

1 **Post-fire changes in plant growth form**
2 **composition in Andean páramo grassland**

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12

13 **Abstract**

14 Questions

15 Fire suppression policies have been widely adopted in the páramo grasslands of the northern
16 Andes to protect their biodiversity and ecosystem services. Páramos have been regularly
17 burned for many years, and it is not clear how páramo vegetation will respond to significant
18 changes in their fire regimes. This study investigates differences in plant growth form
19 composition, light levels and soil temperatures in páramo plots representing a range of
20 recovery times since the last fire.

21 Location

22 Reserva Ecológica El Ángel and La Bretaña Nature Reserve, Carchi, Northern Ecuador.

23 Methods

24 We assessed the frequency of ten páramo growth forms, vegetation height, soil temperature,
25 and light intensity in fifteen fire sites with historical records of fire (<1 – 15 years since fire), and
26 one recently unburned site (at least 40 years since fire). A chronosquence of sites was used to
27 assess potential changes in plant community composition in post-fire succession of páramo.

28 Results

29 The recovery of páramo vegetation after fire comprised three phases: initial recruitment with
30 high growth form diversity, followed by reduced diversity, light and soil temperatures in dense
31 tussock vegetation, and ultimately canopy height stratification with a return of diversity. All but
32 one plant growth forms were represented in each of the three phases, and the changes
33 reflected differences in relative abundance.

34 Conclusions

35 Post-fire páramo succession is characterized by clear shifts in the relative abundance of plant
36 growth forms, ending with (co-)dominance of upright shrubs. The long-term consequences of
37 such shifts for biodiversity and ecosystem function, given the widespread adoption of fire
38 suppression policies in the páramo need careful, evidence-based consideration.

39 Key words: burning, succession, vegetation recovery, phase shift, fire ecology, fire
40 management, tropical alpine, Ecuador

41 **Introduction**

42 The páramos are the largest extension of tropical alpine ecosystems, forming a discontinuous
43 belt throughout the northern Andes, with outliers in Panama and Costa Rica. The páramo has
44 the most diverse mountain flora in the world (Smith and Cleef 1988), and these grasslands
45 sustain ecological processes, carbon storage, and supply water for millions of people,
46 agriculture and industry at lower latitudes (Buytaert et al. 2011).

47 Fires are the most significant human impact in the páramos (Horn and Kappelle 2009; Laegaard
48 1992; Ramsay and Oxley 1996) and people have burned these grasslands for thousands of years
49 (White 2013). Putative fire suppression policies have been introduced to counter a reported
50 increase in burning frequencies in some areas (Armenteras et al. 2020), a conservation strategy
51 that stems from the common perception of fire as a threat to ecosystem integrity and services
52 in the high Andes (Horn and Kappelle 2009; Keating 2007; Matson and Bart 2013).

53 Understanding biodiversity and community level responses to such strategic decisions in the
54 páramo requires an in depth knowledge of both fire regimes and how páramo vegetation
55 recovers through time after fire (Matson and Bart 2013; Ramsay 2001).

56 Fire disturbance might represent a powerful mechanism of promoting and maintaining species
57 diversity in páramo grasslands (Horn and Kappelle 2009; Keating 2007; Sklenář and Ramsay
58 2001). Regular burning in the páramo promotes a destruction-renewal cycle that has resulted in
59 a landscape composed of a mosaic of patches in varying stages of recovery (Grubb 1977;
60 Ramsay 1999; Ramsay 2001; Smith and Young 1987). Fine-scale heterogeneity in vegetation
61 structure leads to patchy distribution of fuel and variable fire temperatures, which results in
62 differential plant mortality, and post-fire establishment and growth (Ramsay 2001; Ramsay and
63 Oxley 1996). Such patchiness and variability in recovery after fire have been linked to higher
64 levels of biodiversity at the landscape scale (Keating 2007; Sklenář and Ramsay 2001) and at a
65 finer scales (Ramsay and Oxley 1996; Sarmiento and Frolich 2002).

66 Studies of post-fire vegetation development have been carried out in Ecuador, Colombia,
67 Venezuela, and Costa Rica and have shown variable changes in composition, cover and stature
68 (Horn and Kappelle 2009). Only a few studies have monitored vegetation recovery through time
69 after fires in Ecuador. Bremer et al. (2019), Keating (2007) and Ramsay (2001) concluded that
70 páramo vegetation recovery does not follow one particular successional trajectory. Fires can

71 have very different effects on vegetation, depending on the intensity and extent of a particular
72 fire (Keating 2007; Luteyn 1999; Sklenář and Ramsay 2001; Suárez and Medina 2001; Zomer
73 and Ramsay in review). Fire behaviour is determined by the pre-fire community structure
74 (physical vegetation structure and fuel accumulation) and fire event conditions (Zomer and
75 Ramsay in review).

76 Rates of tussock grass regeneration have been observed to be high (Gutiérrez-Salazar and
77 Ramsay in press), but the impacts of fire on other páramo life forms vary widely (Horn 1989;
78 Horn 1997; Janzen 1973; Keating 1998). Most páramo species have adaptations that help them
79 to survive fires (Laegaard 1992), but the mechanisms vary among species, making the
80 recognition of community-level successional trends at this taxonomic level difficult. A credible
81 alternative for recognizing community assembly patterns is the use of plant functional types
82 (Smith and Huston 1989): “nonphylogenetic groupings of species that show close similarities in
83 their resource use and response to environmental and biotic controls” (Wilson 1999). To assist
84 in such studies, Ramsay and Oxley (1997) proposed ten plant growth forms for the páramos,
85 each summarising the responses of its component species.

86 One difficulty in developing a better understanding of páramo fire ecology is the lack of well-
87 documented study sites. Some studies have observed post-fire recovery without knowing what
88 conditions were like before or during the fire (e.g., Kovář 2001; Ramsay 2001). In other cases,
89 fires have been set experimentally, sometimes with the addition of a fire stimulant (Keating
90 1998; Ramsay and Oxley 1996). Longer term studies are impeded by the lack of fire records,
91 noting when, where and how páramo fires took place (Bremer et al. 2019; Horn and Kappelle
92 2009; Matson and Bart 2013).

93 Using a fire register for the Reserva Ecológica El Ángel, northern Ecuador, we recorded diversity
94 and abundance of growth forms in a chronosequence (space for time substitution; Walker et al.
95 2010) of páramo sites burned from 2000–2014, and from a site that had not been burned for at
96 least 40 years. We also measured light levels and soil temperatures in the same plots. Our aim
97 was to determine the key phases in post-fire vegetation succession in the páramo, and the
98 mechanisms driving the changes.

99 **Methods**

100 **Study areas and fire records**

101 The Reserva Ecológica El Ángel (REEA) is located in the Western Cordillera of northern Ecuador,
102 and protects part of a contiguous páramo that is shared with Colombia. The buffer zone around
103 the reserve is dominated by agricultural land use, where fires often occur. In the past, fires
104 have also been common in parts of the reserve itself. Typically, such fires were started to
105 stimulate livestock forage, aid hunting, or happened by accident (Ramsay 2001). An inventory
106 of known fires since 2000 in the reserve and its buffer zone has been kept with the help of
107 reserve officials and local fire brigades (Bustos Insuasti 2008; Valdospinos Navas 2008). More
108 recently, the fire brigade in San Pedro de Huaca, Carchi, has also begun recording páramo fires
109 for parts of the Eastern Cordillera in northern Ecuador, providing further opportunities for
110 study.

111 Using these records, twelve sites in REEA and its buffer zone (Western Cordillera) and three
112 additional sites from the páramo of La Bretaña (Eastern Cordillera) were selected for study,
113 representing fires that burned from 2000–2014, from <1 to 15 y before our survey, at
114 elevations of 3500–3900 m. Each fire site was located with GPS coordinates obtained from the
115 records. In addition, one site known to be unburned for at least 40 years was included, making
116 a total of 16 study sites. The páramo grasslands of these study areas were dominated by
117 *Calamagrostis* tussock grasses and giant rosettes of *Espeletia pycnophylla* Cuatrec. (at densities
118 of 1300–5400 adult plants ha⁻¹).

119 **Data collection in the field**

120 One 50m x 2m plot was randomly selected within each fire site. The plot was divided into 100 x
121 1 m² quadrats. In each of these 1 m² quadrats, the presence or absence of ten páramo plant
122 growth forms, defined by Ramsay and Oxley (1997), was recorded: stem rosettes, basal
123 rosettes, tussock grasses, acaulescent rosettes, cushions/mats, upright shrubs, prostrate
124 shrubs, erect herbs, prostrate herbs, and trailing herbs.

125 Vegetation height was measured in each 1 m² quadrat using the drop-disc technique (Stewart
126 et al. 2001), with a 20 cm diameter disc, 190 g in weight, allowed to fall to rest on top of the
127 vegetation (excluding *Espeletia*).

128 Soil temperature was measured at 20 cm depth using Signstek 3 1/2 6802 II Dual Channel
129 Digital Thermometer with 2 K-type thermocouple sensor probes. Measurements were taken at
130 five regular intervals along the longest axis of each plot, at 5 m, 15 m, 25 m, 35 m, and 45 m. At

131 each place a temperature reading was taken in each of three shading conditions: beneath
132 dense tussocks (shaded), on the edge of tussocks (intermediate) and in open intertussock areas
133 (open).

134 Light at ground level was determined by measuring the percentage of incident
135 photosynthetically active radiation (PAR) using a SunScan Canopy Analysis System with BF2
136 Beam Fraction Sensor (Delta-T Devices Ltd, Cambridge, UK) . The sunscan probe was held at
137 ground level underneath the vegetation at 1 m intervals along the length of the plot (50 in
138 total). Each reading consisted of 64 simultaneous measurements of the percentage of total light
139 (above the canopy) reaching the sensors on the ground. The median percentage of the light
140 above the canopy which reached ground level was calculated for each 1 m interval along the
141 transect, and subsequent analysis was based on these median values ($n=50$ for each plot).

142 Shannon's diversity index (using \log_e) was calculated for growth forms for all sites. Non-metric
143 multidimensional scaling (MDS) was carried out with Primer 6 (PRIMER-E, Plymouth, UK) to
144 compare growth form composition between the fire intensity plots. Other standard statistical
145 tests were performed with R version 3.4 (R Core Team 2019).

146 **Results**

147 Diversity of growth forms in sites through time after fire followed a three phased pattern (Fig
148 1). In phase 1, there was a rapid increase to the highest levels of diversity within 2 years.
149 Unfortunately, we had access to just one site <1.5 y after fire. In phase 2, diversity decreased,
150 with the lowest levels occurring 8–10 y after fire. The bulk of our plots were burned within this
151 time range. In phase 3, diversity increased from 10 to 15 y after fire and was even higher in the
152 plot which had not been burned for at least 40 y, almost reaching the same level of diversity
153 registered in at the start of phase 2.

154 Changes in the composition of plant growth forms did not follow a straightforward pattern (Fig.
155 2). Community compositions were fairly similar among sites 1.5–5.6 y after fire and among sites
156 8–10 y after fire. The unburned control was most similar in composition to sites 1.5–5.6 y after
157 fire.

158 Analysis of only those sites burned 1.5–10 y after fire (Phase 2 in Fig. 1) shows that diversity
159 decreased as time since fire increased (regression: $F_{1,11}=14.3$, $p=0.003$; Fig 3a). Richness of
160 growth forms did not vary significantly through time from 1.5 to 10 y after fire (regression:

161 $F_{1,11}=0.145$, $p=0.710$; Fig. 3b). The majority of sites had nine of the ten growth forms present.
162 Lowest richness was found in two sites, both 9 y after fire (five and seven growth forms
163 respectively).

164 The frequencies of several growth forms within the 100 m² plots decreased as time since fire
165 increased from 1.5 to 10 y: prostrate herbs (regression: $F_{1,11}=10.1$, $p=0.009$; Fig. 4A), prostrate
166 shrubs (regression: $F_{1,11}=17.9$, $p=0.001$; Fig. 4B), cushions and mats (regression: $F_{1,11}=6.9$,
167 $p=0.024$; Fig. 4C), and giant basal rosettes (regression: $F_{1,11}=9.3$, $p=0.011$; Fig. 4D).

168 Six growth forms did not follow a distinct pattern of changing frequencies from 1.5–10 y after
169 fire. Tussock grasses were present at high frequency in all plots (99%–100%; Fig. 5A). Giant
170 stem rosettes varied in frequency (40–99%; Fig. 5B), as did upright shrubs (20–65%; Fig. 5C) and
171 erect herbs (1–81%; Fig. 5D). Acaulescent rosettes were found at low abundance (0–11%; Fig
172 5E), and trailing herbs were absent from most plots and were found just once each in two plots
173 (Fig. 5F).

174 Mean vegetation height increased by approximately 25 cm on average as time since fire
175 increased from 1.5–10 y (regression: $F_{1,11}=13.7$, $p=0.040$; Fig 6A). In contrast, soil temperatures
176 at depth decreased (regression, $F_{1,11}=34.3$, $p<0.001$; Fig 6B). Median percentages of incident
177 PAR reaching ground level decreased (regression: $F_{1,647}= 491.0$, $p<0.001$,; Fig. 6C), while the
178 proportion of ground with heavy shading (<10% incident light at ground level) increased as time
179 since fire increased from 1.5–10 y since fire (regression: $F_{1,11}=23.7$, $p<.001$; Fig. 6D). For
180 context, the plot unburned for at least 40 y had a median PAR of 12.4% and the proportion of
181 the readings with heavy shading was 62%.

182 **Discussion**

183 This study considered broad patterns in plant growth forms, since it is the interaction between
184 these forms that helps to explain the mechanisms of succession. However, many distinct
185 species belong to each growth form, and do not all respond to fires in a similar way. Further
186 investigation is needed at the species level to fully understand the implications for biodiversity
187 of different successional trajectories or fire suppression. Particular attention should be focused
188 on endemic species and other species of conservation concern (Matson and Bart 2013), as well
189 as the contribution of different páramo growth forms to the provision of ecosystem services
190 (Bremer et al. 2019).

191 Although community assembly dynamics are known to be highly variable after páramo fires
192 (Keating 2007; Ramsay 2001), our study highlighted three key phases in terms of growth form
193 diversity and composition. The mechanisms responsible for these successional patterns are
194 proposed here to be the consequence of differential survival and recruitment after fire,
195 followed by competitive interactions between growth forms, driving temporal changes in
196 environmental conditions as the structure of vegetation developed (summarised in Fig. 7, and
197 discussed in more detail below).

198 **Fire event leading to Phase 1**

199 Vegetation composition soon after a fire is determined by plants' fire survival strategies and
200 their regeneration mechanisms immediately after fire. Subsequently, most plants are able to
201 grow well in light conditions and warmer soil temperatures. This phase can be considered
202 founder-controlled, where the abundance of plants is driven by survival and recruitment
203 processes.

204 Tussock plants are rarely killed by fires (Hofstede et al. 1995) as their deeply-seated shoot
205 apices and buds are protected against heat in the centre of the tussock base (Laegaard 1992;
206 Ramsay and Oxley 1996). Nevertheless, partial mortality is often observed, leading to
207 fragmentation of plants and a smaller basal area (Gutiérrez-Salazar and Ramsay in press;
208 Laegaard 1992; Ramsay 1999; Suárez and Medina 2001). In the initial recovery phase after a
209 fire, there is a tussock-building phase caused by the growth of surviving fragments and
210 recruitment of new seedlings in open areas (Ramsay 2001; Ramsay and Oxley 1996; Vargas-Ríos
211 1997; Vargas Ríos 2011). During this period, the height of tussocks is restricted, permitting
212 more light at ground level and increased soil temperatures (Gutiérrez-Salazar and Ramsay in
213 press). This allows other growth forms time and space to recover after the fire.

214 Adult giant stem rosettes tolerate fire well, protecting apical buds in at the heart of their
215 rosettes (Laegaard 1992). Germination and establishment of *Espeletia pycnophylla*, co-
216 dominant in our study plots, is known to be enhanced after fires (Laegaard 1992; Suárez and
217 Medina 2001). This is consistent with the initial rise in frequency of giant stem rosettes in our
218 study, which also included *Blechnum* stem rosette ferns.

219 Giant basal rosettes (*Puya hamata* in our plots) also survive fires well by shielding their buds
220 against high fire temperatures (Garcia-Meneses and Ramsay 2014). Recruitment of new *Puya*

221 plants can be enhanced significantly in the open conditions that are typical after a páramo fire,
222 but only if seed-producing adults are present nearby since seed dispersal is poor (Garcia-
223 Meneses and Ramsay 2014; Miller and Silander 1991). This can result patchy distribution
224 patterns of *Puya* at the landscape scale, with consequences for the behaviour of pollinating
225 hummingbirds and the genetic diversity of the plants and their seeds (Garcia-Meneses and
226 Ramsay 2012; Rivadeneira et al. 2020).

227 Some upright shrubs regenerate well after fire, from insulated buds or roots (Horn and Kappelle
228 2009; Ramsay and Oxley 1996) and the abundance of some species might benefit from
229 repeated burning (Keating 2007). The abundance of upright shrubs in our plots did not change
230 markedly with time since fire, suggesting plants maintained their presence from the early
231 stages of recovery, perhaps with occasional colonization from seed.

232 Other growth forms survive fires at or below the soil surface, where fire temperatures are
233 lower (Ramsay and Oxley 1996): cushion and mats, acaulescent rosettes, prostrate herbs,
234 prostrate shrubs, and erect herbs. Survivors of these growth forms, plus new plants recruited
235 from seed rain (Vargas-Ríos 1997), benefit from the open conditions during this initial phase to
236 establish and grow.

237 Trailing herbs, usually growing through the canopies of tussocks do not survive fires well, since
238 they hold their buds in the zone of maximum fires temperatures (Ramsay and Oxley 1996).
239 Plants belonging to this growth form are less abundant in burned páramos, and they were
240 completely absent from our plots in the early phase of post-fire recovery. It is worth noting that
241 even growth forms which are vulnerable to mortality from fire can survive by chance in small
242 islands of vegetation that the fire missed (Laegaard 1992). The relative abundance of these
243 islands, and their later importance in determining the composition of the vegetation merits
244 more attention.

245 **Phase 2**

246 Phase 2 of recovery showed a decrease in growth form diversity from 1.5–10 y after fire,
247 though growth form richness did not vary greatly. The compositional analysis also supports the
248 conclusion that the changes reflect shifts in relative abundance rather than local exclusion of
249 growth forms.

250 In this second phase, tussock grasses increase their dominance. Gutiérrez-Salazar and Ramsay
251 (in press) have shown that the height of the tussocks increases steadily during this phase,
252 resulting in a consistent shading effect and decline in temperature at ground level. The
253 dominance-controlled plant community during Phase 2 is thus characterized by the suppression
254 of potential competitors by the tussocks.

255 The lack of light and lower temperatures at the soil surface inhibits the establishment of growth
256 forms that grow over the soil surface (prostrate herbs, prostrate shrubs, cushions). Although
257 large giant basal rosettes prevent neighbouring tussocks from shading their leaves, smaller
258 plants are vulnerable to being outcompeted for light by taller tussocks. It is this loss of smaller
259 plants and low recruitment of new plants beneath the tussock canopy that explains their
260 decline during Phase 2 (Garcia-Meneses and Ramsay 2014).

261 Long-lived giant stem rosettes and upright shrubs did not show any consistent trend in
262 response to time since fire during this second phase of succession. Their height means they are
263 mostly unaffected by the density of the tussock grass canopy.

264 The abundance of acaulescent rosettes was relatively low, but stable, throughout this phase.
265 These plants favour the canopy gaps where more light reached the ground (all plots had some
266 places which received 50–60% incident light at ground level). Although these gaps were rare in
267 plots representing the later stages of phase 2, they still provided appropriate conditions for
268 some acaulescent rosettes. Erect herbs often grow alongside the tussock leaves in the canopy,
269 or in canopy gaps, and did not show a trend through time in Phase 2.

270 Trailing herbs were only found in sites 8–10 y after fire. They rely on physical support of tussock
271 grasses, but their late arrival suggests poor seed dispersal and/or germination for the species
272 present in our study area.

273 It is noteworthy that one plot, 7 y after fire, was dissimilar in composition to the other plots. It
274 was located on the edge of REEA's buffer zone, adjacent to agricultural fields, and was the only
275 plot in this study to be regularly grazed by cows. This grazing had a visible effect on the
276 vegetation with large spaces between tussocks, providing suitable light conditions for a greater
277 abundance of erect herbs and acaulescent rosettes, but with far fewer *Espeletia* stem rosettes.
278 Grazing disturbance often occurs alongside fire in páramo grasslands and such combined

279 disturbance regimes maintain fragmented tussock grasses and more open conditions (Hofstede
280 et al. 1995; Ramsay and Oxley 1996; Verweij and Kok 1992).

281 **Phase 3**

282 The longer-term absence of fire in some parts of our study area gave some insight into
283 successional change in plots 10 y or more after fire: Phase 3 in our proposed scheme. During
284 this phase, the diversity of growth forms increased with another shift in relative abundances.
285 Our “control” plot, unburned for at least 40 y, had growth form diversity and composition
286 similar to the highest levels recorded in sites 1.5–5.6 y after fire. This was an unexpected
287 trajectory, and while it is important to be cautious before assuming this observation is typical, it
288 raises some interesting ideas about what might happen if more páramo areas were fire-free.

289 In our study, the 15 y since fire and the older “control” site had notably less tussock grass cover
290 (only 89% and 79% frequency respectively) and the highest frequencies of upright shrubs (68%
291 and 73% respectively). It seems that upright shrubs begin to outcompete the tussock grasses as
292 time since fire passes. Such woody encroachment into unburned grassy páramo has been
293 suggested before (e.g., Laegaard 1992), and could be maintained by positive feedbacks in
294 temperature, soil moisture or nutrient availability (Brandt et al. 2013; Matson and Bart 2013).
295 Woody encroachment is a concern to environmental managers of grasslands because it can
296 alter ecosystem structure and function (Knapp et al. 2008; Zavaleta and Kettley 2006) and can
297 lead to declines in biodiversity (Costello et al. 2000; Ratajczak et al. 2012). The implications of
298 growth form shift in unburned páramos for services such as water provision and carbon storage
299 is unclear. High vegetation cover of tussock grasses is often associated with protecting and
300 promoting the ecosystem function of páramo soils, *i.e.*, providing water regulation, storing and
301 sequestering soil carbon (Bremer et al. 2019; Minaya Maldonado 2017). Molina et al. (2019)
302 demonstrated higher rates of chemical weathering in páramo-zone soil under trees with soil
303 beneath tussock grassland in southern Ecuador.

304 While our study and those of Matson and Bart (2013) and Bremer et al. (2019) suggest that
305 diversity and growth form richness may not decrease in a shrub dominated páramo, species
306 composition is likely to shift. It is not clear how many páramo species require disturbance gaps
307 for their survival, but it is likely that many species of conservation interest would see reductions
308 in their abundance in areas where burning was prevented for many decades.

309 From an ecological perspective, the existence of páramo without fire is a relatively recent and
310 rare phenomena (White 2013) and is only beginning to be studied. If fire suppression does lead
311 to the transition from grass páramo to a shrub dominated páramo with potentially altered
312 ecosystem function, the potential consequences are of conservation concern and should be
313 evaluated (Armenteras et al. 2020; Matson and Bart 2013). It is important to recognise that
314 conservation-motivated policies to exclude fire in páramo areas might result in different
315 ecological outcomes from those desired by the policy makers.

316 **Conclusions**

317 We suggest that the recovery of páramo vegetation after fire comprises three phases.
318 Immediately after fire, a survival and recruitment phase occurs in more open conditions, with
319 high diversity of growth forms. As time passes, the growth of tussock grasses prevents many
320 other plants from establishing, reducing diversity. With yet more time, shading from taller
321 plants thins out the tussock cover nearer the ground, allowing certain growth forms to establish
322 which had been mostly excluded in the previous phase—leading to a return of growth form
323 diversity. We have less confidence in this last phase, because of a lack of replication in our
324 study, but it is consistent with observations reported by other researchers.

325 At present, the prominent fire management strategy in many páramo regions is to prohibit
326 fires, with the aim of protecting the integrity of the grassland ecosystem, promoting carbon
327 storage and water provision. It is not yet clear whether this strategy will result in the desired
328 outcomes. Some authors have concluded that this conservation strategy is unrealistic and
329 difficult to enforce with local farmers (Keating 2007), that total burn exclusion is unnecessary to
330 conserve plant species richness, growth form richness or vegetation cover (Bremer et al, 2019),
331 and that it is not consistent with the environmental and cultural history of these fire-dependent
332 páramos (Horn and Kappelle 2009; White 2013). We agree with this assessment and urge policy
333 makers to consider the ecological evidence associated with the strategies being adopted. At
334 very least, long-term studies should be employed to monitor future changes in composition and
335 ecosystem function in response to policies of fire suppression. It would be prudent to support
336 important policy decisions with careful evidence-based consideration of the outcomes.

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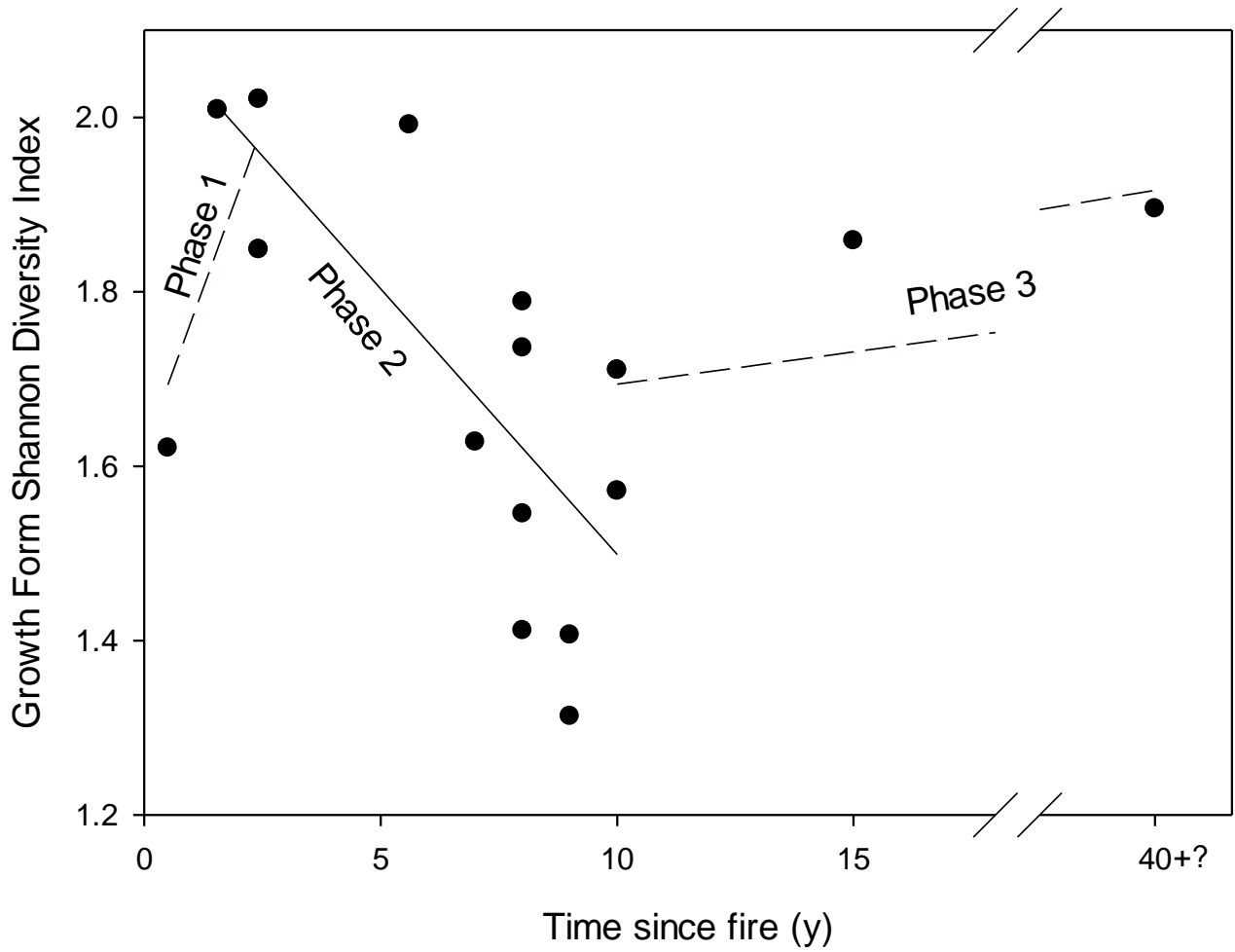
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470 altitude Andean grassland. *Biodiversity and Conservation*
- 471

472 **Fig. 1**

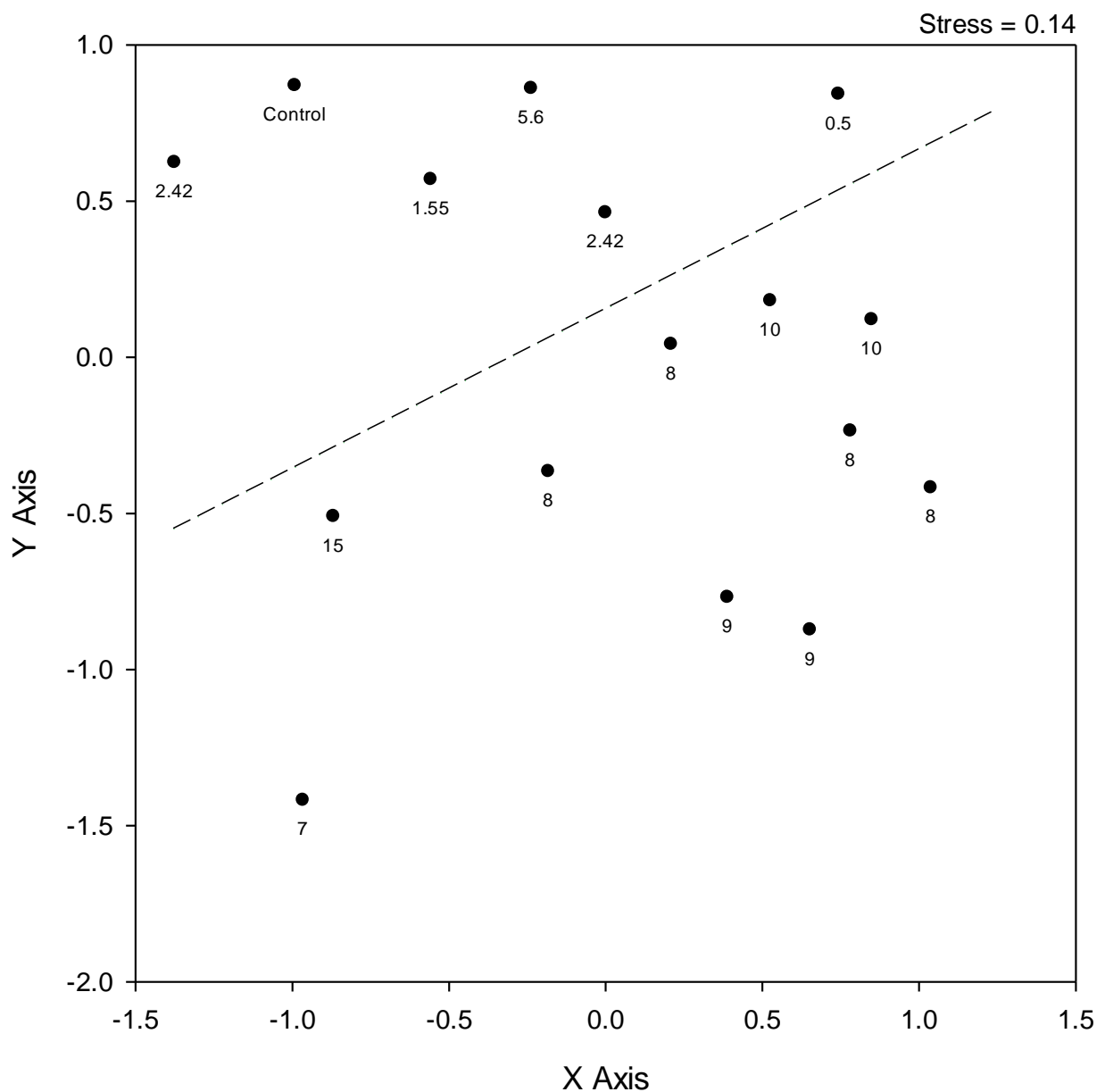
473 Fig. 1. Three phases of plant growth form diversity response through time after fire for 16 plots.
474 The plot at 40 y since fire was not burned during this time and might have been unburned for
475 even longer. Part of the x-axis has been omitted.



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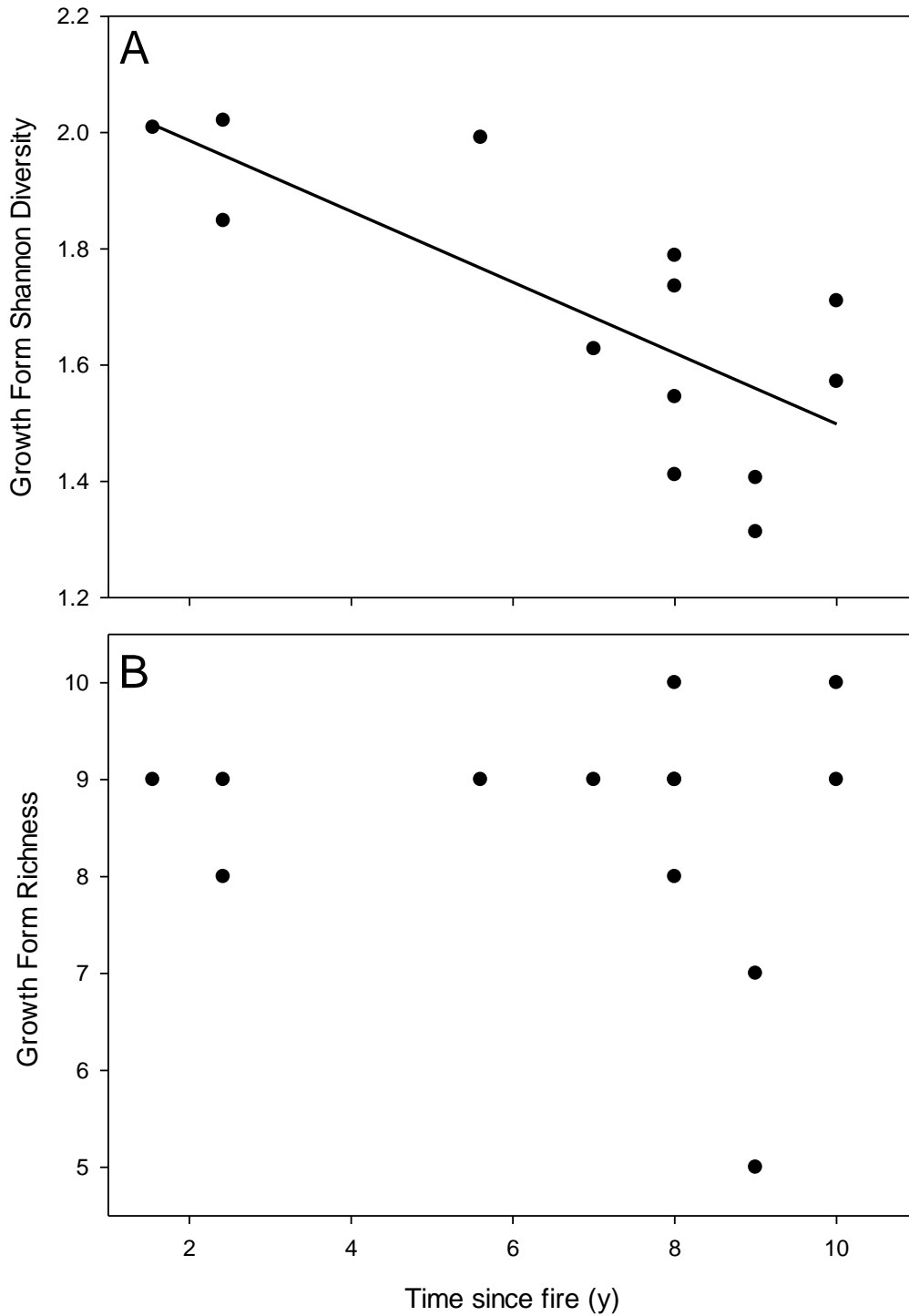
478 Fig. 2. Non-metric Multidimensional Scaling ordination of plant growth form composition based
479 on presence absence data for 100m² plots. Each plot is represented by a point, labelled with
480 the time since fire in years. The distance between plots in the ordination diagram shows the
481 difference between them in growth form composition. The further a site is from another in the
482 diagram, the greater the difference in composition. The dotted line highlights a divide between
483 plant growth form assemblages 0.5–5.6 year since fire and 7–10 y since fire.



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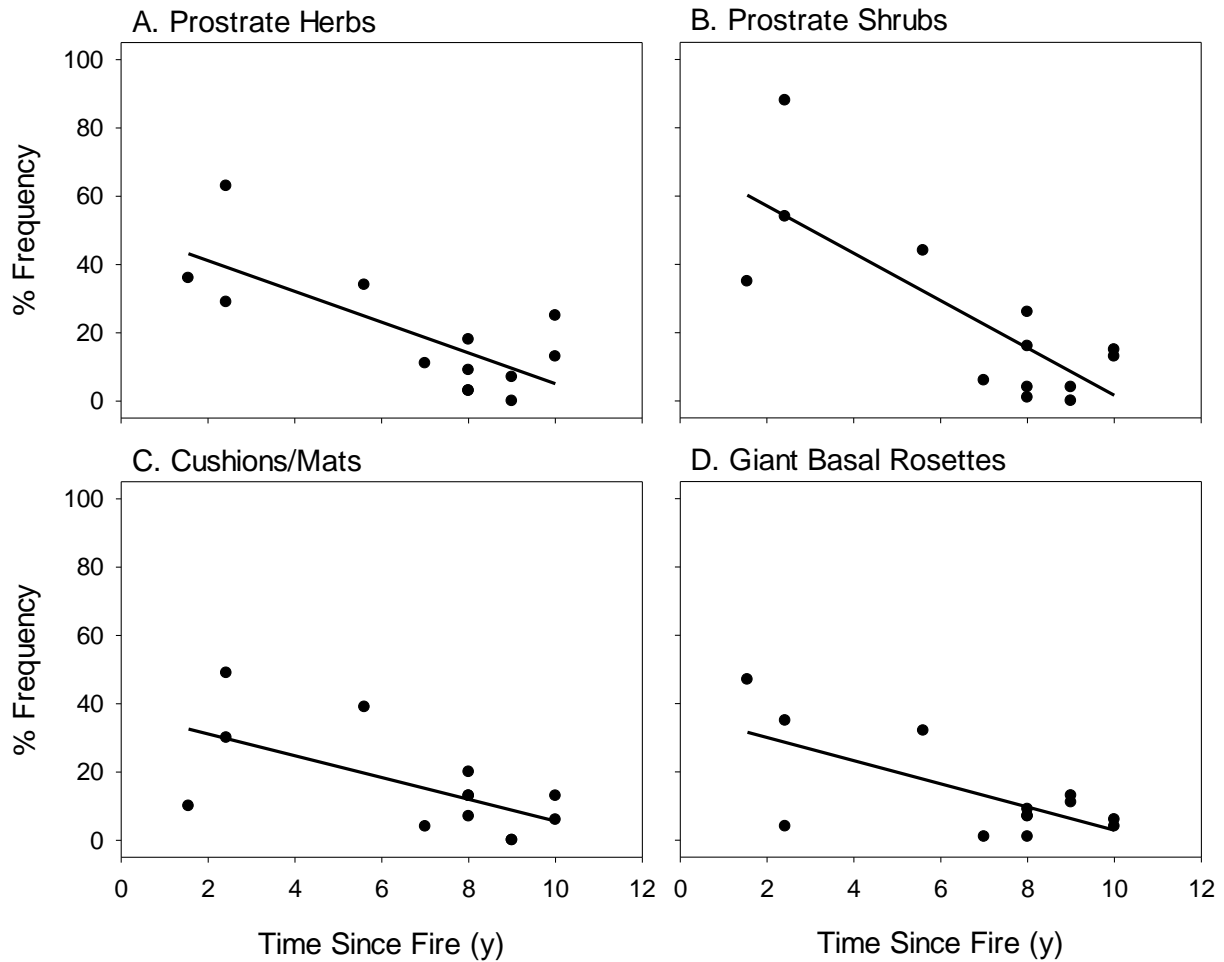
486 Fig. 3. Growth form diversity and richness in thirteen páramo sites, 1.5–10 y after fire. A.
487 Shannon's diversity index ($R^2=0.565$, fitted line $y=2.11-0.06x$). B. Growth form richness (of 10
488 growth forms).



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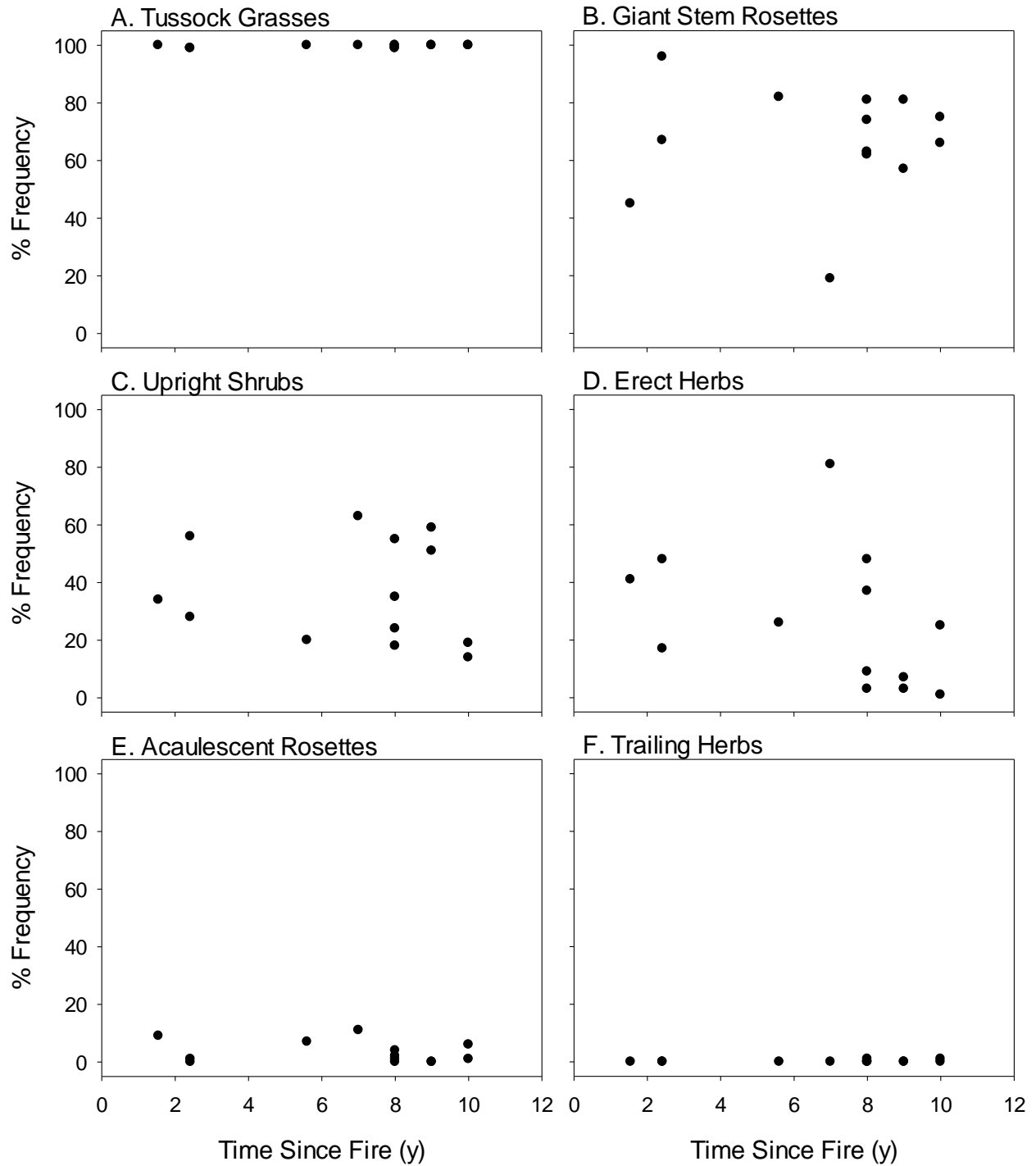
491 Fig. 4. Frequency of four plant growth forms in 100m² plots of differing times since fire, 1.5–10
492 y after fire. (a) prostrate herbs ($R^2=0.551$, $y=50.14-4.5x$) ; (b) prostrate shrubs ($R^2=0.621$,
493 $y=71.01-6.93x$) ; (c) cushions & mats ($R^2=0.385$, $y=37.52-3.19x$); (d) giant basal rosettes
494 ($R^2=0.459$, $y=36.82-3.39x$).



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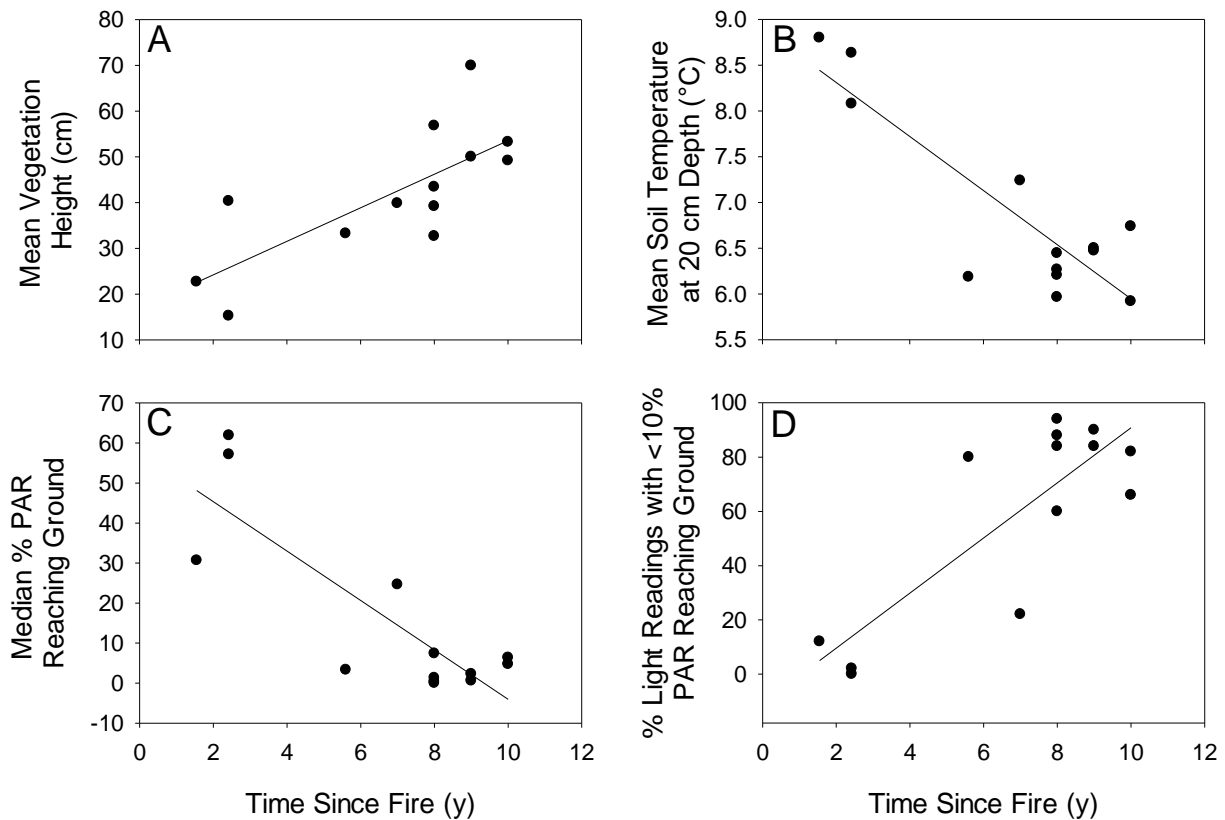
497 Fig. 5. Frequencies of six growth forms in 100 m² plots in plots 1.5–10 y after fire. A. Tussock
498 grasses. B. Giant stem rosettes. C. Upright shrubs. D. Erect herbs. E. Acaulescent rosettes. F.
499 Trailing herbs.



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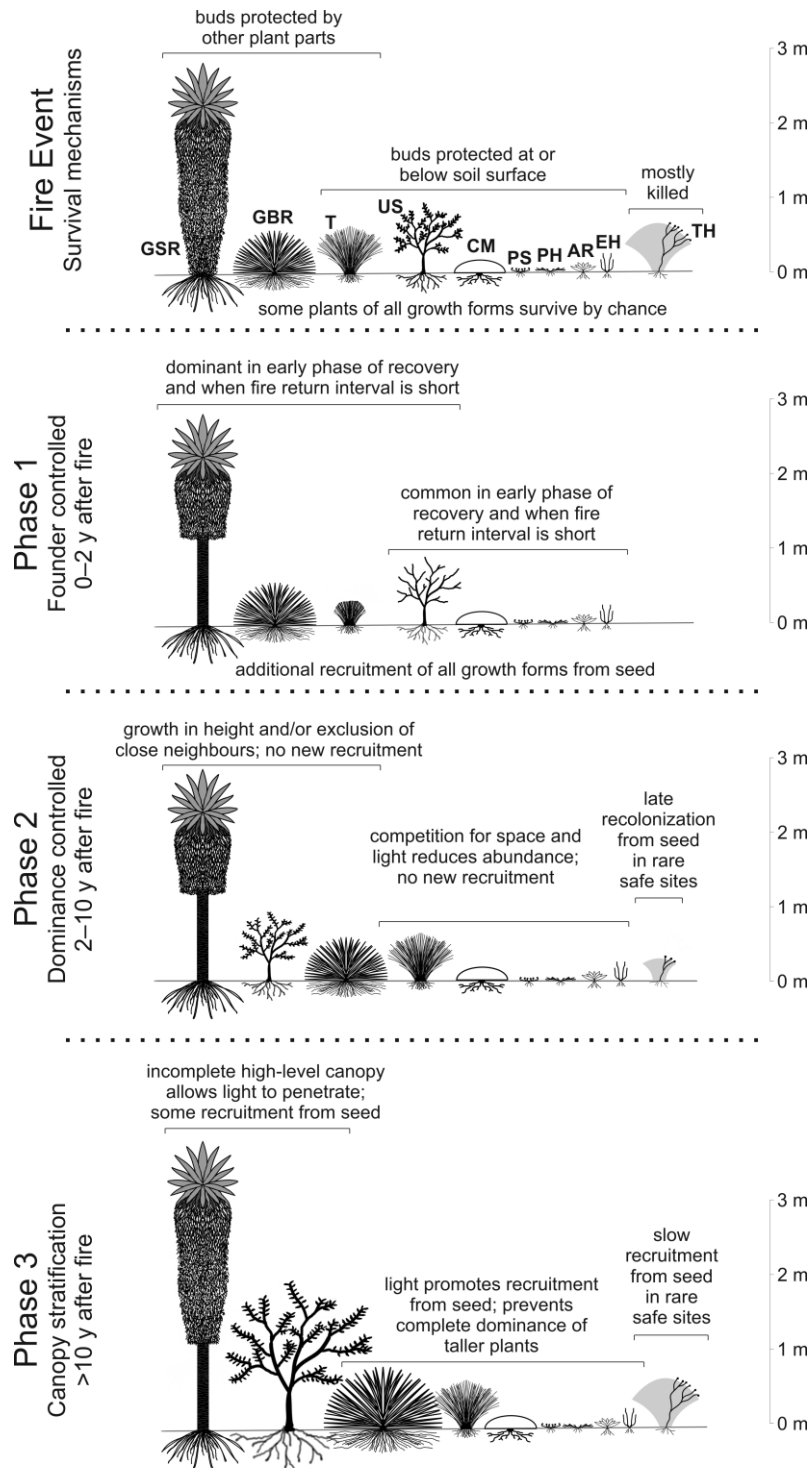
502 Fig. 6. Changes in vegetation height, soil temperature and light conditions at the soil surface. A.
503 Mean vegetation height ($R^2=0.553$, $y=16.91+3.67x$). B. Mean soil temperatures at 20 cm depth
504 ($R^2=0.757$, $y=8.9-0.3x$). C. Medians of photosynthetically active radiation (PAR) reaching ground
505 level, as a percentage of the incident light above the vegetation canopy ($n=50$ for each plot;
506 $R^2=0.431$, $y=55.5-5.51x$). D. Proportion of medians that were <10% incident PAR reaching
507 ground level ($n=50$ for each plot; $R^2=0.683$, $y=10.16x-10.78$).



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510 Fig. 7. Schematic summary of responses of ten páramo growth forms to fire and their
 511 interactions during three phases of post-fire succession. Growth forms: GSR = giant stem
 512 rosette, GBR = giant basal rosette, T = tussock, US = upright shrub, CM = cushion or mat, PS =
 513 prostrate shrub, PH = prostrate herb, AR = acaulescent rosette, EH = erect herb, TH = trailing
 514 herb.



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