ECOLOGY, BEHAVIOR AND BIONOMICS

Diversity and Distribution Patterns of Pronophilina Butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an Altitudinal Transect in North-Western Ecuador

Tomasz W Pyrcz, Janusz Wojtusiak, Rafał Garlacz

Zoological Museum of the Jagiellonian University, Ingardena 6, 30-060 Kraków, Poland; pyrcztomasz@hotmail.com; wojt@zuk.iz.uj.edu.pl; rafgar@wp.pl

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Diversidad y Patrones de Distribución de Mariposas de la Subtribu Pronophilina (Lepidoptera: Nymphalidae: Satyrinae) en un Transecto Altitudinal en el Nor-Oeste de Ecuador

RESUMEN - Se realizó en Ecuador un muestreo de mariposas de la subtribu Pronophilina con el fin de evaluar los efectos de altitud sobre los patrones de distribución, diversidad y estructura de la comunidad en un transecto altitudinal. Se demostró una correlación significativa de todos los índices de diversidad y altitud. El máximo de diversidad expresado por la riqueza de especies, fue reportado a 2600 m. Se identificaron dos grupos de especies en la parte inferior y superior del transecto. La comparación de los coeficientes de similitud indicó valores menores en la franja de altitud intermedia. Se demostró que varios pares de especies relacionadas morfo y ecológicamente tienen distribuciones altitudinales mutuamente exclusivas. La comparación con estudios semejantes revelaron una congruencia muy notable en cuanto a los patrones de diversidad altitudinal de los Pronophilina en varias áreas de la cordillera Andina. En particular, el índice de Shannon llega a valores máximos entre 2600 m y 2850 m, aproximadamente 400 - 500 por debajo del limite superior del bosque nublado. El aumento de la diversidad de los Pronophilina con la altitud puede ser relacionado tan solo de manera marginal con la mayor disponibilidad de los recursos limitados. La menor presión por parte de los depredadores, parasitoides y ectoparásitos en mayores altitudes puede contribuir a la mayor abundancia pero no directamente a la diversidad. Esta última, está relacionada con las características intrínsicas del grupo, tales como el solapamiento de grupos faunísticos elevacionales y la tasa de especiación más rápida en el límite superior del bosque.

PALABRAS CLAVES: Distribución altitudinal, bambú *Chusquea*, especie parapátrida, especiación, riqueza de especies

ABSTRACT - Samplings of Pronophilina, a species-rich group of neotropical montane butterflies, were carried out along an elevational transect in Ecuador to assess the effect of altitude on their distribution patterns, diversity and community structure. All diversity indices were significantly correlated with altitude. Maximum diversity expressed in species-richness, Shannon index and Fisher alpha was recorded at 2600 m. Two assemblages of species were identified in the lower (below 2100 m) and upper (above 2300 m) sections of the transect by means of correspondence (CA) and cluster analysis. A comparison of Sørensen similarity coefficients showed lower values, thus higher turnover in the intermediate elevational band. Several closely related morphologically and ecologically species were found to have mutually exclusive altitudinal distribution patterns. A comparison with similar studies in Venezuela, Colombia and Peru revealed far reaching congruency of the patterns of altitudinal diversity of Pronophilina in distant areas of the Andes. In particular, the Shannon index reaches its maximum values at 2600-2850 m, which invariably correspond to ca. 400-500 m below the upper limit of cloud forest. Increase of diversity of Pronophilina with altitude is marginally related to higher limited resource availability. The lower pressure of predators and parasites at higher elevation can contribute with higher abundance, but cannot be directly correlated with higher diversity. Higher diversity is related with intrisic characteristics of the group, such as aggregated diversity by overlapping of elevational faunal assemblages and higher speciation ratio towards high elevations, particularly near timberline.

KEY WORDS: Altitudinal spread, *Chusquea* bamboo, parapatric species, speciation, species-richness

In the recent years research on altitudinal distribution patterns in insects, and Lepidoptera in particular, has gained some attention (Sánchez-Rodríguez & Baz 1995, Fagua 1999, Pyrcz & Wojtusiak 1999, 2002, Brehm *et al* 2003b, 2005). Most studies in altitudinal patterns dealt with large taxonomic entities, families or orders (Holloway *et al* 1990, Olmstead & Wood 1990, Sanders 2002, Brehm & Fielder 2003, Brehm *et al* 2003a). Distribution patterns of extremely species-rich and diverse groups are exponents of a vast array of ecological factors, usually acting in different ways on different smaller subunits that make up the large taxon. This makes their thorough assessment by statistical methods extremely complex. The results are usually a conglomerate of numerous uncorrelated or loosely correlated factors. In consequence, conclusions concerning altitudinal patterns are generalisations yielding such issues as the decrease of diversity from above sea level (Fernandes & Price 1988, McCoy 1990, Stevens 1992, Brühl *et al* 1999) or hump-backed distributions (Janzen *et al* 1976, Gagné 1979, Holloway *et al* 1990, Olson 1994, Sanders 2002). The lack of a systematic framework is common, therefore studies in most cases employ the morphospecies category (Axmacher & Fiedler 2008).

This study is concerned with a relatively small group of species, belonging to the neotropical subtribe Pronophilina, systematically and zoogeographically well known montane specialists occupying similar ecological niches (Adams 1986, Pyrcz & Viloria 1999, Pyrcz 2004, Pyrcz & Rodríguez 2005). Elevational distributions of the Pronophilina have attracted the attention of naturalists since the early twentieth century (Fassl 1918, Krüger 1924) and have been explored somewhat more extensively within the last two decades (Adams 1985, Pyrcz & Wojtusiak 1999, 2002, Prieto 2003, Pyrcz 2004). This study uses robust statistical data in order to test the hypothesis that closely related species have mutually exclusive parapatric distributions. It focuses on how intrinsic taxa characteristics, such as niche partitioning, interspecific relations and evolutionary dynamics, shape altitudinal patterns.

Material and Methods

Study area. The study area is situated at the confluence of major geographic and biogeographical regions - the Andes and the Chocó. It is located in extreme north-western Ecuador in the region referred to as the Nudo de Pasto, a complex knot of volcanoes, where three Colombian Cordilleras (Western, Central and Eastern) diverge from the main Andean stem. The main field work took place in the Cerro Golondrinas ecological reserve (0°49'N, 78°08'W) situated on the peripheries of the Volcán Chiles (4748 m). The reserve covers an area of about 1400 ha. It encompasses low and mid elevation cloud forest and elfin forest between 1300-3100 m. Nearly 70% of the reserve includes primary forests (own estimates). Secondary forests and non-forested areas in different stages of succession are concentrated along trails and in the proximity of the river La Carolina. The area is characterized by high annual rainfall, exceeding 3000 mm at an elevation of 1500 m. The rainy season extends from November to June. Yearly mean temperatures oscillate from 12°C to 20°C. The protected area is extremely fragile and is under severe stress by local inhabitants from lower and upper elevations, especially due to extensive grazing and forest burning above 3000 m (Picket 2001).

Data collecting and taxonomy. Material (adult Pronophilina) was collected along an altitudinal transect comprised between 1600 m and 2600 m a.s.l. along the trail crossing the Golondrinas reserve. It was conducted through a mixture of primary and secondary forest, without crossing larger open (logged or burnt) secondary areas, which could be an important disturbance factor to the elevational patterns of the Pronophilina (Adams 1985), and with continuous presence of *Chusquea* bamboo-host plants for many species in the Pronophilina. The transect could not be extended above 2600 m a.s.l. due to extremely harsh topography, nor below 1600 m due to the absence of bamboo. Altitudes were measured with calibrated altimeters and cross checked against GPS data and a topographic map of the area (Instituto Geográfico y Militar de Ecuador). The transect consisted of 21 standard baited traps as described in Owen (1971) or DeVries (1987), daily provided with bait consisting of excrements of carnivorous mammals. They were installed at every 50 m in elevation. Trap intervals of 50 m are considered optimal for this kind of research. On one hand they allow establishing exactly altitudinal ranges of individual species, and identifying possible overlapping zones of parapatric pairs. On the other hand, they are far enough from each other to avoid cross interference with the baits.

The sampling took place in June 1999, which corresponds to the late rainy season. This season proved to be a particularly appropriate period for adult butterfly sampling considering their life histories (Owen 1971, DeVries 1987). Two persons operated the traps over 22 days, performing daily data gathering from each trap. All the individuals collected in the traps were placed in separate paper envelopes, duly marked *in situ* with the date and altitude of the corresponding trap.

The sampling technique applied was used successfully in previous studies focused on altitudinal distributions of Pronophilina. This method takes advantage of adult Pronophilina being attracted to baits made of decomposing organic matter, allowing the collection of robust ecological data suitable for statistical analysis within short periods of time (Raguso & Gloster 1993, Lees 1996, Pyrcz & Wojtusiak 1999, 2002, Pyrcz 2004). By contrast, other species-rich groups of montane diurnal Lepidoptera (most Lycaenidae, Hesperidae and Pieridae) are not attracted to baits, thus their sampling is usually random, whereas those attracted to baits (Charaxiinae, Limenitidinae) are little diverse in montane habitats. The use of a passive collecting method proved to be extremely informative in the studies on patterns of diversity along ecological gradients, as well as in other diverse taxa attracted to dung baited traps, such as the Scarabaeidae beetles (Hanski & Niemelä 1990, Lobo & Halffter 2000, Scheffler 2005). A standardized method of collecting in geographically widely dispersed localities is a very efficient method of accumulating valuable information for comparative analysis and uncovering wide-scale patterns (Grytnes 2003, Rahbek 2005).

The collected material was examined in the Zoological Museum of the Jagiellonian University, Kraków, Poland (MZUJ) and compared against the type specimens deposited in major collections in Europe and America (BMNH: The Natural History Museum, London UK; ZMHB: Zoologische Museum Humboldt Universität, Berlin, Germany; MUSM: Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru). All taxa were identified to species and whenever necessary to subspecies level. For taxonomically complex species a number of male genitalia dissections were made following the standard procedure, involving the maceration in hot 10% KOH, and permanently preserving the genitalia in glycerol. Additionally, morphological micro-structures, such as the male androconia, wing venation and head parts were examined under an Olympus SZX9 stereomicroscope. Taxonomic and biogeographic information was cross-checked against authors' data gathered throughout Ecuador and the northern Andes in the period from 1999 to 2008 (Pyrcz *et al* 1999, Pyrcz & Viloria, 1999, Pyrcz 2004).

Statistical analysis. For statistical analysis, abundance and the number of species recorded at each elevational station were given. Two diversity measures, Fisher alpha and Shannon index, were calculated. The former is relatively unaffected by sample size, although some authors indicate that the recommended minimum number of specimens in a sample should be at least 100 specimens (Hayek & Buzas 1997). The latter is more sensitive to sample size (Magurran 2004), however it is still a commonly used diversity index, and is highly indicated for comparative studies (DeVries & Walla 1999, Picket 2001, Scheffler 2005). The Berger-Parker index was used as a measure of dominance. Based on presence-absence data, the Sørensen similarity coefficient was calculated in order to compare faunal composition between all altitudinal stations. The use of this index was justified, because the sample was exhaustive as compared to the overall number of species occurring in the study area and the number of singletons in the sample was limited. The results, presented in a Trellis diagram were grouped in four categories by the similarity level: 0-0.29; 0.3-0.49; 0.49-0.69; 0.7-0.89; 0.9-1 (Southwood 1978). A non-parametric Spearman correlation (*r*) was used to correlate all the indices and proportions of genera with altitude. A species correspondence analysis (CA) was performed in order to demonstrate the ordination of species distributions, and a cluster analysis using Ward's method with squared Euclidean distance was applied (Holloway 1970, Intachat & Holloway 2000), in both cases using the proportion of individuals of species excluding singletons. The Mann-Whitney U-Test was applied in order to assess the degree of overlap of the parapatric species (Pyrcz & Wojtusiak 2002). Species accumulation curve was not calculated. The species-richness estimators were not used because the sample was considered to represent a complete faunal inventory (Brose & Martínez 2004, Brehm *et al* 2005). Statistical analysis was carried out with the Statistica 6.0 software package (Tulsa, USA) and Species Diversity and Richness III software (Pisces Conservation).

Results

Community structure and individual distributions. A total of 2,326 individuals belonging to 48 species and 16 genera were collected in baited traps along the Golondrinas altitudinal transect (online Supporting Material 1), including six new species and six new subspecies, described in separate papers (Pyrcz 1999, Pyrcz & Viloria 1999, Pyrcz & Rodríguez 2005, Pyrcz *et al* 2006). Six species were found to occur along the entire elevational transect, exhibiting a 1000 m elevational range spread. These were *Pronophila orcus* (Latreille), the most common in the sample, *P. simpla* Thieme and *P. montagna* Adams & Bernard, the third and fourth most common species in the sample respectively. Two of the most common species of the genus *Corades* (*C. enyo* Hewitson and *C. pannonia* Hewitson) were also found along the entire transect (Fig 1).

Species abundance appear to be positively correlated with the spread of altitudinal distribution (r = 0.79; P < 0.0001). In other words, common species are characterised by wide altitudinal ranges, and rare species by narrow altitudinal ranges. Nine of the most common species, with ≥ 90 individuals each, accounted for 1,734 individuals representing 74.7% of the sample. Seven of these species belong to the genus *Pedaliodes* Butler. All 17 species of *Pedaliodes* accounted for 1,910 individuals, representing 82.1% of the sample. The most common species in the sample was, however, *P. orcus*, with 387 individuals, constituting 16.5% of the sample. As many as 17 species (35.4% of the sample) were represented by less than 10 individuals. Eight species were singletons. It is important to point out that the species represented by singletons in the sample have been reported in literature as widespread but occurring at low abundance, i.e. *Thiemeia phoronea* (Doubleday), *Panyapedaliodes muscosa* (Thieme), or generally found at higher elevations than covered by the transect, i.e. *Lymanopoda labineta* Hewitson (Adams 1986, Pyrcz *et al* 1999, Pyrcz & Rodríguez 2005).

The species recorded on the transect are grouped by genera and by related (according to actual state of knowledge based on morphological and molecular data) groups of genera (Fig 2). The genus *Pedaliodes sensu lato* (including *Panyapedaliodes* Forster) and the "Pronophila group" constitute more than 90% of the Pronophilina community at each elevation, except at 2600 m. A strong positive correlation was observed between the proportion of the "Pedaliodes group" and altitude (r = 0.71; P < 0.001). On the other hand, a negative correlation is observed between the proportion of the "Pronophila group" and altitude (r = -0.79; P < 0.000). For the remaining groups the correlation was not statistically significant.

The species CA shows two groups corresponding to the assemblages of species with overlapping altitudinal distribution patterns. One of them falls within the lower (~1600-2100 m), and the other within the upper section of the transect (~2300-2600 m) (Fig 3). A cluster analysis

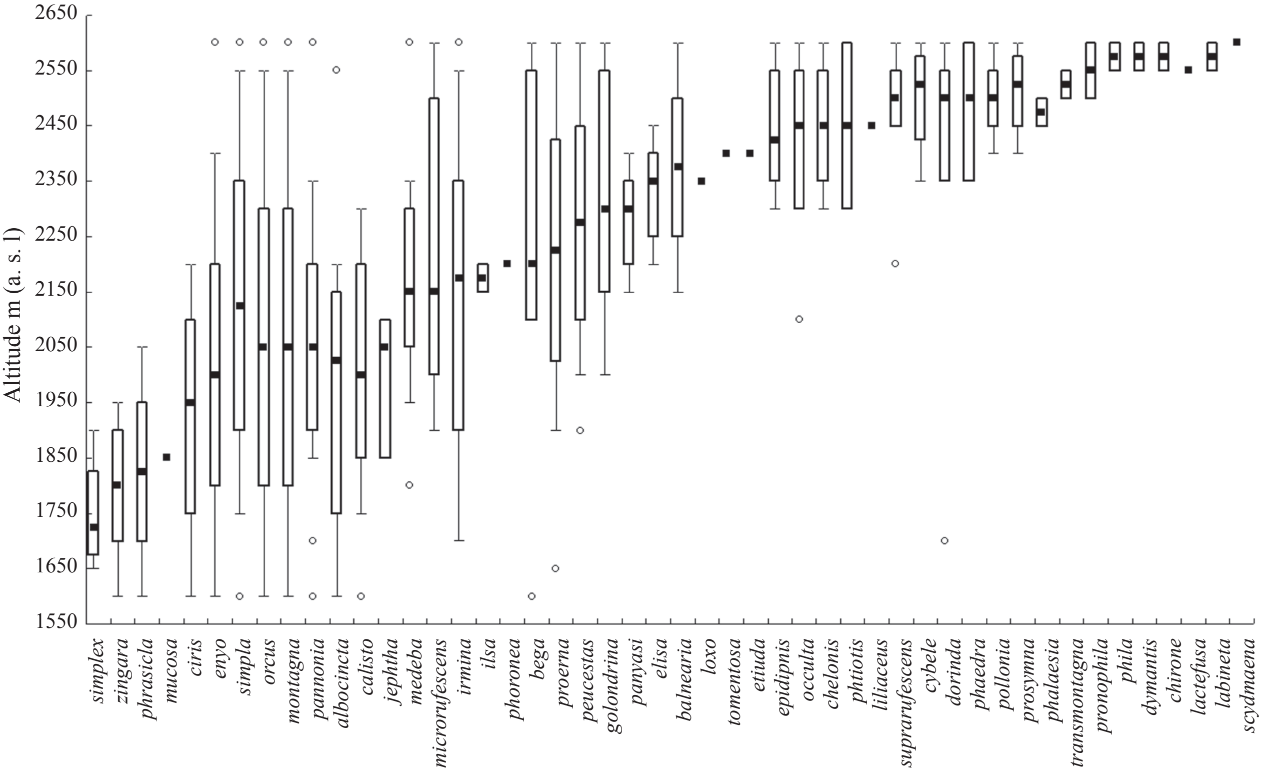


Fig 1 Altitudinal distribution pattern of 48 species collected along the Golondrinas transect. Box and whiskers plot with median, lower and upper quartile, minimum and maximum and outside values of distribution spread.

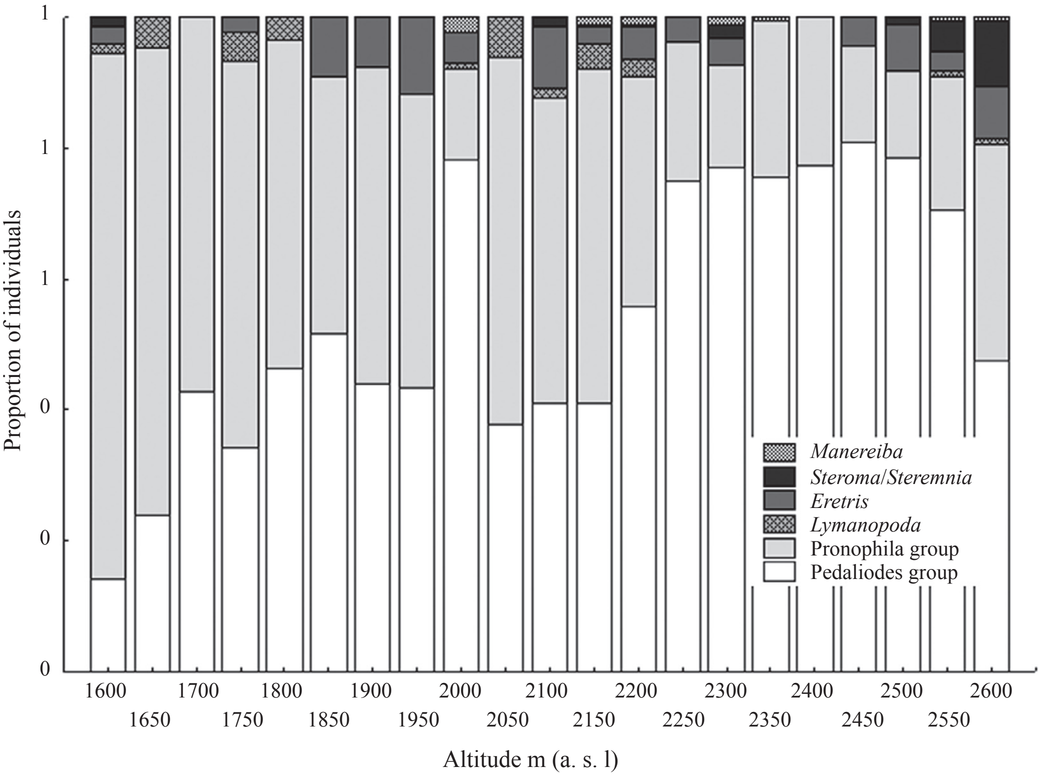


Fig 2 Proportion of individuals belonging to six genera and groups of genera. “Pronophila group” includes the genera: *Corades, Daedalma, Junea, Lasiophila, Mygona, Oxeoschistus, Pronophila, Pseudomaniola* and *Thiemeia*. “Pedaliodes group” includes the genera: *Pedaliodes* and *Panyapedaliodes*.

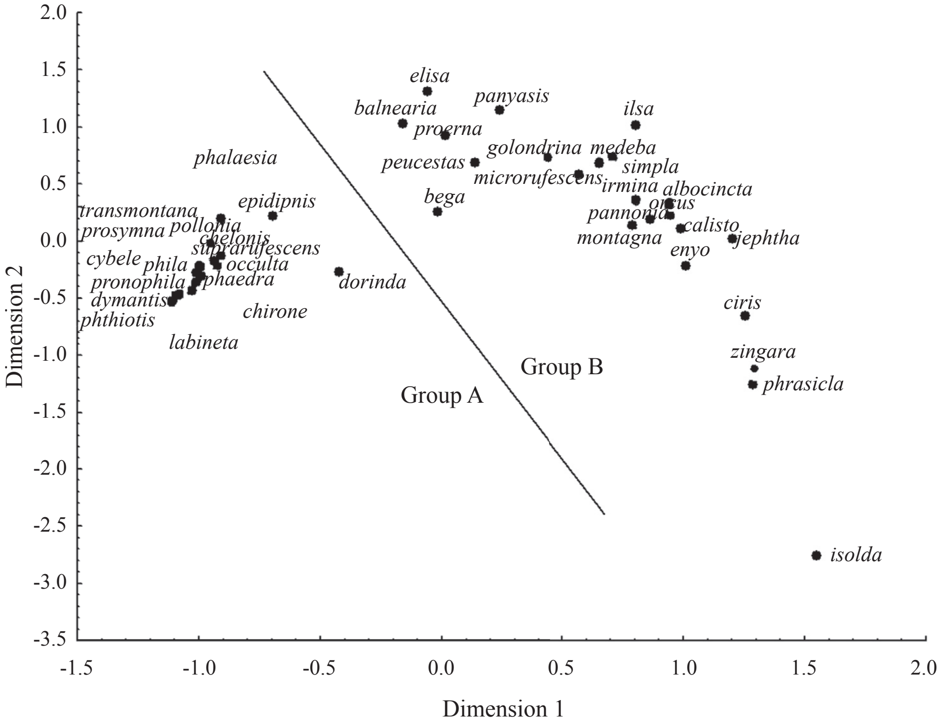


Fig 3 Species correspondence analysis (CA) using the proportion of individuals. Inertia of first axis: 22.7%, inertia of second axis: 15.0% (singletons excluded).

Group A: *Corades chelonis, C. chirone, C. cybele, C. dymantis, Eretis suprarufescens, Junea dorinda, Lasiophila phalaesia, Lasiophila prosymna, Lymanopoda labineta, Panyapedaliodes phila, P. occulta, P. phaedra, P. phthiotis, P. pollonia, P. transmontana, Pronophila epidipnis, Steremnia pronophila*.

Group B: *Corades enyo, C. medeba, C. pannonia, Daedalma elisa, Eretris calisto, E. microrufescens, Lasiophila ciris, Lymanopopda albocincta, Manerebia golondrina, Mygona irmina, Oxeoschistus ilsa, Panyapedaliodes jephtha, P. panyasis, Pedaliodes balnearia, P. montagna, P. peucestas, P. phrasicla, P. proerna, P. simpla, P. zingara, Pronophila orcus, Pseudomaniola ilsa, Steroma bega*.

yielded similar results, showing two well-defined groups corresponding to two elevational assemblages of species (Fig 4). The difference between the two analyses is that four species corresponding with the upper group in CA were grouped as a sister-cluster to the lower group in the cluster analysis. This happened basically because three of these species (*Lasiophila phalaesia* Hewitson, *Pedaliodes pollonia* Adams and *P. transmontana* Pyrcz & Viloria) occured exclusively in the upper section of the transect, whereas the less abundant *J. dorinda* is also represented by one specimen at 1700 m. The Trellis diagram shows a tendency towards a sharper species turnover within the intermediate elevational band (2100-2300 m). It is illustrated by lower Sørensen similarity values between the lower and upper stations, as well as between adjacent stations within this elevational band (C_s: 0.59; 0.65) (Fig 5).

Several closely related or sister-species reported along the transect demonstrated parapatric distributions, understood as adjacent, mutually exclusive or narrowly overlapping elevational zones (Bull 1991). Three pairs, each including a "lower assemblage" and an "upper assemblage" species, were particularly well documented: *Pronophila orcus* and *Pr. epidipnis* Thieme; *Eretris microrufescens* Pyrcz & Willmott and *E. suprarufescens* Pyrcz & Willmott; *Pedaliodes peucestas* (Hewitson) and *P. phaedra* (Hewitson). The overlapping zone between the lower and upper parapatric species corresponded generally with the intermediate band of altitude (2000-2300 m). In the case of *Pronophila*, it extends over 2300-2600 m, but *Pr. epidipnis* is relatively more abundant than its congener above 2450 m. The Mann-Whitney U-Test showed that in two cases (*Pronophila, Pedaliodes*) the observed distributions were effectively parapatric, and in one case (*Eretris*) distributions were not significantly different. The latter result seems an artefact of the insufficient number of records though (Fig 6).

Abundance, richness and diversity. A total of 56 species of Pronophilina were found in the Golondrinas Reserve. Added to the 48 species trapped on the transect, eight species were collected by hand with entomological nets at lower (one below 1600 m) and higher (seven above 2600 m) elevations.

Maximum species richness (29 species) is recorded at the top elevation of the transect at 2600 m, and the second highest value (25 species) immediately below, at 2550 m. Other elevations present neatly inferior values, 8-13 species at 1600-2050 m, and 10-21 species at 2100-2500 m. Species-richness was positively correlated with altitude ($r = 0.73$; $P < 0.002$). The highest value of the Shannon index ($H = 2.92$) corresponded to the highest elevation of the transect, at 2600

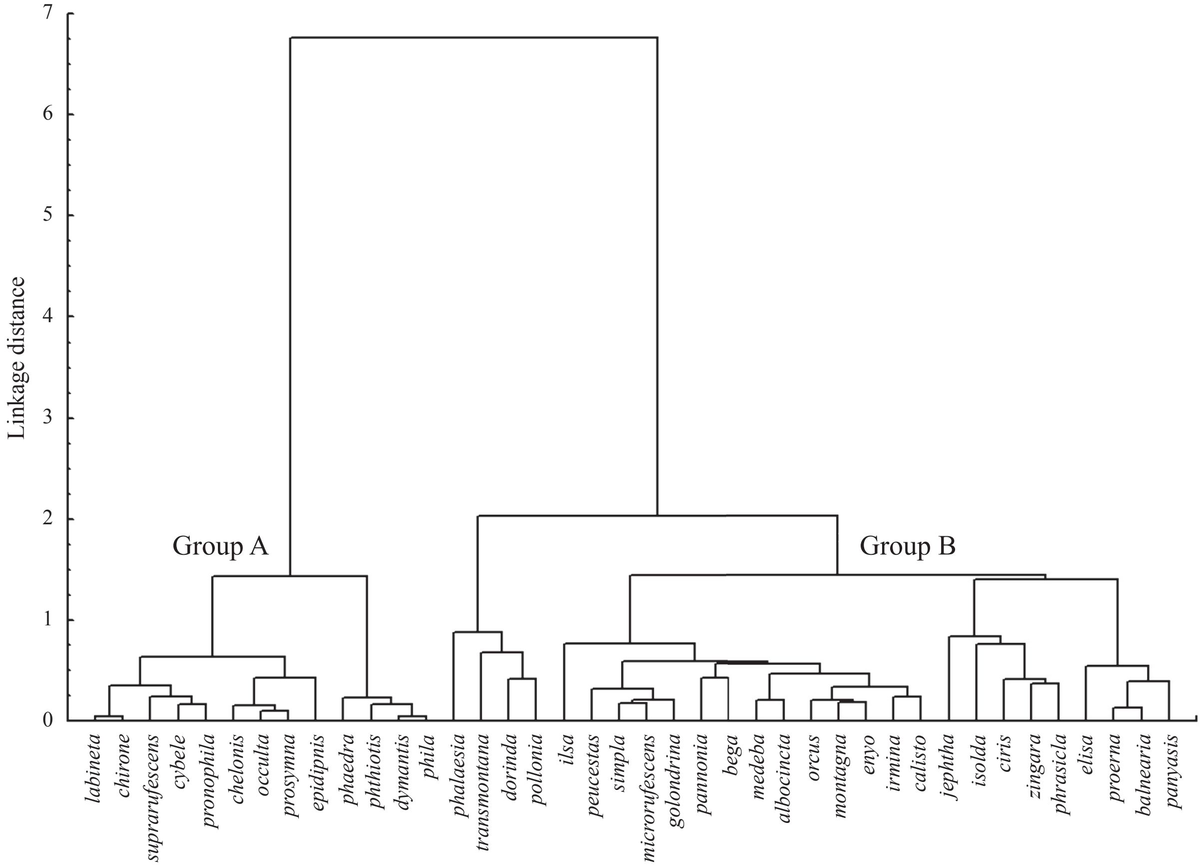


Fig 4 Cluster analysis of the proportions of species (singletons excluded) using the proportion of individuals. Euclidean distances, grouping by Ward's method.

m. The lowest value was observed at the lowest station, 1600 m (H = 1.51). The highest value of Fisher alpha (8.86) was also recorded at the highest station and the lowest (3.03) at 1700 m. Both indices were positively correlated with altitude (Shannon: 0.61; $P < 0.003$; Fisher alpha: 0.66; $P < 0.001$) and with each other ($r = 0.73$; $P < 0.000$).

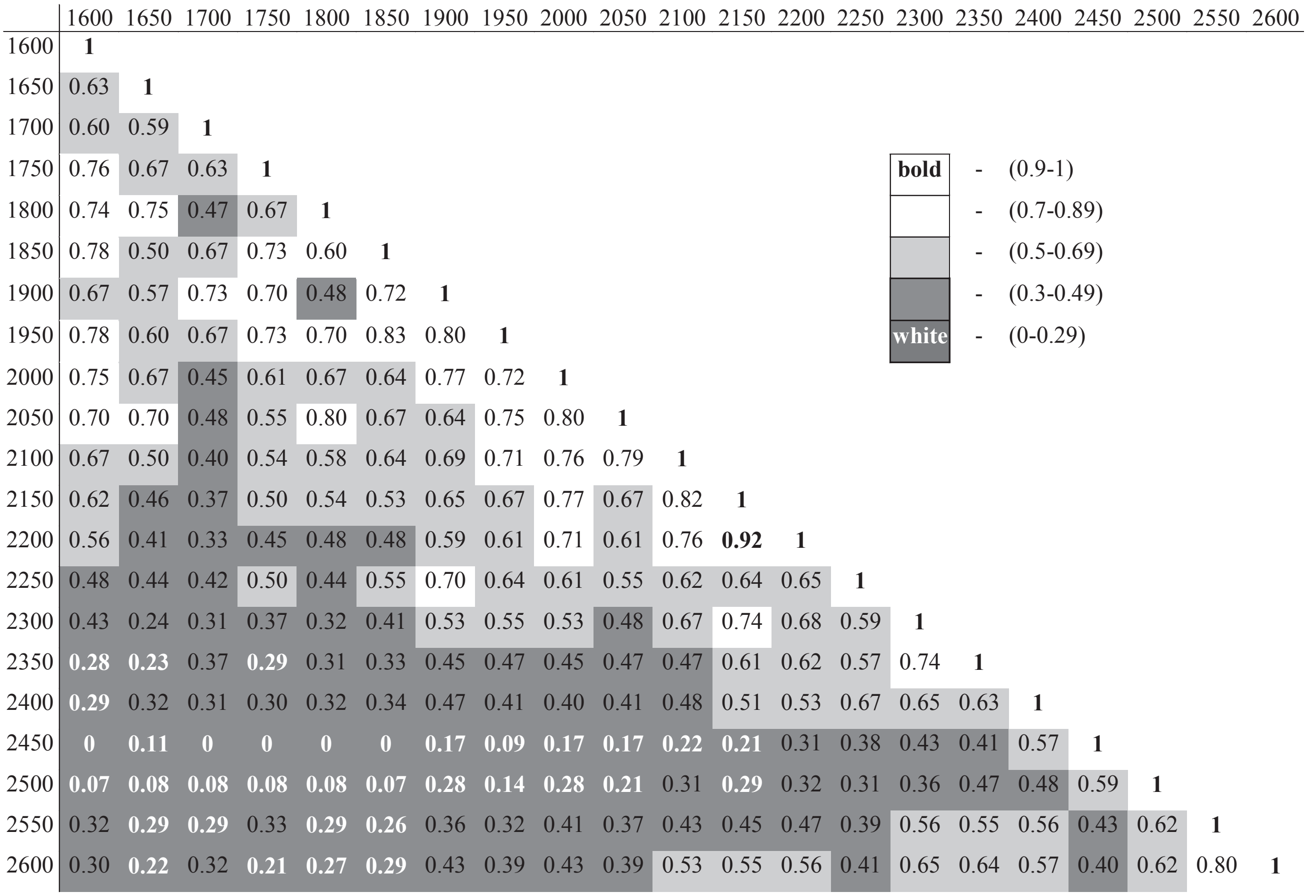
The Berger-Parker dominance index basically yielded opposite results, with the highest value (0.49) at 2350 m (due to the very high relative abundance of *Pedaliodes proerna* (Hewitson) compared to other species at this elevation), and lowest at the highest elevations of the transect at 2550-2600 m (0.01). The dominance index did not indicate a significant correlation with altitude (-0.09 $P < 0.68$ ns) (Table 1).

Maximum abundance on the transect was recorded at 2200 m. The second marked abundance peak corresponded to the top elevation of the transect at 2600 m (314 individuals). Generally, high abundance was maintained throughout the upper half of the transect at 2150-2600 m. Two neatly inferior values were recorded at 2250 m and 2450 m, which was probably due to the less favourable position of the traps. Abundance was found to be significantly positively correlated with the altitude ($r = 0.61$; $P > 0.004$). Abundance depends on local conditions in sites where traps are set, and especially on the presence or absence of dense stands of host plants and the neighbourhood of key areas enhancing adult activity, such as forest clearings or tall trees.

Discussion

Diversity in the Pronophilina was positively correlated with altitude and increased from lower to higher elevations. This is congruent with the results of other three studies in widely dispersed Andean transects in Colombia (Tambito), Venezuela (Monte Zerpa) and Peru (Molinopampa) (Pyrcz & Wojtusiak 1999, 2002, Pyrcz 2004), despite important differences in sample size, faunal composition and altitudes covered of these four transects, only the Molinopampa and Monte Zerpa were extended to the timberline. They showed maximum diversity values at 2600-2800 m (Monte Zerpa, Molinopampa), and revealed a sharp decrease of diversity at the cloud forest – páramo grassland ecotone at 3050-3250 m. Transects in Golondrinas and Tambito culminate in mid- to high elevation cloud forest, and indicate maximum diversity values at the highest sampled elevation.

The lack of data from higher elevations in Golondrinas does not allow us to speculate whether diversity still increases above 2600 m. We know however, from additional sampling carried out above Golondrinas (in 2003), that species richness sharply falls at timberline at 3100-3200 m. A decline of diversity at timberline was also observed by Brehm *et al* (2003b) for the Andean Larentiinae moths (Geometridae). This pattern is linked with the presence of a sharp ecological threshold, corresponding with climate change (lower temperature and humidity, strong wind), vegetation structure



	1600	1650	1700	1750	1800	1850	1900	1950	2000	2050	2100	2150	2200	2250	2300	2350	2400	2450	2500	2550	2600
1600	**1**																				
1650	0.63	**1**																			
1700	0.60	0.59	**1**																		
1750	0.76	0.67	0.63	**1**																	
1800	0.74	0.75	0.47	0.67	**1**																
1850	0.78	0.50	0.67	0.73	0.60	**1**															
1900	0.67	0.57	0.73	0.70	0.48	0.72	**1**														
1950	0.78	0.60	0.67	0.73	0.70	0.83	0.80	**1**													
2000	0.75	0.67	0.45	0.61	0.67	0.64	0.77	0.72	**1**												
2050	0.70	0.70	0.48	0.55	0.80	0.67	0.64	0.75	0.80	**1**											
2100	0.67	0.50	0.40	0.54	0.58	0.64	0.69	0.71	0.76	0.79	**1**										
2150	0.62	0.46	0.37	0.50	0.54	0.53	0.65	0.67	0.77	0.67	0.82	**1**									
2200	0.56	0.41	0.33	0.45	0.48	0.48	0.59	0.61	0.71	0.61	0.76	**0.92**	**1**								
2250	0.48	0.44	0.42	0.50	0.44	0.55	0.70	0.64	0.61	0.55	0.62	0.64	0.65	**1**							
2300	0.43	0.24	0.31	0.37	0.32	0.41	0.53	0.55	0.53	0.48	0.67	0.74	0.68	0.59	**1**						
2350	**0.28**	**0.23**	0.37	**0.29**	0.31	0.33	0.45	0.47	0.45	0.47	0.47	0.61	0.62	0.57	0.74	**1**					
2400	**0.29**	0.32	0.31	0.30	0.32	0.34	0.47	0.41	0.40	0.41	0.48	0.51	0.53	0.67	0.65	0.63	**1**				
2450	**0**	**0.11**	**0**	**0**	**0**	**0**	**0.17**	**0.09**	**0.17**	**0.17**	**0.22**	**0.21**	0.31	0.38	0.43	0.41	0.57	**1**			
2500	**0.07**	**0.08**	**0.08**	**0.08**	**0.08**	**0.07**	**0.28**	**0.14**	**0.28**	**0.21**	0.31	**0.29**	0.32	0.31	0.36	0.47	0.48	0.59	**1**		
2550	0.32	**0.29**	**0.29**	0.33	**0.29**	**0.26**	0.36	0.32	0.41	0.37	0.43	0.45	0.47	0.39	0.56	0.55	0.56	0.43	0.62	**1**	
2600	0.30	**0.22**	0.32	**0.21**	**0.27**	**0.29**	0.43	0.39	0.43	0.39	0.53	0.55	0.56	0.41	0.65	0.64	0.57	0.40	0.62	0.80	**1**

bold - (0.9-1)
□ - (0.7-0.89)
▒ - (0.5-0.69)
▓ - (0.3-0.49)
white - (0-0.29)

Fig 5 Trellis diagram. Comparison of Sørensen similarity coefficients of all altitudinal stations.

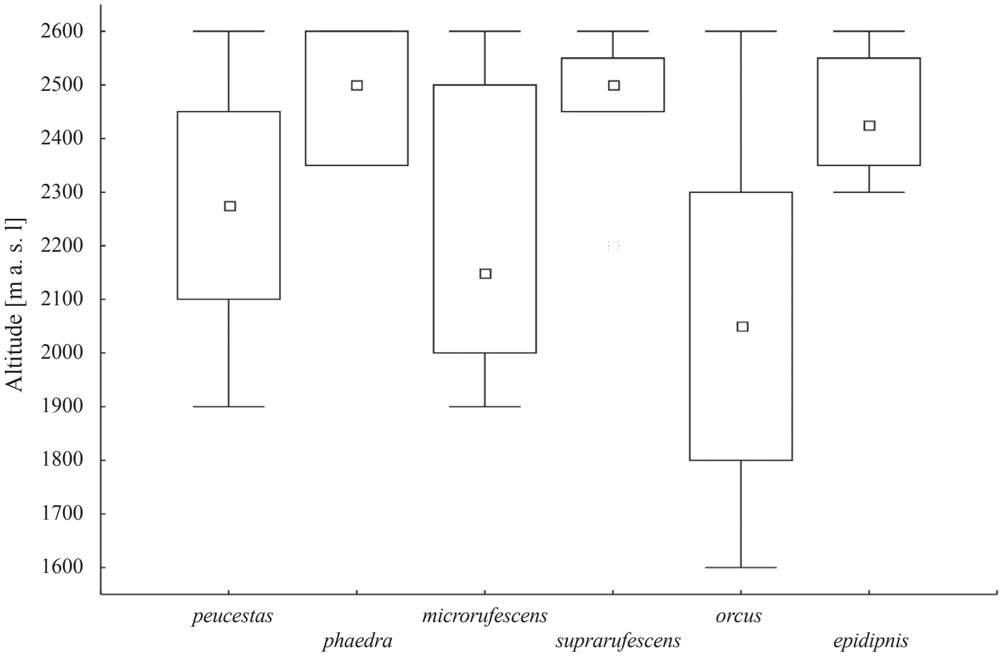


Fig 6 Altitudinal spreads of three pairs of parapatric species. Box and whisker plot with median, lower and upper quartile, minimum and maximum of altitudinal range. *Pronophila orcus* - *Pronophila epidipnis* (Mann-Whitney *U*-test = 39; P < 0.000)*;* *Eretris microrufescens* - *Eretris suprarufescens* (Mann-Whitney *U*-test = 207; P > 0.73, not significantly different); *Pedaliodes peucestas* - *Pedaliodes phaedra* (Mann-Whitney *U*-test = 92.5; P < 0.001).

Table 1 Abundance, species richness (S), Shannon diversity index (H), Fisher alpha and Berger-Parker dominance index along the Golondrinas transect.

	1600 m	1650 m	1700 m	1750 m	1800 m	1850 m	1900 m	1950 m	2000 m	2050 m	2100 m	2150 m	2200 m	2250 m	2300 m	2350 m	2400 m	2450 m	2500 m	2550 m	2600 m
Abundance	71	21	56	44	28	66	66	60	128	96	73	263	314	52	96	197	154	47	98	172	225
Species richness [S]	11	8	9	10	8	12	13	12	13	12	16	18	21	10	17	18	17	11	16	25	29
Shannon index [H]	1.51	1.63	1.55	1.91	1.66	2.04	2.19	2.23	1.91	1.88	2.30	2.08	2.30	2.05	2.28	1.76	2.04	1.93	2.03	2.58	2.92
Fisher alpha	3.64	4.72	3.03	4.04	3.74	4.29	4.85	4.51	3.61	3.62	6.33	4.38	5.08	3.68	6.00	4.83	4.88	4.52	5.43	8.04	8.86
Berger-Parker index	0.08	0.14	0.25	0.14	0.25	0.35	0.18	0.15	0.27	0.21	0.11	0.20	0.17	0.31	0.05	0.49	0.39	0.30	0.08	0.01	0.01

and lower plant diversity above the tree line (Monasterio 1980, Veillon 1989).

Higher diversity of Pronophilina at high elevations cannot be directly correlated to resource availability, the most important of which is the availability of larval host plants in case of specialized phytophagous insects. The larvae of Pronophilina feed on montane bamboos, mostly on *Chusquea* (Schultze 1929, DeVries 1987, Pelz 1997, Heredia & Viloria 2004). This is the most diverse genus of neotropical bamboo with over 250 species occurring in the Andes from ca. 800 m to nearly 4000 m (Judziewicz *et al* 1999), thus within the same altitudinal range as covered by the subtribe Pronophilina. Although their maximum diversity has been defined as falling within the altitude band 2000-3200 m (Soderstrom *et al* 1988), roughly corresponding with the elevation band at which Pronophilina reach their maximum diversity, the knowledge of species-level systematics of *Chusquea* remains insufficient and does not allow establishing precise elevational diversity patterns. Also, the species of Pronophilina, similarly to other grass feeding Lepidoptera, are mostly oligophagous (breeding experiments conducted with *Junea* and *Pedaliodes* (Pyrcz & Greeney unpubl.) and can use a vast array of bamboos. Therefore, the presence or absence of a particular *Chusquea* species cannot be generally a limiting factor. Moreover, a possible correlation of *Chusquea* and Pronophilina diversity is not always supported by biogeographical data. For example, the Brazilian Atlantic premontane and montane forests ecologically similar to the Andean cloud forests, are extremely bamboo-rich with at least 40 species of *Chusquea* (Judziewicz *et al* 1999), but their Pronophilina fauna accounts for less than 10 known species (Lamas *et al* 2004).

The increase in Lepidoptera diversity at high elevations has been correlated with the lower diversity of predators and parasites. Brehm *et al* (2003b), in a study of Geometridae in Ecuador, pointed out the lower diversity of bats, insectivorous birds and ants at higher elevations as a possible contributing factor to the higher diversity of these insects. Indeed, there is a sharp decrease of ant diversity with altitude, and in the tropical forests they are restricted to altitudes below 2300 m (Brown 1973, Brühl *et al* 1999, Fagua 1999). Ants are known to be important predators and a factor regulating population density of many invertebrates (Hölldobler & Wilson 1990). It is therefore not unlikely that their virtual absence from high elevation Andean forests may have a positive effect on Pronophilina populations. Yet, the interactions between ants and pronophilines larvae have not been studied, and this apparent correlation may be coincidental. On the other hand, parasitoids, ruled out by Brehm *et al* (2003b), may play an important role in population density regulation. Over 40% of Pronophilina larvae were found to be infected with parasitoids in mid-elevation cloud forest (Ecuador, Yanayacu). Also, abundant *Acaria* ectoparasites were observed on the bodies and wings of Pronophilina in particularly humid environments (Greeney pers. comm.). Both are presumably important limiting factors which have to be taken into consideration. Nevertheless, we must emphasize that all these restricting factors can limit abundance, but do not have a visible influence on species richness. Ants, bats and ectoparasites are generally not species-specific, thus exert similar pressure on the entire Pronophilina species assemblages.

Diversity peaks at some high altitudes can be explained by the intrinsic characteristics of the Pronophilina community. High species-richness generally falls within the overlapping zones of species belonging to lower and upper faunal assemblages. In some cases, high diversity index within this zone may be somewhat attenuated by the lower abundance effect. It is clear that species occurring within the overlapping zone are at the extremes of their altitudinal ranges, not at their optimum. Our sampling in Golondrinas uncovers such a pattern. Species CA and cluster analysis demonstrated that the Pronophilina reported along the transect falls into two assemblages of species occurring within similar bands of altitude, overlapping at 2100-2300 m (Table 1). The existence of such an overlapping zone can be detected by the higher turnover, as shown by Sørensen similarity coefficients of adjacent altitudinal stations. The presence of pairs of closely related species replacing each other in altitude, which are frequently important components of lower and upper faunal assemblages, also give supports to the existence of this overlapping zone. Similar results have been observed in Colombia (Pyrcz & Wojtusiak 1999), although supported by rather weak quantitative data, and particularly in Venezuela (Pyrcz & Wojtusiak 2002).

Our conclusions on this point differ somewhat from those of Brehm & Fiedler (2004) on altitudinal distributions of Geometridae moths in southern Ecuador. They stated that their results did not indicate the presence of distinct categories of communities, such as "lower montane" or "cloud forest" assemblages, but rather show a smooth transition in which particular species are steadily replacing each other. We believe this conclusion was driven by the accumulation of data coming from species-rich taxonomical/ecological groups and the insufficient knowledge on taxonomy at the species level. This is particularly important to enable the morphological discrimination of closely related parapatric species, which requires extensive comparative material, thorough taxonomical study and fine tuned altitudinal data.

Another factor contributing with the increasing diversity of Pronophilina with altitude is the higher speciation rate at high elevations, particularly near timberline, as indicated by the high ratio of neoendemics at 3000-3200 m, which are "young species" usually belonging to groups of closely related allopatric species (Adams 1985, Pyrcz 2004). It was postulated that the strong divergent selection for local adaptations at forest- páramo ecotone decreases the waiting time for speciation (Smith *et al* 1997, Gavrilets *et al* 2000, Schilthuizen 2000). However, extinction rate at upper forest limit is also very high due to environmental instability, as this zone is the most affected by rapid climate changes and local disturbance. Therefore, we may predict that the maximum diversity would not be registered at the forest- páramo ecotone but at some lower elevation, within an elevation range where speciation rate (influenced by the proximity of the ecotone) is still high, but extinction rate is lower (due to higher ecological stability) than at timberline. Adams (1985), based on thorough field studies in the Colombian and Venezuelan Andes, estimated (without resorting to the method of quantitative altitudinal sampling) the maximum diversity of Pronophilina at 2800 m, and all the above mentioned studies indicated that the maximum diversity in this group of butterflies falls at 2600-2850 m. This is some 400-500 m below the upper limit of cloud forests, which agrees with the above prediction of higher speciation rate at higher elevations.

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Online Supporting Material 1

Pyrcz T W, Wojtusiak J, Garlacz R (2009) Diversity and distribution patterns of Pronophilina butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an altitudinal transect in North-Western Ecuador. Neotrop Entomol 38(6): 716-726.

Data matrix

Species	1600 m	1650 m	1700 m	1750 m	1800 m	1850 m	1900 m	1950 m	2000 m	2050 m	2100 m	2150 m	2200 m	2250 m	2300 m	2350 m	2400 m	2450 m	2500 m	2550 m	2600 m	Total indiv.
Corades chelonis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	4	1	2	12	19	40
Corades chirone	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	7	11
Corades cybele	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	2	7	11
Corades dymantis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	10	11
Corades enyo	3	3	4	-	1	4	4	4	3	2	1	6	4	1	-	-	1	-	-	-	1	42
Corades lactefusa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Corades liliaceus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
Corades medeba	-	-	-	-	1	-	-	1	-	4	2	13	7	-	3	4	-	-	-	-	1	36
Corades pannonia	15	-	1	-	-	2	1	1	3	7	1	5	4	-	1	5	-	-	-	-	3	49
Daedalma elisa	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	1	3	3	-	-	-	11
Eretris calisto	2	-	-	1	-	6	4	7	3	-	5	3	7	2	4	-	-	-	-	-	-	44
Eretris microrufescens	-	-	-	-	-	-	1	-	3	-	2	4	6	-	-	-	-	-	2	-	1	19
Eretis suprarufescens	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	2	5	5	17	31
Junea dorinda	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1	1	5
Lasiophila ciris	1	1	-	4	1	5	-	10	2	1	2	1	3	-	-	-	-	-	-	-	-	31
Lasiophila phalaesia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	5	-	-	6
Lasiophila prosymna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4	9	10	24
Lymanopoda albocincta	1	1	-	2	1	-	-	-	1	6	1	10	9	-	-	-	-	-	-	1	-	33
Lymanopoda labineta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	3
Manerebia golondrina	-	-	-	-	-	-	-	-	3	-	-	3	4	-	1	1	-	-	-	1	1	14
Mygona irmina	-	-	1	1	-	11	16	6	-	-	9	17	34	4	2	5	6	-	-	2	2	116
Oxeoschistus isolda	-	1	1	6	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
Panyapedaliodes jephtha	-	-	-	-	-	1	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	4
Panyapedaliodes muscosa	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Panyapedaliodespanyasis	-	-	-	-	-	-	-	-	-	-	-	1	1	-	2	1	2	-	-	-	-	7
Panyapedaliodes phila	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	7	8
Panyapedaliodes tomentosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Pedaliodes balnearia	-	-	-	-	-	-	-	-	-	-	-	2	1	5	10	28	26	8	1	7	2	90
Pedaliodes etiuda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
Pedaliodes montagna	6	3	14	6	7	23	12	9	34	20	8	52	52	5	5	2	1	-	-	2	1	262
Pedaliodes occulta	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	7	4	8	36	39	96
Pedaliodes peucestas	-	-	-	-	-	-	1	-	31	3	2	3	33	8	20	15	13	1	12	19	9	170
Pedaliodes phaedra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	9	11
Pedaliodes phrasicla	1	1	9	7	4	6	4	2	2	3	-	-	-	-	-	-	-	-	-	1	-	40
Pedaliodes phrasiclea	2	-	1	1	-	1	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	10

Continue

Data matrix Continuation

Species	1600 m	1650 m	1700 m	1750 m	1800 m	1850 m	1900 m	1950 m	2000 m	2050 m	2100 m	2150 m	2200 m	2250 m	2300 m	2350 m	2400 m	2450 m	2500 m	2550 m	2600 m	Total indiv.
Pedaliodes phthiotis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	13	14
Pedaliodes pollonia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	11	43	31	12	98
Pedaliodes proerna	-	1	-	-	-	-	2	2	2	1	8	18	20	5	23	97	60	14	5	14	9	281
Pedaliodes scydmaena	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Pedaliodes simpla	1	-	-	1	2	2	7	11	31	7	10	32	68	16	12	5	7	-	5	4	5	226
Pedaliodes transmontana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	7	-	9
Pronophila epidipnis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	4	1	-	2	9	19
Pronophila orcus	38	10	24	15	11	4	10	5	10	39	19	91	54	3	7	26	16	-	-	1	4	387
Pseudomaniola ilsa	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-	-	**3**
Pseudomaniola loxo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1
Steremnia pronophila	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	6	21	28
Steroma bega	1	-	-	-	-	-	-	-	-	-	1	1	1	-	2	-	-	-	-	2	2	10
Thiemeia phoronea	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1