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9 **Title**10 The influence of natural fire and cultural practices on island ecosystems: insights from a 4800 year
11 record from Gran Canaria, Canary Islands

12

13 **Short running title: A 4800-year palaeoecological record from Gran Canaria**

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56 **Data accessibility**

57 The data that support the findings of this study are being uploaded onto the openly available Neotoma
58 Palaeoecology Database at [<https://www.neotomadb.org/>]. Data can also be accessed through request
59 to the corresponding author.

60 **Abstract**

61 **Aim:** Long-term ecological data provide a stepped frame of island ecosystem transformation after
62 successive waves of human colonization, essential to determine conservation and management
63 baselines. However, the timing and ecological impact of initial human settlement on many islands is
64 still poorly known. Here we report analyses from a 4800-year sedimentary sequence from Gran
65 Canaria (Canary Islands), with the goal of disentangling forest responses to natural fire from early
66 human pressure on the island.

67 **Location:** La Calderilla, a volcanic maar caldera at 1770 m a.s.l. on Gran Canaria.

68 **Taxon:** plants and fungi.

69 **Methods:** A core from the caldera infill was analysed for sediment properties, pollen, micro- and
70 macrocharcoal, with radiocarbon and biochronology dating. Fossil data were statistically zoned and
71 interpreted with the help of cross-correlation and ordination analyses. Surface samples and a pollen–
72 vegetation training set were used as modern analogues for vegetation reconstruction.

73 **Results:** Before human settlement (4800–2000 cal. yr BP), pine (*Pinus canariensis*) pollen dominated.
74 Extensive dry pine forests characterised the highlands, although with temporary declining phases,
75 followed by prompt (sub-centennial scale) recovery. Towards 2280 cal. yr BP there was a shift to open
76 vegetation, marked by an increase in coprophilous spores. Coincidental with independent evidence
77 of human settlement in the pine belt (2000–470 cal. yr BP) there was a decline of pine and a peak in
78 charcoal. Following historic settlement (470–0 cal. yr BP), pollen producers from anthropogenic
79 habitats, secondary vegetation and coprophilous fungi increased in abundance, reflecting higher
80 pressure of animal husbandry and farming. Modern moss polsters reflect extensive reforestation since
81 1950 CE (Common Era).

82 **Main conclusions:** From 4800 cal. yr BP, the pristine vegetation covering the Gran Canaria highlands
83 was a mosaic of dry pine forests and open vegetation. The pine forests sustained intense fires, which
84 may well have promoted habitat diversity. Human interference was initiated around 2280 cal. yr BP
85 probably by recurrent cultural firing and animal husbandry, triggering a steady trend of forest
86 withdrawal and expansion of grasses and scrubs, until the final disappearance of the pine forest locally

in the 20th century. Grasslands were found to be of ancient cultural origin in the summit areas of Gran Canaria, although they underwent an expansion after the Castilian Conquest.

Keywords: ancient grasslands, fire ecology, forest disturbance, human impact, island ecology, palaeoecology, *Pinus canariensis*, reforestation.

Main text

1 Introduction

Evidence of vegetation changes, as testified by sedimentary archives, has been used to detect signals of human settlement, climate change and to assess their impact on ecosystems (Willis and Birks, 2006; Whitlock, Colombaroli, Conedera & Tinner, 2017). One of the most promising research strategies for disentangling human from natural disturbances is a synoptic comparison of long-term ecosystem dynamics in oceanic islands (Connor et al., 2012). Because of their isolation, small area, strong elevational and climate gradients, and recent human colonization, oceanic islands offer a laboratory to reconstruct natural environments and to study the ecological consequences of human impact over the recent millennia (Nogué et al., 2017).

In the Canary Islands (Fig. 1a), analysis of long-term environmental change, e.g. the impact by volcanic activity and by climate change, and their interactions with the human history have been hampered by a paucity of well-preserved fossil archives (Anderson et al., 2009) and by poorly constrained archaeological record. In particular, the timing and circumstances of human colonization remain the subject of considerable uncertainty. An emerging view, supported by an array of evidence (archaeological, palaeontological, palaeoecological), places colonization towards the end of the first millennium BCE (Atoche, 2008; Rando, Alcover, Galván & Navarro, 2014; Velasco et al., 2019; de Nascimento et al., 2020).

Recent palaeoecological analysis of sedimentary cores from three sites in Tenerife, La Gomera and Gran Canaria, have provided first insights into the vegetation history of the last 9000 years. The three sites are located on the mid-elevational belt (600 to 1250 m a.s.l.) and thus mostly featuring pollen types characteristic of the laurel forest and elements of the thermophilous woodland belt. The forest history recorded in the La Laguna basin in the humid belt of North Tenerife (Fig. 1b) highlighted a pre-anthropogenic laurel-dominated forest phase (de Nascimento, Willis, Fernández-Palacios, Criado & Whittaker, 2009). The onset of aboriginal disturbance at about 2000 cal. yr BP deeply impacted the forest ecosystems, well before the Castilian conquest in the 15th Century. An early aboriginal impact

119 over dominant vegetation also emerged from our previously reported pollen sequence from Gran
120 Canaria. The mid-elevation caldera sediments of Laguna de Valleseco (Fig. 1b) recorded a first
121 change in vegetation 2300 years ago and reveal cereal fields as early as 1800 years ago (de
122 Nascimento et al., 2016). The only pollen record extending as far back as the early Holocene is from
123 a pond in the humid watersheds of La Gomera (Fig. 1b; Nogué, de Nascimento, Fernández-Palacios,
124 Whittaker & Willis, 2013), showing 9600 years of climate change and vegetation dynamics. In that
125 (comparatively) high-elevation sequence, a mid-Holocene climate change was indicated by a
126 decrease in the hygrophilous *Phoenix-Salix* groves and an expansion of the *Morella-Erica* woody
127 heath. At that site, there was no direct evidence of human-induced changes in the forest composition
128 or of human-introduced plants.

129 Overall, fire evidence and other forest clearance proxies from the three islands is consistent with the
130 onset of human impacts between 2300–1800 cal. yr BP. Archaeological and historical data suggests
131 that between the 10th and 15th century CE the aboriginal population grew, settlement expanded and
132 land use changed (Morales et al., 2009). The Castilian conquest (1402–1496 years CE) and the
133 subsequent European acculturation are known to have had disruptive and immediate effects on forest
134 ecosystems in most Canary Islands (Quirantes, Núñez, García & Viña, 2011; Santana, 2001).

- coring sites (Fig. 1b and 1e)
- ◆ moss polsters M1-M3
- 0 - bare fan and scree
- 1 - bare rocks
- 2 - petrophytic sparse veg
- 3 - pine forest
- 4 - *Teline*-scrub
- 4a - with plantations
- 5 - Mixed broom scrub
- 6 - chestnut plantations
- 7 - Stands of *Marrubium vulgare*
- 8 - Cliff with broom groves
- Volcanic eruptions in Gran Canaria, 2100 to 1900 yrs cal BP (Fig. 1c)

136 Figure 1 (a-b) Geographic position of the Canary Islands and location of palaeoecological sites
137 mentioned in the text. (c) Average rainfall contour lines of Gran Canaria (mm year⁻¹) for the 1949/50–
138 2005/06 period (CIA, 2015) and climate diagram from Cuevas Blancas - Los Juncos in the most
139 recent thirty years (1981–2012), nearby to La Calderilla (Gran Canaria) (AEMET, 2012). (d) Modern
140 distribution of pine forest in Gran Canaria (del Arco et al., 2006); in red, areas affected by Bandama
141 pyroclastic deposits, 1920 cal. yr BP (median probability), and by El Garañón lava flow, 1940 cal. yr
142 BP (median probability) (Rodriguez-Gonzalez et al., 2009). (e) Detailed physiognomic vegetation
143 map of La Calderilla (original).

144
145 In this paper we complement these research studies with a high-elevation site to analyse how pine
146 forest responded to past environmental change. Our record extends up to the last sixty years of
147 landscape change, allowing the comparison of vegetation changes in Canarian prehistory, post-
148 Castilian conquest and up to very recent landscape dynamics. A view of the highland landscape in
149 the Canary Islands in 1950 CE would have placed, at the upper timberline limit (2400 m a.s.l.,
150 Höllermann, 1978; timberline terminology according to Holtmeier, 2009), a wide range of open
151 vegetation types. These include summit scrub, pachycaul herbs and dwarf shrubs forming petrophytic
152 semi-deserts (del Arco et al., 2006) and grasslands, the latter especially developed in Gran Canaria,
153 although its maximum elevation (1949 m a.s.l.) stands below the timberline ecotone. Geologic events
154 (volcanic eruptions) and anthropic impacts, and consequent increased soil drought (Gieger &
155 Leuschner, 2004), lowered the timberline, replacing pine and juniper by shrubby legumes or by
156 grassland pastures. The usual narrative assumes that human-induced timberline depression began
157 with the Castilian conquest (1478-1483 years CE in Gran Canaria), with pine forest exploitation and
158 burning for fuel, tar for ship, livestock and crop husbandry, intensifying during the 16–17th centuries
159 (Pérez de Paz et al., 1994; Viera y Clavijo, 1790) and resulting in the traditional treeless highland
160 photographs of the 1940s. Reconstructions based on historical documentation in Gran Canaria suggest
161 that, before the Castilian conquest, human interference was not intense (Santana, 2001). We present
162 the first long-term record from the upper forest belt through an integrated palaeoecological analysis
163 of the pine forest timberline ecotone with high elevation grasslands for the last 4800 years. We discuss
164 driving factors such as human impact and volcanic activity, approaching a synoptic view with the
165 other recently published records from the Canaries.

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167

168 2 Material and methods

169 2.1 Ecogeographical setting of Gran Canaria highlands

170 Gran Canaria is the third largest Canary Island in area (1561 km²), reaching 1949 m a.s.l. (Pico de las
171 Nieves). North-eastern ravines, with more than 400 mm year rainfall (Fig. 1c), host the remnants of
172 a laurel forest belt and of thermophilous woodlands, but also xerophytic formations featuring
173 *Dracaena* and groves of *Phoenix* and *Salix* (del Arco et al., 2006). The western and southern flanks
174 preserve the best remnants of open pine forests (400–1500 m) (Fig. 1d), extending above a semi-
175 desert lowland scrub. At the beginning of the 20th century, pine forest reached up the summit in only
176 two locations (Tamadaba, top at 1444 m and Inagua, 1498 m), while most highlands were occupied
177 by grasslands and scrub formed by endemic shrubs and bush legumes (*Teline microphylla* (DC.) P.E.
178 Gibbs & Dingwall and *Adenocarpus foliolosus* (Aiton) DC.) (Naranjo-Cigala, 1995; Naranjo-Cigala,
179 Salas & Almeida, 2001). A reforestation program, started in the 1950s, promoted pine plantations,
180 which now occupy most of the highlands (Fig. 1d). The scrub characteristic of Tenerife and La Palma
181 summits (Fernández-Palacios & de Nicolás, 1995) is missing in Gran Canaria, although several
182 shrubs of diverse Canarian genera (e.g. *Argyranthemum*, *Sideritis*, *Erysimum*, *Echium* and
183 *Pterocephalus*) characterize rocky habitats in its timberline ecotone (Naranjo-Cigala, 1992).

184

185 2.2 Geological history and ecological setting of the volcanic complex of La Calderilla

186 The volcanic complex of La Calderilla, originated around 88±5 ka (Guillou et al., 2004), was one of
187 the last basaltic eruptions on Gran Canaria preceding the Holocene reactivation. It is composed of a
188 phreatomagmatic maar (200 m in diameter, extending down to 1770 m a.s.l.), and a strombolian cone
189 growing in its ESE flank. The sedimentary infill of the caldera formed during the Late Pleistocene
190 and the Holocene, and accumulated to a depth of 14 m on the NE side (see Appendix S1 in Supporting
191 Information). The most recent sedimentation has been generated by an alluvial fan, and by slope
192 deposits mantling all the inner caldera slopes, including organic-rich andosols and their colluvial
193 reworked products.

194 Mean annual precipitation in the last thirty years is estimated at 670 mm (Fig. 1c); the mean annual
195 temperature being 12.6 °C. The vegetation today is dominated by planted *Pinus canariensis* C. Sm.,
196 bush legumes (*Teline microphylla* and *Adenocarpus foliolosus*), and a petrophytic scrub formed by
197 nanophanerophytes and chamaephytes (*Argyranthemum*, *Sideritis*, *Erysimum*, *Pterocephalus*) (Fig.
198 1e). The caldera bottom is occupied by therophytes, partly non-native herbs. Individuals of *Castanea*
199 and *Malus* were planted in the 1950s. More chestnut trees and pine plantations occur outside the
200 volcanic complex (del Arco et al., 2006), while on well-developed soils a few grassland patches
201 merge with scrubby vegetation dominated by leguminous shrubs (Naranjo-Cigala, 1995).

202

203 2.3 Sampling, dating and analysing

204 In May 2013 we retrieved an 8.7 m sediment core by technical drilling (CAL1, Fig. 2, Appendix S1).
 205 The sedimentary sequence down to 6.3 m was sampled for geochemical (170 samples),
 206 sedimentological (30), palynological (55) and charcoal (55) analysis.

207 Thermogravimetric loss-on-ignition was determined on 1g sediment sample with an automated
 208 LECO TGA 601 analyser through four heating steps (in parentheses the parameter obtained): 105 °C
 209 (water content), and, in % over the dry height: 375 °C (non-pyrogenetic organic matter), 550 °C (total
 210 organic matter and sulphides, TOM), 980 °C (carbonates) and the residue (silicate rock fragments
 211 and oxides).

212 Seven samples of bulk sediment and charcoal were radiocarbon dated at the ¹⁴CHRONO Center at
 213 Queen's University Belfast and Beta Analytic (Appendix S1, Table S1.1). Calibration was performed
 214 using the Intcal13 calibration dataset (Reimer et al., 2013). Geochronometric dating, independent
 215 biochronological markers and other stratigraphic tools (Appendix S1) served to constrain the age-
 216 depth model solutions, calculated using OxCal 4.2 (Bronk Ramsey, 2008). The biochronological
 217 evidence is presented in Table 1 and discussed in section 4.1.

218 Pollen extraction (1 cm³ sediment samples) followed chemical treatment, micro-filtration and
 219 acetolysis. *Lycopodium* spore tablets were added to calculate pollen and microcharcoal
 220 concentrations. At least 500 pollen grains for each sample have been identified, except for rare
 221 samples with poor concentrations. Ferns, green algae and fungal spores indicative of animal
 222 husbandry were also analysed (Appendix S2). Poaceae pollen grain size was measured, to detect
 223 evidence of grass crops introduced in the Canaries.

224 Percentage pollen diagrams were drawn in Tilia 1.7.16. Pollen zonation was obtained by a constrained
 225 incremental sum of squares cluster analysis, using Cavalli-Sforza's chord distance as the dissimilarity
 226 coefficient (package CONISS, Grimm, 1987).

227 A recent training set for pollen rain-vegetation calibration sampled in Tenerife (de Nascimento et al.,
 228 2015), coupled with moss polsters and vegetation data obtained at the studied site, was used to adjust
 229 pollen signals to modern vegetation and to evaluate changes that affected highland ecosystems in
 230 Gran Canaria (Annendix S3).

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241 Figure 2 The studied core section CAL1 (La Calderilla, Gran Canaria) spanning the last 4800 years.
242 Sedimentary log, thermogravimetric proxies and age–depth model. Dark horizontal banding
243 highlights intervals of pyrogenetic organic matter, appearing as dark layers in the log. Most important
244 dark layers also correspond to intervals of accumulation of charcoal fragments sized over 10 μm (see
245 Fig. 3). The adopted age–depth model solution is shown by the yellow envelope. Refer to Appendix
246 S1, for details on age–depth model and for the key to the lithological patterns.

247

248 Microcharcoal fragments (size-classes 10–50 and 50–150 μm) and coprophilous spores were counted
249 during routine pollen analysis. Macrocharcoal fragments between 150 μm and 1 mm and > 1 mm
250 were wet sieved from sediment samples (1 cm^3) and counted under a stereomicroscope.

251 To check similarities between percentage pollen data of *Pinus canariensis* and macrocharcoal data
252 series and to detect positive/negative/lead/lag relationships between them, we computed the cross-
253 correlation function of the two time series using the software MYSTAT 12 (Systat Software Inc., CA,
254 USA). In order to avoid non-stationarities and minimise the problem of unstable sedimentation rate,
255 we computed offsets in distance between samples using short series, centred on charcoal
256 accumulation events (Fig. 4). To analyse the temporally variable strength of the relationship between
257 the same data series, Pearson correlation values (r) were obtained using a 10-interval moving-
258 correlation (Fig. 7) using MS Excel.

259 The major compositional changes within fossil dataset and between fossil and modern surface
260 samples were assessed with principal components analysis (PCA). Ordinations were carried out with
261 PC ORD 4.2. To reduce asymmetry in the pollen dataset, square root transformation and range
262 normalisation were performed before running the PCAs.

263 To compare palaeoecological results from La Calderilla with evidence of human occupation derived
264 from the archaeological record, we compiled 253 radiocarbon ages from pre-Castilian archaeological
265 sites (see Appendix S4) into a summed probability density function using OxCal 4.2.

266

267 **3 RESULTS**

268 **3.1 The caldera infill and chronology**

269 The lowermost section of the core (870–650 cm) is made up of slope deposits and associated andosols,
270 incorporating abundant woody charcoal, formed on the wall of the strombolian cone. In the middle
271 segment (650–290 cm) andosols are embedded with silty layers deposited after sheet flows. These
272 fine silts form the complete uppermost caldera infill (290–0 cm). No true pyroclastic falls were
273 noticed throughout the entire sequence; only sedimentary layers from reworked pyroclastic deposits
274 occur (Fig. 2, Fig. S1.1).

275 Seven radiocarbon dates were obtained from bulk samples rich in charcoal particles, from dark soils
276 and silty layers (Appendix S1, Table S1.1). Given that organic carbon consists mostly of charcoal
277 (Fig. 2), without aquatic vegetation, no reservoir effect is expected for these ^{14}C measurements.
278 However, an overlap between the two uppermost ages is suspect, as they are separated by regular,
279 partly laminated, fine sedimentation (Fig. 2). Reworking of charcoal particles most likely occurred in
280 the uppermost interval, after the level of local charcoal accumulation event F4 (see section 3.4) dated
281 2200 ± 42 ^{14}C yr BP. Hence input of secondary “old” charcoal in the upper 350 cm makes ^{14}C ages
282 unreliable. An increase in pollen of cultural indicators allowed identification of the Castilian conquest
283 of Gran Canaria (1478–1483 CE) in the sedimentary record matching the 57 cm depth statistical
284 boundary. This biostratigraphic marker has been included in the final age-depth model, while the core
285 top was given an age of 0 cal. yr BP on the base of its pollen content (Fig. 2, Appendix S3).

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287 **3.2 Modern vegetation - pollen rain**

288 The pollen composition of moss polsters from the caldera rim and bottom (Fig. 1e) records the
289 dominance (Appendix S3) by the main pollen producers currently widespread in the area (*Pinus*,
290 *Castanea*, Brassicaceae, Asteraceae, *Teline*). We observed relationships between pollen rain and
291 plants occurring within the caldera rim (diameter 160–220 m), which will be assumed as the relevant
292 pollen source area. Important pollen producers from lower vegetation belts (*Artemisia*, *Quercus*,
293 *Morella*) occur with low frequencies. The main anthropogenic pollen producers include *Artemisia*,
294 Brassicaceae, Polygonaceae and Chenopodiaceae. The pollen composition of moss polsters displayed

295 marked differences from the core top samples (Appendix S3, Fig. S3.5), pointing to large-scale
296 vegetation cover changes in recent years.

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298 3.3 The long-term charcoal record

299 The gravimetric percentage of pyrogenetic organic matter ($3 \pm 0.7\%$) over Total Organic Matter,
300 TOM ($12.1 \pm 2.8\%$) (Fig. 2) indicates a significant and persistently high charcoal contribution to
301 TOM. Peaks of macrocharcoal occur in zones Z1–Z4 (Fig. 3). The abundance of particles > 1 mm in
302 these layers indicates local forest fires at a maximum distance of 100 m from fire margin for particles
303 aerially transported (Ohlson & Tryterud, 2000). Considering the small size of the caldera watershed,
304 slopewash and floods cannot have carried macrocharcoal from further distances.

305 The most prominent macrocharcoal accumulation events (Fig. 3) are: F1 (620–600 cm), F2 (498–450
306 cm), F3 (420–397 cm), F4 (340–320 cm) and F5 (276–240 cm). F1–F3 appear to correlate with
307 temporary, coeval declines of pine pollen percentages, but only the F3 correlation values are
308 significant. Decline is followed by a prompt recovery. The F4 event shows a strong correlation with
309 the declining pine trend, without later recovery; finally, in F5, macrocharcoal and pine pollen do not
310 show any significant correlation (Fig. 4). The highest charcoal peaks F4–F5 are lagged by a
311 pronounced stratigraphic tail (320–214 cm), which includes pyrophytic fungi (*Gelasinospora*). The
312 observed pattern fits the typical sequence of primary-to-detrital charcoal deposition caused by a local
313 fire, starting with immediate charcoal input by direct fall-out, followed by microbiological decay of
314 litter charcoal and by a secondary input of detrital charcoal driven by runoff (e.g. Colombaroli &
315 Gavin, 2010). The prompt pine recovery after events F1–F3 represents novel fossil evidence for the
316 Canarian pine forest's known resilience to fire. But the missing recovery after event F4, enhancing
317 runoff and protracting secondary deposition is intriguing.

318 Macrocharcoal input decreased in zones Z5 and Z6 to below 200 particles/cm³, mirrored by a further
319 decline of pine pollen below 40% (Fig. 4). This may indicate limited fuel availability and further pine
320 contraction in the local watershed. Persistently high microcharcoal supply can likely be linked to
321 background secondary deposition and / or to regional fires.

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Figure 3 Pollen diagram and record of other palaeoecological proxies from core CAL1 (La Calderilla, Gran Canaria) against age (cal. yr BP) and depth (cm). Data are expressed in percentage unless otherwise stated. The biostratigraphic discriminant cluster of taxa distinguishing zone Z6 was separated at the right side of the upper panel. These latter taxa include pollen types obtained by

329 constrained clustering together with other palynomorphs also discriminant for zone Z6
 330 (*Sporormiella*). Continuation in lower panel: sporadic pollen taxa (i.e. pollen types with average
 331 abundance below 2%), pollen zonation, charcoal proxies and charcoal events F1-F5.

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Figure 4 (a-e) Correlograms showing correlation between macrocharcoal abundance and pine pollen percentage at reduced time windows from core CAL1 (La Calderilla, Gran Canaria). Significance levels ($r \geq 0.5$) are indicated by red lines. (f) Pine pollen abundance versus macrocharcoal concentration (particles / cm³). F1 to F5 main fire events (see Fig. 3). Notice the progression of *Pinus* percentage levels from events F1 to F4 (grey arrow); a pollen decline from F4 to F5, and the subsequent drop of macrocharcoal abundance at 40% pine pollen (black arrow), marking the transition between pollen zone Z4 and Z5. Sample labels are stratigraphic depths.

3.4 The pollen record

The pollen record (Fig. 3) is clustered in six pollen zones grouped into two major stratigraphic biozones (Table 1): the lower one (Z1–Z3, 4800–2000 cal. yr BP) characterized by high abundance of pine pollen with several oscillations; and the upper super-zone (Z4–Z6, 2000–0 cal. yr BP), with reduced pine and high proportion of Poaceae and Asteraceae pollen. A sharp transition at 337–318 cm (2300–2000 cal. yr BP), coeval to fire event F4, separates both groups. The transition interval is clustered in zone Z3.

Interval / Pollen Zone	Time Span	Pollen and NPP Types	AP %	Vegetation Changes	Affecting Factors (→ Possible Concurrent Triggers)
Recent pollen deposition	Last 60 yrs	<i>Pinus canariensis</i> (48%, minimum = 40%), <i>Castanea sativa</i> (12%), Brassicaceae (14%), <i>Sporormiella</i> , Sordariaceae	55	Planted pine forest and secondary legume scrublands	Fire suppression, reforestation, pasture abandoning
Z6 (57–0 cm)	470–0	Cichorioideae (30%), Brassicaceae (25%), Poaceae (20%), Fabaceae (<10%), <i>Sporormiella</i> , <i>Pinus canariensis</i> (6%, minimum 3%), Sordariaceae	<10	Pastures and shrublands. Timberline depression	Human caused fires, timber cutting, animal husbandry
Z5 (225–57 cm)	1405–470	<i>Pinus canariensis</i> (35%, minimum = 24%), Poaceae (30%), Cichorioideae (25%), Brassicaceae (5%), Sordariaceae	35	Residual open forest, scrubs, grasslands, petrophytic open vegetation	Human caused fires, timber cutting, animal husbandry

Z4 (318–225 cm)	1997–1405	<i>Pinus canariensis</i> (50%, minimum = 37%), Poaceae (25%), Cichorioideae (20%), Sordariaceae	50	Forest withdrawal, shift towards open pine forest, soil erosion	Human caused fires, timber cutting? animal husbandry (→ persistent climate drought?)
Z3 upper (376–318 cm)	2281–1997	<i>Pinus canariensis</i> (85%, minimum = 60%), Cichorioideae (5%), Poaceae (<10%) Sordariaceae	80	Signs of declining pine forest, early perturbation of the timberline ecotone	Intense fires (→ human caused), animal husbandry
Z3 lower (447–357 cm)	2746–2281	<i>Pinus canariensis</i> (85%, minimum = 60%), Cichorioideae (5%), Poaceae (<10%), <i>Glomus</i>	85	Dry pine forest full density	Wildfires (→ volcanic activity 1.9–2.1 ka?), human arrival in Gran Canaria
Z2 (567–447 cm)	3705–2746	<i>Pinus canariensis</i> (70%, minimum = 55%), Cichorioideae (12%), Poaceae (<10%), <i>Glomus</i>	70	Dry pine forest canopy density oscillating	Wildfires (→ volcanic activity 3.3–2.3 ka ?)
Z1 (638–567 cm)	4760–3705	<i>Pinus canariensis</i> (45%, minimum = 25%), Cichorioideae (35%), Poaceae (10%), <i>Glomus</i>	45	Post-fire open dry pine forest with scrubs and grasslands	Wildfires (→ volcanic activity between 4.7–4.5 ka ?)

Table 1. Outline of the environmental history at La Calderilla (Gran Canaria) by pollen zone (Z1 to Z6), indicating time span (cal. yr BP, modelled medians of range limits), main pollen and non-pollen palynomorph (NPP) types (major components and ecological proxies) and percentage of arboreal pollen (AP) in the last 4800 years. Interpretation of the reconstructed vegetation changes, of intervening factors and possible triggers is summarized in the last two columns.

3.5 Numerical analysis

Fossil pollen and moss polster samples are shown in the PCA biplot (Fig. 5). Axis 1 (26% of variance) reflects a gradient from pristine forest cover, with *Pinus* and *Morella*, to herbs, cultivated trees, coprophilous spores and other anthropogenic indicators (*Artemisia*, Brassicaceae). Fabaceae are also associated with anthropogenic vegetation, since their pollen is absent in the pristine vegetation phase. Moss samples are plotted apart, along the second axis, adding further variance distinct from the palaeo-ecosystem signal. Moving-correlation analysis highlights significant negative correlation values between charcoal and *Pinus* pollen abundance during events of charcoal accumulation F1 (620–600 cm) and F3–F4 (420–320 cm) (Fig. 7a).

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Figure 5 PCA biplot of La Calderilla (Gran Canaria) fossil and moss polsters. Taxa highlighted in blue show a significant correlation with the PCA Axes 1 and 2 ($r > 0.5$).

4 DISCUSSION

4.1. Environmental reconstruction

Dynamics of the Canarian pine forest

The basal zone (Z1, 4800–3700 cal. yr BP) is characterized by *Pinus* and Asteraceae pollen. After the fire event F1 pine pollen decreases from 60 to 30%. These percentages, calibrated to the pollen–vegetation relationships in Tenerife pine ecosystems (de Nascimento et al., 2015) suggest relatively open pine woodland, corresponding with an average pine forest cover of 55% (Fig. 6). The high percentages and concentration peaks of Asteraceae (*Sonchus* type, *Carlina* type, *Argyranthemum* type), Poaceae, and Caryophyllaceae, likely represent the response of pioneer species to increased openness triggered by fire disturbance. Locally the site hosted an ephemeral puddle in the wet season, as shown by occurrence of *Ranunculus acris* type, *Spyrogyra* and other Zygnemataceae with low values.

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Figure 6 *Pinus canariensis* pollen percentage fossil values from core CAL1 (La Calderilla, Gran Canaria, GC) compared with minimum and maximum threshold values determined in a training set of modern pollen rain from pine forest sites in Tenerife (TF) (de Nascimento et al., 2015).

The next zones (Z2, Z3, 3700–2000 cal. yr BP) record the recovery of pine forest. A high pine pollen proportion reached in zone Z3 (84%), coupled with a sharp reduction of open habitat *taxa*, and with the absence of wet pine forest indicators (*Erica*, *Morella*), points toward extensive dry pine forest cover. Pollen composition in modern Canarian pine forests is influenced by exposure to trade winds, with lower and less variable percentages of pine pollen typifying windward (wet) sites (Fig. 6). Thus, the observed high pine pollen values appear to indicate a dry pine forest reaching extensive cover but lower tree density. Further fire peaks (F2, F3) mark the progressive phase, coeval to temporary pollen declines of pine and increases of scrub plants. However, open vegetation maintained a significant pollen representation, suggesting that forest patches and rocky habitats kept their open structure within a mosaic landscape.

Forest withdrawal and the emergence of grasslands

At the Z3/Z4 boundary, a steady pine pollen decline is visible, initiated around 2280 cal. yr BP, from 80 to 35–40% and an opposing increase in Poaceae and Asteraceae, representing a shift from pine

465 forest to more open vegetation, lasting up to recent times. This change is coeval to the main fire event
466 F4. According to the morphometric data, only wild grasses are recorded. Medium to large-sized
467 Poaceae pollen (40–47 μm , e.g. *Anisantha*, *Avena*, *Bromus*, *Hordeum* in the native flora) occur in low
468 frequency. Following forest decline a shift towards small pollen-sized Poaceae suggests an expansion
469 of wild grasses (Appendix S2, Fig. S2.4). There are no pollen indicators for cultivated fields in zones
470 Z4–Z5, 2000–470 cal. yr BP. Nevertheless, the continuous record of Sordariaceae coprophilous
471 spores, starting with a large peak around 2280 cal. yr BP, is indicative of animal husbandry.
472 Sordariaceae, although sometimes occurring within forest soils, mostly grow on droppings, even at
473 low levels of grazing pressure, replacing saprophytic fungi (Doyen & Etienne, 2016). For instance,
474 modern mosses and soils in Gran Canaria that are occasionally visited by introduced herbivores,
475 contain abundant Sordariaceae spores (Appendix S3, Fig. S3.5). Furthermore, this peak marks the
476 decline of *Glomus*, an endomycorrhizal saprophytic fungus growing on organic matter, mostly
477 restricted to earlier intervals with abundant decaying charcoal.

478 Overall, our findings indicated that by ca. 2280 cal. yr BP the local watershed of La Calderilla
479 underwent an expansion of scrubs and grasslands, likely related to the introduction of animal
480 husbandry, as corroborated by modern pollen/spores-vegetation relationships. This suggests that the
481 emergence of open grassy vegetation in the summit landscape of Gran Canaria represents an ancient
482 cultural landscape, not a secondary product of recent deforestation.

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484 **Land use changes after the Castilian conquest**

485 The uppermost core section (Z5–Z6, 700 cal. yr BP to about 70 years ago) is marked by the appearance
486 and expansion of *Artemisia*, Asteraceae, Brassicaceae, Caryophyllaceae and Fabaceae (*Teline* and
487 *Adenocarpus* types), and by *Sporormiella* and Sordariaceae coprophilous spores (Fig. 3). There is a
488 further decline of pine and appearance of *Quercus robur* type with very low values. The final step of
489 pine decline in zone Z6 is unrelated to changes in charcoal, suggesting that most of the local pine
490 population had been depleted at La Calderilla and that a regional forest reduction affected residual
491 pine stands.

492 The statistical boundary Z5/Z6 at 57 cm (470 cal. yr BP) shows quantitative changes of the main
493 pollen producers, i.e. pine and *Artemisia*, but also the expansion of wind-pollinated herbs and shrubs
494 from ruderal habitats (*Artemisia*, *Polygonum*, Chenopodiaceae and Asteraceae), which today grow in
495 most secondary vegetation zones of Gran Canaria, regardless of elevation. At the same time, an
496 increase in Caryophyllaceae and Brassicaceae may be related to local weeds living today in grazed
497 areas and on the caldera floor (Fig. 1). The evidence of animal husbandry in the caldera in the last

498 400 years is indicated by the increase of *Sporormiella* spores, which do not disperse far from source,
499 being quantitative indicators of local livestock (Davis & Shafer, 2006).

500 The increase in anthropogenic indicators at the Z5/Z6 boundary, and its stratigraphic position, above
501 the midpoint of the last two millennia, are consistent with land use changes and timing of the Castilian
502 conquest and the subsequent rural development that affected Gran Canaria between 16th and the onset
503 of 20th century CE (Naranjo-Cigala, 1995; Santana, 2001). Chestnut and walnut are absent throughout
504 the core up to its top, dated to the 1950s or a little earlier (Appendix S3, Fig. S3.6). These trees were
505 actually planted in the area only around the 1950s CE.

506

507 **4.2 Fire ecology and disturbance in Canarian pine forests**

508 The pollen and charcoal stratigraphy showed the occurrence of a pine forest in the higher areas of
509 Gran Canaria for the past 4800 years, which changes in plant cover in response to fire.

510 The Canarian pine is considered to be adapted to high-intensity fires (Climent, Tapias, Pardos & Gil,
511 2004; Keeley & Zedler, 1998) through traits including: (1) thick bark insulating cambium; (2)
512 epicormic resprouting; (3) serotinous cones. Tall growth habit, longevity, long needles and deep
513 rooting add further adaptation to crown fires connected with great fuel accumulation. Modern pine
514 forests experience both surface and crown fires, favouring understory biodiversity (Otto, García del
515 Rey, Gil Muñoz & Fernández-Palacios, 2010), but the natural fire return interval is significantly
516 longer than the estimated time of recovery (13 years) for natural stands of pine forest on the island of
517 La Palma in at least the last 50 years (Morales, 2010). On the other hand, soil erosion and leaching in
518 the first years after fire may lead to nutrient losses that are not recovered in a 20 years perspective
519 (Durán, Rodríguez, Fernández-Palacios & Gallardo, 2008). The palaeoecological record presented
520 here is the first to show how this fire disturbance regime could have been sustained at the millennial
521 scale in a pre-anthropogenic scenario and how anthropic impacts may have disrupted this long-term
522 equilibrium.

523 Throughout the forested interval (4800–2000 yr cal. BP) we recorded a high TOM and high rate of
524 pyrogenetic organic matter, suggesting massive soil incorporation of woody charcoal. Stratigraphic
525 continuity is not ensured, as we cored a colluvial wedge between the caldera floor and the nearby
526 slope foot. Nonetheless, this 2800-year record contains an interesting succession of runoff and flood
527 events, and the evidence for three fire events, triggering forest cover oscillations and driving slope-
528 wash movements. High rate of organic matter incorporation improved water retention capacity and
529 soil water balance, well exploited by the deep rooting of the Canarian pine. Furthermore, fire
530 clearance and runoff increased habitat diversification.

531 It has previously been debated (e.g. Naranjo-Cigala, 1995) whether endemic shrubs, such as *Sideritis*,
532 *Erysimum*, *Pteroccephalus*, represented by several species in the summits of the highest islands
533 (Tenerife and La Palma) (Kunkel, 1991), survived and evolved in Gran Canaria highlands.
534 Alternatively, they may be seen as orographic relicts from a presumed treeless coenocline indicative
535 of a disrupted summit ecosystem, which may have existed under Pleistocene colder climates. Our
536 data suggest that, even under pre-anthropogenic Holocene pine forest cover, fire disturbance maintained
537 long-term open habitats with shrubs and herbs on denudated ridge tops, walls and caldera floors.

538 The resilient dry pine communities of the highlands were sustained by intense natural fires for more
539 than two millennia between 4800 and 2000 cal yr BP. In general, our historical reconstruction agrees
540 with the potential vegetation model of the Gran Canaria highlands envisaged by modern
541 bioclimatology and based on relationships between instrumental climatologies and vegetation (del
542 Arco et al., 2006). The success of pine plantations in re-afforesting this zone over the last 60 years
543 (Appendix S3, Fig. S3.6) provides further support for this conclusion.

544

545 **4.3 Triggering forest withdrawal since 2.2 ka: volcanic eruptions and humans**

546 The palaeoecological record of La Calderilla displays a long history of forest decline in the timberline
547 ecotone, so that at the time of the Castilian arrival the high elevation pine forest was considerably
548 depleted both in the pollen and macrocharcoal source area. A fire phase at 2200–2000 cal. yr BP
549 appears to have initiated forest decline and soil degradation, continuing until recent times without
550 signs of recovery. This event disrupted millennial dynamics in a pine forest that had previously
551 sustained several intense fire episodes and allowed the emergence of open grassy vegetation. We may
552 therefore hypothesize a forcing external to the natural ecosystem dynamics, either an irreversible
553 impact by early human interference (e.g. as recorded in many Pacific Islands, Prebble & Wilmshurst,
554 2009), or a harsh warming period, triggering severe droughts, e.g. in old pine forests of U.S. (Pierce,
555 Meyer & Timothy Jull, 2004), or an explosive pyroclastic eruption.

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559 Figure 7 Summary figure showing (a) La Calderilla record 10-intervals moving-correlation values
 560 between charcoal > 150µm and *Pinus canariensis* pollen percentage. (b) La Calderilla record charcoal
 561 > 150µm counts. (c) La Calderilla record pollen PCA Axis 1 summarising forest cover changes. (d)
 562 La Calderilla record *P. canariensis* pollen %; (e) Chronology of Middle to Late Holocene volcanic
 563 eruptions and of intervening quiescent periods (Rodriguez-Gonzalez et al., 2009). In red –
 564 strombolian eruptions; in violet – subplinian eruption (Bandama volcanic complex). (f) Human

565 peopling of Gran Canaria before the Castilian Conquest according to the archaeological and
566 documentary record. Probability density function of radiocarbon ages from pre-Castilian
567 archaeological sites (see Fig. S4.7). This panel also shows the time spanned (arrow) by the quote
568 reported by Pliny the Elder about settlement ruins as well as the age of the grindstone found under
569 the Bandama eruption lapilli fall (Barroso & Hansen, 2008). All panels are plotted on the original
570 chronostratigraphic scale of La Calderilla core.

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572 Archaeological research showed that the aboriginal population of Gran Canaria grew significantly
573 following initial occupancy, although arrival and early settlement phases remain poorly constrained
574 by radiocarbon ages. According to radiocarbon chronology (Appendix S4), settlements reliably
575 dating to the 3rd–4th centuries CE occur in the pine belt, at Risco Chimirique and Cueva del Rey and
576 at Artenara (Martín, 2000; Velasco, 2014). These prehistoric settlements, located in the highlands at
577 1000–1500 m elevation, imply the existence of pre-historic highland grazing, affecting pine forests
578 (Jiménez, 1999). Anthracological evidence shows the importance of pine as a wood resource for the
579 aboriginal population, since at least 1700 cal. yr BP (Jorge-Blanco, 1989; Machado, 2009).

580 There is further evidence indicating that Gran Canaria was actually occupied earlier (Fig. 7). The first
581 reliable historical report of human settlements in Gran Canaria before the onset of the Common Era
582 is given by Pliny the Elder's *Naturalis Historia* (Fig. 7f, Appendix S4). Another early, but generally
583 neglected, date (ca. 1900 cal. yr BP) originates from a grindstone found under a pyroclastic flow
584 during the volcanic eruption of Bandama (Barroso & Hansen, 2008; location in Fig. 1d; timing in
585 Fig. 7e).

586 The palaeoecological evidence from La Calderilla suggests an even older onset of human impact, in
587 agreement with the mid-elevation caldera record of Laguna de Valleseco (Fig. 1b). Here, there is a
588 first change in vegetation 2300 years ago and in situ cereal fields settled 1800 years ago (de
589 Nascimento et al., 2016). Consistent evidence of increasing fire frequency is found in Tenerife, La
590 Gomera and Valleseco in Gran Canaria (de Nascimento et al., 2009, 2016; Nogué, de Nascimento,
591 Fernández-Palacios, Whittaker & Willis, 2013) about the same time as in La Calderilla, and all these
592 events are dated (between 2300 and 1800 years ago) very close to the timing of forest decline we
593 recorded in the Gran Canaria highlands.

594 It has been shown worldwide that often, when humans reach new areas and occupy natural forest,
595 there tends to be an immediate drop in forest biomass, in excess of that caused by other potential
596 concurrent factors (e.g. McWethy et al., 2010; Pini et al., 2017). In this perspective, we cannot exclude
597 a multifactorial explanation, such as firing in connection with a drought phase, and recurrently, with

598 a frequency high enough to prevent resprouting and regeneration. This technique was effectively
599 practiced by Mediterranean shepherds since the introduction of animal husbandry in the Neolithic, to
600 clean up large landscapes and increase the productivity of their husbandry activities (Walsh, 2013).
601 In the studied record we clearly observed grasslands replacing the pine forest, with indicators of
602 animal husbandry at low levels of grazing pressure. Thus, more frequent (cultural) fires would have
603 impeded the pine forest recovery, although the site experienced only a low human pressure until the
604 time span of European settlement from the 15th Century onwards.

605 The second hypothesis based on the influence of an eruptive phase is not to be discarded. Several
606 strombolian eruptions affected the northern flank of Gran Canaria in the Late Holocene (Fig. 7e).
607 They may have enhanced fire frequency and charcoal plume dispersal on the windward slope of the
608 highlands, also affecting the area of La Calderilla. Thus, strombolian and lava flow activity may be
609 included in the natural disturbance driving the observed long-term dynamics of pine forests. Actually,
610 the time around the beginning of the Common Era was marked both by a nearby strombolian eruption
611 of low explosiveness (El Garañón, median age = 1940 cal. yr BP, Fig. 1d), and by a very explosive
612 event (Bandama, median age = 1920 cal. yr BP, Fig. 1d, Fig. 7e). Pyroclastic flows are known to
613 produce immediate effects on plant cover, but explosive volcanic disturbance is generally followed
614 by swift recovery, whenever primary or secondary ecological succession is allowed to proceed
615 unhindered (Whittaker, Bush & Richards, 1989). Furthermore, expanding pyroclastic flows from
616 Bandama to La Calderilla would conflict with their rheology and dominant trade winds. These flows
617 typically collapse down-slope from the eruption centre toward the south (Fig. S1.2) or south east,
618 while the uplands were at much higher elevation than the Bandama volcano (about 570 m) and west-
619 oriented.

620 The initiation of the forest decline (calibration extremes 2σ age range = 2218–2332 cal. yr BP, median
621 age = 2228) and the early peak of coprophilous spores (modelled median age = 2281 cal. yr BP) both
622 substantially pre-date these volcanic events, thus excluding a causal link, while being consistent with
623 the timing of early forest clearance at the nearby site of Valleseco (calibration extremes 2σ age range
624 = 2259–2474 cal. yr BP, median age = 2368) (de Nascimento et al., 2016; Fig. 1c).

625 From the overall evidence, we argue for an explanation external to the natural ecosystem dynamics
626 for this early forest decline, most probably triggered by recurrent human burning. We infer that the
627 alteration of the timberline ecotone was initiated by aborigines with cultural firing and by wood
628 collection, producing an enhanced signal of fires in the early stage of island colonization, marking
629 intensification of human activities in the summit. The introduction of large herbivores (goat and
630 sheep) to the island's ecosystems and the practice of firing woodlands for land use, including pastures,
631 are considered to have had a great impact on the ecology of these islands (de Nascimento et al., 2009;
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632 Morales et al., 2009). Pressure over the timberline belt persisted during aboriginal times, along with
633 later fires possibly triggered by the most recent volcanic events, and then, finally, after the Castilian
634 conquest, the intensification of wood collection for ships, houses and tools, fuel, tar production and
635 sugarmills caused the final reduction of the timberline in the Gran Canaria highlands.

636

637 **4.4 Conclusions**

638 This study provides the first historical ecological insights into the last 4800 years of the pine forest
639 dynamics of the highlands of the Canary Islands. The record indicates that extensive pristine
640 communities of dry pine forests characterised the Gran Canaria highlands for more than two millennia
641 from the start of the record. Pine forests appear to have been resilient to recurrent disturbance by
642 natural fires. Alteration of the timberline ecotone was initiated around 2280 years ago, most probably
643 by anthropogenic burning practices that increased 2000 years ago, and lasted until recent times. The
644 early phase of this landscape alteration appears to be coeval, within the dating uncertainties, with the
645 first charcoal peak in a previous study from a middle elevation site in Gran Canaria (de Nascimento
646 et al., 2016), while failing to match the timing of volcanic eruptions and predating the earliest known,
647 dated, human settlements on the island. These data suggest that people were on the island several
648 centuries earlier than recorded by archaeological dates so far available. Recurrent cultural fires and
649 animal husbandry appear to have impeded the pine forest recovery since then. Pressure in the
650 timberline zone persisted, along with later fires triggered by the most recent volcanic events, and
651 finally, the Castilian conquest caused a definitive depression of the timberline. The evidence of
652 remaining “pristine” stands of pine forests in the Gran Canaria highlands supports a bioclimatic
653 rationale for the reforestation program carried out in the 20th century. It appears that some of the sites
654 converted in the 20th century to pine plantations were a 2000 years old cultural landscape of relatively
655 diverse highland grasslands established soon after initial human colonization.

656

657 **References**

- 658 AEMET, Agencia Estatal de Meteorología (2012) *Climate atlas of the Archipelagos of the Canary*
659 *Islands, Madeira and the Azores*. Agencia Estatal de Meteorología de España, Ministerio de
660 Agricultura, Alimentación y Medio Ambiente.
- 661 Anderson, C.L., Channing, A. & Zamuner, A.B. (2009) Life, death and fossilization on Gran Canaria
662 – implications for Macaronesian biogeography and molecular dating. *Journal of Biogeography*, 36,
663 2189–2201.

- 664 Atoche, P. (2008) Las culturas protohistóricas canarias en el contexto del desarrollo cultural
665 mediterráneo: propuesta de fasificación. In R. González, F. López & V. Peña (Eds.), *Los Fenicios y*
666 *el Atlántico* (pp. 317–344). Madrid: Centro de Estudios Fenicios y Púnicos.
- 667 Barroso, V. & Hansen, A.R. (2008) Los primeros canarios. In A.R. Hansen & C.J. Moreno (Eds.) *El*
668 *Gran Volcán—La Caldera y El Pico de Bandama* (pp. 193–216). Gran Canaria: Consejería de Medio
669 Ambiente y Aguas del Cabildo de Gran Canaria.
- 670 Bronk Ramsey, C. (2008) Deposition models for chronological records. *Quaternary Science Reviews*,
671 27, 42–60.
- 672 CIA-Consejo Insular de Aguas de Gran Canaria (2015) *Gran Canaria hydrological plan*.
673 <http://www.aguasgrancanaria.com/>
- 674 Climent, J., Tapias, R., Pardos, J.A. & Gil, L. (2004) Fire adaptations in the Canary Islands pine
675 (*Pinus canariensis*). *Plant Ecology*, 171, 185–196.
- 676 Colombaroli, D. & Gavin, D.G. (2010) Highly episodic fire and erosion regime over the past 2,000 y
677 in the Siskiyou Mountains, Oregon. *Proceedings of the National Academy of Sciences*, 107, 18909–
678 18914.
- 679 Connor, S.E., van Leeuwen, J.F.N., Rittenour, T.M., van der Knaap, W.O., Ammann, B. & Björck,
680 S. (2012) The ecological impact of oceanic island colonization – a palaeoecological perspective from
681 the Azores. *Journal of Biogeography*, 39, 1007–1023.
- 682 Davis, O.K. & Shafer, D.S. (2006) *Sporormiella* fungal spores, a palynological means of detecting
683 herbivore density. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 237, 40–50.
- 684 de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C. & Whittaker, R.J. (2009) The
685 long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of*
686 *Biogeography*, 36, 499–514.
- 687 de Nascimento, L., Nogué, S., Fernández-Lugo, S., Méndez, J., Otto, R., Whittaker, R.J., ...,
688 Fernández-Palacios, J.M. (2015) Modern pollen rain in Canary Island ecosystems and its implications
689 for the interpretation of fossil records. *Review of Palaeobotany and Palynology*, 214, 27–39.
- 690 de Nascimento, L., Nogué, S., Criado, C., Ravazzi, C., Whittaker, R.J., Willis, K.J. & Fernández-
691 Palacios, J.M. (2016) Reconstructing Holocene vegetation on the island of Gran Canaria before and
692 after human colonization. *The Holocene*, 26, 113–125.

de Nascimento L., Nogué S., Naranjo-Cigala A., Criado C., McGlone M., Fernández-Palacios E.,
 Fernández-Palacios J.M. (2020) Human impact and ecological changes during prehistoric settlement
 on the Canary Islands. *Quaternary Science Reviews*, 239. doi.org/10.1016/j.quascirev.2020.106332

del Arco, M.J., Wildpret, W., Pérez de Paz, P.L., Rodríguez, O., Acebes, J.R., García A, ..., García,
 S. (2006) Mapa de Vegetación de Canarias. Santa Cruz de Tenerife: GRAFCAN.

Doyen, E. & Etienne, D. (2016) Ecological and human land-use indicator value of fungal spore
 morphotypes and assemblages. *Vegetation History and Archaeobotany*, 26, 357–367.

Durán, J., Rodríguez, A., Fernández-Palacios, J.M. & Gallardo, A. (2008) Changes in soil N and P
 availability in a *Pinus canariensis* fire chronosequence. *Forest Ecology and Management*, 256, 384–
 387.

Fernández-Palacios, J.M. & de Nicolás, J.P. (1995) Altitudinal patterns of vegetation variation on
 Tenerife. *Journal of Vegetation Science*, 6, 183–190.

Gieger, T. & Leuschner, C. (2004) Altitudinal change in needle water relations of *Pinus canariensis*
 and possible evidence of a drought-induced alpine timberline on Mt. Teide, Tenerife. *Flora*, 199,
 100–109.

Guillou, H., Pérez Torrado, F.J., Hansen, A.R., Carracedo, J.C. & Gimeno, D. (2004) The Plio-
 Quaternary volcanic evolution of Gran Canaria based on new K-Ar and magnetostratigraphy. *Journal*
of Volcanology and Geothermal Research, 135, 221–246.

Grimm, E.C. (1987) CONISS: a FORTRAN 77 program for stratigraphically constrained cluster
 analysis by the method of incremental sum of squares. *Computer & Geosciences*, 13, 13–35.

Höllermann, P. (1978) Geoecological aspects of the upper timberline in Tenerife, Canary Islands.
Arctic and Alpine Research, 10, 365–382.

Holtmeier, F. (2009) *Mountain Timberlines*. The Netherlands: Springer Netherlands.

Jiménez, J.J. (1999) *Gran Canaria Prehistórica*. Santa Cruz de Tenerife: Centro de la Cultura Popular
 Canaria.

Jorge-Blanco, M.S. (1989) Restos vegetales de un túmulo arqueológico de la necrópolis de Arteara,
 Gran Canaria. *Botánica Macaronésica*, 18, 47–58.

Keeley, J.E. & Zedler, P.H. (1998) Evolution of life histories in *Pinus*. In D.M., Richardson (Ed.)
Ecology and Biogeography of Pinus (pp. 219–250). Cambridge: Cambridge University Press.

Kunkel, G. (coord., 1991) *Flora y Vegetación del Archipiélago Canario. Tratado florístico de*
Canarias. 2º parte. Dicotiledóneas. Las Palmas: Edirca.

- 724 Machado, M.C. (2009) El combustible: la antracología. In P. González, M.A. Moreno & A.M.
725 Jiménez (Eds.) *El yacimiento arqueológico de La Cerera, un modelo de ocupación en la isla de Gran*
726 *Canaria* (pp. 299–317). Las Palmas de Gran Canaria: Cabildo de Gran Canaria.
- 727 Martín, E. (2000) Dataciones absolutas para los yacimientos de Risco Chimirique (Tejeda) y Playa
728 de Aguadulce (Telde). *Vegueta*, 5, 29–46.
- 729 McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., ..., Cook,
730 E.R. (2010) Rapid landscape transformation in South Island, New Zealand, following initial
731 Polynesian settlement. *Proceedings of the National Academy of Sciences*, 107, 21343–21348.
- 732 Morales, G. (2010) Análisis del impacto del fuego en la composición específica, estructura y función
733 del pinar canario a lo largo de una cronosecuencia de incendios en la isla de La Palma (Canarias).
734 PhD thesis. Santa Cruz de Tenerife: Universidad de La Laguna.
- 735 Morales, J., Rodríguez, A., Alberto, V., Machado, C., Criado, C. & Rando, J.C. (2009) The impact
736 of human activities on the natural environment of the Canary Islands (Spain) during the pre-Hispanic
737 stage (3rd–2nd Century BC to 15th Century AD): an overview. *Environmental Archaeology*, 14, 27–
738 36.
- 739 Naranjo-Cigala, A. (1992) Evolución del paisaje vegetal en la Cumbre Central de Gran Canaria (Islas
740 Canarias). Una aproximación a la dinámica recolonizadora de la vegetación. *Vegueta*, 0, 263–278.
- 741 Naranjo-Cigala, A. (1995) *Evolución del paisaje vegetal en la Cumbre Central de Gran Canaria*
742 *(1960-1992)*. Las Palmas: Universidad de Las Palmas de Gran Canaria.
- 743 Naranjo-Cigala, A., Salas, M. & Almeida, R.S. (2001) La vegetación del Paisaje Protegido de Las
744 Cumbres (Gran Canaria-Islas Canarias): el matorral de leguminosas (Telino-Adenocarpion,
745 Andryalo-Ericetalia, Pruno-Lauretea). *Vieraea*, 29, 59–70.
- 746 Nogué, S., de Nascimento, L., Fernández-Palacios, J.M., Whittaker, R.J. & Willis, K.J. (2013) The
747 ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. *Journal*
748 *of Ecology*, 101, 368–377.
- 749 Nogué, S., de Nascimento, L., Froyd, C.A., Wilmshurst, J.M., de Boer, E.J., Coffey, E.E.D., ..., Willis,
750 K.J. (2017) Island biodiversity conservation needs palaeoecology. *Nature Ecology & Evolution*, 1,
751 Article number: 0181.
- 752 Ohlson, M. & Tryterud, E. (2000) Interpretation of the charcoal record in forest soils: Forest fires and
753 their production and deposition of macroscopic charcoal. *The Holocene*, 10, 519–525.

- 754 Otto, R., García del Rey, E., Gil Muñoz, P. & Fernández-Palacios, J.M. (2010) The effect of fire
755 severity on first-year seedling establishment in a *Pinus canariensis* forest on Tenerife, Canary Islands.
756 *European Journal of Forest Research*, 129, 499–508.
- 757 Pérez de Paz, P.L., Salas, M., Rodríguez, O., Acebes, J.R., del Arco, M.J. & Wildpret, W. (1994)
758 *Atlas cartografico de los pinares canarios. IV. Gran Canaria*. Santa Cruz de Tenerife: Viceconsejería
759 de Medio Ambiente, Gobierno de Canarias.
- 760 Pierce, J.L., Meyer, G.A. & Timothy Jull, A.J. (2004) Fire-induced erosion and millennial scale
761 climate change in northern ponderosa pine forests. *Nature*, 632, 87–90.
- 762 Pini, R., Ravazzi, C., Raiteri, L., Guerreschi A., Castellano, L. & Comolli, R. (2017) From pristine
763 forests to high-altitude pastures: an ecological approach to prehistoric human impact on vegetation
764 and landscapes in the western Italian Alps. *Journal of Ecology*, 105, 1580–1597.
- 765 Prebble, M. & Wilmshurst, J.M. (2009) Detecting the initial impact of humans and introduced species
766 on island environments in remote Oceania using palaeoecology. *Biological Invasions*, 11, 1529–
767 1556.
- 768 Quirantes, F., Núñez, J.R., García, D.A. & Viña, A. (2011) *Los montes de Tenerife a través de su*
769 *historia*. La Laguna: Universidad de La Laguna.
- 770 Rando, J.C., Alcover, J.A., Galván, B. & Navarro, J.F. (2014) Reappraisal of the extinction of
771 *Canariomys bravoii*, the giant rat from Tenerife (Canary Islands). *Quaternary Science Reviews*, 94,
772 22–27.
- 773 Reimer, P.J., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G., Bronk Ramsey, C., ..., van der Plitch,
774 J. (2013) IntCal13 and MARINE13 radiocarbon age calibration curves 0-50000 years cal BP.
775 *Radiocarbon*, 55, 1869–1887.
- 776 Rodriguez-Gonzalez, A., Fernandez-Turiel, J.L., Perez-Torrado, F.J., Hansen, A., Aulinas, M.,
777 Carracedo, J.C., ..., Paterne, M. (2009) The Holocene volcanic history of Gran Canaria island:
778 Implications for volcanic hazards. *Journal of Quaternary Science*, 24, 697–709.
- 779 Santana, A. (2001) *Evolución del paisaje de Gran Canaria*. Las Palmas de Gran Canaria: Ediciones
780 del Cabildo de Gran Canaria.
- 781 Velasco, J. (2014) El tiempo de los antiguos canarios. *Boletín Electrónico de Patrimonio Histórico*,
782 2, 12–14.

- 783 Velasco J., Alberto V., Delgado T., Moreno M., Lecuyer C. & Richardin P. (2019) Poblamiento,
784 colonización y primera historia de canarias: el C14 como paradigma. *Anuario de Estudios Atlánticos*,
785 66, 1–24.
- 786 Viera y Clavijo de, J. (1790) *Extracto de las actas de la Real Sociedad Económica de Amigos del*
787 *País de Las Palmas (1777-1790)*. Las Palmas de Gran Canaria: Real Sociedad Económica de Amigos
788 del País de Gran Canaria.
- 789 Walsh, K. (2013) *The Archaeology of Mediterranean Landscapes. Human-Environment Interaction*
790 *from the Neolithic to the Roman Period*. Cambridge University Press.
- 791 Whitlock, C. & Millspaugh, S.H. (1996) Testing assumptions of fire history studies: an examination
792 of modern charcoal accumulation in Yellowstone National Park. *The Holocene*, 6, 7–15.
- 793 Whitlock, C., Colombaroli, D., Conedera, M. & Tinner, W. (2017) Land-use history as a guide for
794 forest conservation and management. *Conservation Biology*, 32, 84–97.
- 795 Whittaker, R.J., Bush, M.B. & Richards, K. (1989) Plant recolonization and vegetation succession on
796 the Krakatau Islands, Indonesia. *Ecological Monographs*, 59, 59–123.
- 797 Willis, C. & Birks, H.J.B. (2006) What is natural? The need for a long-term perspective in biodiversity
798 conservation. *Science*, 314, 1261–1265.

799

800 Biosketch

801 Cesare Ravazzi is a researcher working at the National Research Council in Milano, leading a group
802 on vegetation, climate, and human interactions.

803 Author contribution: J.M.F.-P., L.d.N., C.C. and R.J.W. initiated the project; C.R. coordinated the
804 research; M.M. carried out most pollen counting, and contributed to data analysis and figures; M.M.,
805 L.G., R.P. analysed pollen, charcoal and thermogravimetric data; C.C., F.J.P.-T., J.M.F.-P., A.N.,
806 L.d.N., M.M. and C.R. contributed to coring, sampling and interpreting chronological data and
807 volcanic and sedimentary environments; A.N. interpreted the contemporary vegetation dynamics;
808 M.M., C.R. and R.P. made statistical analysis; C.R. and M.M. wrote the paper with the help of all co-
809 authors.

810

811 Supporting Information

812 **Appendix S1 Introductory geology, litho- and chronostratigraphic information on La**
813 **Calderilla (Gran Canaria) core CAL1**

814 Introductory geology to La Calderilla (Gran Canaria).
815 Sedimentary log and sedimentary environments from La Calderilla (Gran Canaria) core CAL1.
816 Geochronometry, biochronological markers and age-depth model design of La Calderilla (Gran
817 Canaria) core CAL1.
818
819 **Appendix S2 Bibliographical reference for pollen, spores and charcoal analysis; morphometry**
820 **of Poaceae pollen**
821 List of references for the identification of palynological taxa, algae and fungi, and of macrocharcoal
822 morphotypes.
823 Morphometric analysis of Poaceae pollen.
824
825 **Appendix S3 Information on pollen rain – modern vegetation and land use relationships**
826 Pollen rain of individual pollen types recorded from mosses and modern vegetation.
827 Land use changes in the last 60 years in La Calderilla (Gran Canaria).
828
829 **Appendix S4 Radiocarbon archaeological chronology and early historical record of Gran**
830 **Canaria**
831 Early historical record of nature features and human artifacts on Gran Canaria at the onset of Current
832 Era (Pliny the Elder).
833 Probability density function of radiocarbon ages from pre-Castilian archaeological sites of Gran
834 Canaria.

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