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1 ***Espeletia* giant rosette plants are reliable biological**
2 **indicators of time since fire in Andean grasslands**

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***Espeletia* giant rosette plants are reliable biological indicators of time since fire in Andean grasslands**

1 Abstract

Páramo grasslands in the tropical Andes are fire prone ecosystems and an understanding of their fire ecology is fundamental to biodiversity conservation and ecosystem management. Fire registers are normally impractical in these remote, cloud-covered landscapes, but *Espeletia* giant rosette plants have been proposed as biological indicators of time since fire in páramos. *Espeletia* giant stem rosettes tolerate fire well, protecting apical buds in at the heart of their leaf rosettes, and for some species, germination is known to be enhanced by fire. As the plant grows, its dead leaves remain attached to the stem, but fire removes these and resets the “leaf clock”. This study uses a unique register of fires in one Ecuadorian páramo to assess the robustness of this biological indicator. Dead leaf cover on *Espeletia pycnophylla* giant rosette plants was measured in fifteen different sites with known fire dates from 2000 to 2014. The growth rates of plants at four different elevations were measured over a two-year period and used to estimate time since fire based on dead leaf cover in the known sites. Estimates were accurate to ± 2 y. Thus, where fire records are missing, relatively easy measurements of growth rates and dead leaf cover of *Espeletia* giant rosette plants can provide reliable estimates across a wide range of times since fire. This approach has value for direct investigations into fire ecology but also for studies in which controlling for fire dynamics is necessary to reveal underlying patterns. Therefore, this approach also offers a means to obtain better information on other landscape-scale processes such as the impact of climate change on biodiversity or the provision of ecosystem services.

Key words: páramo, burning, growth rates, fire regimes, fire history, landscape ecology

2 Introduction

Fires occur in nearly every terrestrial biome on Earth, simply because wherever vegetation grows there is the potential for it to burn (McKenzie et al. 2011). Fires represent a ‘punctuated’ form of disturbance and can instantly ‘reset’ vegetation succession, plant

37 community composition, species dominance, and spatial patterns (McKenzie et al. 2011;
38 Ramsay 2014). These drastic effects of fire are not always aligned with and can conceal the
39 subtler signals of more continuous ecological processes, such as climate change.

40 Understanding fire regimes and the current stage of vegetation in the fire recovery cycle is
41 crucial to separate fire responses from longer-term ecological trends and thus facilitate
42 investigations into the general response of biodiversity to environmental change in fire
43 prone ecosystems. Satellite imagery and remote sensing have revolutionized the study of
44 fires in landscapes, but are not feasible methods in some cases where cloud cover and lack
45 of resources limit these technology dependent methods (Ramsay 2014). It would be useful
46 to have a simple, on the ground method to reconstruct recent fire history. It has been
47 proposed that plants might provide a way of estimating time since fire, if their growth after
48 fire is predictable.

49 Tropical alpine regions support fire-prone ecosystems in which the lack of fire records
50 hampers studies into fire ecology, biodiversity conservation and management, and the
51 monitoring of climate change. Tropical alpine ecosystems occur in the upper regions of the
52 Andes, the Afroalpine belt and to a lesser extent, Indonesia and Papua New Guinea
53 (Buytaert et al. 2011). The high altitude grasslands of the Northern Andes, known as
54 *páramos*, are the largest extension of tropical alpine ecosystems, covering an area of around
55 35,000 km² (Madriñán et al. 2013). The páramos are hotspots of biodiversity and endemism
56 (Myers 2006) and provide essential ecosystem services, such as water provision and carbon
57 storage (Buytaert et al. 2011) that sustain biological processes on both local and global
58 scales, and support the livelihoods of millions of people (Buytaert et al. 2006). Global
59 climate change is predicted to displace ecosystem boundaries and the increased isolation of
60 remaining páramo patches is expected to induce species extinction and biodiversity loss
61 (Buytaert et al. 2011). Drier and warmer soil conditions are predicted to cause faster organic
62 carbon turnover, decreasing below ground organic carbon storage. These changes may have
63 major impacts on water supply (Buytaert et al. 2011). Thus, conservation and sustainable
64 management of the páramo is vital.

65 Páramo landscapes have been burned regularly by people for thousands of years (Laegaard,
66 1993; Horn & Kappelle, 2009). The páramos are used extensively for grazing of livestock,
67 and burning of vegetation encourages new, more nutritious growth for grazing (Laegaard
68 1992; Ramsay & Oxley 1996). The frequency of burning depends on vegetation recovery but
69 is typically every 2 to 5 years (Ramsay & Oxley 1996). Accidental fires have increased as
70 visitor numbers have grown in recent decades (Ramsay 2001). These fires play an intrinsic
71 ecological role in the páramo and local fire regimes have been shown to impact biodiversity,
72 vegetation composition and ecological dynamics, agricultural production, soils, and
73 hydrology (Ramsay 2014; Sklenář & Ramsay 2001). The páramos contain a wide array of
74 specialized plant species extraordinarily well adapted and resilient to fire (Laegaard 1992).
75 Fire disturbance creates a competitive advantage for those plants with suitable adaptations
76 and without doubt determines the detail of biodiversity composition and ecological
77 dynamics of modern páramo grasslands (Horn & Kappelle 2009; Ramsay 2014). A better
78 understanding of the nature of fire regimes, the ability and time needed for páramo plant
79 communities to recover from burning, and the impacts of fire on ecosystem service
80 provision is essential to determine whether management decisions are beneficial from an
81 ecological perspective (Hardesty et al. 2005).

82 Unfortunately, investigations of post-fire dynamics in the páramo are limited by the lack of
83 information about fire history. Fire records are very rarely kept, and even when they are,
84 they are incomplete. Monitoring fires on the ground is difficult in the remote and rugged
85 páramos, and high cloud cover limits remote sensing and satellite imagery methods of
86 assessment (Ramsay 2014). The use of ecological indicators has been proposed as a possible
87 approach to determine time since fire at a landscape scale in the páramo. In Costa Rican
88 páramos, the growth rings of certain shrubs can be used to date fires (Horn 1989; Kerr et al.
89 2017; Williamson et al. 1986), but this approach is limited in the páramos of northern
90 Ecuador because shrubs do not reliably form annual growth rings there (personal
91 observation by authors). Garcia-Meneses and Ramsay (2014) investigated the use of *Puya*
92 giant rosettes plants to estimate time since fire. Pulses of recruitment of *Puya* occur soon
93 after fires and result in a cohort of plants of the same age. However, there was found to be

94 a large margin of error as the recruitment pulse may take place within a window of several
95 years after fire.

96 Ramsay (2014) proposed that *Espeletia* giant rosette plants have potential to indicate recent
97 fire history more accurately. *Espeletia* giant rosettes are characteristic plants of the
98 Northern Andes (Diazgranados 2012) and of ecological importance because they represent a
99 large proportion of the biomass in páramo ecosystems, help to regulate the hydrological
100 cycle, and prevent soil erosion (Garcia et al. 2004). The subtribe Espeletiinae currently has
101 eight recognized genera, 141 species, and 17 subspecies (Diazgranados 2012). *Espeletia*
102 cover large areas of the páramos of Colombia, Venezuela and northern Ecuador
103 (Diazgranados 2012; Luteyn et al. 1992), with the potential to act as an indicator of time
104 since fire throughout these grasslands. *Espeletia* giant rosettes have a peculiar morphology,
105 specifically adapted to the high elevation and harsh climate of the tropical mountain
106 environment (Carlquist 1994; Ramsay 2014). *Espeletia* are very resilient to fire, protecting
107 apical buds in giant leaf rosettes lifted above the ground (Laegaard 1992). Ramsay (2014)
108 documented mortality of adult *Espeletia* plants at 2.5% in unburned vegetation, but higher
109 after burning (8% for a low intensity fire to 56% for a very high intensity fire). Germination
110 of some species eg. *Espeletia pycnophylla* is known to be enhanced by fires due to the
111 availability of open space, light and nutrients (Laegaard 1992; Suárez & Medina 2001). Many
112 species of *Espeletia* retain dead leaves on the stem (known as marcescence), which serve to
113 insulate the water reserve inside the plant during cold nights (Goldstein & Meinzer 1983).
114 These marcescent leaves are normally burned away during a fire, but clothe the stem that
115 grows afterwards. If the stem growth rate of the population is known, then the time taken
116 to grow the stem that appears after a fire can be calculated—a kind of “leaf clock”.

117 This study builds upon Ramsay’s (2014) proposal, seeking to test the effectiveness and
118 limitations of the approach and to refine it across a wide range of study sites and times
119 since fire. A unique set of historical fire dates since 2000 has been recorded for the páramo
120 of El Ángel and Volcán Chiles, northern Ecuador, which is dominated by *Espeletia*
121 *pycnophylla* Cuatrec., a species typical of the páramos of this region, including parts of
122 southern Colombia (Diazgranados 2012). We compared recorded fire dates with time-since-

123 fire estimates, based on *Espeletia* leaf cover and growth rates, to check the accuracy and
124 robustness of the indicator approach. For the longer-term, we wanted to demonstrate the
125 use of *Espeletia* species more generally to assess recent fire histories in páramos across the
126 northern Andes, in order to inform sustainable management of these important
127 ecosystems, and to promote the use of plants as indicators of fire in ecosystems around the
128 world.

129 **3 Methods**

130 **3.1 Study areas**

131 The Reserva Ecológica El Ángel (REEA) is part of the Ecuadorian system of protected areas,
132 and is managed by the Ministry of Environment. The reserve was set up to protect semi-
133 natural and natural ecosystems (mostly high-altitude páramo grasslands) and is surrounded
134 by landscapes where agriculture is the main land use. Contiguous with the northern
135 boundary of the REEA is the páramo of Volcán Chiles, now managed as a private reserve by
136 the Comuna Esperanza, historically a farming cooperative, based in nearby Tufiño. Like most
137 páramo grasslands in Ecuador, fires have been frequent in REEA and Volcán Chiles in recent
138 decades. Typically, fires have been set to improve livestock forage, to facilitate hunting, or
139 by accident (Ramsay 2001). Concerned by the potential ecological damage caused by these
140 fires within the reserve, the Pontificia Universidad Católica del Ecuador carried out two
141 studies with help from park officials and local fire brigades, and technical assistance from
142 Randi Randi, an NGO. The first project created an inventory of known fires from 2000–2008
143 (Valdospinos Navas 2008), while the second established a protocol for registering fires after
144 2008 (Bustos Insuasti 2008). These projects also included the páramo beyond the strict
145 limits of the reserve itself in the agricultural buffer zone. As a consequence, good quality
146 information exists in and around REEA about known fire dates in particular places. Before
147 2008, these dates were recorded only at the level of year, but subsequently precise dates
148 have been recorded. The information is not comprehensive, in that some fires might have
149 occurred without being recorded, especially smaller ones, but many fires have been noted.
150 These records appear to be unique in the páramos for this span of time and represent a
151 valuable resource for studying the effects of fire on this ecosystem.

152 To establish whether *Espeletia* giant rosette plants can be used to successfully estimate time
153 since fire, fifteen locations on the Western Cordillera within REEA and its buffer zone were
154 selected to represent a range of times since fire (burned from 2000–2014, representing <1
155 to 15 y ago at the time of survey) at elevations of 3500–3900 m. All were within two hours'
156 walking access from a road, for logistical reasons as well as the likelihood that fire records
157 nearer to the roads would be more comprehensive than in less frequently visited, remote
158 places. Each fire site was located with GPS coordinates obtained from the records.

159 More recently, the fire brigade in San Pedro de Huaca, Carchi, Ecuador, has also begun
160 recording fires in páramo grasslands on the Eastern Cordillera in northern Ecuador. Three
161 additional sites were included from the páramo of La Bretaña, all at elevations of 3600–
162 3750 m and burned within 2½ years of the survey.

163 The páramo grasslands in the study areas were dominated by *Calamagrostis* tussock grasses
164 and giant rosettes of *Espeletia pycnophylla* Cuatrec. This species of *Espeletia*, like many
165 others in the northern Andes, retains marcescent leaves on the stem. These plants are
166 found at high densities throughout these páramos, counted at 1300–5400 adult plants ha⁻¹.
167 Some plants achieve heights of more than 4 m, but most die or fall over before they reach
168 that size.

169 **3.2 Field measurements and data analysis**

170 Growth rates of *Espeletia* plants were measured from March 2012 to March 2014. At the
171 start of the period, ten plants approximately 1 m tall were randomly selected at each of four
172 elevations on Volcán Chiles (3600, 3800, 4000, and 4200 m) and the well-defined lower limit
173 of the living rosette was marked with string around the stem. Close to two years later, the
174 difference between the string and the new lower limit of the living rosette was measured to
175 the nearest centimetre. From these measurements and the time difference between
176 observations, mean annual stem growth rates were calculated for each elevation.

177 At each of the fifteen fire sites, we randomly selected 50 *Espeletia* plants with a lower limit
178 of marcescent leaf cover 1–1.5 m above the ground. This indicated that these plants would
179 have been 1–1.5 m tall at the time of the last fire, a height which showed consistent leaf
180 removal by flames in an earlier study (Ramsay 2014). The marcescent leaf cover of each

181 plant was measured: the length of stem with accumulated dead leaf blades (not leaf bases
182 alone) from their attachment point on the stem to the base of the living rosette (Fig. 1). In
183 rare cases of asymmetrical fire damage, measurement was always taken from the side of
184 the plant where the fire burned highest on the stem.

185 The mean growth rates and dead leaf cover were combined to estimate time since fire.
186 Simply, the height of stem with marcescent leaves attached was divided by the growth rate
187 to give the number of years needed to grow that amount of stem. Ramsay (2014) suggested
188 an adjustment to correct for unrepresentative growth rates during an initial period after the
189 fire. However, we did not apply such an adjustment in this study. Although there might be
190 potential for underestimating time since fire, because the rosettes might have initially
191 grown more slowly as they recovered from the fire, an overestimation is also possible, since
192 green leaves in the living rosette are often killed but not destroyed by the fire. The
193 marcescent leaves formed by these leaves do not indicate post-fire regrowth. The balance
194 between these processes of under- and overestimation is unknown at present, and so no
195 attempt was made to adjust estimates in this way.

196 Ramsay (2014) also recommended removing the greatest and lowest 10% of marcescent
197 leaf cover measurements from a 50-plant sample, leaving an 80% core of 40 plants. This was
198 intended to remove outliers of unusual fire experience or subsequent regrowth from the
199 calculations. To explore further the effect of this approach, the consistency of marcescent
200 leaf cover measurements was evaluated by comparing leaf cover statistics for a range of
201 different subsample sizes from the 50 measured plants at each site (all plants; 96%; 80%;
202 60%; 40%). A check was also made to see if variability in dead leaf cover within populations
203 at each site changed predictably with time since fire.

204 Ultimately, a comparison was made between known times since fire—from the records—
205 and those estimated from marcescent leaf cover. Standard statistical tests were performed
206 with IBM SPSS statistics for Macintosh (Version 23, Armonk, New York, USA).

207 **4 Results**

208 *Espeletia* annual growth rates fell into two groups: plants at 3600 and 3800 m elevations
209 grew at just over 9 cm y^{-1} , while plants at 4000 and 4200 m grew 2–3 cm y^{-1} less (Kruskal-
210 Wallis $X^2=35.908$, $df=3$, $p<0.001$; Fig. 2). At 3600 m elevation, the mean growth rate of
211 *Espeletia* plants was 9.28 cm y^{-1} . This figure was used to calculate estimates of time since
212 fire for all but one of the plots, since they were located at similar elevations. One plot was
213 located at 3900 m, so a different figure of 7.89 cm y^{-1} was used for the calculations there.

214 Marcescent leaf cover on *Espeletia* stems was measured for 50 plants at each of the sites.
215 Table 1 presents five options for calculating the mean for use in the subsequent estimates.
216 With no or few outliers removed (all or 96% subsamples), the higher variability among the
217 plants at a site made distinguishing between sites less clear-cut (indicated by the multiple
218 comparison of means tests). With a larger number of plants excluded from the extremes
219 (60% and 40% subsamples), distinguishing between sites became compromised by the
220 smaller sample size. The most effective option was removing five plants from each extreme
221 of the distribution (80% subsampling). This was the option used to calculate the estimates
222 that follow.

223 As time since fire increased, mean marcescent leaf cover increased predictably (regression:
224 $F_{1,14}=82.51$, $p<0.001$; Fig. 3A). In addition, the variability of mean marcescent leaf cover also
225 increased predictably (regression: $F_{1,14}=21.69$, $p<0.001$; Fig. 3B).

226 Estimates of time since fire made on the basis of marcescent leaf cover matched well with
227 known fire dates (regression: $F_{1,14}=115.96$, $p<0.001$; Fig. 4), with 14 out of 15 fire sites within
228 1.8 years of the known fire date.

229 **5 Discussion**

230 *Espeletia pycnophylla* marcescent leaf cover showed predictable growth after fire, and
231 measurements of marcescent leaf cover in known sites provided effective estimates of time
232 since fire, up to 15 years after fire. The use of *Espeletia*'s "leaf clock" for estimating when
233 the last fire happened at a particular site seems to be reliable well within the timeframe of

234 typical fire cycles in the páramo grasslands of the northern Andes, normally at intervals of
235 2–5 years (Keating 2007; Ramsay & Oxley 1996).

236 However, the variability of marcescent leaf cover increased as time since fire elapsed. The
237 standard deviation of marcescent leaf cover measurements reached the equivalent of 8–9
238 months of growth by 5 y after a fire, and just over two years of growth by 15 y after a fire.
239 This is an acceptable level of error, where no other means of estimating time since fire
240 exists, and is consistent with the concept of a population where individual growth rates vary
241 slightly from plant to plant. As time goes by, these differences accumulate and variation in
242 marcescent leaf cover increases within a sample of plants. Microtopographic factors might
243 promote or restrict growth of individual plants, for example by affecting water availability
244 (Pérez 1987). Competition with neighbours and genetic variation could also contribute to
245 individual growth rate variability. *Espeletia* height has also been shown to affect individual
246 growth rates (Ramsay 2014). As plants grow taller, night-time rosette temperatures
247 decrease and slower metabolism, even damage to the plant's apical meristem, becomes
248 more likely. However, at lower elevations, this is likely to be outweighed by warmer
249 temperatures and improved daytime growth. *Espeletia* plant stems hold an inner reservoir
250 of water that, insulated by the marcescent leaves, provides a supply of unfrozen water to
251 the leaves in early morning when soil water is potentially still too cold to be of use
252 (Goldstein & Meinzer 1983). Therefore, as time passes after a fire, surviving *Espeletia* plants
253 at the elevations studied here would be expected to increase in growth rate as they grow
254 taller—and this might also contribute to the increased variance in leaf cover over time.

255 To some extent, the variability in individual growth rates can be taken into account by
256 removing outliers with particularly rapid or slow growth, compared with the more general
257 population. In this study, we followed Ramsay's (2014) original proposal for including only a
258 core 80% of 50 plant measurements. It did provide a suitable protocol for removing unusual
259 outliers, while maintaining an appropriate sample size. Apart from the reasons noted above,
260 outliers are also likely in variable, low intensity, fast moving fires that occasionally miss
261 entire plants, leaving their leaves intact (Ramsay, 2014). Since this situation does not always
262 reflect the fire conditions, it is not surprising that excluding outliers did not make much of a

263 difference to the mean estimates of most sites. Nevertheless, excluding outliers routinely
264 does provide some confidence that the potential impact of this issue would be addressed.
265 Furthermore, in cases of asymmetrical marcescent leaf cover, the accuracy of our
266 estimations suggests that measuring the side of plant where the fire burned highest on the
267 stem was an effective approach.

268 In addition to differences in leaf cover between plants within a site, there are likely to be
269 variations in growth rate between sites, at the population level. The intensity of the fire
270 might have an impact on the recovery and subsequent growth rates of surviving plants. Fires
271 burning upslope, with the wind, are likely to be of low intensity, burning quickly and lightly
272 across the area. The vegetation would be damaged less and likely to recover more quickly.
273 Some *Espeletia* plants might be missed by such fires altogether. Contrastingly, slowly
274 burning, intense fires might result in high levels of mortality and much longer periods of
275 reduced growth afterwards. For example, the time since fire of one of the sites included in
276 this study was not estimated well. The site was known to have been burned 9 years before
277 the observations were made, but leaf cover measurements overestimated this time by
278 nearly three years, suggesting growth rates were faster at this site. The site was located on
279 steep slope and the vegetation was unusually dense, with tall shrubs and tussock grasses.
280 The slope and topography could have created conditions for a low intensity fire. We found a
281 high standard deviation of leaf cover measurements at this site, consistent with the
282 expectations of a low intensity fire.

283 Elevation strongly influenced *Espeletia* growth rates. Growth rates varied from 6.64–
284 9.28 cm y⁻¹, with a marked decrease between 3800 and 4000 m. *Espeletia* growth depends
285 strongly on light and temperature. The moist adiabatic lapse rate is around 5–6 °C per
286 kilometre increase in elevation, and would be expected to reduce growth rates. However, in
287 these tropical mountains, soil temperature is strongly linked to solar radiation, which in turn
288 is controlled partly by cloud cover. Based on observations in the study area over 25 y by one
289 of the authors, the cloud base in the páramo of El Ángel and Volcán Chiles usually sits
290 around 3900 m. Plants below the cloud base receive more light, while those above the line
291 of the cloud base are in the cloud, resulting in foggy conditions with lower levels of light and

292 temperature. This helps to explain the marked decline in growth rate from 3800 to 4000 m.
293 Mountain topography can also affect growing conditions, such as that found at the 4100 m
294 road pass on Volcán Chiles from east (exposed, mostly cloudy) to west (sheltered, mostly
295 sunny). The growth measurements at 4200 m were made on the ridge in a zone where the
296 cloud dissipated as it began to descend down the western flanks of the mountain. *Espeletia*
297 growth was not significantly different at this elevation compared with plants 200 m lower
298 down the mountain in more constant cloud cover. These variations in plant response to
299 local conditions illustrate the value of measuring growth rates in a number of different
300 locations within a páramo landscape. Since these measurements only require some string, a
301 tape measure, and the ability to relocate marked plants at a future date, we recommend
302 collecting as much data on growth rate as is practical.

303 Another factor influencing growth rates is the variation in climate from year to year. In
304 particular, plant responses in the páramos have been linked to the El Niño Southern
305 Oscillation or ENSO (Luteyn 1999), which often results in less humidity in the mountains of
306 Ecuador and Colombia (Buytaert et al. 2006). In areas where water is not normally limiting,
307 plant growth could be promoted by the clearer skies. As an example, Ramsay (2014)
308 measured a mean *Espeletia* growth rate of 14.8 cm y⁻¹ at 3600 m elevation in northern
309 Ecuador, immediately after the 2009–2010 ENSO. This contrasts with the slower growth
310 rates of 9.28 cm y⁻¹ presented in this current study, from the same páramo and elevation,
311 but obtained over two years between ENSO events. It highlights the need to measure
312 growth rate over several years, and the need to consider the influence of climatic events like
313 the ENSO in interpreting variations in leaf cover in sites with different fire histories.

314 The success of using giant rosette marcescent leaf cover and growth rates to estimate time
315 since fire has important implications for future ecological research in the *Espeletia*-
316 dominated páramos of northern Ecuador and Colombia. To this point, investigations of fire
317 impacts have been limited by the absence of fire records. The ability to estimate time since
318 fire allows for more comprehensive investigations of the direct impacts of fire on plant
319 communities, soils, and water provision through time. Fire histories are also influential in
320 investigations of longer term changes in the páramo, such as the impact of climate change

321 or elevation on biodiversity. Fire causes greater shifts in both environmental conditions and
322 plant community composition than the subtler effects of long term change. It is therefore
323 important to know the stage of the fire cycle of each study site to control for the fire effects.
324 This method will allow investigations to control for time since fire and will provide a means
325 to carry out better studies in future (Ramsay 2014).

326 To encourage the use of this simple approach elsewhere in the northern Andes, we provide
327 a protocol that explains clearly how to measure *Espeletia* growth rates and marcescent leaf
328 cover (Online Resource 1). It includes examples of simple calibration graphs could be taken
329 into the field for rapid assignment of a site to a time since fire. Similar calibration graphs
330 could be developed for other páramos where fires are common.

331 Although this study was restricted to just one species of *Espeletia*, other species have
332 potential as indicators, such as *Espeletia grandiflora* Humb. & Bonpl. in Colombia. Initial
333 work with this species in Chingaza National Park has shown similar results to those
334 published here, but more detailed studies should be carried out to confirm the suitability of
335 this approach with other indicator species.

336 Of course, this approach to estimating time since fire is only directly applicable in regions
337 with *Espeletia*. However, the principles of this indicator method may also have potential in
338 the fire prone mountain grasslands of East Africa, where convergent evolution has produced
339 a strikingly similar collection of plant forms (Smith 1994). The morphology, seedling
340 establishment and growth of Andean *Espeletia* and East African *Senecio keniodendron* are
341 remarkably alike, as are the life history strategies of Andean *Puya* (also with potential as a
342 fire indicator) and East African *Lobelia* (Garcia-Meneses & Ramsay 2014).

343 Southern Ecuador, Perú, Costa Rica, and Panamá all have páramos with tussock grasses, but
344 without *Espeletia* giant rosettes species. These regions have regular fire disturbance too,
345 and face the same challenges of habitat conversion, climate change, and the need for
346 sustainable management (Horn & Kappelle 2009). It would be useful to have a field method
347 of indicating time since fire in these regions also. Tussock grass development through time
348 after fire has potential in this regard, but other indicators should also be considered such as
349 growth rings or zones in shrubs (Kerr et al. 2017).

350 While time since fire is a very important factor of fire regimes, it is not the whole story. This
351 method of indicating time since fire from *Espeletia* marcescent leaf cover does not reveal
352 the frequencies of fire events or the intensity of the last fire. Fire frequency, ‘the number of
353 fires per unit time in a particular stand of páramo’ (Horn & Kappelle 2009), is thought to
354 determine the vegetation structure and fuel availability of a site, influencing the spatial
355 extent and intensity of fires (Keating 2007). Fire intensity is a very important factor of fire
356 regimes and has been shown to have differential and significant impacts on the survival of
357 plants during fire and the trajectory of plant community recovery. More research on fire
358 frequencies and intensity is needed.

359 **6 Conclusions**

360 *Espeletia pycnophylla* marcescent leaf cover can be used as an effective indicator of time
361 since fire in *Espeletia*-dominated páramo grasslands of Ecuador and potentially Colombia,
362 given known growth rates. This approach is relatively inexpensive and simple, requiring no
363 special equipment. Simple growth studies are needed to calibrate this method to local
364 conditions. This indicator approach can be included in all future studies for which fire
365 histories are influential. Relevant studies include direct investigations of the impacts of fire
366 on biodiversity and vegetation recovery in the páramo. Indirect studies include those of the
367 subtler impacts of longer term environmental change in the landscape, where signals of
368 change are often confused by the more immediate effects of fire. The wider applicability of
369 this indicator approach is to facilitate studies of fire effects on ecosystem services, such as
370 water provision and carbon storage, in the páramo. Ultimately, this study contributes to the
371 understanding of how fires can be included in management planning for these grasslands
372 and how plants themselves can be used as biological indicators of fire.

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384 used in Fig. 1.

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458 **9 Tables**

459 **Table 1.** Consistency of *Espeletia* leaf cover measurements with different subsampling of the
 460 complete sample. Mean \pm standard error of marcescent leaf cover calculated for subsample
 461 sizes selected from the total of 50 plants of each site (all plants; 96%, 80%, 60%, 40%).
 462 Means sharing a letter were not significantly different according to a Student-Newman-
 463 Keuls test, following a Kruskal Wallace test ($df=14$ and $p < 0.001$ in every case).

Time since Fire (y)	Observed Mean \pm SE marcescent leaf cover in subsample				
	All (n=50)	96% (n=48)	80% (n=40)	60% (n=30)	40% (n=20)
0.5	10.7 ^e \pm 1.5	9.5 ^g \pm 0.7	8.9 ^g \pm 0.3	8.9 ⁱ \pm 0.2	9.0 ^k \pm 0.2
1.6	12.4 ^e \pm 0.7	12.1 ^{fg} \pm 0.5	12.1 ^{fg} \pm 0.4	12.0 ^{hi} \pm 0.4	11.9 ^{jk} \pm 0.3
2.4	17.4 ^e \pm 0.4	17.3 ^f \pm 0.4	17.2 ^f \pm 0.3	17.0 ^g \pm 0.2	16.9 ⁱ \pm 0.2
2.4	15.5 ^e \pm 0.6	15.4 ^{fg} \pm 0.5	15.1 ^f \pm 0.4	14.9 ^{gh} \pm 0.3	14.8 ^{ij} \pm 0.2
5.7	57.3 ^d \pm 1.3	57.4 ^e \pm 1.3	57.5 ^e \pm 1.2	58.0 ^f \pm 1.0	57.9 ^h \pm 0.9
7	64.4 ^{cd} \pm 2.3	64.4 ^e \pm 2.2	63.8 ^e \pm 1.9	63.8 ^e \pm 1.7	64.6 ^f \pm 1.4
8	63.5 ^{cd} \pm 2.0	63.4 ^e \pm 2.0	63.0 ^e \pm 1.7	62.9 ^{ef} \pm 1.2	62.8 ^{fg} \pm 1.0
8	61.0 ^d \pm 1.2	60.9 ^e \pm 1.1	60.8 ^e \pm 0.9	60.8 ^{ef} \pm 0.7	60.3 ^{gh} \pm 0.6
8	62.7 ^{cd} \pm 1.3	62.7 ^e \pm 1.2	62.6 ^e \pm 1.0	62.5 ^{ef} \pm 0.8	62.5 ^{fg} \pm 0.8
8	81.7 ^b \pm 2.1	81.1 ^{bc} \pm 1.8	80.6 ^b \pm 1.4	80.8 ^b \pm 1.1	81.0 ^c \pm 0.9
9	69.7 ^c \pm 1.4	69.8 ^d \pm 1.3	69.5 ^d \pm 1.1	69.2 ^d \pm 0.9	69.4 ^e \pm 0.6
9	110.1 ^a \pm 3.7	110.1 ^a \pm 3.6	111.1 ^a \pm 3.1	110.9 ^a \pm 2.8	110.8 ^a \pm 2.2
10	82.8 ^b \pm 1.6	82.9 ^b \pm 1.5	83.3 ^b \pm 1.0	83.0 ^b \pm 0.8	83.0 ^c \pm 0.6
10	76.7 ^b \pm 2.1	76.1 ^c \pm 1.8	75.7 ^c \pm 1.5	75.4 ^c \pm 1.3	74.9 ^d \pm 1.1
15	108.0 ^a \pm 4.5	108.3 ^a \pm 4.3	108.6 ^a \pm 3.6	107.3 ^a \pm 3.3	106.0 ^b \pm 2.7

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466 **10 Figures**

467 **Fig. 1.** Typical morphology of a burned *Espeletia pycnophylla* plant. Marcescent leaves
468 remain attached to the stem beneath the living rosette leaves. Burning removes marcescent
469 leaf blades and, after repeated fires, also removes the clasping leaf bases. The length of
470 stem covered by accumulated marcescent leaves was measured in this study as an indicator
471 of time since fire.

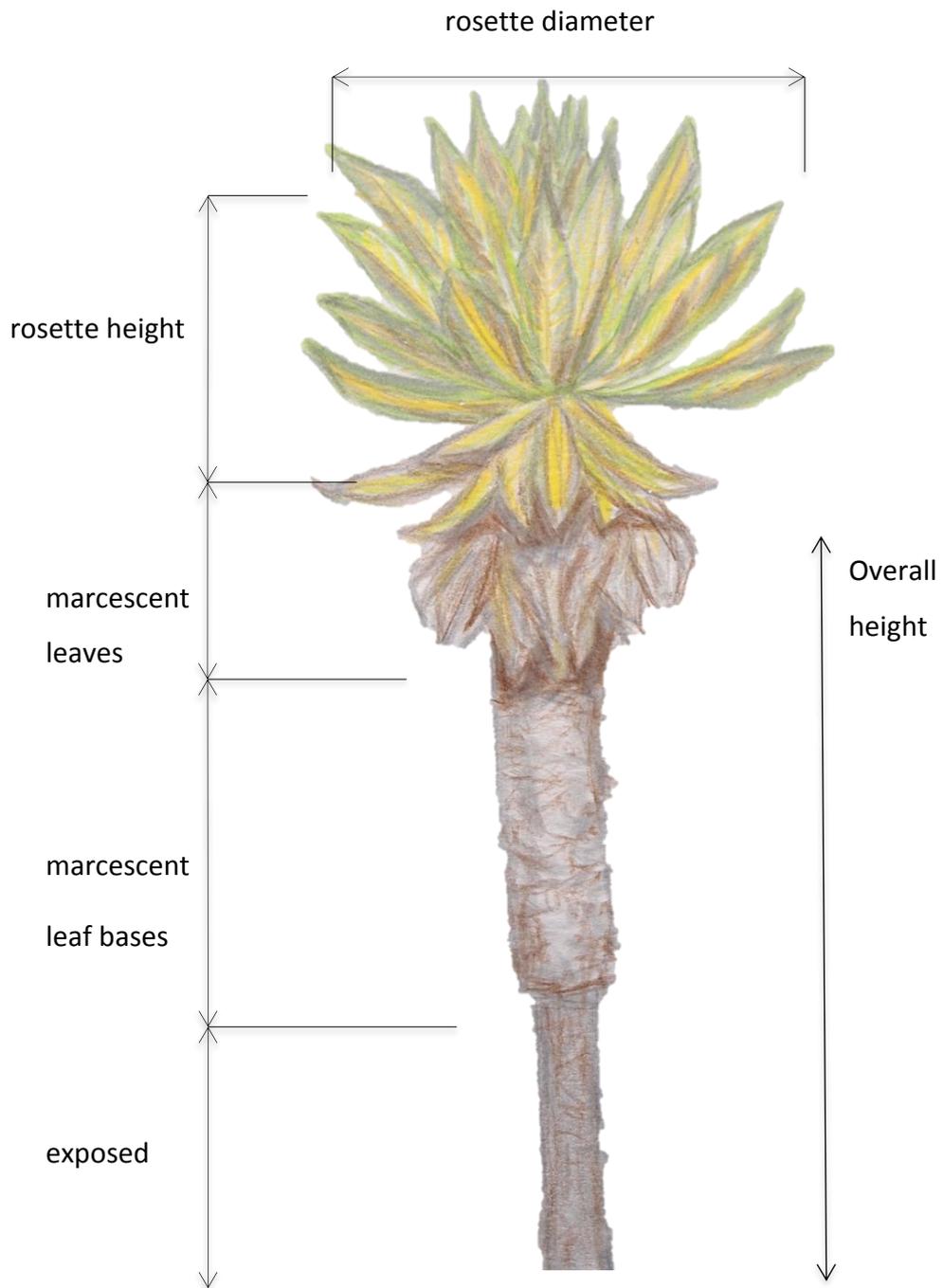
472 **Fig. 2.** Mean stem growth rates for *Espeletia pycnophylla* at four elevations on Volcán Chiles
473 over a two-year period, 2012–2014. Error bars represent SE. Means sharing a letter were
474 not considered significantly different according to a Student-Newman-Keuls multiple
475 comparison of means test.

476 **Fig. 3.** Relationship between known time since fire and marcescent leaf cover of *Espeletia*
477 plants at fifteen fire sites. (A) Mean marcescent leaf cover ($y=4.39 + 7.88x$; $r^2= 0.864$). (B)
478 Variability (standard deviation) of marcescent leaf cover ($y=0.42 +1.26x$; $r^2= 0.625$). In both
479 cases, statistics were calculated from 80% core subsamples of 50 plants, excluding five
480 measurements from each tail of the distribution.

481 **Fig. 4.** Relationship between known and estimated time since fire for fifteen sites ($y=0.06 +$
482 $0.93x$; $r^2=0.899$). Calculated with growth rates of 9.28 cm y^{-1} at 3600 m and 7.89 cm y^{-1} at
483 3900 m.

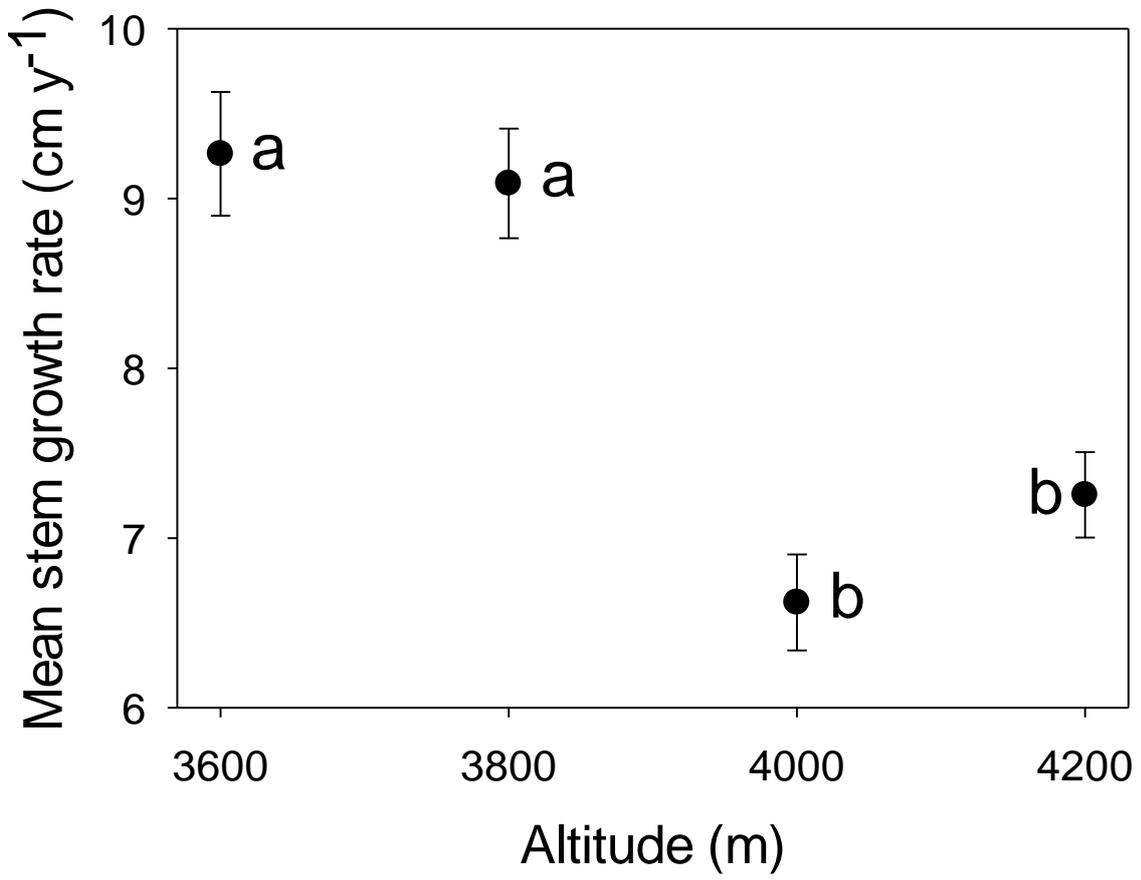
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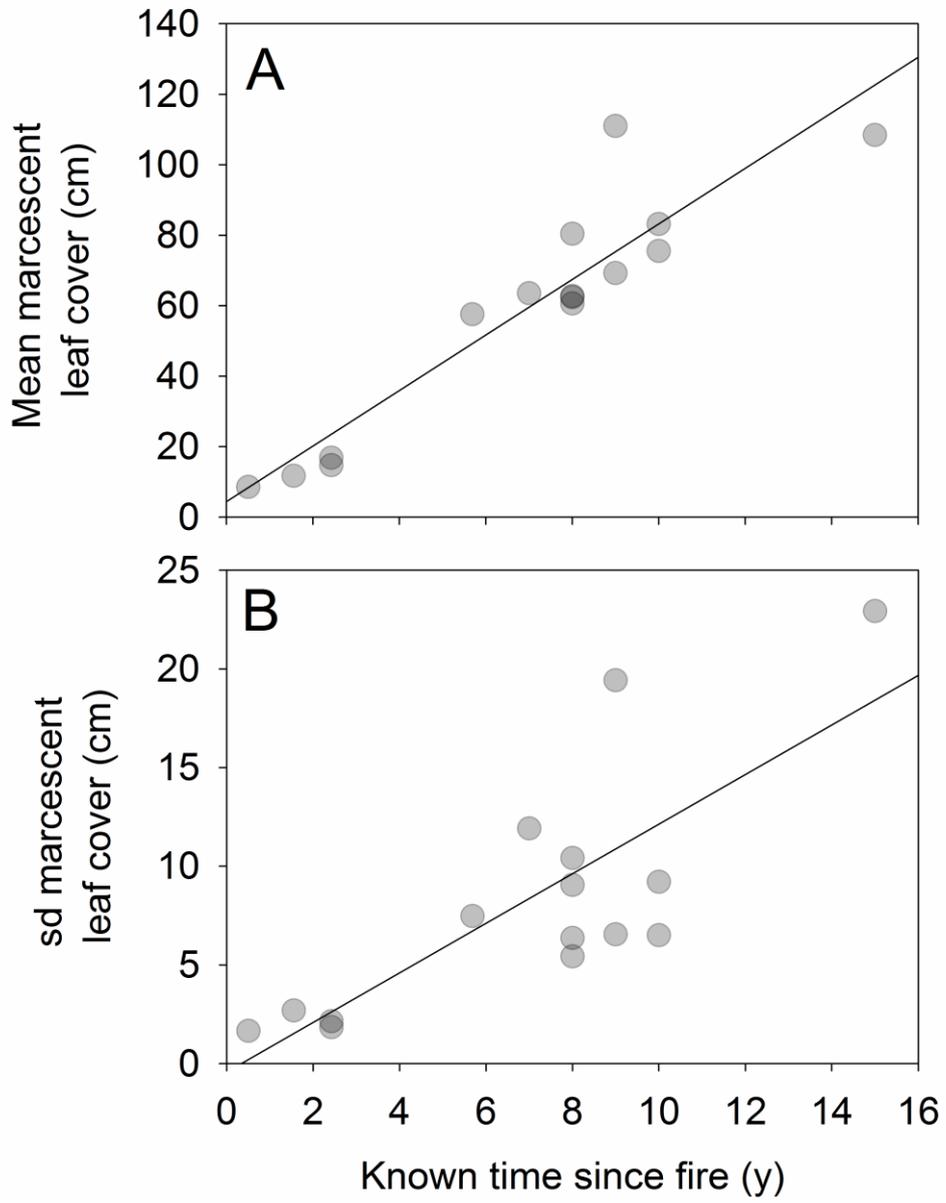
485 Fig. 1



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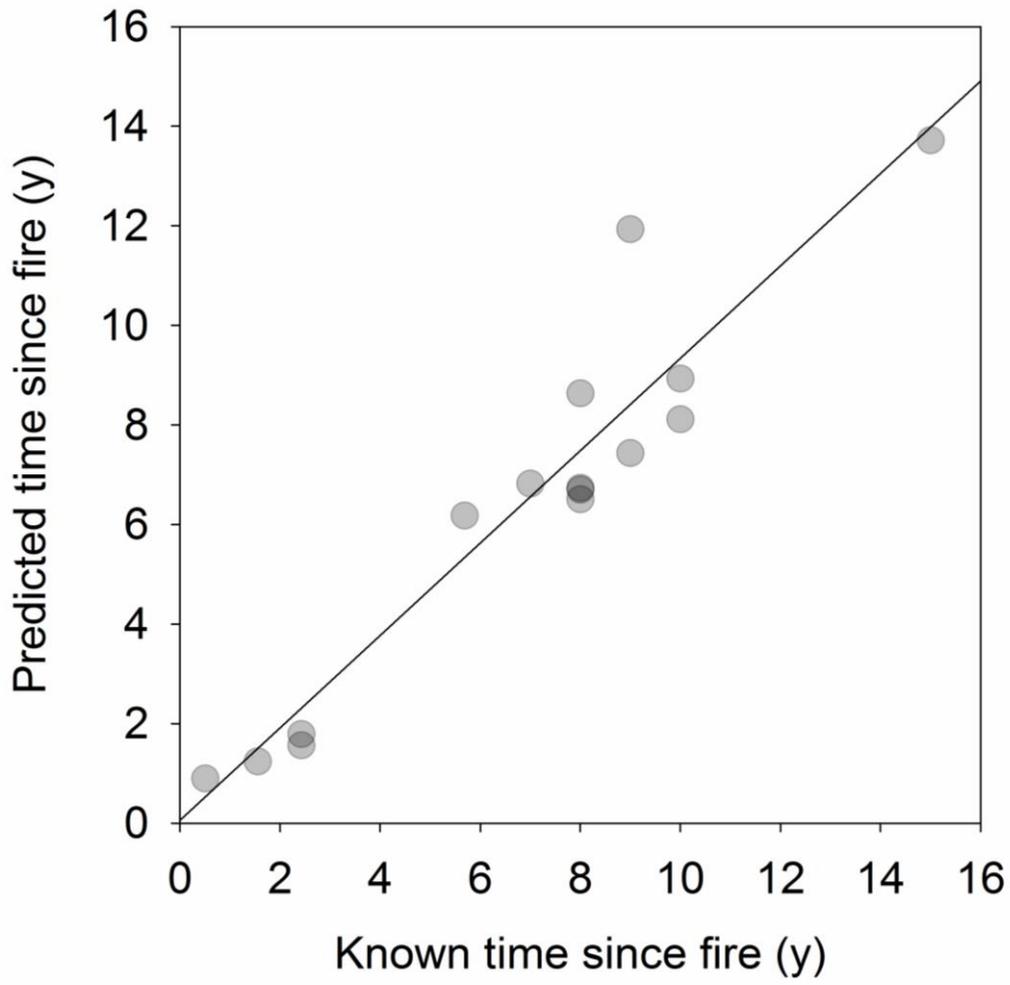




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494 Fig. 4



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