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Modern pollen-vegetation relationships along a steep temperature gradient in the Tropical Andes of Ecuador

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Abstract: The characterization of modern pollen rain assemblages along environmental gradients is an essential prerequisite for reliable interpretations of fossil pollen records. In this study, we identify pollen-vegetation relationships using modern pollen rain assemblages in moss polsters (n = 13) and lake sediment surface samples (n = 11) along a steep temperature gradient of 7°C (3100–4200 m above sea level) on the western Andean Cordillera, Ecuador.

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22 The pollen rain is correlated to vascular plant abundance data recorded in vegetation relevées
23 (n = 13). Results show that pollen spectra from both moss polsters and sediment surface
24 samples reflect changes in species composition along the temperature gradient, despite
25 overrepresentation of upper montane forest taxa in the latter. Estimated pollen transport
26 distance for a lake (Laguna Llaviucu) situated in a steep upper montane forest valley is 1–2
27 km, while a lake (Laguna Pallcacocha) in the páramo captures pollen input from a distance of
28 up to 10–40 km. *Weinmannia* spp., *Podocarpus* spp., and *Hedyosmum* sp. are indicators of
29 local upper montane forest vegetation, while *Phlegmariurus* spp. and *Plantago* spp. are
30 indicators for local páramo vegetation.

31

32 **Keywords:** Tropical Andes; Pollen rain; Pollen transport distance; Cajas National Park;
33 Páramo; Montane forest; High-elevation lakes

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38 INTRODUCTION

39 A robust understanding of the Holocene vegetation and climate history of the Tropical
40 Andes (8°N, 26°S) is key for understanding long-term ecosystem dynamics (Bush et al.,
41 2004; Cárdenas et al., 2011) and variability in large-scale climate systems, such as the El
42 Niño–Southern Oscillation (Moy et al., 2002; Muñoz et al., 2017) and the Intertropical
43 Convergence Zone (Muñoz et al., 2017). Fossil pollen have been widely used in the Tropical
44 Andes to reconstruct vegetation and climate history (Liu and Colinvaux, 1985; Bush et al.,
45 2004; Hooghiemstra and Van der Hammen, 2004; Cárdenas et al., 2011; Flantua et al., 2016;
46 Schiferl et al., 2017). Such pollen records are especially valuable when they are calibrated to

47 a modern pollen-climate-vegetation dataset. In the Tropical Andes, several calibration studies
48 show that modern pollen rain reflects the surrounding vegetation composition (Weng et al.,
49 2004; Reese and Liu, 2005) and that compositional changes in modern pollen assemblages
50 closely track altitudinal gradients (Weng et al., 2004; Moscol-Olivera et al., 2009; Urrego et
51 al., 2011b). As such, when calibrated locally, pollen assemblages can be used to reconstruct
52 changes in the position of the upper forest line (Niemann et al., 2010; Groot et al., 2011;
53 Urrego et al., 2011a) and, by inference, palaeotemperature (Weng et al., 2004; Groot et al.,
54 2011).

55 Yet, calibrating modern pollen assemblages to vegetation and climate in the Tropical
56 Andes is challenging. First, differences in plant pollination syndromes (Bush, 1995; Moscol-
57 Olivera et al., 2009), heterogeneous vegetation (Jantz et al., 2013), and upslope wind
58 dispersal of pollen (Bush, 2000; Weng et al., 2004; Moscol-Olivera et al., 2009; Niemann et
59 al., 2010; Urrego et al., 2011b) result in a biased representation of pollen taxa in the pollen
60 record. For example, upslope wind dispersal leads to overrepresentation of mostly arboreal
61 taxa above the upper forest line (Weng et al., 2004; Moscol-Olivera et al., 2009; Niemann et
62 al., 2010; Jansen et al., 2013). Second, modern pollen calibration studies in the Tropical
63 Andes are mostly based on pollen rain in moss polsters (Weng et al., 2004; Moscol-Olivera et
64 al., 2009; Urrego et al., 2011b; Cárdenas et al., 2014), soil samples (Weng et al., 2004; Reese
65 and Liu, 2005), or pollen traps (Moscol-Olivera et al., 2009; Niemann et al., 2010; Jantz et
66 al., 2013;), while reconstructions of past vegetation dynamics are usually based on pollen
67 records from lake sediments (Colinvaux et al., 1997; Hansen et al., 2003; Urrego et al., 2005;
68 Schiferl et al., 2018). Pollen records from lake sediments likely represent temporal and spatial
69 scales different than moss polsters (Gaudreau et al., 1989; Fall, 1992), but so far no local
70 studies in the Tropical Andes are available to quantify this. Hence, the characterization of
71 modern pollen rain assemblages from lakes is an essential prerequisite for accurate

72 reconstructions. Furthermore, reliable interpretations of fossil pollen records require
73 information on the transport distance of pollen in the landscape to determine the spatial scale
74 of the reconstructed vegetation (Gaudreau et al., 1989), and establish dominantly local and
75 regional elements of the pollen rain. Yet, knowledge on pollen dispersal and transport
76 distance in South American neotropical landscapes is limited to a few sites (e.g., Bush and
77 Rivera, 1998; Whitney et al., 2018) and local studies in the Tropical Andes to quantify first-
78 order estimates of pollen transport distances between plants and lake-surface sediments
79 across different vegetation zones are so far not available.

80 Here, we analyse the modern pollen rain captured in surface samples from lake
81 sediments and moss polsters in relation to the vegetation in along an altitudinal gradient
82 between 3100 and 4200 m above sea level (asl) in the Tropical Andes. The transect covers a
83 temperature gradient of ca. 7°C and the transition from the upper montane forest to the
84 páramo. The aims of our study are (1) to assess to what degree the altitudinal and temperature
85 gradients drive species composition changes in the modern pollen rain in both moss polsters
86 and sediment surface samples from Andean lakes; and (2) to assess qualitative and
87 quantitative relationships between pollen assemblages and its parent plant communities in the
88 Tropical Andes of Ecuador.

89 **STUDY REGION: CAJAS NATIONAL PARK, ECUADOR**

90 Cajas National Park (CNP) in southwest Ecuador provides an ideal location for
91 investigating modern pollen rain across an altitudinal and environmental gradient because of
92 the presence of more than 200 pristine lakes across an altitudinal gradient; several of these
93 lakes have been used for reconstructions of vegetation and climate history (Colinvaux et al.,
94 1997; Moy et al., 2002; Hansen et al., 2003).

95 CNP is situated on the western Cordillera of the southern Ecuadorian Andes
96 (2°46'46"S, 79°13'27"W), ca. 25 km west of Cuenca in the province of Azuay, and ca. 300

97 km south/southwest of Quito (Fig. 1). Elevation in the park ranges from 3100 to 4500 m asl
98 with a plateau at ca. 4000 m and several deep valleys and mountain rivers draining to the
99 west and east (Rodbell et al., 2002). The geomorphology of the area has been shaped by
100 glacial expansion and retreat, resulting in an abundance of lakes, valleys, and moraines
101 (Hansen et al., 2003). The montane forests and páramos in the region are a biodiversity
102 hotspot (Myers et al., 2000), with many endemic species occurring in narrow altitudinal
103 distribution ranges (Gentry, 1992) and the region has been identified as a “priority landscape
104 for biodiversity conservation” (Cuesta et al., 2017). The vegetation in CNP follows an
105 altitudinal zonation (Fig. 1). The vegetation in the lower reaches of the park (3100–3500 m
106 asl) is a continuous upper montane Andean forest reaching a height of 15–20 m, with multi-
107 stemmed trees, contorted tree growth, and giant shrubs, with epiphytes and lianas covering
108 the trees. Herbaceous flora such as grasses, sedges, and ferns cover the forest floor.
109 Following Bakker et al. (2008), we define the upper forest line as the uppermost contour of
110 closed continuous forest. Isolated patches of small dwarf trees (e.g., *Polylepis* spp.) are not
111 considered upper montane forest. The upper montane forest transitions into grass páramo
112 with small patches of *Polylepis* spp. forest at 3500 m asl. The grass páramo (i.e., pajonal) at
113 3500–4000 m asl is dominated by bunch grasses, with scattered herbs and shrubs, such as
114 *Puya* spp. In the higher reaches of the park (>4000 m asl), the vegetation is mainly
115 characterized by shrub and cushion páramo, where cushion plants dominate and bunch
116 grasses and small shrubs are scattered across the landscape (Hansen et al., 2003).
117 Anthropogenic impact on the vegetation is minimal, with minor grazing by llamas, and the
118 area has been protected since 1996. In proximity of the park (5 km from Llaviucu) are
119 plantations of *Eucalyptus* spp. and *Pinus* spp.

120 Lapse rate for mean temperature is ca. 6.88°C/km in CNP (Córdova et al., 2016) and
121 temperature shows a strong diurnal variation averaging from ca. -1.8 to 17.8°C (Carrillo-

122 Rojas et al., 2016). Precipitation in the inter-Andean valley, where the city of Cuenca is
123 situated (Fig. 1), is relatively low (800–1500 mm/yr) because the air masses lose most of
124 their moisture on the western and eastern Andean flanks (Vuille et al., 2000). Spatial
125 variability in rainfall is very high in the region and can differ 25% within distances of <4 km
126 (Buytaert et al., 2006). Fogs and rain occur frequently >3000 m asl, with a mean annual
127 precipitation of ≥ 2000 mm (Hansen et al., 2003). The western Andean slopes near CNP
128 experience positive precipitation and temperature anomalies during warm El Niño events
129 (Vuille et al., 2000; Moy et al., 2002). Prevailing winds are from the east, southeast, or
130 northeast during non-El Niño years (Carrillo-Rojas et al., 2016) but the area farthest west in
131 CNP could also be influenced by westerly winds from the Pacific (Fig. 1; Hansen et al.,
132 2003).

133 **METHODS**

134 We use a combination of vegetation surveys, modern pollen assemblages from moss
135 pollsters and lake sediments, and a quantitative spatial analysis to characterize the modern
136 pollen rain in CNP along altitudinal and temperature gradients. Temperature data along the
137 altitudinal gradient are based on meteorological stations in CNP and were obtained from
138 Córdova et al. (2016).

139 **Vegetation survey**

140 To assess qualitative and quantitative relationships between pollen assemblages and
141 their parent plant communities, we conducted a vegetation survey in August 2015 along an
142 altitudinal transect from 3100 to 4200 m asl. In total, 13 vegetation relevés (10 × 5 m for
143 forests and 5 × 5 m for páramo) were made in homogeneous vegetation types and located in
144 the vicinity of the research lakes (Fig. 1). The relevés were arbitrarily chosen following the
145 “stratified random” technique to represent the major vegetation communities in CNP. The
146 vegetation relevés along the transect included upper montane forest, *Polylepis* spp. stands,

147 grass páramo, and cushion páramo (Fig. 1). For every relevé, a list of vascular plants was
148 recorded along with their percentage cover using the Braun Blanquet method adjusted by
149 Barkman et al. (1964). In forest relevés we identified and counted all trees with a diameter at
150 breast height (= 1.3 m) of >1 cm, at species level when possible. All Braun Blanquet data
151 were converted to percentage cover for further analysis by using the mean of the upper and
152 lower limit of the range. For each relevé species richness (i.e., number of taxa) was calculated
153 per standardized plot area (25 m²) and converted to the same taxonomic level as found in the
154 modern pollen rain (adjusted species richness) for comparison. Altitude and slope were
155 measured with a GPS device.

156 **Modern pollen rain**

157 In August 2015, samples for the analysis of modern pollen and spore rain were
158 obtained through 13 moss polsters taken from the centre of each vegetation relevé (Fig. 1)
159 and through sediment surface samples from seven lakes (Table 1) collected with an UWITEC
160 gravity corer. Along the sampled gradient no suitable lakes were found at 3200–3500 and
161 3600–3800 m asl. To assess variability in pollen rain within a lake we analysed replicates
162 from four of the seven lakes. We expanded our dataset by adding data on pollen rain in
163 sediment surface samples previously collected and analysed by Hansen et al. (2003) from
164 four additional lakes (Laguna Pampiada [Pamp], Laguna Chorreas [Chor], Highest Lake
165 [HL], and Upper Lake [UL]) and one additional sample from Laguna Pallcacocha, resulting
166 in a total n = 11 and total replicates n = 5.

167 To extract pollen from the moss polsters, approximately 100 cm² of each moss polster
168 was washed with ethanol (90%). Extracts were centrifuged and decanted. The lake sediment
169 surface samples were freeze-dried and ~0.5 g was used for pollen analyses. Sediment and
170 moss samples were spiked with 4 mL *Lycopodium clavatum* solution (i.e., ~8339 spores). To
171 remove humic acids, coarse fragments, and to disaggregate the sediments, samples were

172 treated with 10% KOH at 70°C and sieved over 200 µm mesh. Samples were dewatered with
173 99% acetic acid and acetolysed for 10 minutes at 100°C in a 1:9 mixture of sulphuric acid
174 and acetic anhydride (Faegri and Iversen, 1989). The sediment surface samples were floated
175 over sodium polytungstate (d = 2.0) to remove minerals. Residues were mounted in glycerol
176 and analysed to a minimum of 300 pollen grains and spores with a Leica DM2500 light
177 microscope at 400× magnification. Pollen types were identified to the lowest taxonomic level
178 possible following descriptions by Hooghiemstra (1984), and by comparison with the
179 reference collections at the University of Amsterdam and Utrecht University. In routine
180 pollen analysis, pollen grains from the dwarf tree *Polylepis* spp. cannot be morphologically
181 separated from grains of *Acaena* spp. (Smit, 1978). Van't Veer et al. (2000) argued that most
182 pollen grains of the *Polylepis* spp.-*Acaena* group reflect *Polylepis* spp. Following this line of
183 reasoning, we only identified *Polylepis* spp. in our samples. Species richness in the pollen
184 samples was determined with rarefaction calculations (Birks and Line, 1992) to remove the
185 effect caused by variations in the pollen sum amongst samples. The rarefaction method was
186 applied by using the “individual rarefaction” option in the software PAST (version 2.01;
187 Hammer et al., 2001). Pollen percentages for each taxon were calculated relative to the total
188 pollen number found in the specific sample (total pollen sum included all pollen and spore
189 types except aquatic taxa such as *Isoëtes* spp.). Percentage diagrams were plotted with C2
190 version 1.7.7 (Juggins, University of Newcastle, UK).

191 **Data treatment and spatial analysis**

192 Following previous studies in the Tropical Andes (e.g., Moscol-Olivera et al., 2009),
193 the relationship between the vegetation and modern pollen rain in moss and sediment surface
194 samples was determined through the association index (A; Davis, 1984). This index is based
195 on presence-absence data and calculations were conducted following Davis (1987). A
196 provides a relative measure for a pollen type in a moss or sediment sample to indicate the

197 presence of the plant in the local vegetation sampled. The values range between 0 and 1, with
198 $A = 1$ when the pollen type and the plant taxon are both present and $A = 0$ when the pollen
199 type or the parent plant either are absent or do not co-occur (Davis, 1984). The production
200 bias between plant community cover (i.e., upper montane forest or páramo) and the
201 respective pollen types was assessed by comparison of pollen percentages and vegetation
202 cover percentage from the relevé data for both moss and sediment surface samples.
203 Subsequently, a first-order estimate of mean pollen transport distances for Laguna Llaviucu
204 and Laguna Pallcacocha was made, since both lakes have been used as sites for
205 reconstructions of vegetation and climate history (Colinvaux et al., 1997; Moy et al., 2002).
206 Laguna Llaviucu is situated within the upper montane forest and Laguna Pallcacocha in the
207 páramo, providing the opportunity to identify the effect of landscape openness on mean
208 pollen transport distance. To identify the spatial range of the regional pollen rain in the lake
209 samples, we used vegetation maps with a land cover classification at 30 m spatial resolution
210 created by the Ministerio del Ambiente, Ecuador (2014) in collaboration with the Food and
211 Agriculture Organization of the United Nations. We calculated the land cover percentage in
212 stepwise buffers (1, 5, and 10–45 km) around Laguna Pallcacocha and Laguna Llaviucu to
213 make a first-order estimate of the mean pollen transport distance. We compared relative
214 vegetation cover of upper montane forest, páramo, and *Polylepis* spp. stands with the
215 equivalent units based on the pollen data from both lakes for the stepwise increasing buffers.
216 In addition, the closest recorded stands of important forest elements were compared to the
217 computed vegetation cover. This approach does not consider production biases of individual
218 taxa, but provides a first-order estimate of the main pollen transport distance. All spatial
219 analyses were conducted with ArcMap software version 10.3.1 (ESRI, Redlands, CA, US).

220 **Statistics**

221 Ordination analyses were performed on the pollen data to summarize changes in
222 species composition across the upper montane forest-páramo ecotone and to explore
223 differences in composition between sediment and moss pollen samples. Pollen percentages
224 were log transformed (Šmilauer and Lepš, 2014), and rare species (<2%) were deleted to
225 minimize their influence on the outcomes. We applied a scaling focus on inter-sample
226 distances, and species scores were centred and divided by their standard deviation. For moss
227 sample nine (M9) we excluded *Azorella* spp. from the total pollen sum for the ordination
228 analysis. The sample contained an exceptionally high concentration of *Azorella* spp. with
229 pollen grains in some cases still attached to each other, pointing to the possibility that the
230 moss sample also included *Azorella* spp. plants and/or flowers. Canonical correspondence
231 analysis (CCA) was performed separately for the lake sediment surface samples and moss
232 polsters with air temperature (°C) as the only constraining variable (CCA_{temp,moss} and
233 CCA_{temp,sed}). To visualize the relationship between temperature at the sampling locations and
234 species composition, temperature measured at each lake sampling location was plotted
235 against its CCA axis 1 score. To test differences in composition between lake sediment
236 surface samples and moss polsters we conducted a CCA analysis (CCA_{sample}) with sample
237 type as the only constraining variable and a permutation test (n = 499) for testing
238 (dis)similarity. All ordination analyses were conducted with Canoco v.5 (ter Braak and
239 Šmilauer, 2012).

240 **RESULTS**

241 **Vegetation survey**

242 A total of 40 plant families, 72 genera, and 107 species of plants were recorded in the
243 13 vegetation relevés and adjacent areas in CNP. A selection of the results of the vegetation
244 survey is plotted as percent cover together with the modern pollen rain in Figure 2. The
245 vegetation relevés in the upper montane forest at 3148–3178 m asl are characterized by

246 *Hedyosmum* sp., Melastomataceae, Poaceae, *Oxalis* spp., *Berberis* spp., and *Weinmannia* spp.
247 In the vegetation relevés in the upper limit of the upper montane forest at 3300 m asl we
248 mostly recorded Melastomataceae, Piperaceae, and some Asteraceae. Above 3500 m asl, the
249 vegetation relevés are characterized by páramo taxa such as Asteraceae (e.g., *Baccharis* spp.,
250 *Chuquiraga jussieui*, and *Loricaria* spp.), Cyperaceae (e.g., *Isolepis* spp.), *Plantago* spp.,
251 Poaceae (e.g., *Calamagrostis* spp. and *Cortaderia* spp.), Apiaceae (e.g., *Azorella*
252 *pedunculata*), Ericaceae (e.g., *Disterigma empetrifolium*), Geraniaceae (e.g., *Geranium* spp.),
253 Hypericaceae (e.g., *Hypericum* spp.), Grossulariaceae (*Ribes* spp.), Rosaceae (e.g.,
254 *Lachemilla* spp.), and Valerianaceae (e.g., *Valeriana microphylla* and *Valeriana rigida*). The
255 taxa mentioned in brackets above are examples of the most common taxa in the vegetation,
256 pollen morphologically these taxa cannot be identified on this detailed level. Scattered in the
257 páramo are patches of *Polylepis* spp. forest.

258 **Pollen spectra in moss polsters**

259 In total, 48 pollen taxa (i.e., 44 families, 31 genera, and 3 species) could be identified
260 in the modern pollen rain of all moss and sediment surface samples. Asteraceae, Apiaceae,
261 Cyperaceae, Valerianaceae, and Poaceae are common families in the páramo, but pollen from
262 these taxa are difficult to identify on the species level, reducing the palynological richness. In
263 the moss polsters, 44 taxa were identified with 22 pollen taxa also found in the vegetation
264 relevés, while 18 taxa recorded in the relevés were not represented by pollen grains. On
265 average we found 22 (SD = 4.22) pollen taxa per moss polster.

266 With increasing elevation, there is a clear sequence in dominance of different pollen
267 taxa (Fig. 2). At the lowermost site, Melastomataceae dominate (41% at 3148 m asl),
268 followed by Chloranthaceae type (unknown parent plant taxa, pollen resemble
269 Chloranthaceae but do not belong to the *Hedyosmum* genus) in the upper montane forest
270 between 3148 and 3554 m asl, and *Polylepis* spp. at the upper forest line (3554 m asl). Other

271 common taxa at 3100 m asl, included *Alnus acuminata*, *Weinmannia* spp., and *Podocarpus*
272 spp. Some bisaccate pollen grains could originate from the *Pinus* spp. plantation outside
273 CNP. In the páramo moss polsters (3933 m asl) Poaceae dominate the pollen spectrum. At the
274 uppermost site (4228 m asl), the moss polsters from the páramo showed a dominance of
275 Asteraceae pollen. Other common taxa are Cyperaceae and *Plantago* spp.

276 Rarefied pollen taxa richness for moss polsters has a significant positive relation to
277 species richness in the vegetation, adjusted for taxonomical resolution of the palynological
278 analysis (Pearson's R : $P = 0.04$; Fig. 3). This means that the palynological richness in moss
279 polsters reflects the richness of the local vegetation. The CCA_{sample} , clearly separated the
280 moss polsters and sediment surface samples ($P = 0.002$), indicating that the pollen
281 assemblage captured by sediment surface samples differs significantly in composition from
282 the pollen assemblages captured by moss polsters (Fig. 4). The $CCA_{\text{temp,moss}}$ reveals clear
283 changes in the composition of the pollen assemblages along the temperature gradient. Axis 1
284 represents 30.5% of the variability of the dataset ($P = 0.004$; eigenvalue = 0.18). Upper
285 montane forest taxa such as Melastomataceae, *Hedyosmum* sp., and *Weinmannia* spp. have
286 positive scores on Axis 1, and páramo taxa such as *Phlegmariurus* spp., Apiaceae, *Plantago*
287 spp., and Valerianaceae have negative scores (Fig. 4).

288 **Pollen spectra in lake-surface sediments**

289 In the sediment surface samples 37 taxa were identified of which 18 pollen taxa are
290 recorded locally as plant in the relevés. The sediment surface samples contained 28 (SD =
291 1.93) pollen taxa on average. There is a clear sequence in dominance of different pollen taxa
292 along the altitudinal gradient (Fig. 2). At the lowermost lake Llaviucu (3150 m asl), pollen
293 from Poaceae (29%) dominate the pollen assemblage, while other frequently found pollen
294 taxa are *A. acuminata*, Choloranthaceae pollen type, *Hedyosmum* sp., Melastomataceae,
295 *Myrica* spp., *Podocarpus* spp., and *Weinmannia* spp. The pollen assemblage from Laguna

296 Taitachugo, situated just above the upper forest line (3550 m asl), is dominated by Poaceae
297 (19–25%). Other common taxa in the sediment record of this lake are *Podocarpus* spp. and *A.*
298 *acuminata*. In the pollen assemblages from the lakes situated within the páramo, *A.*
299 *acuminata* pollen become more abundant, reaching a maximum of 19% at 4230 m asl;
300 Poaceae, Asteraceae, and *Phlegmariurus* spp. are other frequently found pollen types.
301 Rarefied pollen taxa richness is not significantly related to the adjusted species richness in the
302 vegetation, indicating that the sediment surface samples do not capture local vegetation
303 species richness (Pearson's R : $P = 0.69$; Fig. 3).

304 The $CCA_{temp, sed}$ revealed clear changes in the composition of the pollen assemblages
305 along the temperature gradient. Axis 1 represented 14.7% of the variability of the dataset ($P =$
306 0.01 , eigenvalue = 0.03). Upper montane forest taxa such as Melastomataceae, *Podocarpus*
307 spp., *Hedyosmum* sp., and *Weinmannia* spp. have positive scores on Axis 1, and páramo taxa
308 such as *Phlegmariurus* spp., *Polylepis* spp., and *Plantago* spp. have negative scores (Fig. 4).

309 **Pollen representation**

310 The comparison of the association indexes for the 67 taxa found in the vegetation and
311 modern pollen rain samples are given in Table 2. In the moss polsters 19 taxa showed an $A >$
312 0 , indicative of pollen taxa with an identified local parent plant in the vegetation relevés. For
313 the sediment surface samples, 14 taxa were found with $A > 0$. Overall, association indices for
314 a certain taxon are within the same range in moss polsters and sediment surface samples. The
315 vegetation relevés each contained taxa that were not represented in the modern pollen rain in
316 moss and sediments. These silent taxa ($A = 0$) include *Berberis* spp., Rosaceae, *Geranium* sp.,
317 *Oxalis* spp., *Sibthorpia* sp., and Orobanchaceae. The pollen from these taxa is probably
318 absent in the modern pollen rain because they are likely entomophilous or autogamous and
319 consequently have a low pollen productivity or do not disperse their pollen far from the
320 parent plant. Other taxa for which $A = 0$ are those that were not found in the vegetation

321 relevés but were recorded in the modern pollen rain. These are generally anemophilous upper
322 montane forest species, e.g., *A. acuminata*, Moraceae, *Juglans neotropica*, *Vallea* spp.,
323 *Rapanea* spp., *Alchornea* spp., *Podocarpus* spp., and *Myrica* spp. The highest association
324 indices (~0.7–1) were recorded for Poaceae, Asteraceae, and Ericaceae in the moss polsters,
325 while in the sediment surface samples the highest association indices were found for Poaceae,
326 Asteraceae, Valerianaceae, and Apiaceae. Taxa that are underrepresented in the pollen rain
327 relative to their abundance in the vegetation were *Ribes* spp., Solanaceae, Caryophyllaceae,
328 *Weinmannia* spp., and *Puya* spp. These taxa are underrepresented in the modern pollen rain
329 because of their pollination syndromes, being primarily entomophilous, zoophilous, and/or
330 ornithophilous (Moscol-Olivera et al., 2009).

331 At the vegetation type level (Fig. 5), our results show that in the pollen spectra from
332 moss polsters there is a significant relationship between páramo vegetation cover in the
333 relevée and páramo pollen abundance (Pearson's R : $P = <0.001$). For the upper montane
334 forest species this relationship is also significant ($P = <0.001$). For the lake sediment surface
335 samples, we do not observe a correlation between percentage upper montane forest pollen
336 and the upper montane forest cover in the nearest vegetation relevée, or the percentage of
337 páramo pollen and páramo vegetation. The pollen spectra from Laguna Llaviucu and Laguna
338 Pallcacocha show that the montane forest taxa make up 40 and 50%, respectively, of the total
339 pollen sum. Our spatial analysis showed that a 40 and 50% montane forest land cover is
340 reached at a 1.2 km radius around Laguna Llaviucu and a >40 km radius around Laguna
341 Pallcacocha. The first appearance of montane forest in the sensitivity analysis is at ~10 km
342 radius around Laguna Pallcacocha. Therefore, the estimated pollen transport distance for
343 pollen rain in Laguna Llaviucu is 1 to 2 km, while pollen transport distance in Laguna
344 Pallcacocha is between 10 and 40 km (Fig. 6).

345 **DISCUSSION**

346 **Pollen spectra along a temperature gradient: moss versus sediment**

347 Pollen spectra from the moss polster transect spanning a temperature gradient of ca.
348 7°C in the western Andean Cordillera in Ecuador show clear differences in the distribution of
349 pollen taxa. Pollen rain of the upper montane forest was characterized by Melastomataceae
350 (41%) and *Hedyosmum* sp. (10%) reflecting local forest taxa recorded in the vegetation
351 relevés. The position of the modern upper forest line at ~3500 m asl is reflected in the pollen
352 rain of moss polsters by a decrease of upper montane forest taxa Melastomataceae (<41%)
353 and *Hedyosmum* sp. (<10%) and an increase to above 17% of (dwarf) tree taxa typically
354 growing above the upper forest line (e.g., *Polylepis* spp.) accompanied with an increase of
355 páramo taxa to above 40% (e.g., Poaceae, Asteraceae, and *Phlegmariurus* spp.).
356 Melastomataceae can occur above the forest line and reach into the lower páramo (Cleef,
357 1981; Moscol-Olivera, 2009a), making them less suitable for the interpretation of forest line
358 dynamics. A previous study in Podocarpus National Park (PNP), located on the eastern
359 Cordillera of the Ecuadorian Andes approximately 150 km southeast of CNP, showed that the
360 position of the modern upper forest line between 2730–3040 m asl was reflected in the pollen
361 composition, recorded by pollen traps, by upper montane forest pollen taxa levels at 25%
362 (Niemann et al., 2010), which is considerably lower than the 60% in our study. In the
363 Colombian Andes, at the high plain of Bogotá, the position of the upper forest line is
364 represented by levels of about 40% of arboreal pollen and 20% of Poaceae (Hooghiemstra,
365 1984). This difference highlights the need to locally calibrate the upper forest-line pollen
366 signal.

367 Upper montane forest taxa are overrepresented in the moss polsters above the upper
368 forest line, supporting previous studies on modern pollen rain in the Tropical Andes (Weng et
369 al., 2004; Moscol-Olivera et al., 2009; Urrego et al., 2011b). However, this regional pollen

370 distribution signal does not eliminate the effect of temperature in the composition of moss
371 pollen spectra ($CCA_{\text{moss, temp}}$). The ordination analyses also show that pollen spectra from the
372 upper montane forest at ~3100 m asl/9.7°C (T_{mean}) are compositionally different from those at
373 higher elevations/lower temperature (e.g., ~4050 m asl/3.5°C T_{mean}). Previous work in Peru
374 on the Amazonian Andean flank also reported that compositional changes observed in moss
375 pollen spectra along an elevation gradient (~3100 m range) were most likely driven by an
376 elevation-driven temperature gradient (Weng et al., 2004; Urrego et al., 2011b). Yet, a direct
377 analysis of the effect of temperature on compositional changes was not made. Here, we show
378 that temperature is indeed a significant driver of compositional changes in pollen spectra of
379 moss polsters.

380 Composition of pollen assemblages in moss polsters is significantly different from
381 sediment surface samples. For the lake-sediment surface samples, overrepresentation of upper
382 montane forest taxa in the pollen spectra is much more pronounced than in the moss polsters.
383 We show that pollen rain in moss polsters closely tracks the local vegetation, whereas
384 samples from lakes reflect a more regional vegetation cover. For example, *A. acuminata*
385 reaches a maximum of ~20% in the upper páramo samples, but is entirely absent in the
386 vegetation relevés. *A. acuminata* does not grow above the upper forest line, demonstrating its
387 high pollen productivity as well as upslope wind-transport of its pollen. This corresponds
388 with observations in the Colombian Andes, where the first 20% of *A. acuminata* was
389 considered to be mainly a background effect and only a percentage above 20% indicates that
390 *A. acuminata* occurred *in situ* (Hooghiemstra, 1984). Pollination strategies in neotropical tree
391 taxa (mostly anemophilous) contribute to a biased representation of these taxa in lake
392 sediments (Bush and Rivera, 2001; Moscol-Olivera et al., 2009). The relatively open
393 structure of the páramo, combined with upslope wind pollen dispersal (Bush, 2000; Weng et
394 al., 2004; Moscol-Olivera et al., 2009; Niemann et al., 2010; Urrego et al., 2011b) and

395 convection (Ledru et al., 2012) in the Andean mountains most likely further amplifies the
396 relatively high deposition of upper montane forest pollen in the sediment surface samples of
397 lakes in the páramo.

398 Yet, despite overrepresentation, differences in the distribution of pollen taxa in
399 samples from the lakes along the temperature gradient are observed. Overall, the association
400 indices show that Apiaceae, Asteraceae, Cyperaceae, *Hypericum* spp., *Phlegmariurus* spp.,
401 Melastomataceae, *Plantago* spp., *Polylepis* spp., and Valerianaceae represent mostly local
402 vegetation signals. *R* values (Davis, 1963) or *t/P* values (Grabandt, 1980, 1985) were not
403 calculated because of the limited dataset of less than 30 paired pollen-rain-vegetation samples
404 (Moscol-Olivera et al., 2009), yet our data provide first-order estimates that are greatly
405 needed in this part of the Andes. The ordination analyses show that pollen spectra from the
406 upper montane forest at ~3100 m asl/9.7°C (T_{mean}) are compositionally different from those at
407 higher elevations/lower temperature (e.g., ~4050 m asl/3.5°C T_{mean}). Samples from the lake
408 situated in the upper montane forest (Laguna Llaviucu) consistently reflect local forest taxa
409 recorded in the vegetation relevés. With the necessary caution to infer conclusions from a
410 small dataset that does not cover the entire range of the montane forest (<3100 m asl), our
411 results suggest that *Podocarpus* spp., *Hedyosmum* sp., and *Weinmannia* spp., could serve as
412 indicator species for upper forest line dynamics in palaeorecords. Indeed, *Weinmannia* spp. is
413 a common entomophilous tree in the Andean forest (Moscol-Olivera et al., 2009b) and
414 various studies have reported pollen abundance peaks in samples from the upper montane
415 forest >2800 m asl (Rull, 2006; Moscol-Olivera et al., 2009; Urrego et al., 2011b). Earlier
416 observations in northern Ecuador and the eastern Cordillera of Colombia have shown that
417 pollen signals of *Weinmannia* spp. give a reliable indication of the presence of local Andean
418 forest (Grabandt, 1980; Moscol-Olivera et al., 2009). Our results extend these observations to
419 the western Cordillera of the southern Ecuadorian Andes. Although previous research

420 indicated that *Podocarpus* spp. shows a large elevational range in field observations (Groot et
421 al., 2013), our results suggests that in the CNP *Podocarpus* spp. is a local signal of montane
422 forest. Pollen spectra from páramo lakes (>3500 m asl/<7°C T_{mean}) are characterized by
423 páramo taxa such as *Phlegmariurus* spp. and *Plantago* spp, while pollen spectra from moss
424 pollsters are also characterized by Apiaceae and Valerianaceae. In northern Ecuador, pollen
425 spectra obtained from moss pollsters and pollen traps indicate that Apiaceae, Poaceae, and
426 Cyperaceae point at the presence of local páramo vegetation (Moscol-Olivera et al., 2009).

427 Previous work in the northern Tropical Andes showed that altitude—and by inference
428 temperature—is the main controlling factor for the composition of pollen assemblages (Rull,
429 2006), thus allowing the estimation of palaeoaltitudes and palaeotemperatures from pollen
430 records (Hooghiemstra, 1984; Wille et al., 2001; Rull, 2006; Groot et al., 2011). We show
431 that temperature is indeed a driver of compositional changes in pollen spectra in sediment
432 surface samples as has been suggested for other Andean locations (Rull, 2006). Our results
433 suggest that compositional changes in the pollen spectra from sediment surface samples can
434 be used as a tool to estimate species optima and consequently to estimate palaeotemperature
435 in the Tropical Andes, although palaeoclimatological reconstructions have pointed at other
436 possible drivers (e.g., pCO₂) of floral compositional change (Groot et al., 2011).

437 The palynological richness documented in the moss polsters was significantly
438 correlated to local vegetation richness, supporting earlier work in the Tropical Andes (Weng
439 et al., 2007; Jantz et al., 2013). The palynological richness documented in the moss polsters is
440 reflecting local vegetation diversity (alpha diversity), which is in line with earlier work in the
441 Tropical Andes, showing that palynological richness reflects the richness of the local
442 vegetation (Weng et al., 2006; Jantz et al., 2013). In contrast to moss polsters, our results
443 show that palynological richness in sediment surface samples does not reflect local floral
444 species richness. The relatively higher palynological richness for the sediment surface

445 samples likely reflects diversity from a diverse landscape (beta diversity). Hence,
446 reconstructions of plant diversity in the fossil pollen record should clearly consider the
447 diversity of the local parent plant vegetation (alpha diversity), pollination syndromes of the
448 parent plants, and landscape heterogeneity (beta diversity; Gosling et al., 2018).

449 **Pollen transport distance in high-elevation Andean lakes**

450 Our study provides a first-order estimate of pollen transport distance between
451 vegetation and lake sediments from high-elevation Andean lakes in both upper montane
452 forest and páramo settings. Laguna Llaviucu, which is located in the upper montane forest,
453 has a much lower mean pollen transport distance (1–2 km) compared to Laguna Pallcacocha
454 (10–40 km), which is situated in the páramo. Possibly, the closed canopy of the forest
455 combined with weak winds in the trunk space reduced the pollen dispersal distances. Above
456 the upper forest line, the relatively open structure of the páramo combined with upslope
457 pollen dispersal most likely increases the pollen transport distance for high-elevation Andean
458 lakes (Bush, 2000; Weng et al., 2004; Moscol-Olivera et al., 2009; Niemann et al., 2010;
459 Urrego et al., 2011b). This means that, based on the vegetation composition buffers,
460 palaeoecological reconstructions based on lake sediments from the upper montane forest
461 represent local vegetation dynamics within a 1–2 km radius around the lake. On the other
462 hand, fossil pollen records from lakes in the páramo of CNP capture a regional signal up to
463 and possibly even above a 40-km radius. The difference in pollen representation between
464 lakes immersed in upper montane forest and lakes immersed in páramo is supported by
465 multiproxy evidence in Jansen et al. (2013), where the molecular biomarker-signal from a
466 mire in northern Ecuador was used to reconstruct the upslope migration of the upper forest
467 line during the late Holocene. For post-glacial forest development, the study by Jansen et al.
468 (2013) found a significant lag between pollen (earlier) and biomarkers (later), suggesting that
469 the upslope movement of the forest line happened later in time than would be expected on the

470 basis of pollen alone. Molecular biomarkers are not influenced by aeolian transport and
471 provide a good proxy for *in situ* vegetation dynamics (Jansen et al., 2013). When compared to
472 the pollen record of the mire in northern Ecuador, the results from Jansen et al. (2013) show
473 that a pollen record from a site that was always located in the páramo was influenced by
474 upslope aeolian pollen transport while, in pollen records from sites below the upper forest
475 line, upslope aeolian pollen transport does not influence the reconstruction. Therefore,
476 multiproxy analyses can significantly improve local vegetation reconstructions in páramo
477 sites. In the context of quantitative reconstructions of past vegetation using a modelling
478 approach, e.g., the REVEALS model (Sugita, 2007), our results show that conventional
479 theories in pollen-vegetation relationships in non-mountainous areas cannot be directly
480 applied to areas with steep topography and high landscape heterogeneity. Landscape
481 reconstructions models such as REVEALS, however, hold great potential for
482 palaeoecological reconstructions in the Tropical Andes, since such models can correct for
483 biases in pollen percentages caused by differences in pollen productivity and dispersal
484 between taxa (Sugita, 1994; Hellman et al., 2008). Given the overrepresentation of arboreal
485 taxa in the páramo of CNP, Ecuadorian Andes, we suggest that more attention should be paid
486 to developing, testing, and validating models such as REVEALS for regions with steep
487 vegetation and altitudinal gradients such as the Tropical Andes.

488 **CONCLUSION**

489 Pollen spectra from moss polsters and sediment surface samples along an upper-
490 montane-forest-páramo ecotone reflect changes in species composition along a temperature
491 gradient of 7°C (altitudinal gradient: 3100–4200 m asl), despite overrepresentation of upper
492 montane forest taxa in the pollen rain. The pollen rain spectra from moss polsters reflect the
493 local vegetation, while pollen spectra from páramo lake sediments reflect a regional
494 vegetation cover up to 2–40 km distance depending on position within the landscape (upper

495 montane forest or páramo). The ordination analysis show that in the pollen spectra from lakes
496 *Weinmannia* spp., *Podocarpus* spp., and *Hedyosmum* sp. are indicators of local upper
497 montane forest vegetation and could be indicator species for upper forest line dynamics,
498 while *Phlegmariurus* spp. and *Plantago* spp. are indicators of local páramo vegetation. Other
499 taxa representative of local vegetation include Asteraceae, Cyperaceae, *Hypericum* spp.,
500 *Plantago* spp., *Polylepis* spp., and Valerianaceae. Palynological richness in the moss polsters
501 was significantly related to local vegetation richness (alpha diversity), but this relationship
502 was not found for the sediment surface samples because the pollen rain in sediment surface
503 samples likely reflects diversity from a diverse landscape (beta diversity). Important factors
504 influencing the modern pollen rain, and subsequently the palynological richness, are
505 variations in pollination syndromes, open vegetation structure, and upslope wind pollen
506 dispersal, which consequently contribute to the size of the mean pollen transport distance of
507 high-elevation Andean lakes. Estimated pollen transport distance for a lake situated in the
508 upper montane forest is 1–2 km, while lakes in the páramo capture pollen from a distance of
509 10–40 km.

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691 **Table 1.** Coordinates, altitudes, and estimated sizes of lakes sampled in 2015.

692 **Table 2.** Association indices for taxa found in the vegetation and/or in the modern pollen
693 rain. $A = 1$ when the pollen type and the plant taxon are both present; $A = 0$ when either the
694 pollen type or the parent plant is absent.

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698 **Figure 1.** (color online) Study region. (A) Elevation map showing the location of CNP in
699 Southern Ecuador (SRTM data, USGS 2014). (B) Map showing vegetation types in CNP
700 region and sampling locations of this study. (C) Elevation profile across the Ecuadorian
701 Andes (SRTM data, USGS 2014) with the research location, major vegetation types, and
702 wind patterns.

703 **Figure 2.** (color online) Diagrams with pollen percentages of total pollen from moss polsters,
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708 **Figure 4.** Ordination analyses. (A) Canonical correspondence analysis (CCA) performed on
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710 sample type as the constraining variable. (B) CCA performed on percentage data of pollen
711 taxa found in moss polsters with temperature as the constraining variable. (C) Temperature
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718 **Figure 6.** (color online) Sensitivity analysis of land cover percentages at a certain radius (km)
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