Desert up to 5000 m. Ferrú & Elgueta (2011), in a list of Coleoptera from the extreme north of Chile, indicated a large number of species over 4000 m, including two species of Tenebrionidae at 5200 m, Laguna Verde in the province of El Loa. The first records of extreme altitudes of coccinellids in South America were published by Hofmann (1970), with two records of *Eriopis minima* Hofmann in Bolivia at 4500 m. Many years later, Bustamante & Yábar (2006) highlighted the altitudes reached by several species of the genus *Eriopis* in southern Peru, again mentioning *E. minima* that was found at a maximum altitude of 4150 m. Molina-Montenegro *et al*. (2006, 2009) described the presence of *Hi. variegata* and *Eriopis chilensis* Hofmann (as *E. connexa*) in the Andes of central Chile at 3200 and 3600 m, respectively, associated with the cushion plants (*Azorella monantha* Clos and *Laretia acaulis* (Cav.) Gill. & Hook), which would confer to these insects a protection to the stressful and changing microclimatic conditions at those altitudes. Recently, Grez *et al* (2017) recorded the presence of the invasive species *Ha. axyridis* in the Andes of Central Chile at 3578 m, the highest reported altitude for this species in the world. Along with it, numerous specimens of the exotic species *Hi. convergens* and *Hi. variegata* were found, while *E. chilensis* was found at 3380 m, being the only native species recorded in this study at these altitudes.

Climate change is threatening the survival of populations and species. Urban (2015) analyzed 131 studies of climate change and extinction, finding that South America was the continent with the highest risk of extinction associated with this phenomenon (23%, against 5% and 6% for North America and Europe, respectively). Also, this author proposed that invertebrates have an 8.8% risk of extinction, being surpassed only by reptiles (9.0%) and amphibians (12.9%), and that endemic species in the study area had a 6% higher risk of extinction than non-endemic species in the same area. Pepin *et al* (2015) established that warming due to climate change occurs more rapidly at extreme altitudes in contrast to medium and low altitudes, and that this puts at risk many high-altitude ecosystems and the habitat of many rare and endangered species. Nowadays, given the growing importance of studying the effects of climate change, which could alter the fauna of high altitudes due to changes in temperature and the removal of glaciers, it is necessary to have information on the maximum altitude that numerous species of insects currently occupy.

Records of Coccinellidae at high altitudes in South America are reported in this study, providing so far unknown and relevant biogeographical information and endemism

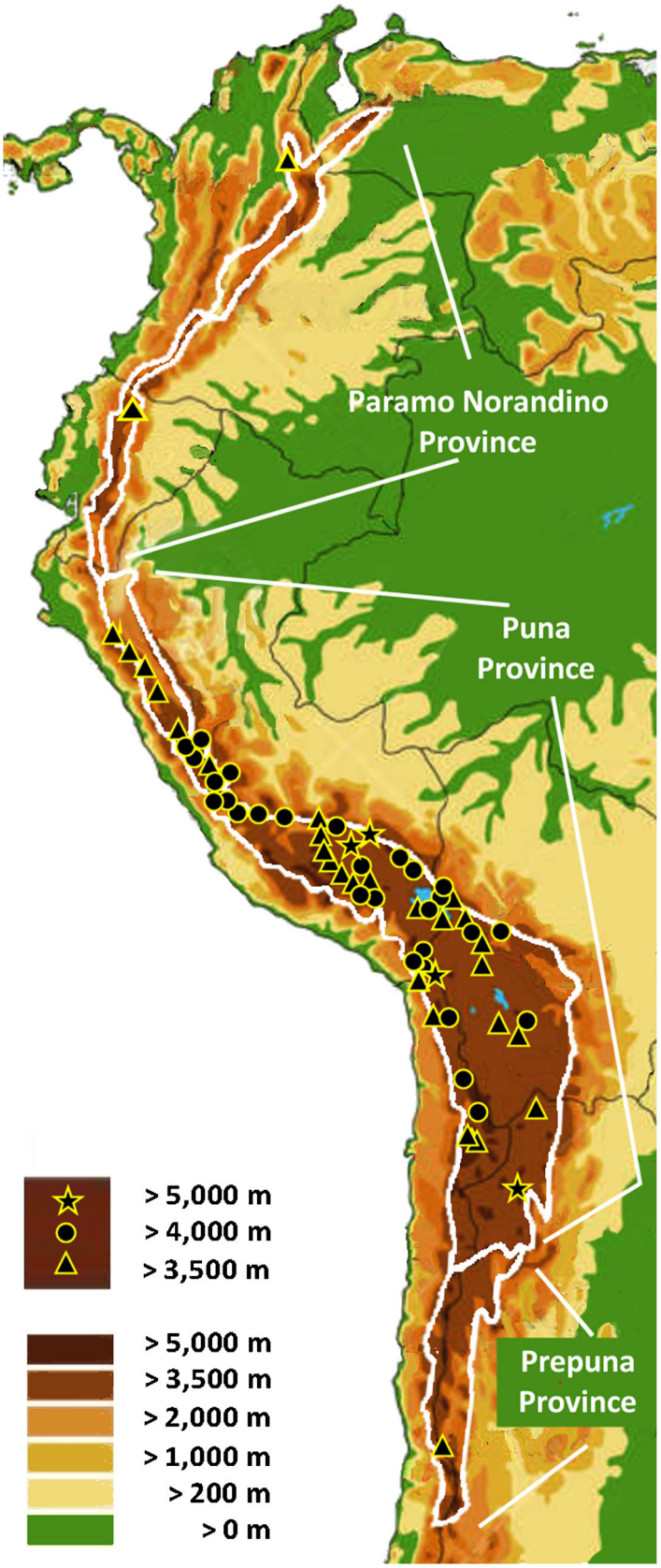

Fig 1 Biogeographic provinces (adapted from Morrone 2001) and geographic distribution of localities with presence of coccinellids in the Andes, according to altitude ranges.

data for this family. This will allow specialists to have precise information of locations where species of coccinellids are found to date at extreme altitudes, and in the future could allow evaluating the progress of the effects of climate change on that fauna.

Materials and Methods

The literature on South American coccinellids was reviewed in order to extract the data of the altitudes of specimens collected at over 3000 m in the high Andes of Argentina, Bolivia, Colombia, Chile, Ecuador, and Peru. Also, material from collections and museums used for the development of the website on coccinellids of Chile and other South American countries (www.coccinellidae.cl) was reviewed. This material includes photographs with labels with taxonomic identification and locality information of the collected specimens. The collections and museums consulted were as follows: CEUC: Entomological Collection of the University of San Antonio Abad of Cusco, Peru; CPFR Private collection of Francisco Ramírez, Santiago, Chile; CPGG Private collection of Guillermo González, Santiago, Chile; CPMD Private collection of Manuel Diéguez, Santiago, Chile; MKRB Entomology Museum Klaus Raven Búller, Agrarian University La Molina, Lima, Peru; MUSM Museum of Entomology of the National University of San Marcos, Lima, Peru; USAM Universidad Nacional Santiago Antúnez de Mayolo, Ancash, Peru; USNM U.S. National Museum of Natural History, Smithsonian Institution, Washington, USA, and UTAR Entomological Collection of the University of Tarapacá, Arica, Chile. The altitudes of the records were obtained from the references of the literature and the labels of the specimens and verified by the altitudes obtained in the "Google Earth" program, either by the name of the locality or by the geographic coordinates present in the records. In some cases, the website "Centros Poblados de Peru" (https://www.deperu.com/centros-poblados/) was used. The altitudes obtained by these methods are indicated in brackets less than–greater than "< >". When the original reference indicates a given amount of kilometers in some direction referred to a locality, the measurement was made at a point displaced from the locality at the indicated distance and direction. When the reference to a given locality was very extensive (e.g., province, district, mountain), a range of altitudes was assigned. If there was a noticeable difference with the altitude of the record, we examined if there were places with the indicated altitude in the vicinity of the locality, up to 5 km. In the case where no places with the indicated altitude were found, a question mark "**?**" was added. When it was not possible to find the locality, < s/i > "without information" was indicated. In some cases, the department, province, or other data that did not appear in the original record are indicated between square brackets "[]." With this information, a list of the species that reach altitudes higher than 3500 m on the continent was made, ordered from higher to lower altitudes and grouped according to the altitudinal zones proposed by Villagrán *et al* (1982). For each species, the records exceeding 3000 m were listed, including altitude, locality, record origin (bibliographic reference or collection acronym), and altitude range (verified from Google maps). To review the levels of endemism of the species of Coccinellidae studied it was necessary to review the geographical and altitudinal distribution of each of the species below the limit of 3000 m established for the study, which was done using the same sources already indicated.

Results

Records of 35 species of Coccinellidae were obtained with at least one collection over 3500 m elevation. These records include the genera *Cycloneda* (ten species), *Eriopis*, (15 species and one subspecies), *Harmonia* (one species), *Hippodamia* (two species), *Mimoscymnus* (two species), *Psyllobora* (one species), and *Stenadalia* (four species) (Fig 2). Only three species were not identified; all of them probably not described so far. Records were obtained from a total of 184 locations, of which 119 were between 3000 and 4000 m (Puneño zone), 57 between 4000 and 4900 m (Altoandino zone), and eight above 4900 m (Subnival zone). The records do not indicate the number of specimens, but in many of these locations, several specimens of the indicated species were observed. All the records were obtained in the Paramo Norandina, Puna, and Prepuna provinces (Fig 1), all of them in the Paramo Puneña biogeographic sub-region.

Subnival zone (above 4900 m).
Sub-desert vegetation.

5.250 m *Eriopis minima* Hofmann 1970 (Fig 3a).

- 5250 m, Peru, Cusco, Quispicanchis, Ocongate, Nevado Ausangate (CEUC) < 4800–5040? m > (Fig 4b) (Comment 1)
- 5100 m, Chile, Parinacota, Casiri Macho lagoon (CPGG) < 4925 m–5300 m > (Fig 4h) (Comment 2).
- 4500 m, Bolivia, [La Paz], Illimani (Hofmann 1970) < 4300–5000 m >.
- 4500 m, Bolivia, Potosí (Hofmann 1970) < 3888? m >.
- 4400 m, Chile, Tamarugal, Quebrada Blanca (MNHN) < 4367 m >.
- 4300 m, Chile, Parinacota, Caquena (CPFR) < 4415 m >.
- 4150 m, Peru, Cusco, Tucsa (CEUC) < 4280 m >.

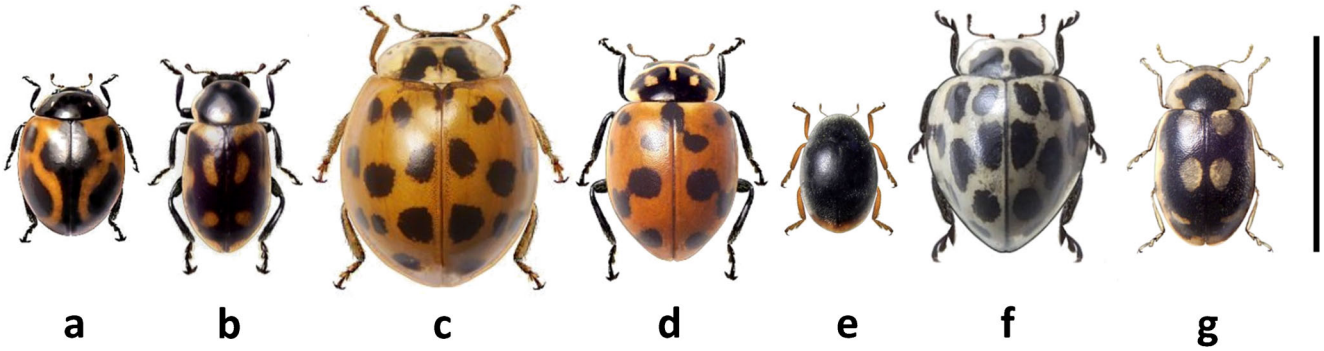

Fig 2 Habitus of representative genera and species of extreme altitudes; (a) *Cycloneda andresi*, (b) *Eriopis alticola*, (c) *Harmonia axyridis*, (d) *Hippodamia variegata*, (e) *Mimoscymnus terminatus*, (f) *Psyllobora constantini*, (g) *Stenadalia marieae* (scale: 5 mm).

- 4097 m, Chile, Tamarugal, Cancosa (González 2014a) < 3936 m > .
- 4100 m, Chile, Parinacota, Camino a Surire (CPGG) < 4100 m >.
- 4030 m, Bolivia, La Paz, La Paz (González 2014a) < 3600–4100 m >.
- 4000 m, Bolivia, [La Paz], Titicaca (Hofmann 1970) < 3815 m >.
- 4000 m, Bolivia, La Paz, Huarina (Hofmann 1970) < 3847 m >.
- 4000 m, Bolivia, [La Paz], Illimani (Hofmann 1970) < 4300–5000 m > (Comment 3).
- 4000 m, Bolivia, Cochabamba, Tunari (Hofmann 1970) < 4050 m >.
- 4000 m, Chile, Parinacota, Visviri (González 2014a) < 4083 m > (Fig. 4g).
- 4000 m, Chile, [Parinacota], Ancocalani (Hofmann 1970) < 4032 m >.
- 3950 m, Peru, Cusco, Canchis, Patatinta (Bustamante & Yábar 2006) < 4041 m >.
- 3920 m, Chile, [El Loa], Tumbre (Hofmann 1970) < 3920 m >.
- 3900 m, Peru, Cusco, [Quispicanchis,] Urcos (Hofmann 1970) < 3110 m > (Comment 4).
- 3850 m, Bolivia, [La Paz], Titicaca, Guaqui (Hofmann 1970) < 3969 m >.
- 3820 m, Bolivia, [La Paz], Achacachi (Hofmann 1970) < 3829 m >.
- 3804 m, Bolivia, Oruro, Ventanilla Caracollo (González 2014a) < 3775 m >.
- 3800 m, Peru, Puno, Juli (CEUC) < 3888 m >.
- 3650 m, Chile, Parinacota, Putre (CPGG) < 3551 m >.
- 3600 m, Bolivia, [La Paz], La Paz (Hofmann 1970) < 3600–4100 m >.
- 3500 m, Chile, [Parinacota], Putre (Hofmann 1970) < 3551 m >.
- 3446 m, Peru, Cusco, Checacupe (Bustamante & Yábar 2006) <3439 m >.
- 3400 m, Chile, [Parinacota], Putre (CPGG) < 3551 m >).
- 3300 m, Chile, [Parinacota], Belén (Hofmann 1970) < 3071 m >.
- 3000 m, Chile, Parinacota, Socoroma (González 2014a) < 3306 m >. Comments: (1) The specimens collected near Ausangate, the fifth highest peak in Peru at—the eastern foothills of the Ausangate glacier (Fig 4b) (Anahí Oróz, personal communication); however, the altitude indicated in the label is not consistent with the altitudes present in the indicated location, with a bias of about 210 m. (2) On the slopes of the Casiri Macho lagoon there are altitudes of up to 5300 m less than 1 km away

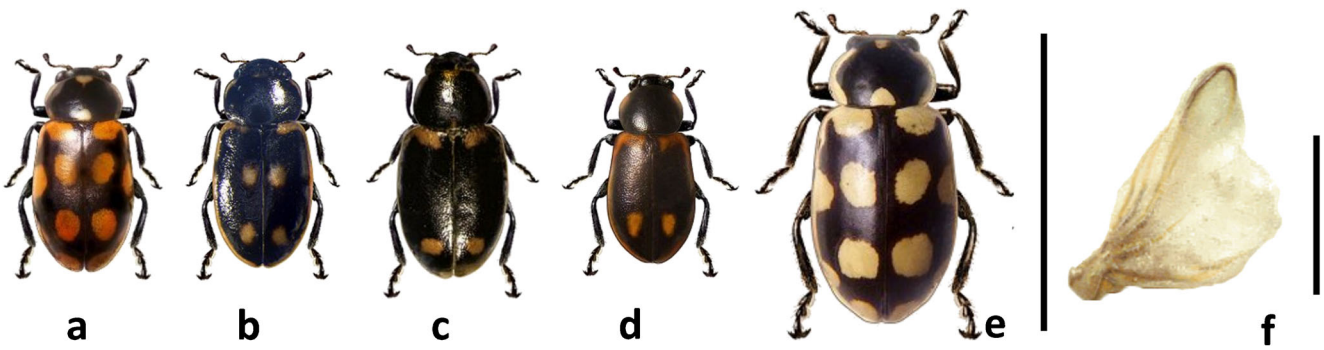

Fig 3 Genus *Eriopis*; (a) *E. minima.* (b) *E. huancavelicae*. (c) *E. santiagoi*. (d) *E. lawalawani*. (e) *E. connexa*. (f) Brachyptera metasternal wing of *E. minima*. Scale of habitus: 5 mm, of wing: 1 mm.

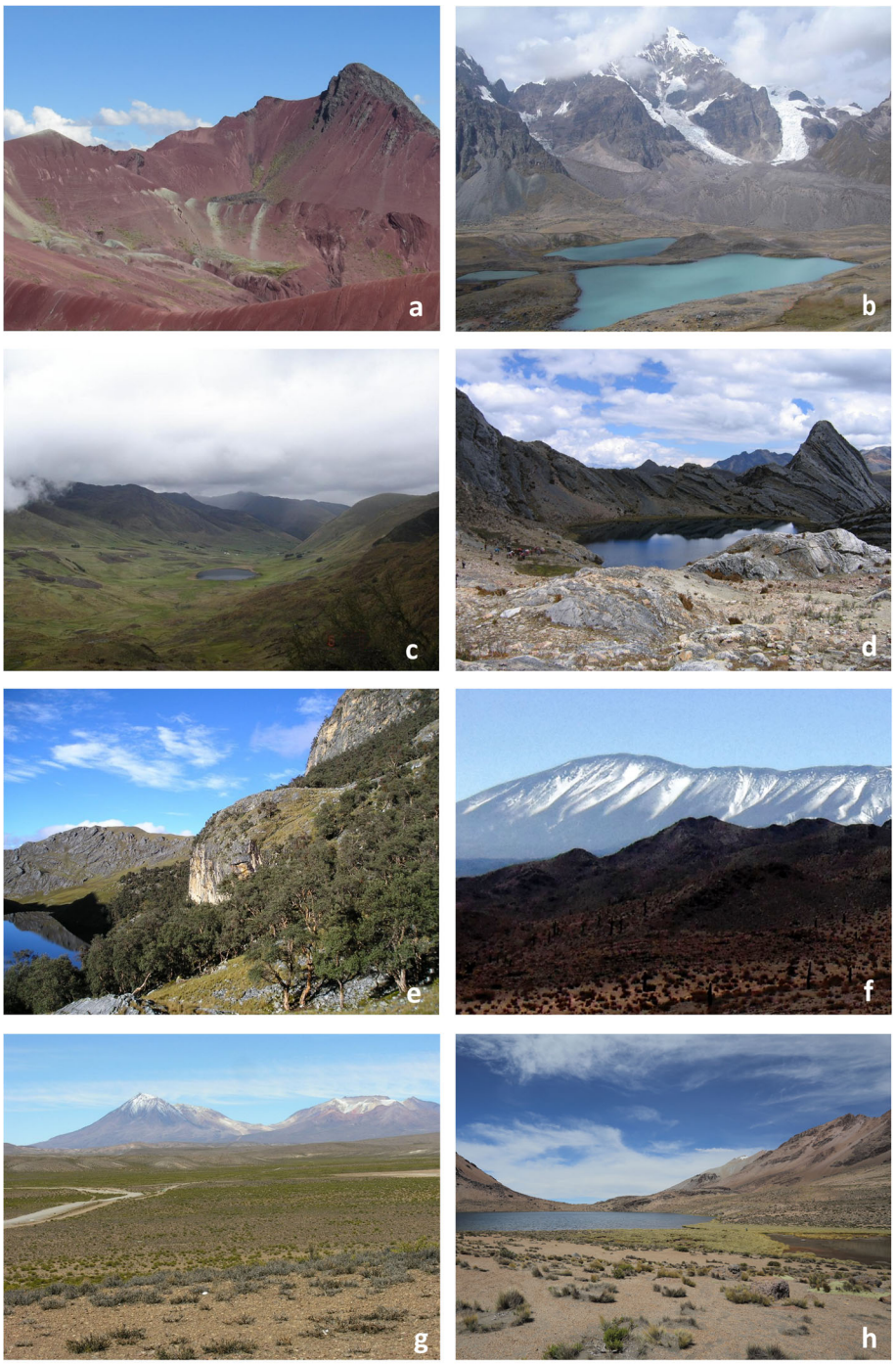

Fig 4 Localities; (a) Montaña de Siete Colores (Cusco, Peru). (b) Pumacocha Lagoon and Nevado Ausangate (Cusco, Peru). (c) Usmay (Ayacucho, Peru). (d) Jupaymarca (Áncash, Peru). (e) Canrash (Áncash, Peru). (f) Nevado de Cachi (Salta, Argentina). (g) Visviri (Parinacota, Chile). (h) Laguna Casiri (Parinacota, Chile). (a–f) Abdhiel Bustamante, (g) Margarita Ruíz de Gamboa, (h) Sergio Rothmann.

(Hugo Benítez, personal communication). (3) There is no precise locality with the name Illimani in La Paz; however, in the foothills of the mountain of that name that reaches 6462 m, there are innumerable areas with altitudes between 4200 and 5000 m. (4) The town of Urcos is only at 3110 m, but less than 5 km away, there are roads that climb steeply up to 4000 m within the district of the same name.

5230 m *Eriopis alticola* Hofmann 1970 (Fig 2b).

- 5230 m, Peru, Cusco, Quispicanchis, Ocongate, Pumacocha [Pumacocha lagoon] (CEUC) < 4570–5100? m > (Fig 4b) (Comment 5).
- 4294 m, Peru, Áncash, Pampa Silvestre (MUSM) < s/i > (Comment 6).
- 4167 m, Peru, Cusco, Quebrada Chaisamayo (CPMD) < 4200 m > (Comment 7).

- 4070 m, Peru, Cusco, Paucartambo, Challabamba (MUSM) < 4074 m >.
- 3900 m, Peru, Cusco, Urcos (Hofmann 1970) < 3110 m > (Comment 8).
- 3855 m, Peru, Áncash, Chuchucora (MUSM) cf. < 3147–4188 m > (Comment 9).
- 3754 m, Peru, Cusco, Urubamba, Ocuman (Bustamante & Yábar 2006) <3724 m >.
- 3691 m, Peru, Cusco, Acomayo (Bustamante & Yábar 2006) < 3691 m >.
- 3370 m, Peru, Cusco, Anta, Aparquilla (Bustamante & Yábar 2006) < 3323 m >.

Comments: (5) Regarding the specimens collected on the shores of the Pumacocha lagoon, north of the Ausangate glacier (Fig 4b), even though the altitude of the lagoon is 4570 m, there are places less than 1 km away that reach altitudes of 5100 m. A GPS was used with a barometric altimeter (Walter Cosio, personal communication); even so, the altitude indicated on the label is 130 m higher than the verified altitudes obtained in Google Maps. (6) The town of Pampa Silvestre in Ancash could not be located. (7) Quebrada Chaisamayo in Cusco also could not be located, but by the coordinates present on the label, it was possible to determine its location and altitude. (8) For the Urcos locality, see comments under *Eriopis minima*. (9) The locality of Chuchucora in Áncash is at 3147 m, but the coordinates present on the label, about 50 km north of Chuchucora, correspond to the Pierina Mine at an altitude of 4188 m.

5230 m *Cycloneda andresi* Oróz *et al* 2009 (Fig 2a).

- 5230 m, Peru, Cusco, Quispicanchis, Ocongate, Pumacocha [Pumacocha lagoon] (Oróz *et al* 2009) < 4570 a 5100? m > (Fig 4b) (Comment 10).
- 4122 m, Peru, Áncash, Jupaymarca (Oróz *et al* 2009) < 4312 m > (Fig 4e).
- 3850 m, Peru, Ayacucho, Usmay (Oróz *et al* 2009) < 4039 m > (Fig 4c).
- 3506 m, Peru, Ayacucho, Callenueva (CEUC) < 3585 m >.
- 3170 m, Peru, Cusco, Ur [Urubamba], Chicón (CEUC) < 2871 m > (Comment 11).

Comments: (10) For the locality Pumacocha (Fig 4b), see comment under *Eriopis alticola*. (11) The town of Urubamba is at only 2871 m, but less than 2 km away, on the way to the Chicón mountain that rises to 5530 m, there are altitudes of up to 3200 m.

5230 m *Eriopis andina* Hofmann 1970.

- 5.230 m, Peru, Cusco, Quispicanchis, Ocongate, Pumacocha [Pumacocha lagoon] (CEUC) < 4570 a 5100? m > (Fig 4b) (Comment 12).
- 4400 m, Peru, Huancavelica, Huachocolpa (MUSM) < 3996 m > (Comment 13).
- 3900 m, Peru, Cusco, Calca, Pampacorral (Bustamante & Yábar 2006) < 4142 m >.
- 3750 m, Chile, Parinacota, Putre (CPGG) < 3551 m > (Comment 14)
- 3600 m, Chile, Parinacota, Arica-Putre (CPFR) < 3551 m >.
- 3506 m, Peru, Ayacucho, Callenueva (Oróz *et al* 2009) < 3585 m >.
- 3430 m, Chile, Parinacota, Altos de Socoroma (González 2014a) < 3306 m>.
- 3350 m, Chile, [Parinacota], Putre (Hofmann 1970) < 3551 m >.
- 3300 m, Chile, Tamarugal, Chusmiza (UTAR) < 3593 m >.
- 3250 m, Chile, [Parinacota], Belén (Hofmann 1970) < 3071 m >.
- 3200 m, Chile, Parinacota, Lupica (González 2014a) < 3458 m >.
- 3150 m, Peru, Cusco, Lares (Bustamante & Yábar 2006) < 3227 m >.
- 3000 m, Chile, Parinacota, Socoroma (González 2014a) < 3306 m >.

Records of *Eriopis andina boliviana* Hofmann 1970.

- 4000 m, Bolivia, [La Paz], Huatajata (Hofmann 1970) < 3861 m >.
- 3800 m, Bolivia, [La Paz], Titicaca, Achacachi (Hofmann 1970) < 3829 m >.

Comments: (12) and (13) for the localities Pumacocha and Huachocolpa see comments for *Cycloneda andresi* and *Eriopis alticola*, respectively. (14) Although the town of Putre is located at 3551 m, less than 2 km east on the international road there are altitudes of 3750 m.

5200 m *Cycloneda lacrimosa* González & Vandenberg 2006.

- 5200 m, Argentina, Salta, Nevado de Cachi (González & Vandenberg 2006) < 4150 a 5300 m > (Fig 4f) (Comment 15).
- 4000 m, Chile, Parinacota, Visviri (MNHN) < 4083 m > (Fig 4g).
- 3733 m, Bolivia, Potosí, Uyuni (CPMD) < 3663 m>.
- 3700 m, Bolivia, Oruro, Oruro (González & Vandenberg 2006) < 3717 m >.

Comments: (15) The Nevado de Cachi record is within the limit of altitudinal vegetation in the area, since there are several records in the province of Salta of plant species between 5200 and 5300 m, e.g., the shrub *Xenophyllum poposum* (Phil.) V.A. Funk reaches 5300 m (www.floraargentina.edu.ar). The altitude indicated corresponds to hiking trails that are in the vicinity of the Nevado (Fig 4f).

5100 m *Eriopis altiplanica* González.
- 5100 m, Chile, Parinacota, Casiri Macho Lagoon (CPGG) < 4925 m > (Fig 4h) (Comment 16).
- 4400 m, Chile, Tamarugal, [Parinacota], Parinacota (González 2014a) < 4386 m >.
- 4097 m, Chile, Tamarugal, Cancosa (González 2014a) < 3936 m >.

Comments: (16). On the slopes of the Casiri Macho Lagoon, less than 1 km away, there are altitudes of up to 5300 m. The altitude of collection was measured with an altimeter (Hugo Benítez, personal communication).

Altoandino zone (4000 to 4900 m).
Shrublands, high wetlands, and cushion plants.

4800 m *Cycloneda* sp. 1 (comment 17).
- 4800 m, Peru, Huancavelica, Huachocolpa (MUSM) < 3996 m > (Comment 18).
- 4611 m, Peru, Pasco, Huallay, Chungar (MUSM) < 4610 m >.
- 4416 m, Peru, Huancavelica, Huando (MUSM) < 4402 m >.
- 4328 m, Peru, Cusco, Espinar, [Cerro] Condorsayana (MUSM) < 4293 m >.
- 4167 m, Peru, Cusco, Quebrada Chaisamayo (MUSM) < 4200 m > (Comment 19).
- 4120 m, Peru, Cusco, Yanacancha (MKRB) < 3970 m >.
- 4086 m, Peru, Áncash, San Marcos, Huaripampa, (MUSM) < 3072 m > (Comment 20).
- 4070 m, Peru, Cusco, Paucartambo, Challabamba (MUSM) < 4074 m > (Comment 21).

Comments: (17) This species has usually been confused with *C. andresi*, but its male genitalia indicate that it is a different species. (18) Although the town of Huachocolpa is at 3996 m and the coordinates that are 8 km to the SW have a similar altitude, the district of Huachocolpa has many altitudes that reach 4800 m and above. (19) For the locality Quebrada Chaisamayo, see comments for *Eriopis alticola*. (20) The altitude for the town of Challabamba is only 2820 m, but the coordinates indicate a place far away but consistent with the indicated altitude. (21) The town of Huaripampa is only 3072 m, but in its surroundings less than 2 km away, on the road to Cotonga, there are altitudes of 4100 m and above.

4692 m *Cycloneda atra* González 2018.
- 4692 m, Peru, Huancavelica, Huachocolpa (MUSM) < 3996 m > (Comment 22).
- 4635 m, Peru, HV [Huancavelica], Pueblo Libre [peasant community] (MUSM). < 4408 m > (Comment 23).

Comments: (22) About Huachocolpa see comment *Cycloneda* sp. 1. (23). The label coordinates correspond to about 3 km south of the town of Pueblo Libre, and the altitude corresponds to that point.

4635 m *Eriopis figueroai* González 2018.
- 4635 m, Peru, HV [Huancavelica], Pueblo Libre [peasant community] (MUSM) < 4408 m > (Comment 24).

Comments: (24) About Pueblo Libre see comment under *Cycloneda atra*.

4611 m *Eriopis canrash* Bustamante *et al* 2007.
- 4611 m, Peru, Pasco, Huallay, Chungar (MUSM) < 4610 m >.
- 4311 m, Peru, Áncash, Huari, San Marcos, Canrash (CEUC). < 4210 m > (Fig 4d).
- 4200 m, Peru, Junín, Junín (Bustamante *et al* 2007) < 4124 m >.
- 4122 m, Peru, Áncash, Jupaymarca (Oróz *et al* 2009) < 4312 m > (Fig 4e).
- 4100 m, Peru, Junín, Carhuamayo (Bustamante *et al* 2007) < 4126 m >.
- 4086 m, Peru, Áncash, San Marcos, Huaripampa (MUSM) < 3072 m > (Comment 25).

Comments: (25) About Huaripampa see comment under *Cycloneda* sp. 1.

4611 m *Cycloneda* sp. 2 (comment 26).
- 4611 m, Peru, PA [Pasco], Huallay, Chungar (MUSM) < 4610 m >.

Comments: (26) Undescribed species of very characteristic appearance, with black elytra flanged with yellow, known from a single specimen.

4500 m *Eriopis huancavelicae* Bustamante *et al* 2009 (Fig 3b).
- 4500 m, Peru, Ayacucho [Huancavelica], [locality] Wasi wasi, (CEUC) <4509 m > (Comment 27).

Comments: (27) The locality is in the border of both provinces, but to the interior of Huancavelica and not of Ayacucho, as the label indicates.

4384 m *Eriopis peruviana* Hofmann 1970.
- 4384 m, Peru, Junín, Carhuamayo, La Victoria (MUSM) < s/i > <4123–4400 m > (Comment 28).
- 4314 m, Peru, [Puno], La Raya (Hofmann 1970) <4123 m >.
- 4221 m, Peru, Junín, Carhuamayo, La Victoria (MUSM) < s/i > <4123–4400 m > (Comment 29).
- 4100 m, Peru, Junín, [Junín] (Hofmann 1970) <4124 m >.

- 3950 m, Peru, Cusco, [Canchis, San Pablo,] Patatinta (Bustamante & Yábar 2006) < 4041 m >.
- 3885 m, Peru, Cusco, [Canchis,] Santa Bárbara (Bustamante & Yábar 2006) < 3958 m >.
- 3810 m, Peru, Cusco, [Canchis, Pitumarca,] Osefina (Bustamante & Yábar 2006) < 3866 m >.
- 3800 m, Peru, Junín, 37 km E. Carhuamayo (Hofmann 1970) < 3600–3900 > .
- 3730 m, Peru, Cusco, [Calca, Taray], Matinga (Bustamante & Yábar 2006) < 3741 m >.
- 3700 m, Peru, Cusco, [Calca], Pampallacta (Bustamante & Yábar 2006) < 2965–3800 m > (Comment 30).
- 3700 m, Peru, Cusco, Chicón (Bustamante & Yábar 2006) < 3600–5451 m > (Comment 31).
- 3625 m, Peru, Cusco, Sequeracay (Bustamante & Yábar 2006) < 3669 m >.
- 3610 m, Peru, Cusco, Huillcapata (Bustamante & Yábar 2006) < 3631 m > .
- 3600 m, Peru, Cusco, Chumbivilcas, Buena Vista (Bustamante & Yábar 2006) < 3437 m >.
- 3585 m, Peru, Cusco, Mandorani (Bustamante & Yábar 2006) < 3856 m >.
- 3545 m, Peru, Cusco, [Canchis, Checacupe], Chari (Bustamante & Yábar 2006) < 3573 m >.
- 3530 m, Peru, Cusco, [Canchis, Pitumarca], Chacachapampa (Bustamante & Yábar 2006) < 3821 m >.
- 3505 m, Peru, Cusco, [Anta, peasant community] Saratohuaylla (Bustamante & Yábar 2006) < s/i > <3345 m > (Comment 32).
- 3480 m, Peru, Cusco, San Jerónimo, Pata pata (Bustamante & Yábar 2006) < 3300 m >.
- 3480 m, Peru, Cusco, [Chumbivilcas,] Llusco (Bustamante & Yábar 2006) < 3663 m >.
- 3450 m, Peru, Cusco, Huayllojo (Bustamante & Yábar 2006) < 3439 m >.
- 3446 m, Peru, Cusco, [Canchis], Checacupe (Bustamante & Yábar 2006) < 3439 m >.
- 3400 m, Peru, Cusco, Huama (Bustamante & Yábar 2006) < 3455 m >.
- 3350 m, Peru, Cusco, Huanchaq, Perayoc (Bustamante & Yábar 2006) < 3370 m >.
- 3330 m, Peru, Cusco, Anta, Aparquilla (Bustamante & Yábar 2006) < 3324 m >.
- 3310 m, Peru, Cusco, Kayra (CEUC) <3384 m >.
- 3250 m, Peru, Cusco, Oropesa (Bustamante & Yábar 2006) < 3093 m >.
- 3210 m, Peru, Cusco, Quispicanchis, Urcos (Bustamante & Yábar 2006) <3110 m > .
- 3210 m, Peru, Cusco, Acomayo, Acos (Bustamante & Yábar 2006) < 2906 m >.
- 3200 m, Peru, Cusco, Tancarpata (Bustamante & Yábar 2006) < 3354 m >.
- 3170 m, Peru, Cusco, Calca, Chicón (Bustamante & Yábar 2006) < 3000–3800 m >.
- 3060 m, Peru, Cusco, Calca, San Salvador, Pillahuara (Bustamante & Yábar 2006) < 3023 m >.
- 3010 m, Peru, Apurimac, Ampay (Bustamante & Yábar 2006) < 2880–3800 m > (Comment 33).
- 3000 m, Peru, [Cusco], Urubamba, Ollantaitambo (Hofmann 1970) < 2847 m >.

Comments: (28) and (29) The locality of La Victoria could not be located; the indicated altitude corresponds to Carhuamayo and surrounding areas, where the roads near Carhuamayo and less than 5 km away have altitudes up to 4400 m. (30) Although the locality of Pampallacta is located at only 2965 m, less than 2 km away there are roads and localities that reach 3800 m. (31) Chicón is a mountain that rises above 5530 m, the collection site should refer to nearby valleys less than 5 km away from the summit, with heights similar to the record. (32) The peasant community of Saratohuaylla could not be located on the map, but it could be established that it was in the district of Anta, whose average altitude is 3345 m. (33) The National Sanctuary of Ampay has altitudes in the range indicated in the record.

4200 m *Eriopis lawalawani* Bustamante *et al* 2007 (Fig 3d).

- 4200 m, Peru, Puno, Coasa, Macusani, Lawalawani (Bustamante *et al* 2007) < 4352 m > (Comment 34).

Comments: (34) The locality could not be located, but the altitude was obtained according to the coordinates. In the area, there are multiple lagoons with altitudes consistent with the indicated one.

4200 m *Eriopis loaensis* González 2014.

- 4200 m, Chile, Antofagasta, El Loa, El Tatio (González 2014a) < 4261 m > (Comment 35).

Comments: (35) The examined specimen has no abdomen, so the presence of the species at that altitude should be confirmed.

4176 m *Eriopis punicola* Hofmann 1970.

- 4176 m, Peru, Pu [Puno], Putina, San Isidro de Torno, Bosque de Torno (CEUC) < 3858 m >.
- 4000 m, Bolivia, [La Paz], Huatajata (Hofmann 1970) < 3861 m >.
- 4000 m, Bolivia, [La Paz], Titicaca (Hofmann 1970) < 3815 m >.
- 3950 m, Bolivia, [La Paz], Santiago de Huata (Hofmann 1970) < 3850 m >.
- 3850 m, Bolivia, [La Paz], Achacachi (Hofmann 1970) < 3829 m > .

- 3800 m, Peru, Puno, Chucuito, Juli (Bustamante & Yábar 2006) < 3888 m >.
- 3700 m, Peru, Puno, Camacani (Hofmann 1970) < 3842 m >.

4122 m *Eriopis nobilis* Mader 1958.
- 4122 m, Peru, Áncash, Bolognesi, Huata, Jupaymarca, 4122 m (Bustamante *et al* 2007) < 4312 m > (Fig 4d).
- 4066 m, Peru, Áncash, Pachapaqui (Bustamante *et al* 2007) < 3916 m >.
- 4066 m, Peru, Áncash, Puhun [Pujun?] (Bustamante *et al* 2007) < 3703 m > (Comment 36).
- 3400 m, Peru, Cajamarca, Cumbemayo (Bustamante *et al* 2007) < 3596 m >.
- 3152 m, Peru, Cajamarca, Porcón Alto (Bustamante *et al*. 2007) < 3492 m >.

Comments: (36) Puhun could not be located, but there is in Ancash a town and district named Pujun, which at less than 2 km, has accessible roads with altitudes consistent with that indicated.

4050 m *Eriopis santiagoi* Bustamante & Oróz 2016 (Fig 3c).
- 4050 m, Peru, [Junín], Conococha (Bustamante & Oróz 2016) < 4020 m > (Comment 37).

Comments: (37) The only known locality of the species, collected on different dates.

4000 m *Stenadalia laskarensis* Gordon 1994.
- 4050 m, Chile, [Parinacota,] Visviri (CPFR) <4083 m > (Fig 4g).
- 3500 m, Chile, [El Loa,] Tumbre (Gordon 1994) < 3912 m >.
- 3500 m, Chile, El Loa, Volcan Laskar (Ferru & Elgueta 2011) < 3800–5369 m >.

4000 m *Cycloneda lucasii* Mulsant 1850.
- 4000 m, [Chile, Parinacota,] Visviri (MNHN) < 4083 m > (Fig 4g).
- 3490 m, Argentina, Jujuy, Abra Pampa (CPMD) < 3490 m >.

Puneño zone (3000 to 4000 m).

Shrubby steppes, relatively rich in species and plant cover. There are many species of coccinellids that have been collected in this zone, including most of those mentioned above. The species for which at least one collection exceeds 3500 m were listed.

3950 m *Hippodamia convergens* Guerin-Meneville 1842.
- 3950 m, Peru, Cusco, Pulpera (CEUC) < 3929 m >.
- 3800 m, Peru, Puno, Juli (CEUC) < 3888 m >.
- 3578 m Chile, Santiago, Valle Nevado (Grez *et al* 2017) < 2607–3936 m > .
- 3506 m, Peru, Ayacucho, Callenueva (CEUC) < 3585 m >.
- 3052 m, Peru, Ancash, Huaraz (CEUC) < 3052 m >.

3949 m *Cycloneda bustamantei* González 2018
- 3950 m, Peru, Cajamarca, nr [norte?] Rio Rejo, Yanacocha (González 2018) < 4011 m >.
- 3807 m, Peru, La Libertad, Sánchez Carrión (González 2018) < 2200? m > (Comment 38).
- 3492 m, Peru, Cajamarca, Porcón Alto (González 2018) < 3492 m >.

Comments: (38): The altitude indicated in the record is not consistent with the coordinates given in the labels, whose altitudes border 2200 m; however, there are altitudes consistent with the one indicated in the province of Sanchez Carrión.

3900 m *Stenadalia amoena* Gordon 1994.
- 3900 m, Bolivia, [La Paz,] Titicaca, Huarisata (Gordon 1994) < 3815 m >.
- 3850 m, Peru, Ayacucho, Usmay (CEUC) < 4039 m >.
- 3506 m, Peru, Ayacucho, Callenueva (Bustamante-Navarrete *et al*. 2017b) < 3585 m >.

3820 m *Eriopis connexa* Germar 1824 (Fig 3e).
- 3820 m, Bolivia, La Paz, Tiwanacu (MNHN) < 3861 m >.
- 3800 m, Bolivia, La Paz, Copacabana (USNM) < 3859 m >.

3810 m *Stenadalia mariae* Gordon 1994 (Fig 2g).
- 3810 m, Bolivia, La Paz, Guatajata (Gordon 1994) < 3861 m >.

3780 m *Psyllobora* sp. (Comment 39)
- 3950 m, Peru, Cusco, Santo Tomás (CEUC) < 3654 m >.

Comments: (39) The species presents similarity of habitus with the species *Psyllobora constantini* González *et al* 2017 (Fig 2f).

3741 m *Hippodamia variegata* (Goeze 1777) (Fig 2d).
- 3741 m, Peru, Cusco, Chumbivilcas (Bustamante *et al* 2017a) < 3665 m >.
- 3600 m, Chile, Santiago, Valle Nevado (Molina-Montenegro *et al*. 2006) < 2607–3936 m >.
- 3578 m, Chile, Santiago, Valle Nevado (Grez *et al* 2017) < 2607–3936 m >.

3740 m *Cycloneda arcula* (Erichson 1847).
- 3740 m, Peru, Cusco, Wañacahua (CEUC) < 3741 m >.
- 3565 m, Peru, La Libertad, Sánchez Carrión, Cungush (MUSM) < 3662 m>.
- 3425 m, Peru, La Libertad, Huamachuco (MUSM) < 3269 m >.
- 3400 m, Peru, Ancash, Wilcawain (USAM) < 3400 m>.
- 3149 m, Peru, Ancash, Huari (USAM) < 3149 m>.
- 3052 m, Peru, Ancash, Huaraz (USAM) < 3052 m>.

3738 m *Stenadalia vittata* Gordon 1994.
- 3738 m, Bolivia, Oruro, Challapata (Gordon 1994) < 3733 m >.

3600 m *Eriopis chilensis* Hofmann 1970.
- 3600 m, Chile, Santiago, Valle Nevado (Molina-Montenegro *et al* 2006) < 2607–3936 m > (identified as *E. connexa* Germar)
- 3578 m, Chile, Santiago, Valle Nevado (Grez *et al* 2017) < 2607–3936 m >.

3578 m *Harmonia axyridis* (Pallas 1772) (Fig 2c).
- 3578 m, Chile, Santiago, Valle Nevado (Grez *et al* 2017) < 2607–3936 m >.
- 3400 m, Perú, Ancash, Wilcawain (USAM) < 3400 m >.
- 3336 m, Perú, Ancash, Olleros (USAM) < 3336 m > .
- 3052 m, Perú, Ancash, Huaraz (USAM) < 3052 m > .
- 3050 m, Perú, Ancash, Pinar (USAM) < 3050 m > .

3501 m *Cycloneda sanguinea* (L. 1763).
- 3501 m Peru, Ancash, Racrachaca (USAM) < 3501 m >.
- 3.149 m Peru, Ancash, Huari (USAM) < 3149 m >.
- 3.100 m Peru, Ancash, Huaraz (USAM) < 3100 m >.

3500 m *Cycloneda marcapatae* Oróz *et al* 2009.
- 3500 m, Peru, Cusco, Quispicanchis (CEUC) < 3143 m >.

3500 m *Mimoscymnus brevicapillus* Gordon 2002.
- 3500 m, Ecuador, Napo, Papallacta (Gordon 2002) < 3151 m >.
- 3457 m, Ecuador, Pichincha, Laguna San Marcos (CPGG) < 3429 m >.
- 3400 m, Ecuador, Napo, Papallacta (Gordon 2002) < 3151 m >.

3500 m *Mimoscymnus terminatus* Gordon 2002 (Fig 2e).
- 3500 m, Colombia, Norte de Santander, 14 km SW Pamplona (Gordon 2002) < 3200 m >.

Localities. The majority of localities could be identified correctly with the information provided in the labels, with the exception of two localities (Pampa Silvestre, 4294 m, and La Victoria, 4384 m). One locality could not be located on Google maps to verify the altitude provided in the label (peasant community Saratohuaylla, 3505 m).

Altitudes. The altitudes indicated by the collectors or authors agree with the reference altitudes obtained in this study, with differences of less than 300 m. This is fully compatible with mountain environments in which small displacements produce appreciable differences in altitude. It is common for collectors to capture their specimens in rural areas and to indicate the nearest locality, which in Andean areas can be located many kilometers away and at a different altitude; in about 15 cases, there are differences greater than 300 m, and in most of them, the presence of the altitudes indicated in the records were verified less than 5 km around the indicated location. Only in six cases was there no concordance between the altitudes indicated in the labels and the altitude of the locality. These cases were denoted with "**?**" in each record.

Other genera and species. Epilachnini in the genera *Epilachna* and *Toxotoma* are strongly associated with the Andes Range, but at altitudes up to 3000 m. No references or specimens exceeding this altitude were found, except for a reference to *E. flavofasciata* LaPorte in the Paramo de Huasca, Colombia, at 3400 m (Gordon 1975), and one record of *E. convergens* in Aija, Ancash, Peru, at 3147 m (USAM). The highest altitude found for a species of the Hyperaspidini/Brachiacanthini tribes was for *Hyperaspis andina* González & Gordon, in the locality of Lupica, Parinacota, Chile, at 3200 m (González & Gordon 2009). Some additional species of the tribe Coccinellini were found between 3000 and 3500 m in the Ancash department, Peru, in Huaraz and other localities, including *Anatis lebasi* (Mulsant), *Eriopis nobilis* Mader, *Neda norrisi* (Guerin-Meneville), *Paraneda pallidula guticollis* Mulsant, and an undescribed *Psyllobora* sp. (USAM). Other genera of Coccinellidae were not recorded over 3000 m. Bustamante *et al* (2007) mention *Cycloneda ancoralis* (Germar) in the town of Jupaymarca (Áncash, Peru) at 4122 m, but the collected specimens were later identified as *C. andresi*.

Ecosystems and habitats. In many places at high altitudes species were not isolated, but were in sympatry with several other coccinellid species. They were well-established, even reproducing. The community at the highest altitude was at the edges of the Pumacocha Lagoon, in the vicinity of Ausangate (Fig 4b) (Cusco, Peru) at 5230 m, where they were found sharing the habitat with *C. andresi*, *E. alticola*, and *E. andina*, in a puna where they fed on moss aphids (Walter Cosio, personal communication). In Jupaymarca (Fig 4d) (Ancash, Peru), at 4122 m, also in a puna that had Poaceae vegetation (grasses), several species were found feeding on moss aphids located below the level of herbaceous plants; the species sharing this habitat were *E. canrash*, *E. nobilis*, and *C. andresi.* For the last species, all the stages of development (eggs, larvae I–IV, pupae, and adults) were found (Bustamante *et al* 2007). In Usmay (Fig 4c) (Ayacucho, Peru), *C. andresi*, *E. andina*, and *S. amoena* were found in sympatry in a puna at 3850 m; at least the first two were feeding on moss aphids in a forest of *Polylepis pepei* B. Simpson (Bustamante-Navarrete *et al* 2017a). In another locality, Callenueva (Ayacucho, Peru) at 3506 m, these same three species were found sharing their habitat with *Hi.*

convergens in a cloud forest of *Polylepis canoi* W. Mendoza, in a marshy habitat where they fed on unidentified aphids (Bustamante-Navarrete *et al* 2017b). In Valle Nevado, Chile, *Hi. variegata*, *Hi. convergens*, *E. chilensis*, and *Ha. axyridis* were found living at 3600 m in a sector of sparse vegetation dominated by cushion plants (Apiaceae): *Azorella madreporica* Clos and *Laretia acaulis* (Cav.) Gill. *et* Hook (Grez *et al* 2017). Some species were the only ones found in each locality, such as *E. huancavelicae* that was collected in the town of Wasi Wasi, Huancavelica, Peru, at 4500 m among the vegetation typical of these places; *Aciachne pulvinata* Benth (Poaceae) and *Azorella* sp. (Apiaceae) (Bustamante *et al* 2009); the species *E. lawalawani* was found in the locality of Lawalawani (Puno, Peru) at 4200 m on plants of *Muelembeckia* on the edge of a *Polylepis* forest (Queuña or Quewiña) (Bustamante *et al* 2007). *Eriopis punicola* was collected in a *Polylepis* forest near the town of Torno (Puno, Peru) at 4176 m (label data).

Adaptations to extreme altitudes. Some morphological adaptations have been observed in these species of extreme altitudes. Among them, Mani (1968) mentions dark body pigmentation or melanism, related to the damage that can be produced by ultraviolet radiation; alar atrophy (brachypterism), related to lower flight efficiency due to oxygen deficiency and low temperatures; and the reduction in body size due to the extreme conditions that delay the metamorphosis and affect development, together with the advantages offered by small body size to use microclimatic niches. Bustamante & Oróz-Ramos (2016) mention two of these adaptations in relation to the genus *Eriopis* in Peru: the small size and the predominantly black color. Both are very evident in some of the species of the genus *Eriopis* indicated, whose size is noticeably smaller than other species of the genus; *E. minima*, *E. huancavelicae*, *E. santiagoi*, and *E. lawalawani* (Fig 3a–d) are around 3 to 4 mm long, compared to about 4 to 6 mm long for other species of the genus (e.g., *E. connexa*, Fig 3e). All except *E. minima* present marked melanism (Fig 3 b–d), which has also been observed in *E. altiplanica* and *E. alticola* (Fig 2b). Total or partial reduction of the membranous wings has been observed in *E. minima*, a species in which both fully apterous or brachypterous specimens were found as well as others with fully functional wings (González 2014a) (Fig 3f).

Endemism and altitude patterns of the species. Most of the species found at high altitudes are endemic to the Puna biogeographic province and are restricted to the Andes Range. The only study that provides data on endemism of coccinellids in South America is González (2014b), where it is established that 21.3% of species present in Argentina are endemic. Among the 35 species found at altitudes greater than 3500 m in South America, only three are not found in the Puna province. Two only inhabit the Paramo Norandino province, *M. brevicapillus* in Ecuador, and *M. terminatus* in Colombia, while *E. chilensis* inhabits the Prepuna province in Chile. None of these records exceeds 4000 m. Among the species present in the Puna province, a group of nine non-endemic species is recognized, including three introduced species (*Hi. convergens*, *Hi. variegata*, and *Ha. axyridis*) and six native species (*C. arcula*, *C. sanguinea*, *E. connexa*, *E. punicola*, *E. chilensis*, and *E. loaensis*). A characteristic of this group of non-endemic species is that they are distributed from sea level (except *E. punicola*, which does not have records lower than 1657 m) up to an altitude not greater than 4200 m. The remaining 23 species are endemic to the Puna province (72%); they are not present at altitudes below 2500 m and have been found up to 5300 m. They belong mainly to three genera: *Eriopis* (10 species), *Cycloneda* (8 species), and *Stenadalia* (4 species). A very restricted geographic and altitudinal distribution group is recognized among these species over 4000 m, which includes *E. altiplanica*, *E. figueroai*, *E. canrash*, *E. huancavelicae*, *E. lawalawani*, *E. santiagoi*, *C. atra*, and *Cycloneda* sp. 1 and sp. 2. These species also share a restricted spatial distribution, some of which are known from a single locality, and all exhibit marked adaptations to altitude, such as melanism and reduced size.

Discussion

This study describes for the first time and in a comprehensive way the geographic distribution, habitat, and precise locations of the coccinellids that live at high altitudes in the Andes Range, providing the highest reports worldwide of these insects. Our results show that the fauna of coccinellids in the Andes Range above 3500 m and up to 5250 m is represented by a great variety of species, especially of the genera *Cycloneda* and *Eriopis*, each with several species associated with these extreme altitudes. Moreover, it was observed that in many places, several coccinellid species coexisted, indicating that these are established communities rather than isolated populations or migrating individuals carried by the wind or looking for places for hibernation, as has been described for other latitudes (Englund *et al* 2010). This is reinforced by the adaptations to altitude such as reduced size, melanism, and brachypterism present in several of the species examined, which suggest that these species have been thriving in these habitats for a long time.

The vast majority of the records obtained over 3500 m are concentrated in the Puna biogeographic province, which is consistent with the average altitude of extensive Altiplano areas. The high level of endemism found in this area is worth

noting, estimated to be 72% of the species. This contrasts with the situation found at lower altitudes, where a large number of species of coccinellids have a much more extensive distribution. For example, in areas of similar longitudinal extension in Argentina, only 21.3% of species are endemic (González 2014b). Additionally, a significant percentage of the species analyzed (28%) does not live below 4000 m, while an even higher percentage of species (44%) does not live below 2500 m, suggesting that altitude could be one of the limiting factors hindering the dispersion of these species to other areas. Another factor that could influence the high endemism in this area is the mountainous terrain; large differences in altitude can be found in relatively small areas, and the areas suitable for coccinellids to develop are often very fragmented and isolated, which does not allow the establishment of continuous populations over large areas, as happens where altitude differences are lower. Endemism is associated with a greater vulnerability of the species given the small and fragmented distribution, as Urban (2015) postulated.

The records of coccinellids at high altitudes are relevant considering the growing evidence of global warming processes associated with climate change, which will strongly affect mountain habitats and the associated fauna (Pepin *et al* 2015). The effects at extreme altitudes will also affect the fauna at medium and low altitudes, given the dependence of these localities on the water supply coming from extreme altitudes, from the melting of the snow and glaciers (Pepin *et al* 2015). Monitoring of populations of extreme altitudes could allow in the future the evaluation of the effects of climate change in critical areas and anticipate their effects in middle and lower zones.

The records presented here are the highest altitudes reported for coccinellids in the Americas. Furthermore, based on the consulted literature, these would be the highest altitudes recorded for coccinellids worldwide, since in other continents, no records of coccinellids have been above 4500 m. Future challenges include the study of the temporal distribution of the species throughout the year, since although most records are in summer, some of them were in autumn and winter. It is also necessary to study the migration of some species that have a high altitudinal range, since the mountain range could be a temporary refuge for them, as was postulated by Grez *et al* (2017) for *Ha. axyridis*.

The information provided in this study emphasizes the importance of conserving these high altitude ecosystems, where an abundant variety of species of the family Coccinellidae can be seen in extreme and fragile environments, with high levels of endemism.

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