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ORIGINAL PAPER

Diversity and community composition of euglossine bee assemblages (Hymenoptera: Apidae) in western Amazonia

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Abstract Tropical forests are known for their diverse insect fauna. We aimed to determine the effect and relative importance of latitude, elevation and climatic factors affecting species richness and turnover in euglossine bee assemblages along a gradient of 18° latitude from tropical rainforests to subtropical, deciduous dry forests in Peru and Bolivia. Sixteen forest sites were sampled during the dry season. Variance partitioning techniques were applied to assess the relative effects of the spatial and environmental variables on species richness and composition. Furthermore, we conducted a Species Indicator Analysis to find characteristic species for the biogeographic zones. There was a significant decrease in species richness towards the subtropical area. The best predictors of species richness were precipitation and its consequences on soil properties as well as temperature seasonality. The abundance of euglossines was most closely related to precipitation and soil-pH, but the causal links of abundance to these factors is unclear since soil-pH itself is correlated to a drastic turnover of vegetation structure. Based on the analysis of assemblage composition we propose three different assemblages with a transitional zone at the southern tropical area. The biogeographical distribution of euglossine bees along our study transect appears to be primarily related to climatic conditions and does not reflect the common subdividion of Amazonia into drainage systems.

Keywords Beta diversity · Bolivia · Euglossini · Indicator species · Latitudinal gradient · Orchid bees · Peru · Species turnover

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Introduction

Tropical rainforests cover only 7% of the world's landmass but are inhabited by approximately 50% of all terrestrial species (Myers 1986). The factors determining and maintaining this enormous biodiversity are still not fully understood. The relative importances of environmental factors and biological interactions against random variation and dispersal limitation have been debated for decades (Whittaker and Levin 1977; Brown 1984; Hubbell and Foster 1986; Hurtt and Pacala 1995; Whitfield 2002; Ren-Cang et al. 2008; Carranza et al. 2011).

Rainforests are not homogeneous but rather consist of a mosaic of different forest types determined by edaphic and climatic factors as well as natural and anthropogenic disturbances (Gentry 1988; Tuomisto et al. 1995). In Peruvian Amazonia alone, Tuomisto et al. (1995) recognized over 100 types of rainforest biotopes from satellites images. Pitman et al. (2001), on the other hand, found homogenous dominant tree oligarchies at large scales in Amazonia even under different environmental conditions. The decrease in species similarity with geographic distance may also be explained by competitive exclusion (Tuomisto et al. 2003a) and neutrality (Condit et al. 2002). The latter rules out competition and produces a stochastic spread and loss of species driven by dispersal limitation (Hubbell 2001). This factor seems to play a role for the steep decline of similarity on small to intermediate scales (Condit et al. 2002; Duque et al. 2002, 2009; Vormisto et al. 2004).

In Amazonia, the majority of studies considering large scale changes in species diversity and composition have focussed on plant communities, while there are only few studies considering animals, mostly vertebrates (e.g. Eberhard and Bermingham 2005; Abrahamczyk and Kessler 2010). The number of studies considering insects is relatively low. Recently, Vasconcelos et al. (2010) studied the beta diversity of ants along the Amazon River, finding that distribution patterns depend mostly on precipitation regimes.

On a worldwide scale bees in general are most diverse in warm, temperate, and xeric regions and decrease towards the humid tropics (Michener 1979). However, bees are still the most important pollinators in the Neotropics (Fleming and Muchala 2008). Among bees, orchid bees (Hymenoptera: Apidae: Apinae: Euglossini) are a distinctive and exclusively Neotropical group of approximately 210 species in five genera (Kimsey and Dressler 1986; Roig-Alsina and Michener 1993; Nemésio and Silveira 2007b). Euglossine bees pollinate a wide array of plant families, especially orchids, in all states of forest succession (Gilbert 1980; Dressler 1982d; Ackerman 1985). About 600–700 species of orchids, roughly 10% of the Neotropical species (Ramírez et al. 2002; Ackerman 1983a, b) are pollinated by male euglossine bees. Other plant families, e.g. Amaryllidaceae, Araceae, Bignoniaceae, and Solanaceae, attract male euglossines as well (Dressler 1982d; Williams and Dressler 1982; Sazima et al. 1993; Braga 2000; Schwerdtfeger et al. 2002). Due to their ability to fly long distances in short times, orchid bees are one of the most important long distance pollinator groups of Neotropical lowland rainforests and thus provide an essential ecosystem function in Amazonia (Janzen 1971; Bawa 1990).

Orchid bees range from southern Arizona and Texas (Minckley and Reyes 1996; Búrquez 1997) to Paraguay and northwestern Argentina (Moure 1967), inhabit preferably densely forested environments (Ducke 1902; Braga 1976; Roubik and Ackerman 1987; Oliveira and Campos 1995; Nemésio and Silveira 2006a, b, 2007a, b), and represent one of the taxonomically and ecologically best studied groups of Neotropical bees (Cameron 2004; Roubik and Hanson 2004; Michener 2007). Nemésio and Silveira (2007b) distinguished three biogeographic zones in orchid bee community composition and diversity: Central America (76 species), the Amazon Basin (127), and the Brazilian Atlantic forest (62).

In Costa Rica and Panama, orchid bees reach their peak in community diversity at approximately 800 m above sea level (Roubik and Hanson 2004), but local diversity patterns in Amazonia, the distributional core of this group of bees (Ramirez et al. 2010), remain largely unknown. The richest local assemblages of orchid bees consist of about 50 species and can comprise 20–30% of the total regional bee diversity (Roubik and Hanson 2004).

Most species of orchid bees have relatively small distribution areas. Thus, only 12 species occur from southern Mexico to southeastern Brazil (Roubik and Hanson 2004). The geographic distribution of individual bee species may be determined by a number of factors such as climate, vegetation structure, competition with similar species (Rosenzweig 1995) as well as resources such as nest sites, resin, pollen and nectar sources, and perhaps even microbial mutualists (Wcislo and Cane 1996). Furthermore, the presence of host bee species is essential for cleptoparasitic Euglossini like *Exaerete* (Wcislo and Cane 1996).

To our knowledge, there are no studies assessing potential factors of species richness and turnover of orchid bees on a large geographical scale. Only several local inventories of euglossine faunas exist (see Nemésio and Silveira 2007b and references therein). In the present study, we surveyed a latitudinal transect of more than 2000 km from tropical Peru to subtropical Gran Chaco region in Bolivia. We evaluated the relative importance of spatial and environmental factors in species turnover and abundances along this precipitation and seasonality gradient.

Materials and methods

Study sites

Between May and October 2008 we sampled orchid bees at 16 sites along a latitudinal gradient from tropical, evergreen rainforests (3.5° S; 73.5° W) in northern Peruvian Amazonia to subtropical, deciduous forests in central Bolivia (21.6° S; 62.5° W; Fig. 1). Study sites were located in primary, lowland forests between 119 m and 954 m a.s.l.. At each locality, we established a 1 km transect inside the forest and a shorter 350 m transect at the forest edge. Sampling was conducted for one to four days per site, depending on logistical considerations and weather conditions. For orchid bees, surveys of a single day have great utility, and may reveal almost as much about local community structure as studies lasting a full year (Roubik 2004a). Soil samples were taken from the non-organic horizon at each site and analysed for pH, cationic exchange capacity (CEC) and base saturation. The Peruvian soil samples were analysed in the soil laboratory of the Universidad Nacional Agraria—La Molina, in Lima, Peru, and the Bolivian ones at the Department of Plant Ecology at the University of Göttingen, Germany. Climate data was extracted from WorldClim (Hijmans et al. 2005; Table 1).

Census techniques

Euglossine bees were baited with the eight most powerful attractants following Ackerman (1983c): 1–8 cineole, benzyl acetate, methyl benzoate, eugenol, methyl salicylate, methyl cinnamate, skatole, vanillin. Additionally to the latter ones, the commercial drugs Olbas, and Gelomyrtol, as well as hydrogendiethylester and tea-tree oil were used in the Bolivian sites because they are known to be highly attractive to orchid bees (M. Schwerdtfeger, "personal communication") and in order to increase sampling coverage. The fluid agents

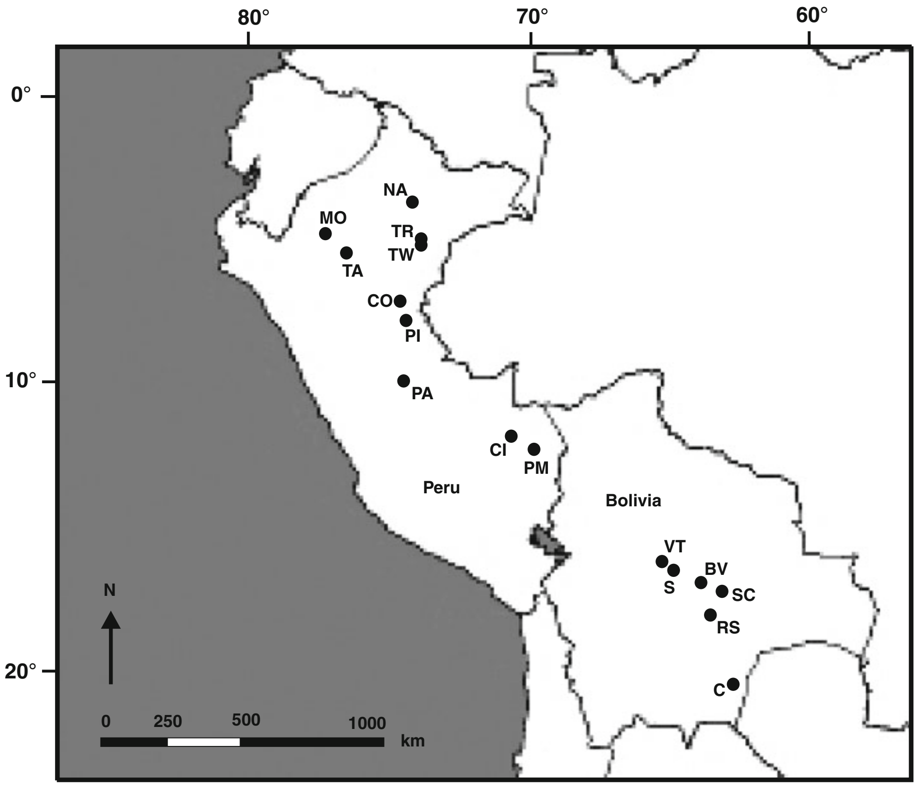

Fig. 1 Location of the study sites in western Amazonia. *BV* Buena Vista, *C* Corbalán, *CI* Centro de Investigación y Capacitación Río Los Amigos (CICRA), *CO* Contamana, *MO* Moyobamba, *NA* Río Nanay, *PA* Panguana, *PI* Pijuayal, *PM* Puerto Maldonado, *RS* Río Seco, *S* Sacta, *SC* Santa Cruz, *TA* Tarapoto, *TR* Río Tapiche I, *TW* Río Tapiche II, *VT* Villa Tunari

were dripped on a sheet of filter paper and refreshed every 30 min. The crystalline chemicals were separately placed in small bags made of thin paper towels. All baits were placed about 15 paces apart and 1.7 m above ground in a straight line. From 7.30 am to 3.30 pm, we patrolled these lines, netting all bees hovering at a bait or trap. Additionally, at the Bolivian sites, self-made modified McPhail traps were used (Steyskal 1977). The bees were killed with ethyl acetate or formol. Specimens were dried on silica gel, put into paper bags for transport, and later pinned for identification. The species were identified following Dressler (1982a, b, c, 1985), Kimsey (1982), Bonilla-Gómez and Nates-Parra (1992), Bembé (2004), Roubik (2004b), Anjos-Silva and Rebêlo (2006), Oliveira (2006) and Nemésio and Silveira (2009).

Data analysis

To assess the effect of incomplete sampling, a linear regression analysis was used to relate the number of species per site to the number of individuals per site. In addition to raw species numbers, we also estimated total species numbers with several species richness estimators (ACE, ICE, Chao 1, Chao 2, Jack 1, Jack 2, Bootstrap, MMMeans, MMRuns) using EstimateS (Colwell et al. 2004). For analyses considering abundances, we divided

Table 1 Table of environmental data and number of species; Δ elevation 5 km = maximum altitudinal range five km around the study site; estimated species numbers are the mean of eight species richness estimators

	Latitude (°)	Longitude (°)	Mean temperature (°C)	Temperature seasonality	Minimum temp. (°C)	Mean prec. (mm)	Precipitation seasonality	Elevation (m)	Δ elevation 5 km (m)	Soil-pH	CEC (μmol$_c$/gTB)	Base saturation (%)	Baited spp.	Estimated spp.
Nanay	−3,533	−73,474	26.3	418	20.5	2910	14	134	34	4.25	75.1	15	16	21.33
Rio Tapiche I	−5,434	−74,003	27.1	411	20.7	2355	21	119	8	4.22	169.3	31	25	36.80
Rio Tapiche II	−5,515	−74,015	27.1	448	20.6	2336	21	121	6	4.16	282.6	5	27	38.49
Moyobamba	−6,043	−76,583	21.9	538	16.4	1493	23	954	647	4.04	64.9	27	17	32.73
Tarapoto	−6,276	−76,174	25.9	394	18.7	2379	28	944	987	3.72	27.1	27	26	36.15
Contamana	−7,129	−74,569	25.7	529	25.5	1993	29	167	401	5.49	53.5	71	19	19.84
Pijuayal	−8,090	−74,192	26.2	589	18.9	1835	37	159	14	3.92	115.5	12	15	21.35
Panguana	−9,368	−74,562	24.4	459	16.7	1896	42	202	88	4.45	36.9	40	19	21.83
Puerto Maldonado	−12,278	−69,278	25.3	1033	17.3	2324	53	164	68	4.83	147.1	48	17	21.29
Cicra	−12,342	−70,059	24.7	1003	16.7	3146	47	230	34	3.85	65.5	17	26	30.68
Villa Tunari	−16,965	−65,413	24.90	1956	14.4	3710	53	400	166	3.91	108.13	41	22	32.51
Sacta	−17,092	−64,781	25.10	2090	14.9	2782	52	204	52	3.81	115.62	53	14	19.76
Buena Vista	−17,516	−63,636	24.10	2182	14.6	2101	55	424	198	5.76	177.25	84	25	33.35
Santa Cruz	−17,782	−63,066	24.10	2231	15.3	1085	49	397	35	6.08	157.97	88	9	9.78
Rio Seco	−18,715	−63,192	24.30	2543	13.3	733	65	434	75	5.69	114.56	79	2	2.10
Corbalán	−21,607	−62,465	23.60	3692	10.3	543	78	268	28	5.34	140.12	84	0	0

the number of individuals collected per site by the number of sampling days to compensate for unequal sampling intensity.

To assess the relationships between the number of raw and estimated species numbers and the number of individuals against the geographic, climatic and edaphic variables, we conducted pairwise linear regression analyses. To test for habitat heterogeneity, we calculated the maximum altitudinal range five km around each study site by using Google Earth maps. We took edaphic variables into account because they are closely related to vegetation types (Tuomisto et al. 1995, 2003b) and thus influence orchid bees indirectly. We repeated the regression analyses of the observed species number against environmental factors excluding *Eufriesea* because species of this genus are known to be seasonal in their occurrence. Then, we calculated multiple linear models in R (R Development Core Team 2007) to select the best combination of explanatory variables. Models were fitted iteratively by the step function and manually using the AICc criterion (Burnham and Anderson 2004). Due to a clear spatial structure shown by the sampling localities, we also conducted general least squares models with the program "Spatial Analysis in Macroecology: SAM" (Rangel et al. 2006) which additionally includes the spatial relationship between the sites.

To analyse changes in assemblage composition between study sites, we first used Detrended Correspondence Analyses (DCA), with downweighting rare species in PcOrd 5.0 (McCune and Mefford 1999). We downweighted rare species because without downweighting, DCA patterns tend to be dominated by rare species whose patterns however are less reliably documented because of their low sampling intensity (Leyer and Wesche 2008). We excluded the southernmost site (Corbalán) since we did not find any orchid bee there. Second, we used simple Mantel tests using Sørensen similarity index to assess the relationships between assemblage composition and environmental factors. The Mantel analysis was done with the original similarity data and with estimated similarity data calculated in Estimate*S* (Colwell et al. 2004) to test whether incomplete sampling had an influence of our results. Third, we used partial Mantel tests in R based on quantitative Sørensen similarity indices (Bray-Curtis), geographical distances and environmental factors.

Finally, we conducted a Species Indicator Analysis (Dufrene and Legendre 1997) as implemented in PcOrd 5.0 by variously dividing the dataset into geographical regions: I. Peru NW of the Amazon and Ucayali Rivers; Peru SE of the Amazon and Ucayali Rivers; tropical Bolivia; subtropical Bolivia. II. Peru; tropical Bolivia; subtropical Bolivia. III. Peru; Bolivia. IV. Peru plus tropical Bolivia; subtropical Bolivia.

Results

In total, we collected 1524 specimens of euglossine bees representing 59 species in five genera (App. 1). Fifty-seven species (96.6%) were identified to species level while the remaining two species were sorted into morphospecies. Eight species (14%) were found at more than ten sites, while 15 (25%) were only found at a single site and seven (12%) at two sites. No euglossine bees were found at the southernmost site (Corbalán). Mean species numbers were 20.4 ± 4.7 for the Peruvian sites, 20.3 ± 5.7 for the tropical Bolivian sites, and 5.5 ± 4.9 for the two subtropical sites.

There was no significant correlation between the number of species per site and the number of sampling days per site ($R = 0.14$, $P = 0.60$). However, the number of individuals collected at a site was significantly correlated to the number of species per site ($R = 0.68$, $P = 0.004$; Table 2). This suggests that sampling completeness may have

Table 2 *R*-values for the simple linear regression analysis of the number of species and individuals corrected by sampling days against environmental factors; Δ elevation 5 km (m) = maximum altitudinal range five km around the study site

	Number of species	Estimated number of species	Number of individuals
Mean temperature	0.44	0.34	0.6*
Temperature seasonality	−0.68**	−0.66**	0.52*
Minimum temperature	0.55*	0.46^	0.50*
Mean precipitation	0.73***	0.68**	0.56*
Precipitation seasonality	−0.60*	−0.64**	0.49^
Latitude	−0.58*	−0.60*	0.05
Elevation	0.04	0.19	−0.17
Δ elevation 5 km	0.28	0.35	−0.33
Soil-pH	−0.52*	−0.61*	0.44^
Base saturation	−0.58*	−0.64**	0.57*
Cationic exchange capacity	0.04	0.09	0.24
Number of individuals	0.68**	0.66**	–
Number of individuals corrected by sampling days	0.75***	0.70***	–
Sampling days	0.08	0.20	–

^ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

affected our species counts. However, when we controlled for incomplete sampling by using species richness estimators (Table 1), results of linear regression analyses between the estimated number of species and the environmental factors were similar to those using the raw species numbers (Table 2). For this reason, all further analyses were conducted with the raw data only. When we repeated the regression analyses of the observed species number against environmental factors excluding *Eufriesea*, we found no qualitative differences compared with the results for the regression analyses of the complete species set. Therefore we do not further report these results.

Looking at all explanatory variables separately, species and individual numbers per site were significantly related to several climatic factors such as mean annual temperature and precipitation or temperature and precipitation seasonality but also to edaphic factors such as base saturation or soil-pH (Table 2; Fig. 2).

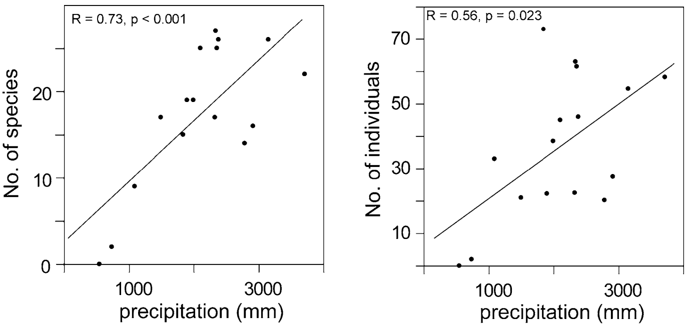

Fig. 2 Relationships of the number of orchid bee species and individuals per site against mean annual precipitation. *R* and *P*-values are based on linear regression analyses

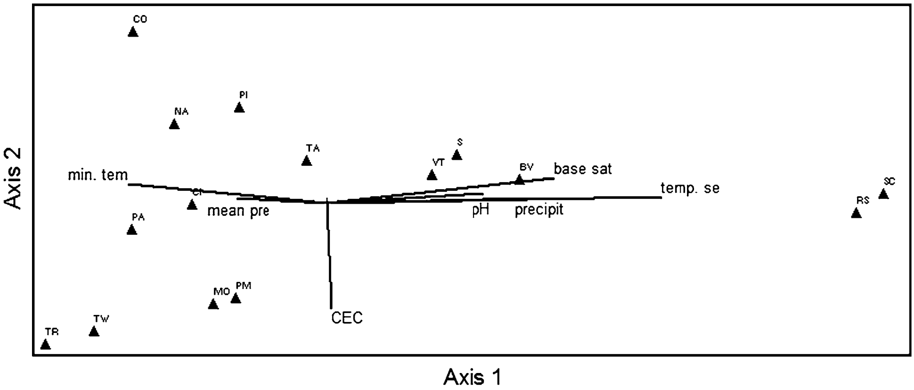

Fig. 3 DCA based on the species composition of the sampled bee assemblages; the *black lines* indicate the environmental factors as marked (Axis 1: eigenvalue = 0.73, length of gradient = 4.56; Axis 2: eigenvalue = 0.13, length of gradient = 1.63); *min. temp* minimum temperature, *mean pre* mean annual precipitation, *CEC* cationic exchange capacity, *precipit* precipitation seasonality, *base sat* base saturation, *temp. se* temperature seasonality, *NA* Nanay, *TR* Rio Tapiche I, *TW* Rio Tapiche II, *MO* Moyobamba, *TA* Tarapoto, *CO* Contamina, *PI* Pijuayal, *PA* Panguana, *PM* Puerto Maldonado, *CI* Cicra, *VT* Villa Tunari, *S* Sacta, *BV* Buena Vista, *SC* Santa Cruz, *RS* Río Seco, Corbalán (not shown)

The multiple linear model best explaining species richness per site ($R^2 = 0.84$, $P = 0.001$; AICc = 110.89) included five factors: temperature seasonality ($P = 0.006$), mean annual precipitation ($P = 0.002$), elevation ($P = 0.07$), CEC ($P = 0.03$), and base saturation ($P = 0.187$). The comparable model for the number of individuals ($R^2 = 0.53$, $P = 0.025$; AICc = 143.1) only included mean annual precipitation ($P = 0.045$), minimum temperature ($P = 0.101$), and CEC ($P = 0.133$). The comparable General Least Squares models in SAM taking spatial structure into account for species numbers ($R^2 = 0.83$, AIC = 120.8) included temperature seasonality ($P = 0.005$), mean annual precipitation ($P < 0.001$), elevation ($P = 0.028$), CEC ($P = 0.009$), and base saturation ($P = 0.086$) and for the number of individuals ($R^2 = 0.54$, AIC = 151.0) mean annual precipitation ($P = 0.001$) and CEC ($P = 0.044$).

The DCA (Fig. 3) revealed clear environmental gradients related to the species composition of the studied euglossine assemblages. Axis 1 was mainly related to a gradient in temperature seasonality and minimum temperature as well as to mean annual precipitation, soil-pH, and soil base saturation. Axis 2 was related to a gradient in soil cationic exchange capacity (CEC). The simple Mantel tests using the original and estimated data (Table 3) disclosed significant relationships of the similarity of species composition between sites to temperature seasonality, mean annual precipitation, precipitation seasonality as well as inter-site distance, but with lower r-values for the estimated data. However, once spatial distance was taken into account by the partial Mantel tests, no other environmental factor showed a significant relationship to species composition.

The Species Indicator Analysis (Table 4) recovered nine species with significantly structured distributions when the study region was subdivided into three components, with three species showing a preference for Peru, four for tropical Bolivia, and two for subtropical Bolivia. When the two Bolivian regions were combined, the analysis recovered nine significant species as well as, four in Peru and five in Bolivia. Finally, only two species showed significant distribution patterns when the subtropical Bolivian sites were contrasted with all other sites (Table 4). All three analyses included *Eulaema meriana* as

Table 3 Regression (R) values for simple the Mantel tests between species composition and environmental factors for original and estimated similarity data

	Original data	Estimated data
Mean temperature	0.11	0.01
Temperature seasonality	0.73***	0.24***
Minimum temperature	0.24	0.10
Mean precipitation	0.49**	0.18*
Precipitation seasonality	0.37**	0.14**
Elevation	0.05	−0.01
Soil-pH	−0.02	0.04
Base saturation	0.08	−0.01
Cationic exchange capacity	0.30	0.13
Inter-site distance	0.59***	0.18***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4 Results of the species indicator analyses

	Peru NW/Peru SE/tropical Bolivia/ subtropical Bolivia	Peru/tropical Bolivia/subtropical Bolivia	Peru/ Bolivia	Subtropical Bolivia/tropical sites
Eufriesea pulchra	–	Peru^	Peru^	–
Euglossa amazonica	Trop. Bolivia**	Trop. Bolivia*	Bolivia^	–
Euglossa cordata	–	–	Bolivia*	–
Euglossa chalybeata	Trop. Bolivia^	Trop. Bolivia^	–	–
Euglossa despecta	–	–	Bolivia**	–
Euglossa fimbriata	Subtrop. Boliva*	Subtrop. Boliva*	Bolivia*	–
Euglossa ignita	Peru NW*	Peru***	Peru***	–
Euglossa imperialis	–	–	–	Topical^
Euglossa intersecta	–	Peru**	Peru**	–
Euglossa laevicincta	–	–	Peru^	–
Euglossa magnipes	Trop. Bolivia**	Trop. Bolivia**	Bolivia*	–
Euglossa mixta	Trop. Bolivia^	Trop. Bolivia*	–	Tropical*
Euglossa modestior	Trop. Bolivia*	Trop. Bolivia^	–	–
Euglossa orellana	Trop. Bolivia**	Trop. Bolivia**	–	–
Euglossa securigera	–	–	Bolivia*	–
Eulaema bombiformis	–	Peru**	Peru**	–
Eulaema meriana	Peru SE^	Peru***	Peru**	Tropical*
Eulaema mocsaryi	–	–	Peru^	Tropical^
Eulaema pseudocingulata	–	–	Peru^	–
Exaerete frontalis	Peru NW^			

^ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

being an indicator species for Peru or tropical sites. *Eulaema bombiformis* and *Euglossa intersecta* were recovered as indicator species for Peru, and *Euglossa fimbriata* and *Euglossa magnipes* for Bolivia in both analyses contrasting Peru with Bolivian regions. The remaining species were only chosen as indicator taxa in single analyses. When we additionally divided the sites in Peru into sites northwest and southeast of the Amazon and

Ucayali Rivers we found only one species significant for the NW-region and one marginally significant each for the NW-and SE-region.

Discussion

This is the first study relating species richness and abundance of orchid bees to abiotic factors along a latitudinal gradient. Overall, we found that climatic and soil conditions captured a substantial amount of the variation in alpha diversity of orchid bees in western Amazonia. Especially the annual amount of precipitation was related to the distribution pattern of orchid bee individuals and species along the gradient (Fig. 2). In striking contrast to other bee families, where the highest species richness is commonly found in drier, subtropical regions (Michener 1979, 2007; Roubik 1989; Radchenko and Pesenko 1994), we found a dramatic loss of species richness from tropical to subtropical ecosystems. This decline between the two biomes may be a response to the transition from low annual amplitudes in temperature and precipitation, no or few arid months, and the absence of frost to a marked seasonality in precipitation and temperature and even occasional nocturnal freezing. This transition goes hand in hand with a marked turnover in plant community composition from evergreen rain forests to seasonally dry, deciduous forests (Justiniano and Fredericksen 2000; Abrahamczyk and Kessler 2010). Whether this latitudinal decline of alpha diversity of orchid bee assemblages is directly related to climatic conditions or some other, proximal factor such as the availability of food plants or plant species adapted to pollination by orchid bees cannot be answered with the data available at present. A comparison with the numbers of individuals recorded does not provide conclusive evidence in this regard. Species richness and individual numbers per site were strongly correlated, and the regression analyses recovered very similar suites of environmental variables.

The latitudinal decline of species richness and it's relationship to climatic factors parallel the situation in many other plant and animal groups (Wiens et al. 2006; Hawkins and De Vries 2009; Hu et al. 2010). The causes for this decline are still unknown, and may involve either the carrying capacity of ecosystems as determined by water availability and temperature (Hawkins et al. 2003), or historical and evolutionary causes (Wiens and Donoghue 2004). In many tropical and subtropical areas in the southern hemisphere, water-related variables are the best predictors of several animal richness patterns (Hawkins et al. 2003). One potential explanation for invertebrates could be that hot environments create problems with desiccation because of their small body size (Hawkins et al. 2003). This is reflected in our study, since bee abundances increased with the amount of mean annual precipitation. In our study, the linear model revealed that additionally to mean annual precipitation and temperature seasonality, elevation, CEC and base saturation also accounted for alpha diversity. However, especially the soil parameters probably only have an indirect effect on bee assemblages via their relationships to plant communities and habitat structure (Tuomisto et al. 1995, 2003b). Geographical distance only played a minor role in determining the differences in species richness of orchid bees, which coincides with the results of Vasconcelos et al. (2010) for ants.

The biogeographic division of the orchid bee assemblages of our study regions into three parts seems to be the best choice based on the DCA. Río Seco and Santa Cruz form one cluster representing the subtropical, seasonal sites climatically differentiated from the others by several arid months and temperatures near zero degrees Celsius. The tropical Bolivian sites Villa Tunari, Sacta and Buena Vista represent the second cluster distinguished from the Peruvian sites by a higher temperature seasonality. We interpret this cluster as a transition zone from tropical, non-seasonal, evergreen rain forests in the north to seasonally drought deciduous forests in the south. The third cluster includes the ten Peruvian sites. Unfortunately, we lack study sites from northern Bolivia so that the possible transition between the second and third cluster remained unsampled.

The biogeographic pattern detected by us disagrees with commonly found separation of Amazonian faunistic regions where assemblages are subdivided by river drainages (Silva & Oren 1996; Bates et al. 1998). For example, we found no clear separation between sites north and south of the Amazon and Ucayali Rivers, usually considered the major biogeographic barrier in western Amazonia. Our results agree with the finding of Dick et al. (2004) who reported that in euglossine bees the phylogenetical structure across a broad spatial scale is weaker than in any other Neotropical group previously examined, and may derive from a combination of Quarternary speciation, population expansion and long distance gene flow. In our case, thus, the biogeographic patterns may reflect past changes in the distribution of vegetation types dring the Pleistocene climatic fluctuations (Nemésio and Silveira 2007b). But although such shifts are undisputed, the actual distribution of different vegetation types at different points in time remain controversial for Amazonia (Hoorn et al. 2010; Ramirez et al. 2010; Werneck et al. 2010). We therefore consider it premature to try to interprete the latitudinal separation of orchid bee assemblages in these terms. Finally, biogeographical subdividions of Amazonia rarely go as far south as our study, which includes sites in the Paraná drainage and in subtropical vegetation types. Considering all the above points, we conclude that the biogeographic patterns detected by us most likely reflect current climatic conditions.

In conclusion, our results support previous studies that patterns of species richness of Amazonian plant and animal assemblages are largely accounted for by climatic and edaphic factors (ter Steege et al. 2003; Wittmann et al. 2006; Vasconcelos et al. 2010). How these factors determine species numbers remains unknown, however. In the case of orchid bees, the abundance and diversity of nesting sites and nesting material, predators and flower phenology and availability may play important mediating roles (Roubik and Hanson 2004). However, detailed data on these factors are very difficult to obtain. Regardless of the underlying causes, the observed relationship between euglossine species richness and local climate have important implications regarding the expected climatic changes resulting from global change and altered land use. The Amazon basin is likely to experience novel climate conditions by the end of the 21st century (Williams et al. 2007). As a census studies of euglossine bees can be conducted quite easily, the present study may represent a baseline against which to assess future changes in species richness or the elvational or latitudinal distribution of species, as predicted for tree species (Toledo et al. 2010).

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Appendix

See Table 5.

Table 5 Species abundance per site

	Peru									
	Nanay	Rio Tapiche I	Rio Tapiche II	Moyobamba	Tarapoto	Contamana	Pijuayal	Panguana	Cicra	Pto. Maldonado
Aglae caerulea				1			1			
Eufriesea distinguenda			1							
Eufriesea magretti					16					
Eufriesea pulchra	1	28	12		4			2	5	2
Eufriesea purpurata					1					
Eufriesea violacea									1	
Eufriesea xantha		1								
Euglossa allosticta					1	2		1		
Euglossa amazonica		1	1		1		2		3	5
Euglossa analis		1	1							
Euglossa augaspis		1	6					3	2	2
Euglossa bidentata		9	1		1		1			
Euglossa chalybeata	2				1	1			9	1
Euglossa chlorina										
Euglossa cognata		4	7		1				1	3
Euglossa cordata										
Euglossa crassipunctata								1		
Euglossa decorata	1							1		
Euglossa despecta				1	2			1	1	
Euglossa dressleri										
Euglossa fimbriata										
Euglossa hemichlora			3						1	
Euglossa heterosticta		1							1	

Table 5 continued

	Peru									
	Nanay	Rio Tapiche I	Rio Tapiche II	Moyobamba	Tarapoto	Contamana	Pijuayal	Panguana	Cicra	Pto. Maldonado
Euglossa ignita	4	5	14	11	2	7	13	2	28	9
Euglossa imperialis	1			2	8	7	7	5	1	3
Euglossa intersecta	9	4	3		2	7	1	7	3	1
Euglossa ioprosopa	1			1	1					
Euglossa iopyrrha			1		1	1				
Euglossa laevicincta	2	1	2		1	1	4			
Euglossa macrorhyncha		1	1							
Euglossa magnipes				2					1	2
Euglossa melanotricha										
Euglossa mixta	12	1	2	1	8	9	14	8	31	
Euglossa modestior		5	7	1	1				3	
Euglossa mourei		1	3						1	
Euglossa occidentalis	1				4	12	4		7	
Euglossa orellana	7			1	6	3	18	4	1	3
Euglossa parvula			1							
Euglossa perviridis			1							
Euglossa pleosticta										
Euglossa prasina		1								
Euglossa retroviridis	1									
Euglossa rugilabris						2	1			
Euglossa securigera					2					
Euglossa spec. I										
Euglossa spec. II										

Table 5 continued

	Peru									
	Nanay	Rio Tapiche I	Rio Tapiche II	Moyobamba	Tarapoto	Contamana	Pijuayal	Panguana	Cicra	Pto. Maldonado
Euglossa stilbonota	1		3							
Euglossa townsendi										1
Euglossa turbinifex				1						
Euglossa viridifrons	2	7	1			1			2	
Eulaema bombiformis	5	4	2	1	1	1		2	7	2
Eulaema marcii		1	1	9	3	3	1	7	12	4
Eulaema meriana	5	1	12	6	6	8	3	16	14	1
Eulaema mocsaryi		9	4	1	5	7		4	6	3
Eulaema nigrita				1	12					1
Eulaema peruviana				1						
Eulaema pseudocingulata		1	7	1	1	1	1	1	1	
Exaraete frontalis		3	7			4		1	1	
Exaraete smaragdina		5	4				3	5	3	2
Total number of species per site	16	24	27	17	26	18	15	18	26	17
Mean species richness per biogeographic zone	20.4 ± 4.7									
Total number of individuals per site	55	96	108	42	92	77	74	71	146	45
Mean number of individuals	87.3 ± 31.55									

	Tropical Bolivia			Subtropical Bolivia		Total number of individuals	Number of sites
	Villa Tunari	Sacta	Buena Vista	Santa Cruz	Rio Seco		
Aglae caerulea			1			3	3
Eufriesea distinguenda						1	1

Table 5 continued

	Tropical Bolivia			Subtropical Bolivia		Total number of individuals	Number of sites
	Villa Tunari	Sacta	Buena Vista	Santa Cruz	Rio Seco		
Eufriesea magretti						16	1
Eufriesea pulchra						54	7
Eufriesea purpurata						1	1
Eufriesea violacea						1	1
Eufriesea xantha						1	1
Euglossa allosticta	1					5	4
Euglossa amazonica	23	17	33	9		95	10
Euglossa analis						2	2
Euglossa augaspis	1					15	6
Euglossa bidentata						12	4
Euglossa chalybeata	15	1	2			32	8
Euglossa chlorina			1			1	1
Euglossa cognata	3	1	1			21	8
Euglossa cordata	1		13	6		20	3
Euglossa crassipunctata						1	1
Euglossa decorata	1		4			7	4
Euglossa despecta	8	1	2	4	3	23	9
Euglossa dressleri	1					1	1
Euglossa fimbriata			1	46	5	52	3
Euglossa hemichlora						4	2
Euglossa heterosticta						2	2
Euglossa ignita						95	10
Euglossa imperialis	1	1	5			41	11
Euglossa intersecta						37	9

Table 5 continued

	Tropical Bolivia			Subtropical Bolivia		Total number of individuals	Number of sites
	Villa Tunari	Sacta	Buena Vista	Santa Cruz	Rio Seco		
Euglossa ioprosopa	11					14	4
Euglossa iopyrrha						3	3
Euglossa laevicincta						11	6
Euglossa macrorhyncha						2	2
Euglossa magnipes	1	7	18	2		33	7
Euglossa melanotricha			2			2	1
Euglossa mixta	21	8	43			158	12
Euglossa modestior	33	4	3	1		58	9
Euglossa mourei						5	3
Euglossa occidentalis						28	5
Euglossa orellana	92	35	2			172	11
Euglossa parvula						1	1
Euglossa perviridis						1	1
Euglossa pleosticta			1			1	1
Euglossa prasina						1	1
Euglossa retroviridis						1	1
Euglossa rugilabris						3	2
Euglossa securigera	2		3	3		10	4
Euglossa spec. I			1			1	1
Euglossa spec. II			1			1	1
Euglossa stilbonota						4	2
Euglossa townsendi	1		1			3	3
Euglossa turbinifex ****						1	1
Euglossa viridifrons						13	5

Table 5 continued

	Tropical Bolivia			Subtropical Bolivia		Total number of individuals	Number of sites
	Villa Tunari	Sacta	Buena Vista	Santa Cruz	Rio Seco		
Eulaema bombiformis						25	9
Eulaema marcii	3	1	2	1		48	13
Eulaema meriana	1	1				74	12
Eulaema mocsaryi	1	1	2			43	11
Eulaema nigrita		2	3	6		25	6
Eulaema peruviana	2					3	2
Eulaema pseudocingulata			1			15	9
Exaraete frontalis						16	5
Exaraete smaragdina	1	1	1			25	9
Total number of species per site	22	14	25	9	2		
Mean species richness per biogeographic zone	20.3 ± 5.7			5.5 ± 4.9			
Total number of individuals per site	224	81	147	78	8		
Mean number of individuals	150.7 ± 75.6			43.0 ± 49.5			

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