The highest known euglossine bee community from a garden in the Bolivian Andes (Hymenoptera, Apidae, Euglossini)

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Abstract
In this contribution, the first observations of euglossine bee species from the Bolivian Prepuna are reported. Euglossa melanotricha Moure, Eufriesea mariana (Mocsáry) and Exaerete dentata (L.) were observed at an elevation of 2640 m in a garden located in San Joaquin, Salancachi (Chuquisaca department, annual precipitation 400–500 mm). This is the highest known record for a population of Euglossa and Eufriesea to date. All of the euglossine bees were observed exclusively on introduced plants. The distributional patterns, biological associations and ecological significance of the observed euglossine bees are discussed.

Keywords
Bolivia, orchid bees, Prepuna, inter-Andean dry valleys

Introduction
Euglossine bees, also known as orchid bees, are a mainly Neotropical tribe of the Apidae that comprises approximately 232 species in five genera (Nemésio and Rasmussen 2011). They have received significant attention in the past century, in particular because they are one of the most important groups of pollinators (e.g. Dressler 1982; Roubik 1989) and the exclusive pollinators of nearly 700 orchid species (Pemberton and Wheeler 2006).
Euglossine bee species are most diverse in tropical evergreen forests (up to 53 spp., see Nemésio and Rasmussen 2014), which is likely because the high precipitation, favorable temperatures, and low seasonality in these forests serve to facilitate a continuous supply of nectar and pollen as well as a generous supply of varied odor substances for courtship displays (see Rebêlo 2001; Roubik and Hanson 2004; Aguiar et al. 2014). The species richness of euglossine bees in Brazil decreases in semi-deciduous Atlantic Forest (~1200 mm/yr) (11 to 19 spp., reviewed by Aguiar and Gaglianone 2012), open habitats such as Cerrado (700–1200 mm/yr) (8 spp., reviewed by Faria and Silveira 2011) and the semi-arid, deciduous Caatinga (500–700 mm/yr) (5 spp., see Lopes et al. 2007). In the sub-Andean areas of Peru and Bolivia, Abrahamczyk et al. (2013) found a negative relationship between euglossine bee species richness and climatic seasonality, which was most pronounced between tropical evergreen rainforests (3710 mm/yr) (26 spp.) and subtropical deciduous dry forests in Bolivia (733 mm/yr) (2 spp.).

In mountainous terrain, little is known about the factors limiting the upper distribution of euglossine bees, although available data suggests that such patterns are influenced by the same factors that shape the latitudinal distribution (see Nemésio 2008; Aguiar et al. 2014). In the higher elevations, commonly found in the Andes (often reaching over 5000 m a.s.l., Fig. 1A), sub-humid and humid mountain forests are replaced by shrub and grasslands in which plant diversity and productivity are restricted by aridity, high radiation, low temperatures, and alkaline and saline soils (Ibisch and Merida 2003). While euglossine bees commonly occur from sea level up to 1700 meters of elevation (Dressler 1982; Dick et al. 2004; Nates-Parra et al. 2006), only four of the 232 known euglossine bee species have been observed at an elevation higher than 2640 m (Euaerete smaragdina (Guérin-Méneville): 2650 m; Eulaema cingulata (F.): 2800 m; El. polychroma (Mocsáry): 3400 m; El. boliviensis (Friese): 3900 m) (reviewed by Ramírez et al. 2002; Gonzalez and Engel 2004). Species of the genus Eufriesea have not been reported from elevations higher than 2050 m (reviewed by Ramírez et al. 2002) and the highest elevations that have been recorded for species of the genus Euglossa are 2050 m (Euglossa nigropilosa Moure) (see Ramírez et al. 2002) and 2560 m (Euglossa ioprosopa Dressler) (Parra-H and Nates-Parra 2007).

Observations of a euglossine bee community are reported herein, including species of Euglossa and Eufriesea, from a garden at an elevation of 2640 m in the semi-arid Prepuna of the Bolivian Andes.

**Material and methods**

The observation of orchid bees were made on a private estate, named “San Joaquin” (19°10’30S; 65°13’25W) in Salancachi, close to the village of Yotala in the department of Chuquisaca in an elevation of 2640 m (Fig. 1). Because the eastern cordillera blocks moisture-bearing winds originating in the Amazon basin and the Atlantic (Strecker et al. 2007), the average annual precipitation in the study area ranges only between 400–500 mm (López et al. 2013). Rainfall is concentrated in a rainy season and there is a pronounced
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Dry season with 6–8 arid months (Ibisch and Mérida 2003). The average temperature is about 12–16 °C, with high temperatures that may exceed 30 °C and low temperatures falling below 0 °C (Ibisch and Mérida 2003). In this contribution, the ecoregion classification proposed by Navarro (2002) has been followed and the vegetation of the altitudinal zone of the inter-Andean valleys situated between 2,100 to 3,200 m a.s.l. is considered as Prepuna (see also Thomas et al. 2010). The vegetation in the Prepuna is characterized by xerophytic shrubs and cacti with a low number of xeric tree species (Thomas et al. 2010).

The tree vegetation in San Joaquin consists mainly of non-native *Eucalyptus* (Myrtaceae) trees (a commonly planted tree throughout the high Andes, see Thomas et al. 2010), *Persea americana* Mill. (Avocado) (Lauraceae), and *Pinus* sp. (Pinaceae). A garden of vascular plants (~260 m²) (Fig. 2B) is maintained with water from a subterranean spring. Among the flowering plants in this garden, *Ismene narcissiflora* (Jacq.) M. Roem. (Amaryllidaceae) is the only vascular species native to Bolivia. *Euphorbia pulcherrima* Willd. ex Klotzsch (Euphorbiaceae) is native to Mexico and Central America (Lee 2000), *Duranta erecta* L. (Verbenaceae) is possibly native to the West Indies, Central America, and/or the Florida Keys, *Pelargonium* sp. (Geraniaceae) and *Agapan-
thus praecox Willd. (Amaryllidaceae) originate from South Africa (Mor et al. 1984) and Hibiscus rosa-sinensis L. (Malvaceae) is introduced from Asia.

The garden of San Joaquin and three transects of about 14 km length were surveyed (Fig. 1D) on three days in September 2012, and in April and December of 2013. The humidity and temperature were measured in December of 2013 with a digital handheld hygrometer in locations where orchid bees were observed. The species were identified following the references in Abrahamczyk et al. (2012). In addition, the taxonomists André Nemésio (Universidade Federal de Uberlândia, Brazil) and Benjamin Bembé (Zoologische Staatssammlung München, Germany) were consulted for the confirmation of the identification of Euglossa melanotricha Moure.

Results

No euglossine bees were observed in the three transects outside of the garden during any of the three surveys. Flowers of Acacia (Fabaceae) trees, shrubs, and vascular plants in these transects were exclusively visited by Apis mellifera L. or other flower visitors.
In September of 2012 a male of *Euglossa melanotricha* (Fig. 3B) was observed hovering over a barbecue in the garden during noon and the next morning a female was found on the back of a chair inside the house. In April of 2013, *E. melanotricha* was abundant (not counted) on flowers of *Hibiscus rosa-sinensis* (Fig. 2C) and *Duranta erecta*.

In December of 2013, individuals of three euglossine bee species (*Euglossa melanotricha* (46♂; 19♀) (Fig. 3B), *Exaerete dentata* (L.) (12♂; 3♀) (Fig. 3A) and *Eufriesea mariana* (Mocsáry) (6♀) (Fig. 3C), were captured in the garden. The bees were active between 0900–1700 h, in temperatures between 21.7–24.3 °C and at relative humidities of 52.7–28.5% (humidity decreasing towards noon).

All three euglossine species were observed foraging in the flowers of *Agapanthus praecox*. *Exaerete dentata* and *Euglossa melanotricha* were also observed in the flowers of *Hibiscus rosa-sinensis*, and *E. melanotricha* additionally in the flowers of *Duranta erecta*. Euglossine bees were the only hymenopteran floral visitors that were recognized in these plants.

No euglossine bees were observed on the flowers of *Ismene narcissiflora*, the only native flowering plant in the garden. The flowers of *Euphorbia pulcherrima* were visited by *Apis mellifera* and several wasp species, but not by euglossine bees.

**Discussion**

The observations reported here are the first published records for euglossine bee species from the Prepuna and the inter-Andean dry valleys in Bolivia, and the elevation of 2640 m is the highest known record for a population of *Euglossa* and *Eufriesea* to date (see Ramírez et al. 2002).
Euglossine species richness in San Joaquin (400-500 mm/yr) is comparable with that of the semi-deciduous lowland forest in Santa Cruz department about 180 km east of the actual study area (733 mm/yr, 2 spp., see Abrahamczyk et al. 2013) and single sites in the Caatinga (500–700 mm/yr, 1-3 spp., Lopes et al. 2007). The euglossine fauna of the Bolivian Prepuna may contain species of the genus *Eulaema* as well: e.g. *El. cingulata* (F.) and *El. nigrita* Lepeletier are the two most common and ubiquitous *Eulaema* species and they are widely distributed in relatively arid areas south of the Amazon basin (Zucchi et al. 1969). Both species have been reported in Bolivia at an elevation of ~2600 m (see Ramírez et al. 2002).

*Eufriesea mariana* has been previously reported in similar habitats (Kimsey 1982; Ramírez et al. 2010; pers. obs., see Perger and Guerra 2013 for data) and co-occurs in several locations in the Argentinean Andes with *Ex. dentata* (Ascher and Pickering 2014). Since species of *Exaerete* are considered obligate nest parasites of species of the euglossine genera *Eulaema* and *Eufriesea* (see Garofalo and Rozen 2001 for references), the presence of *Ex. dentata* in the Andes may be facilitated by parasitizing *Ef. mariana*.

*Euglossa melanotricha* has been reported from semi-deciduous forests, Atlantic forest and the Caatinga (500–1600 mm/yr) at elevations between 400 and 1350 m (Bembé 2004; Nemésio 2009). Judging from the dissimilarities between the conditions (precipitation, seasonality, and elevation) of the Prepuna and the previously reported regions, and the distance of ~190 km between San Joaquin and the nearest reported lowland location at Los Volcanes (Bembé 2004), the establishment of *Eg. melanotricha* in the Prepuna may be explained by long-distance dispersal from suitable habitats in lower elevations over the riparian vegetation of the Rio Grande (Fig. 1 B), and a successful founder event facilitated by the suitable conditions in the garden of San Joaquin.

The exclusive occurrence of the observed euglossine bees on introduced plants in the garden suggests that either they have low host plant specificities or have adapted their host plant preferences to local conditions, as has been previously observed in naturalized or insular euglossine bee populations (Eltz et al. 2005; Pemberton and Wheeler 2006; Ramírez et al. 2010).

The apparent persistence of euglossine bees in an area with low orchid species richness (see Lopez 2003; Thomas 2008) is consistent with the observation that male euglossine bees often obtain the volatiles they use in attracting mates from non-orchid sources (see Whitten et al. 1993; Ramírez et al. 2011). To date, the degree of dependence of euglossine bees on orchids as scent sources is poorly understood and only one study (Pemberton and Wheeler 2006) clearly demonstrates that a euglossine bee species can persistently exist in an area without euglossine bee-associated orchids. Further study of the Prepuna in Bolivia should help our understanding of the biology of euglossine bees in peripheral habitats.

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