# Climate warming effects in the tropical Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador

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**Abstract.** 1. In order to assess the impact of global warming on the biodiversity of the tropical high Andean páramo ecosystem, we compared historical and recent surveys of ground beetle communities along elevational gradients of the Pichincha volcano (Northern Ecuador). The studied datasets date to 1880, 1985/86 and 2013/15.

2. From 1880 to 1985, the bottom range of at least one stenotopic and wingless high-altitude species, *Dyscolus diopsis*, has shifted approximately 300 m upward, with the resulting area reduction of more than 90% from $>12$ km$^2$ to $<1$ km$^2$, which highlights the probability of future local extinctions on the Pichincha as well as on other mountains of Ecuador.

3. Over a shorter period of time, the comparison of the 1985/86 and 2013/14 datasets indicates that the lower limit of the superpáramo ground beetle community has shifted upwards from circa 4300 m to circa 4400 m. Different individual responses are recorded among the species. Some of them did not experience any significant change, whereas the upper limit of one of the grassland generalists has shifted upwards at least 400 m in 28 years.

4. These results suggest that the response to global warming varies from one species to the other, depending on their degree of specialisation and tolerance. They call for the implementation of a monitoring programme that would use carabid assemblages as an indicator of the impact of climate change on the páramo ecosystem, in combination with other proxies.

**Key words.** Andes, carabids, climate change, elevational range shift, endemic species, extinction risk, páramo, tropical biodiversity.

## Introduction

Climate simulations for the northern tropical Andes indicate that warming will be amplified with elevation, reaching up to +4 °C at the highest elevations by the end of the 21st century (Diaz *et al.*, 2014). This change is expected to have a negative impact on the biodiversity of the high Andean páramo ecosystem (Buytaert *et al.*,

2011). Higher temperatures and increased drought lead to an upward shift of stenotopic organisms that depend on low temperatures, and therefore to the fragmentation and progressive reduction in their habitat area (La Sorte & Jetz, 2010), which will eventually cause the inevitable extinction of any endemic species that is restricted to summit areas and has a low dispersion ability (Raxworthy *et al.*, 2008; Wilson & Gutiérrez, 2012), especially in the case of tropical species that have low physiological tolerance ranges and are therefore vulnerable to relatively small climate changes (Colwell *et al.*, 2008).

The elevational shift that has been predicted using climate models has received experimental confirmation

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worldwide for several organisms (Chen *et al.*, 2011a). A growing number of studies are based on a comparison between historical and recent surveys of insect communities along elevational gradients. Most of them concern European mountains (Bässler *et al.*, 2013; Menéndez *et al.*, 2014; Pizzolotto *et al.*, 2014). In the tropics, a significant upward shift of the elevational range of Geometrid moths between 1965 and 2007 has been demonstrated in Borneo mountains (Chen *et al.*, 2009, 2011b). No comparable work has been achieved so far in the Andean region (Larsen *et al.*, 2011), except for a study that uses the indirect evidence of old larval faeces to assess at circa 200 m over 20 years the upslope shift of Lucanid beetles in Southern Ecuador (Onore & Bartolozzi, 2008). More generally, publications dedicated to insect response to climate change are 10 times less numerous in South America than in Europe (Andrew *et al.*, 2013). The aim of this study is to begin to fill this gap, by comparing two sets of historical records (dating to 1880 and to 1985/86) with recent surveys (2013–2015) of ground beetle (Coleoptera, Carabidae) assemblages along an elevational gradient in Ecuadorian Andes.

The beetle family Carabidae was selected for several reasons. Ground beetles have been for decades a prime target for environmental impact studies, due to their abundance, diversity, sensitivity to environmental changes, and easy sampling by means of pitfall traps and hand catches (Kotze *et al.*, 2011). At high elevations in tropical Andes, they are one of the most important components of the macroinvertebrate assemblages. The 204 species that have been collected so far above 3500 m in Ecuadorian páramos have been subject of a systematic and ecological revision (Moret, 2005, 2009). They are present year round in every habitat type of the páramo ecosystem, generally in numerous and diverse assemblages.

Taking advantage of the existence of precisely documented samplings made in Ecuador in 1880, at the end of the Little Ice Age – probably a unique circumstance in tropical alpine environments – two hypotheses will be tested: (i) that some species experienced an upslope shift of their elevational range due to the ongoing climate change, and (ii) that the area reduction that affects suitable cold and wet environments at high elevations leads to a decrease in species diversity.

## Materials and methods

The study area ranges from 3900 to 4780 m a.s.l. on the south and southeast slopes of the Pichincha mountain, situated near Quito in the Western Cordillera of Ecuadorian Andes (0°10′16″S 78°35′53″W). Though forming a single orographic unit, it is a composite volcanic edifice consisting of an older Quaternary stratovolcano at the east, now extinct and largely dissected by erosion (Rucu Pichincha, 4698 m), and a younger one, still active, at the west (Guagua Pichincha, 4784 m). All this area belongs to the páramo ecosystem (Luteyn, 1999). According to its

vegetation structure, the páramo has been divided into several zones. Grass páramo, dominated by bunch- or tussock-forming grasses, occurs on the Pichincha from about 3500 m to 4250 / 4300 m. From 4300 m upwards, the superpáramo is characterised by sclerophyllous shrubs, cushion plants and shortstem grasses, with a vegetation cover that gets increasingly poor and patchy above 4400 m in the so-called upper superpáramo or desert superpáramo (Sklenár & Ramsay, 2001; Sklenár & Balslev, 2005). On the Pichincha, the superpáramo area extends up to 11.6 km$^2$. The upper superpáramo area, above 4400 m, is divided into two separate patches around the Rucu peak (1.8 km$^2$) and the Guagua peak (3.8 km$^2$). As a whole, the páramo area of Guagua and Rucu Pichincha forms a single ecological unit, separated from other páramo areas of the Western Cordillera, and can therefore be considered as a tropical alpine island (Anthelme *et al.*, 2014).

The oldest known entomological collections in the Pichincha area were made on the Guagua peak by the pioneer alpinist Edward Whymper (1840–1911), during his expedition to Ecuador in 1879/80 (Whymper, 1892). He registered with extreme care the date, place and elevation of every botanical or zoological sample he made. The accuracy of his altitudinal measurements, made with a mercury barometer, has been corroborated in every station that could be positioned on a modern topographic map. The specimens found by Whymper in any given place were not mixed with others, as was common practice at that time, but kept in separate vials. After his return to England, mounted specimens received printed labels – or mixed printed and hand-written labels – that bear the name of the mountain, a topographical reference such as 'first camp' or 'summit ridge', and the precise altitude. Only part of this information has been reproduced in the zoological appendix of his publication (Bates, 1891). The complete geographical information was copied in 2013 by the first author (PM) from the original labels of the specimens currently kept in Paris in the entomological collection of the Muséum National d'Histoire Naturelle (MNHN). Whymper's collections on the Guagua Pichincha were made from 21 to 23 of March 1880, at three different sites (Fig. 1).

W1: 14 007 feet [=4269 m] near his first camp 'midway between the two peaks of Pichincha'. Current environment: transitional zone between grass páramo and superpáramo, vegetation cover 90%.

W2: 14 992 feet [=4570 m] near his second camp at the foot of the Guagua summit ridge. Current environment: upper superpáramo, vegetation cover 60%.

W3: from 15 500 feet [=4724 m] 'near summit' to 15 600 feet [=4755 m] on the 'middle peak' of the summit. Current environment: upper superpáramo, vegetation cover less than 10%.

The position of the first two sites is given in Whymper's publication (1892: 208–210), whereas the altitudes of W3 are only known from the original labels of historical specimens preserved in MNHN Paris. The sampling method
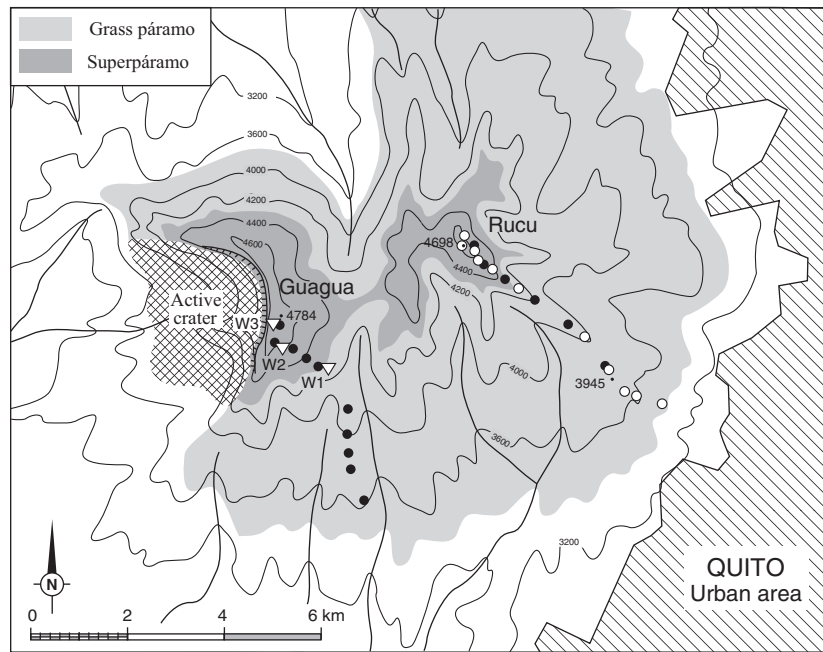
**Fig. 1.** Map of the Pichincha volcano with localisation of the sampling sites. White triangles: 1880 and 2015; black circles: 1985/86; white circles: 2013/14.

was not fully described by Whymper. Most beetles were probably collected by hand in the immediate surroundings of bivouac sites. At the highest elevations, they 'were discovered in course of breaking out rock specimens, and were disinterred from amongst stones which were cemented together with ice' (Whymper's preface in Bates, 1891: viii).

These three sites were resampled twice in 2015 by AB, MAA and PM, in March (same month as in 1880) and in September: W1 at 4270–4280 m in the area of Whymper's first camp (S 0°11′04.7″/W 78°35′21.1″), W2 at 4560–4570 m on the very site of his second camp (S 0°10′42.2″/W 78°35′48.2″), and W3 at 4760–4768 m on the southern peak of Guagua Pichincha, near Whymper's 'middle peak' (S 0°10′34.7″/W 78°35′59.7″). Ground beetles were searched beneath stones and cushion plants, by three persons during 1 h in each spot. Additional material from W2 was collected in 1996 by Augusto Vigna Taglianti (Dipartimento di Biologia, Sapienza Università di Roma, Italy).

The second set of old samplings dates to 1985/86. PM made a complete survey of the Guagua Pichincha Southeast transect, in March 1985 from 3850 to 4500 m and in June 1986 from 4400 to 4700 m, which represents a sampling effort of approximately 12 h in total. He also made a partial survey of the Rucu Pichincha East transect during 4 h in August 1985, from 3900 to 4600. The average distance between these two transects is 4.5 km (Fig. 1). They have the same south-east to east exposure and similar climatic conditions. No differences were observed in the plant zonation, though subject to confirmation by a botanical survey. The sampling method consisted of active

hand searching and was performed by day, mostly beneath stones and cushion plants.

A complete resurvey of the Rucu Pichincha East transect, from Quito cable car station to the summit of Rucu, was conducted by MAA and AB from January to July 2013 and in July 2014, on 10 sampling sites situated at 3305, 3653, 3887, 3979, 4210, 4302, 4383, 4441, 4605 and 4708 m. The total sampling effort amounts to 9 days, with an average number of three collectors working together during 4 h per day. The sampling method was based on intensive hand searching beneath stones and cushion plants. In the grass páramo areas where stones or other natural shelters are much rarer than in the superpáramo, artificial shelters consisting of logs and stones were disposed and periodically surveyed.

Identifications were made to the species level, following the taxonomic arrangement proposed by Moret (2005). From the 10 genera that have been collected so far in the Pichincha páramo area, only four are treated in this study: *Dyscolus*, *Blennidus*, *Dercylus* and *Pelmatellus*. Three other genera (*Bembidion*, *Lebia* and *Oxytrechus*) were excluded considering their small body size (total length under 5 mm) that makes them likely to be significantly underrepresented when the collections only rely on active search by hand. The last three (*Incagonum*, *Glyptolenoides* and *Sericoda*) were discarded because they were registered only once in the studied area, and only at the lower elevations of the grass páramo.

A total of 1301 carabid beetles of the above-mentioned genera were studied (Table 1 and supplementary Table S1). Due to the heterogeneity of the available

**Table 1.** Number of individuals of the genera *Dyscolus*, *Blennidus* and *Dercylus* collected at three sample sites on the Guagua Pichincha, in 1880, 1996 and 2015.

| Genus | Species | W1 4270 m | | W2 4560/4570 m | | | | W3 4720/4760 m | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1880 | 2015 | 1880 | 1996 | 2015 May | 2015 September | 1880 | 2015 May | 2015 September |
| *Dyscolus* | *alpinus* | | 8 | | | | | | | |
| | *denigratus* | | 3 | | | | | | | |
| | *verecundus* | | 1 | | | | | | | 1 |
| | *orthomus* | | | | 29 | 98 | 20 | | | |
| | *megacephalus* | | | | 18 | 37 | 20 | 4 | | |
| | *oopteroides* | | | 3 | 155 | 100 | 72 | | 17 | 3 |
| | *rotundiceps* | | | | | 14 | 2 | | | |
| | *diopsis* | 2 | | 3 | | 3 | | 3 | 15 | 15 |
| *Blennidus* | *mucronatus* | | 3 | | 40 | 38 | 27 | | 3 | 3 |
| *Dercylus* | *cordicollis* | | 1 | | | | | | | |
| Total | | 2 | 16 | 6 | 242 | 290 | 141 | 7 | 35 | 22 |

datasets, a preliminary analysis was performed in order to test the accuracy of the catches and to estimate the theoretical total species richness in each sampling area, according to two indices based on the observed data: the incidence-based coverage estimator (ICE) and the Chao2 estimator (Hortal *et al.*, 2006). ICE and Chao2 estimators of species richness were computed using EstimateS 9.1.0 (Colwell, 2013). The data from sites W1, W2 and W3 in 1880 and 2015 (Table 1) and those from the complete transects in 1985/86 and 2013/14 (supplementary Table S1) were analysed separately.

Based on these data, two comparisons were performed. First, the 1880 data were compared with samplings made 135 years later at exactly the same sites and at the same moment of the year. The very low number of individuals sampled by Whymper in 1880 (15) indicates that his collection was far from exhaustive, and thus cannot yield reliable information as to abundance or species richness. According to the above-mentioned preliminary analysis, both ICE and Chao2 estimated 12 species in the area of sites W1, W2 and W3, whereas the observed gamma diversity amounts to 10 species, which means that 83% of the overall richness was sampled. On the other hand, this analysis confirms that the collection made by Whymper in 1880 represents but a small part of the real species richness. Therefore, the only evidence that can be drawn from his dataset is the presence of a species at a given site, as a member of an otherwise unknown assemblage. Although limited, this positive evidence acquires great significance when there is no record of that species at the same site in 2015, despite intensive and repeated searching.

A second comparison was made between the 1985/86 and 2013/14 surveys. Two variables were studied: the overall elevational range of each species and the species diversity at different elevations. As the sites surveyed in 1985/86 and 2013/14 are not exactly the same, the elevational data of both surveys were distributed in vertical intervals of 100 m, from 3850 m upwards. The Bray–Curtis similarity measure of the sites sampled in 1985/86 and 2013/2014 was computed in order to calculate the species assemblage similarity over the time (Table 2). Bray–Curtis is a popular similarity index for abundance data, and was calculated using the software PAST 3.10 (Hammer *et al.*, 2001). As superpáramo Carabids are wingless and have a low dispersal ability, the risk of a bias due to occasional invaders is considered negligible.

## Results

*First comparison: 1880 and 2015*

Three species of the studied genera were collected by Whymper at sites W1, W2 and W3 on the Guagua Pichincha (Table 1). *Dyscolus megacephalus* and *Dyscolus oopteroides* were found at elevations where they still lived in 1985/86 and 2013/15. *Dyscolus diopsis* is the only species that was collected in 1880 at every site, amounting to the totality (W1), one half (W2) or slightly less than one half (W3) of the samples, whereas in 2015 it was not found at W1, was very rare at W2 (0.7% of the captures), and was abundant only at W3 (53%). The case of W2 deserves a careful attention. In 1996, *D. diopsis* was not found there despite intensive sampling effort (242 individuals collected). In 2015, it was collected at this site in a very small portion of the sampled area, consisting in a coulee of bare loose soil with a vegetation cover limited to less than 10% of the surface. These conditions were the normal ones above 4600 m, where *D. diopsis* appeared with more frequency. On the Rucu Pichincha, despite intensive searching in 1985, 2013 and 2014, *D. diopsis* was never found below 4600 m (supplementary Table S1).

**Table 2.** Bray–Curtis similarity measure of the sampled intervals. Codes as follows: 85 = 1985/86, 13 = 2013/14. Letters A-I refer to the elevational intervals (*A* = 3850–3950 m, *B* = 3950–4050 m, *I* = 4650–4750 m). Bold print highlights the elevations where assemblage composition has changed between 1986 and 2013 (similarity <50%).

|  | 85A | 85B | 85E | 85F | 85G | 85H | 85I | 13A | 13B | 13D | **13E** | 13F | 13G | **13H** | **13I** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 85A | 1.00 | 0.68 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.78 | 0.58 | 0.39 | 0.37 | 0.00 | 0.00 | 0.04 | 0.00 |
| 85B |  | 1.00 | 0.23 | 0.14 | 0.31 | 0.18 | 0.08 | 0.59 | 0.56 | 0.36 | 0.51 | 0.14 | 0.30 | 0.18 | 0.05 |
| **85E** |  |  | 1.00 | 0.13 | 0.34 | 0.24 | 0.27 | 0.00 | 0.11 | 0.18 | **0.22** | 0.13 | 0.32 | 0.11 | 0.14 |
| 85F |  |  |  | 1.00 | 0.46 | 0.43 | 0.48 | 0.00 | 0.15 | 0.06 | 0.33 | 0.75 | 0.32 | 0.69 | 0.28 |
| 85G |  |  |  |  | 1.00 | 0.63 | 0.34 | 0.03 | 0.16 | 0.10 | 0.38 | 0.26 | 0.51 | 0.24 | 0.27 |
| **85H** |  |  |  |  |  | 1.00 | 0.23 | 0.00 | 0.13 | 0.09 | 0.31 | 0.19 | 0.27 | **0.33** | 0.41 |
| **85I** |  |  |  |  |  |  | 1.00 | 0.00 | 0.05 | 0.10 | 0.11 | 0.48 | 0.32 | 0.43 | **0.45** |
| 13A |  |  |  |  |  |  |  | 1.00 | 0.63 | 0.41 | 0.28 | 0.00 | 0.03 | 0.05 | 0.00 |
| 13B |  |  |  |  |  |  |  |  | 1.00 | 0.45 | 0.43 | 0.15 | 0.20 | 0.15 | 0.04 |
| 13D |  |  |  |  |  |  |  |  |  | 1.00 | 0.39 | 0.06 | 0.08 | 0.05 | 0.06 |
| 13E |  |  |  |  |  |  |  |  |  |  | 1.00 | 0.26 | 0.39 | 0.26 | 0.12 |
| 13F |  |  |  |  |  |  |  |  |  |  |  | 1.00 | 0.32 | 0.89 | 0.25 |
| 13G |  |  |  |  |  |  |  |  |  |  |  |  | 1.00 | 0.30 | 0.19 |
| 13H |  |  |  |  |  |  |  |  |  |  |  |  |  | 1.00 | 0.35 |
| 13I |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 1.00 |

To sum up, if we take into account the Rucu and Guagua transects together, *D. diopsis* has never been collected below 4560 m over the past 30 years, despite intensive sampling efforts. From the 929 carabid beetles that have been collected since 1985 on both transects in the 4200–4600 m interval, only three individuals (those collected in 2015 at 4560/4570 m), i.e. 0.3%, belong to this species, whereas five of the eight individuals found by Whymper in the same interval were *D. diopsis*. Its lowest registered elevation was 4267 m in 1880, 4600 m in 1986, 4605 m in 2013, and 4560 m in 2015, which represents a difference of nearly 300 m between the 1880 record and the lowest record of the 1985–2015 period.

*Second comparison: 1985/86 and 2013/14*

The sampling effort was significantly higher in 2013/14 than in 1985/86, with the result that the number of collected individuals was 1.77 times greater in 2013/14 (345 vs. 195). The results as to overall species richness (12) and assemblage composition were exactly the same: eight *Dyscolus* species, two *Blennidus*, one *Dercylus* and one *Pelmatellus* (supplementary Table S1). Moreover, ICE and Chao2 estimators of species richness gave the same result of 12 species, both when merging the two sampling periods and when ran separately for each period, thus confirming the accuracy of the sampling design.

The cluster analysis of the sampled sites produced two main groups that correspond, respectively, to the grassland zone, up to 4200/4300 m, and to the superpáramo (Fig. 2b). This overall pattern remained unchanged from 1985 to 2014. Changes have been detected at the upper limit of the transition zone between these two vegetation belts, despite a sampling gap between 4050 and 4250 m. The Bray–Curtis similarity matrix (Table 2) shows that the assemblage composition has changed significantly in

interval E (4250–4350 m), with a similarity of only 22% between the 1985/86 and 2013/14 samples. According to the cluster analysis (Fig. 2b), interval E belonged in 1985 to the superpáramo cluster along with intervals F to I, whereas 28 years later, in 2013, it was more closely connected with the grass páramo cluster (intervals A to D). Additionally, relatively low similarity values in intervals H (4550–4650 m) and I (4650–4750 m) suggest that there has been more changes in beetle assemblages at the uppermost elevations of the superpáramo, above 4550 m, than in the lower superpáramo.

**Discussion**

Spatial shift of species tracking suitable climatic conditions at regional scale have already been observed in species with high dispersal potential, such as birds or flying insects (Parmesan, 2006; Chen *et al.*, 2011a). This study focuses on ground beetles that are both wingless, thereby with low dispersal ability, and microendemic, hence with small distribution areas. These insects are therefore appropriate fine-grain indicators of the response of high-altitude communities to the current climate change provided that reliable historical data are available. In this respect, Whymper's 1880 samplings offer an opportunity that is unparalleled in tropical Andes.

In case of Mt Pichincha, Whymper's collection only yielded exploitable results for one species, *D. diopsis*, supporting the assumption that the bottom range of this species has shifted approximately 300 m upward in one century. As far as the ecology of *D. diopsis* is known, it is a stenotopic, cryophilous species that lives in high-altitude biotopes characterized by a sparse vegetation cover on rocky or loose sandy ground (Moret, 2005). These conditions are met with in all the sites where this species has been found on the Pichincha since 1985. They do not exist
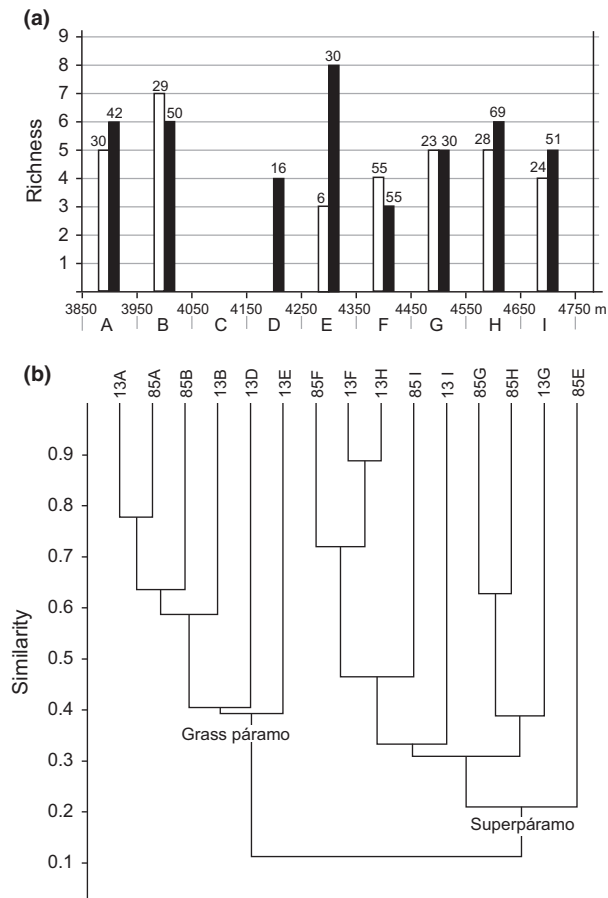
**Fig. 2.** Species richness and similarity along the south-east slopes of Mt Pichincha in 1985/86 and 2013/14, from 3850 m upwards, in vertical intervals of 100 metres. (a) Species richness (white bars: 1985/86; black bars: 2013/14). The total number of individuals collected in each interval is quoted above the bar. (b) Cluster analysis based on the Bray–Curtis similarity matrix of sampled intervals (codes as in Table 2).
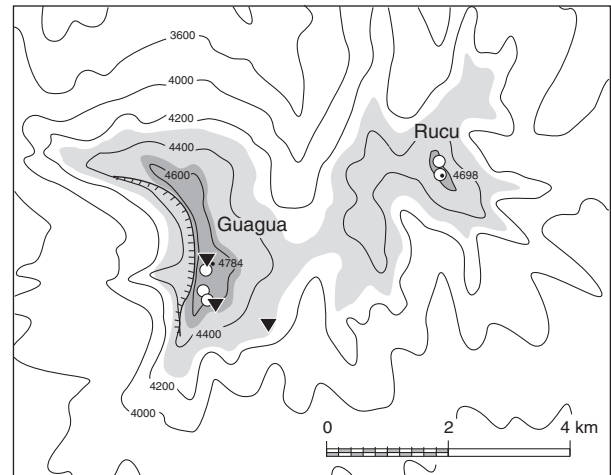


**Fig. 3.** Habitable area of *Dyscolus diopsis* on Mt Pichincha. Black triangles: catches in 1880; white dots: catches since 1985. Light grey: potential area in 1880; dark grey: potential area in 2015.

at present at the lowermost site where *D. diopsis* was collected by Whymper in 1880 (W1, 4270 m). This site is currently a grass páramo mixed with shrubby elements of the lower superpáramo, much more densely covered by vegetation than any current habitat of *D. diopsis* on the Pichincha or on any other mountain in Ecuador. Therefore, its presence there in 1880 lead us to assume that the microclimatic and ecological conditions were significantly different at that time, and that a site that belongs now to the transition zone between grass páramo and superpáramo would a century ago, at least in some places, have the aspect of a desert superpáramo.

As a consequence of the upward shift of its lower limit, the potential area of *D. diopsis* has shrunk dramatically in the span of a century. The contour line of the lowest altitude at which the species was collected gives a rough approximation of its habitable area (Fig. 3): a little more than 12 km$^2$ in 1880 with a contour line at 4270 m, and less

than 1 km$^2$ in 2014/15 with a contour line at 4560 m. Moreover, the current area is divided into two isolated patches on the Guagua and Rucu summits. Although merely indicative, as they ignore local edaphic or microclimatic factors, these figures reflect the order of magnitude of the area reduction caused by a 300 m upslope shift in the particular orographic context of the Pichincha volcano. From these premises, the question of the future extinction of *D. diopsis* necessarily arises, being a species that presents all the traits that make mountain organisms especially vulnerable to global warming: endemism, low dispersion ability, and a narrow ecological niche (Colwell *et al.*, 2008; Raxworthy *et al.*, 2008; Wilson & Gutiérrez, 2012). *D. diopsis* is currently represented by isolated island-like populations on the summits of 12 mountains of northern and central Ecuador (Moret, 2005). Assuming that its upslope shift continues at the pace that has been registered on the Pichincha, local extinctions are likely to occur during the coming century in four mountains that peak below 5000 m and possess small suitable habitats in their summit areas: Pichincha (4784 m), Cotacachi (4939 m), Corazón (4788 m) and Guamaní (4490 m). *Dyscolus diopsis* as a species is not directly endangered, thanks to its presence on several higher mountains with wider habitable areas. Other superpáramo specialists are microendemic to a single volcano (Anthelme *et al.*, 2014), which increases dramatically their vulnerability to climate change and the risk of extinction.

Over a shorter period of time, the comparison of the 1985/86 and 2013/14 samplings provides a broader picture of recent changes in ground beetle elevational ranges. The similarity analysis has shown that the lower limit of the superpáramo carabid community moved upwards from circa 4300 m in 1985/86, to circa 4400 m in 2013/14 (Fig. 2). Further investigations are needed to know if this 100 m upslope shift reflects a parallel upslope expansion of the grass páramo plant community.

Other minor changes observed in the ground beetle assemblages can be linked with different trajectories at species level (Fig. 4 and supplementary Table S1). The sampled species can be clustered in five groups according to their past and current altitudinal distribution.

1. Four grass páramo specialists (*Dyscolus alpinus*, *D. denigratus*, *Blennidus pichinchae* and *Pelmatellus columbianus*) reached 4300 m in 2013/14, at least 100 m higher than their highest record in 1985/86, not only on Mt Pichincha but also among the many hundreds of specimens of these species that have been collected in other mountains of Ecuador between 1984 and 1986 (Moret, 2009), suggesting a moderate upward shift of their upper limit, in accordance with the results of the similarity analysis.

2. One grass páramo specialist, *Dercylus cordicollis*, has experienced a dramatic upslope expansion into the superpáramo, with two records at 4600 m in 2013 and 2014. There are no records of this species above 4150 m in any mountain of Ecuador in 1985/86, which suggests that its upper range limit has shifted upwards at least 400 m in 28 years. It is worth noting that this shift is not related to a parallel expansion of grassland. It therefore implies adaptation to new habitat conditions in terms of vegetation cover, soil composition and microclimate. More information is needed from other mountains in Ecuador to know if this is an isolated case or a general trend for this species.

3. Three páramo generalists (*Dyscolus palatus, D. verecundus* and *Blennidus mucronatus*) were present both in the upper grass páramo and in the superpáramo. The first two were rare in both surveys, so that no reliable trend can be deduced from the available data. As to the latter, there is no evidence of change in its elevational range,
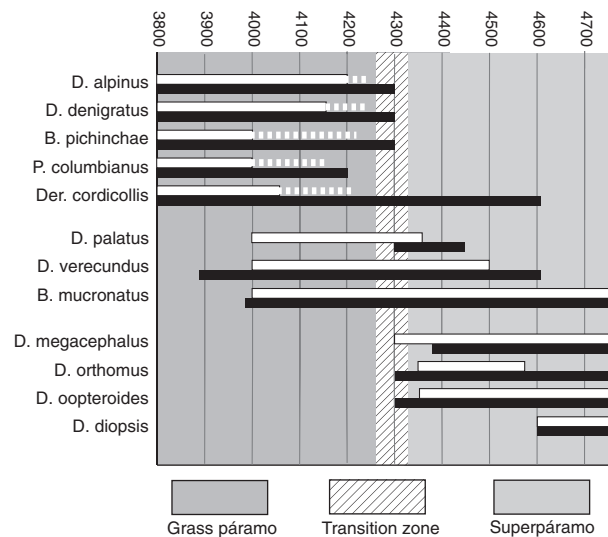
which remains very wide and suggests a high ecological tolerance.

4. Three superpáramo specialists (*D. megacephalus*, *D. oopteroides* and *D. orthomus*) had in both surveys a broad elevational range. No clear changes have been registered between 1986 and 2013, except in the case of *D. orthomus* that has been collected in 2013, 150 m above its upper limit in 1986. This evidence is clearly not sufficient to evaluate the response of the superpáramo community.

5. There is finally one desert superpáramo specialist: *D. diopsis*. The above-mentioned upward shift of its lower limit is likely to have occurred between 1880 and 1985. No appreciable change has been recorded during the last 30 years, at least on the Pichincha. The hypothesis of a recent upward shift of its upper limit should be tested on higher mountains, e.g. the Antisana (5704 m) or the Cotopaxi (5897 m).

In summary, disregarding two species for which we do not have sufficient data, four species did not move significantly between 1986 and 2013, whereas six species experienced during the same period an upward shift of their upper limit, moderately (around 100 or 150 m) in four cases, dramatically (at least 400 m) in the case of *D. cordicollis*.

In accordance with other studies (Brambilla & Gobbi, 2014; Menéndez *et al.*, 2014; Pizzolotto *et al.*, 2014), it can be assumed that the response to global warming varies from one species to another depending on their degree of ecological specialisation, their physiological tolerance, and their different times of response to climatic changes. Important differences among Andean carabids as to cold hardiness and resistance to desiccation have been observed experimentally (Sømme *et al.*, 1996). In another beetle family, a study performed in Costa Rica on mountain-dwelling Chrysomelidae showed that the critical thermal maximum varies among species across elevational gradients (García-Robledo *et al.*, 2016). Physiological limitations are not the only factor that can drive area contractions. Interactions between species are likely to play an important role too. In addition, it is also possible that carabid beetles are responding to changes in their food resources rather than to temperature directly. As their preys depend for subsistence on the páramo vegetation, future research should put emphasis on a parallel study of plant and insect communities.

In the absence of long-term meteorological records at high altitudes in Ecuadorian mountains, a close fit between increasing temperatures and changing distributions cannot be assessed as has been done in other studies (Chen *et al.*, 2011a). Broader regional meteorological reviews give evidence for a warming trend that affects the tropical Andes at least since the mid-20th century. Based on 279 weather stations located between 1°N and 23°S, Vuille *et al.* (2008) showed that air temperature increased by 0.68 °C since 1939. A similar tendency has been obtained from 15 Ecuadorian stations between 1961 and 1990 (Quintana-Gómez, 2000). In the longer term, the pace of glacier retreat provides the best available proxy for assessing climate



**Fig. 4.** Elevational ranges of 12 Carabid species on the southeast slopes of Mt Pichincha. White bars: 1985/86; black bars: 2013/14. Dashed parts of the white bars refer to collections made on other mountains of the same province in 1985/86, according to Moret (2009).

change at high altitudes, owing to the high correlation that exists between glacier melt rate and air temperature. The period in which Whymper explored the mountains of Ecuador corresponds to the end of the Little Ice Age in the Andes (Ledru *et al.*, 2013). His description of the Pichincha summit area, with thick deposits of snow and even ice (Whymper, 1892), points to climatic conditions that were significantly colder than now. The last advance of Ecuadorian glaciers occurred around 1870, after which they entered a phase of continuous retreat, quite pronounced in the late 19th century, moderate during the first half of the 20th century, and accelerated in the last three decades (Rabatel *et al.*, 2013).

The coincidence of Whymper's expedition with the end of the Little Ice Age gives his observations a unique and outstanding value, notwithstanding the small number of collected specimens. The precision of the topographic and elevational data attached to his botanical and zoological material has no parallel in the Andes before the mid-20th century, not to mention the vague descriptions of Humboldt that were recently used to assess upward shifts in the distribution of vegetation zones over a period of 210 years (Morueta-Holme *et al.*, 2015).

## Conclusion

The results of this study suggest that the elevational ranges of Andean páramo ground beetles have changed significantly during the past decades, though not in a uniform way. The most specialised stenotopic high-altitude species experienced an important upslope shift (ca. 300 m) between 1880 and 1985. Among more generalist species, a wide spectrum of upward shift rates was recorded between 1985/86 and 2013/14, presumably as a result of differences in ecological and climatic tolerance at species level. On the other hand, our results do not support the hypothesis that the area reduction in the upper superpáramo environment has led to a dramatic decrease in species diversity, as far as the Pichincha mountain is concerned.

Historical data represent a valuable source of information, hitherto largely unexploited, that can provide novel insights into the transformation process of high alpine environments since the end of the Little Ice Age. This study should be extended to other mountains where Whymper collected insects, such as the Chimborazo, Antisana and Cayambe volcanoes, and should also include his botanical collections. On the other hand, it calls for the creation of a long-term monitoring programme that would use carabids as an indicator of the effects of climate change on the páramo ecosystem.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12173:

**Table S1.** Altitudinal distribution (in 100 m intervals) of the Carabid species of the genera *Dyscolus*, *Blennidus*, *Dercylus* and *Pelmatellus* on the Pichincha volcano in 1985/86 and in 2013/14.

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