

1 **Climate change and the migration of a pastoralist people c.3500 cal. years**  
2 **BP inferred from palaeofire and lipid biomarker records in the montane**  
3 **Western Ghats, India**

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19

20 **Abstract**

21

22 Human migration in response to climate change during the Holocene has been recorded in  
23 many regions of the world. The Todas are a pastoralist people who are believed to have  
24 colonized the higher elevations (>2000 m asl) of the Nilgiris in the Western Ghats, India, not  
25 earlier than about 2000 cal. yr BP. Vegetation shifts in response to changing climate in tropical  
26 montane forest-grassland mosaic of the Ghats have been well documented using stable carbon  
27 isotopes and pollen profiles; however, there have been no corresponding investigations of  
28 human presence and activity at the highest elevations. We used a number of other proxies to  
29 infer the human ecology of this montane region. Radiocarbon dated (~22,000 cal. BP to the  
30 present) peat samples from the Sandynallah basin (2200m asl, Nilgiri hills, Tamil Nadu State)  
31 were used to reconstruct fire history, animal abundance, and human presence since the Last  
32 Glacial Maximum (LGM). While the macro-charcoal record indicates fires at the LGM, macro-  
33 and micro-charcoal counts indicate intense fire at ~3500 cal. yr BP, coprophilous fungal spores  
34 indicate a large population of herbivorous mammals, and steroid biomarkers indicate human  
35 faecal remains for the first time. This period is also characterized by dry arid conditions and  
36 dominant grassy vegetation as inferred from *n*-alkane signatures. We thus infer that a pastoralist  
37 people, most likely the Todas, migrated to the highest elevations of the Western Ghats along  
38 with their buffalo herds in response to prolonged or abrupt climate change in peninsular India,  
39 about 3500 cal. yr BP or at least 1500 years prior to what historical accounts assume.

40 **Keywords:** Palaeoclimate, Holocene, human migration, Toda, buffalo culture, lipid biomarker

41

## 42 **1. Introduction:**

43

44 Climate change is known to have driven human adaption through migration from the earliest  
45 times of human evolution (Carto et al. 2009; Tierney, deMenocal, and Zander 2017) through  
46 to the historical period of the late Holocene (D'Andrea et al. 2011). Some of the best  
47 documented migrations involving nomadic pastoralists and agriculturalists come from Chinese  
48 chronicles (Fang and Liu 1992; Pei 2017). A series of migrations of nomadic people in the  
49 Mongolian grasslands and east-central Asia between 190 BCE and 1880 CE is closely related  
50 to historical cold and dry periods (Fang and Liu 1992). Holocene migrations in the tropics have  
51 been less well documented, though the migration of the Harappan people southward, following  
52 the decline of the extensive Harappan civilization in northwest India and Pakistan, has been  
53 increasingly attributed to the aridification of this region about four millennia ago (Chandran,  
54 1997; Dixit, Hodell, and Petrie 2014; Dutt et al. 2019).

55

56 Peninsular India has been inhabited by modern humans not long after the out-of-Africa  
57 migration (Korisettar 2016) while, at the same time, it has been subject to a changing climate  
58 in tune with global change during the late Pleistocene and Holocene Epochs (Sukumar et al.  
59 1993; Rajagopalan et al., 1997; Bhagwat, Nogué, and Willis 2012). Human societies in the  
60 peninsula have gone through a complex process of transitions from hunter-gatherer through  
61 pastoralist to settled agricultural over this period (Korisettar et al. 2001; Johansen 2004; Fuller,  
62 Boivin, and Korisettar 2007; Fuller 2013; Morrison et al. in press), though their links to climate  
63 have been scarcely investigated. The Western Ghats (sea level up to >2600m in the Nilgiris  
64 and Anamalais) running parallel to the west coast of India have generally been settled much  
65 after the Deccan plateau and its river valleys, perhaps because the Ghats were largely hilly and  
66 densely forested. Although human occupation of the Ghats has only been attributed to the end  
67 of the Palaeolithic, about 12,000 cal. BP (Chandran 1997), it is certain that human influences  
68 along the fringes of the Ghats, both the moister west and the drier east, would have been much  
69 earlier. In any case, no evidence has so far been presented or even suggested for human  
70 occupation at the highest elevations (>2000m asl) of the Ghats prior to about 2000 cal. BP; the  
71 steep slopes, rugged terrain and dense forests at lower to mid-elevation with a history of malaria  
72 may have proved to be difficult barriers for the ascent of humans to the highest elevations. The  
73 Todas, an obligate buffalo-tending pastoral community, are widely believed to be the earliest

74 people to move into the upper Nilgiri plateau perhaps during the 1st millennium CE or later  
75 (Rivers 1906; Noble 1976; Emeneau 1997; Zagarell 1997). Other indigenous people of the  
76 Nilgiris include the artisan Kotas, and the hunter-gather or cultivator Kurumbas and Irulas who  
77 have inhabited the region since early times, while the cultivator Badagas were 16th century  
78 immigrants (Hockings 1980).

79

80 The higher elevation (>2000m asl) of the Nilgiris features a unique ecosystem mosaic  
81 consisting of patches of tropical montane forests (locally known as *sholas*) restricted to the  
82 folds, valleys and depressions, and extensive grasslands on the slopes, ridges and exposed areas  
83 (Meher-Homji 1967; Jose et al. 1994; Das et al. 2015). Late Pleistocene and Holocene  
84 paleoclimatic reconstruction using stable carbon isotope analysis of peat from high-elevation  
85 (>2000 m asl) valleys of the Nilgiris suggests that the region had undergone phases of wet and  
86 arid climate, broadly in tune with well-known global climatic events since the Last Glacial  
87 Maximum, resulting in shifts in the relative dominance of C3 plants (mainly woody vegetation  
88 and herbs other than tropical grasses) and C4 plants (tropical grasses) (Sukumar et al. 1993;  
89 Caner et al. 2007). Evidence from pollen studies also suggests the co-occurrence of grassland  
90 and forest through moister and more arid phases in the Nilgiri region over this period (Vasanthy  
91 1988; Sutra, Bonnefille, and Fontugne 1997). While these studies have provided us with a fairly  
92 good understanding of past vegetation and associated climate, in particular the strength of the  
93 monsoon, they have not specifically investigated the human ecology associated with these  
94 changes.

95

96 At the same time, several other proxies such as macro- and microcharcoal abundance in  
97 sediments to record fires including those of possible anthropogenic origin (Carcaillet et al.  
98 2001; Whitlock and Larsen 2002; Clark 1988), fungal spores associated with dung to assess  
99 animal abundance (Van Geel 2002), leaf wax lipids characteristic of different plant types, and  
100 steroid compounds indicative of animal- and human faeces (Pancost et al. 2002; Meyers 2003)  
101 are useful to understand the relationship between climate, vegetation and human presence or  
102 activity. In particular, lipid biomarkers which are powerful tools in resolving past plant or  
103 animal origins have been hardly explored in paleoecological research in India. Alkanes have  
104 been used to trace their source in sediments from microbes, algae and higher plant types  
105 (Cranwell 1973; Ficken et al. 2000; Pancost et al. 2002; Nichols et al. 2006). *n*-alkane  
106 distributions dominated by carbon chain lengths C<sub>21</sub>, C<sub>23</sub> and C<sub>25</sub> suggest aquatic plant  
107 dominance (Pancost et al. 2002; Nichols et al. 2006). A predominance of C<sub>27</sub>, C<sub>29</sub> and C<sub>31</sub>

108 indicate higher contribution from epicuticular leaf waxes of land plants, with elevated C<sub>31</sub>  
109 presence attributed to inputs from grasses and C<sub>27</sub> or C<sub>29</sub> predominance related to a tree-leaf  
110 origin (Cranwell 1973; Rommerskirchen et al. 2006). Thus,  $nC_{27}/nC_{31}$  ratio has been applied  
111 to understand the changes in relative distributions of grasses and woody plants in peatland  
112 (Schwark, Zink, and Lechterbeck 2002).

113

114 Faecal steroid (stanols and sterols) biomarkers have been used to identify the biogenic origin  
115 in ancient samples as these organic molecules are resistant to diagenetic alteration and  
116 degradation (Bull et al., 1999; Bull et al., 2002; Prost et al., 2017). Stanols are produced by the  
117 microbial degradation process from their  $\Delta^5$ -sterols precursors (Bull et al. 2002; Nash et al.  
118 2005). Coprostanol is the major  $5\beta$ -stanol in human faeces, while the faeces of herbivores such  
119 as cows and sheep contain a higher relative proportion of  $5\beta$ -stigmastanol due to the high  
120 amount of stigmasterol, campesterol and sitosterol derived from their herbivorous diet  
121 (Linseele et al. 2013; Leeming et al. 1996). The ratios of various steroid compounds in dated  
122 archaeological samples have thus been used in identifying human and herbivorous mammalian  
123 faeces and, hence, their presence at a particular site (Linseele et al. 2013; Prost et al. 2017;  
124 Schroeter et al. 2020). Steroid biomarkers have never been used so far in exploring their origins  
125 in any archaeological or paleoecological context in India.

126

127 We thus carried out this study on Late Quaternary paleoecology of the Nilgiris with the  
128 following primary objectives:

- 129 a. To complement the earlier studies on paleo-climatic and paleo-vegetation by using  
130 proxies other than pollen and stable isotopes.
- 131 b. To use charcoal counts in peat to trace fire history and draw inferences on its possible  
132 relationship to past climate and human activity.
- 133 c. To use fungal spores specific to animal dung to determine the past abundance of  
134 herbivorous animals which may also signify presence of domestic animals.
- 135 d. To use lipid steroid biomarkers (associated with faeces) extracted from peat to detect  
136 the presence of domestic livestock and human populations in the Nilgiri plateau.

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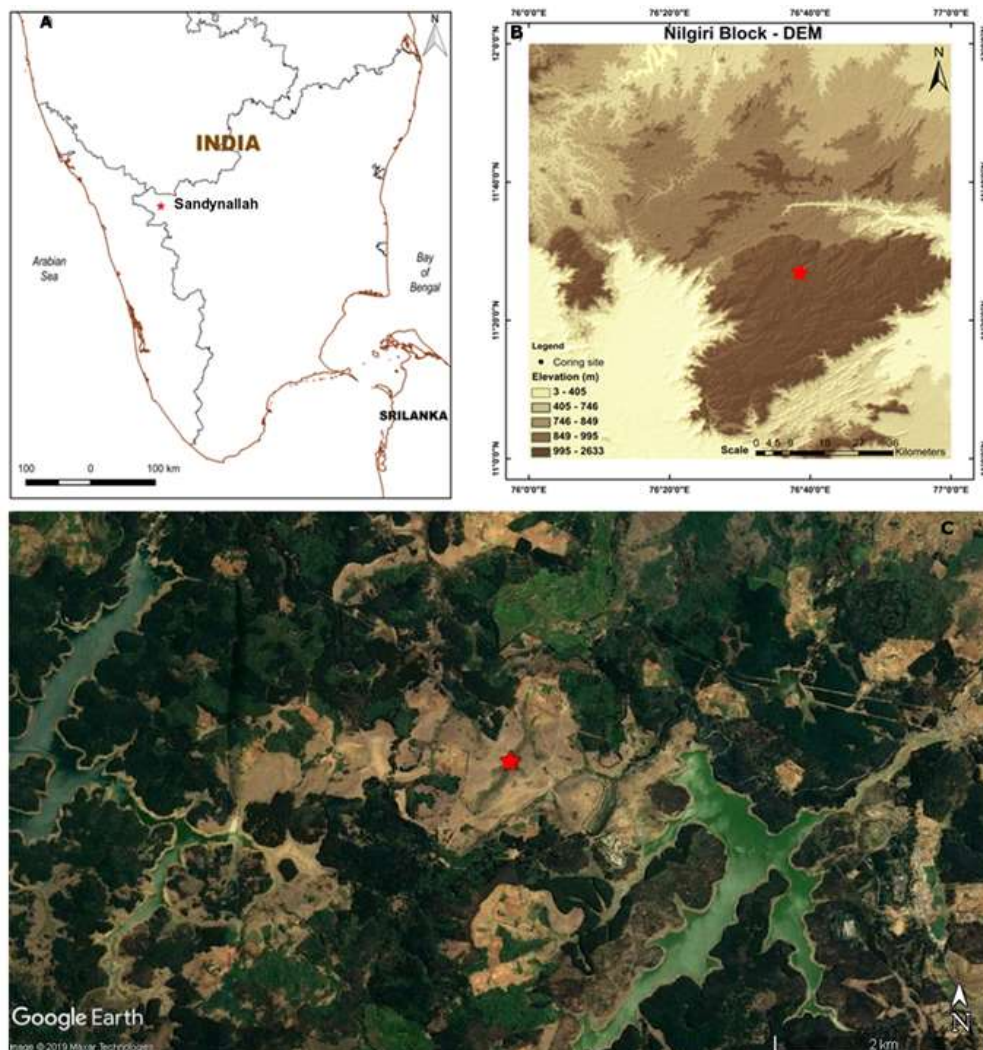
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## 141 2. Methods

### 142 2.1. Study site

143 Our study site, the Sandynallah valley, is located between 11°26'32"N, 76°38'6"E and  
144 11°26'37"N 76°38'8"E at an elevation of ~2200 m above sea level, in the Nilgiri massif of the  
145 southern Western Ghats, India (Fig. 1). Since 1950, the study site is administered by the Sheep  
146 Breeding Research Station (SBRS) of Tamil Nadu University of Veterinary and Animal  
147 Sciences (TANUVAS). Although the site is located in the tropical belt, peat is preserved in  
148 valleys in this mountain range due to cool temperatures (annual average 13.5 °C) and  
149 moderately high precipitation leading to water logging (annual average precipitation of about  
150 1400 mm) (von Lengerke 1977). These tropical mountain ranges feature peat deposits dating  
151 back to >40,000 radiocarbon yr BP which have been studied extensively to reconstruct Late  
152 Quaternary vegetation and climate (Vasanthy 1988; Sukumar et al. 1993; Sutra, Bonnefille,  
153 and Fontugne 1997; Rajagopalan et al., 1997; Ramya Bala 2015; Ramya Bala et al. 2016).

154



155

156 Fig 1. (A) The physical map of peninsular India depicting the Sandynallah site in the Nilgiris  
157 (B) The digital elevation model (source: ASTER GDEM) of the study region with the altitude  
158 range given in the side panel, (C) Google Earth image of Sandynallah and the trenching site  
159 with a mosaic vegetation pattern.

## 160 2.2. Sample collection and $^{14}\text{C}$ dating

161 A pit of ~1.8 m depth was dug close to a location from which a core (labelled as Core 1) had  
162 been previously taken and radiocarbon dated (Ramya Bala et al. 2016), and peat samples  
163 collected as monoliths at regular intervals in a stainless-steel box of dimensions 15.6 cm x 9.3  
164 cm x 3.0 cm. Thirteen samples were collected in zip lock bags, adjacent samples starting from  
165 the surface separated by ~2 cm, down to a depth of ~1.6 m. Sub-samples were freeze dried  
166 (Labconco bulk drier) and crushed into fine powder and stored. Accelerated Mass Spectrometry  
167 (AMS) radiocarbon dating of seven peat samples after standard Acid Alkali Acid (AAA) pre-  
168 treatment (Nakamura et al., 2003) was carried out at the Inter-University Accelerator Centre  
169 (IUAC), New Delhi (Table 1). Blank sample prepared along with the peat samples was used  
170 for background correction, while standard sample OXII (oxalic acid II) was used for  
171 normalization (Sharma et al., 2019). Data quality was monitored with a secondary standard  
172 (IAEA-C7); the consensus value ( $p\text{MC} = 49.53 \pm 0.12$ ) was within the error limits of the  
173 experimental result ( $p\text{MC} = 49.48 \pm 0.12$ ). Calibration of the radiocarbon dates was done using  
174 OxCal (Ramsey, 2013).

175

176 **Table 1.** Details of the AMS  $^{14}\text{C}$  dated peat samples and calibrated dates using OxCal from the  
177 Sandynallah basin

Lab Code	Sample type	Sample ID	Depth range	AMS $^{14}\text{C}$ age $\pm$ Error	Calibrated age range Cal BP ( $2\sigma$ )	Median cal yr BP
IUACD#17C1321	Bulk Peat	PS1	2-11 cm	-159 $\pm$ 31	19 to -2	4
IUACD#17C1322	Bulk Peat	PS3	25-34 cm	1413 $\pm$ 34	1372 to 1285	1320
IUACD#17C1323	Bulk Peat	PS5	47-56 cm	3280 $\pm$ 41	3608 to 3401	3510
IUACD#17C1324	Bulk Peat	PS8	81-90 cm	4202 $\pm$ 45	4852 to 4584	4730
IUACD#17C1325	Bulk Peat	PS10	104-113 cm	6135 $\pm$ 50	7165 to 6894	7035
IUACD#19C2461	Bulk Peat	PS11	115-124 cm	11508 $\pm$ 49	13455 to 13263	13355
IUACD#17C1326	Bulk Peat	PS13	138-147 cm	18235 $\pm$ 97	22361 to 21846	22103

178

### 179 2.3. *Macrocharcoal counts*

180 From each of the 13 samples collected for analyses, 1 gm peat was kept in 10 ml 10% KOH  
181 solution overnight to deflocculate particles followed by NaOCl treatment to remove non-  
182 charred organic matter (Stevenson and Haberle 2005). Particles >125 µm size were collected  
183 for identification. Macrocharcoal particles are visually recognizable as opaque, angular and  
184 usually planar, black fragment and were counted using a stereomicroscope (LeicaS4E) at 10x  
185 magnification (Mooney and Tinner 2011). The extraction was performed thrice for each  
186 sample, and the mean ( $\pm 1$  SD) count calculated.

187

### 188 2.4. *Microcharcoal, pollen count and dung fungal spore analyses*

189 Microcharcoal and fungal spores were extracted from peat using standard methods for chemical  
190 processing of pollen (Faegri and Iversen, 1989). The procedure involves a series of acid  
191 treatments with HCl to remove carbonates, HF to remove silicate minerals and acetolysis (9:1  
192 mixture of acetic anhydride and H<sub>2</sub>SO<sub>4</sub>) to remove polysaccharides (Erdtman, 1960). The  
193 samples were mounted on glass slides with glycerine and frequencies of microcharcoal, pollen  
194 (minimum of 800 pollen grains) and fungal spores were quantified using a microscope  
195 (Olympus CX43). Total pollen counts were done with the help of reference slides at the French  
196 Institute of Pondicherry (Tissot, Chikhi, and Nayar 1994). Black, opaque angular fragments  
197 >10 µm were identified and counted as microcharcoal particles (Clark 1988). We selected 4  
198 common fungal taxa considered as coprophilous and semi-coprophilous, *Sporormiella spp.*,  
199 *Sordaria spp.*, *Delitschia spp.*, and *Trichodelitschia spp.* (Perrotti and van Asperen 2019;  
200 Baker, Bhagwat, and Willis 2013) which were identified and classified at the level of genus or  
201 species based on van Geel et al. (2011); Cugny, Mazier, and Galop (2010). The ratio of  
202 coprophilous fungal spore count to total pollen count was used to estimate fungal spore  
203 abundance.

204

### 205 2.5. *Lipid extraction, quantification, biomarker identification and interpretation*

206 Total lipids were extracted from 0.2 g of the lyophilized peat samples using 9:1 v/v mixture of  
207 dichloromethane and methanol, and recovery standard consisting of 10 mg/l *n*-Hexatriacontane  
208 d<sub>50</sub>. The extracts were separated into two functional groups based on charge and hydrophobicity  
209 by solid phase extraction (SPE), using 6 ml glass columns packed with 500 mg of Supelco  
210 Superclean LC-NH-2 (Kim and Salem 1990). The columns were eluted with hexane (15 ml,

211 Fraction 1: alkanes) CHCl<sub>3</sub>/isopropanol (15 ml of 2:1 v/v, Fraction 2: alkanols). The Fraction  
212 2 was dissolved in 100 µl bis(trimethylsilyl) trifluoroacetamide (BSTFA) and 100 µl of pyridine,  
213 and heated (70 °C for 120 min) to convert all the alkanols into their respective trimethylsilyl  
214 ethers.

215 The two different lipid fractions were quantified in an Agilent 6890N GC (Linköping  
216 University, Sweden) interfaced to an Agilent 5973 MSD mass spectrometer at 70 eV and  
217 scanned from m/z 40–600 (at 2.62 scans/s; following Ghosh, Routh, and Bhadury (2017)). All  
218 eluted solvents were evaporated, Fraction 1 was re-dissolved in hexane, while Fraction 2  
219 samples were re-dissolved in CHCl<sub>3</sub>: MeOH (2:1), prior to injection in splitless mode (1 µl;  
220 inlet pressure of 10 psi with a flow rate 54.3 ml/min) and separated on a HP-5 MS capillary  
221 column (5% diphenyl dimethyl polysiloxane; 30 m length, 0.25mm i.d. and 0.25 µm film  
222 thickness). All the samples were run at constant flow (1.3 ml/min) with He as carrier gas.  
223 Detection limit in the different standards ranged from 0.1 to 1 ng/g. Reproducibility of internal  
224 standards was in the range of 5-10 ppm for different compounds. All the lipid fractions were  
225 identified in samples by comparing their characteristic mass spectra, and generated ion  
226 fragments (base peak and molecular ion), retention time, and elution order published in the  
227 literature (Peters, Walters, and Moldowan 2005), NIST online library, and Archives of Mass  
228 Spectrometry.

229 We employed several *n*-alkane indices based on carbon chain length and ratios of different  
230 compounds to infer their origin from different plant types such as grasses, trees/shrubs, and  
231 aquatic plants. Similarly, stanols and sterols extracted from peat samples were used to infer  
232 their inputs from herbivorous mammal or human faeces (Table 2).

233

234 Table 2. Lipid biomarker ratios used in the present study and their interpretation (References: 1-  
235 Cranwell, 1973, 2- Rommerskirchen et al., 2006, 3-Gagosian and Peltzer, 1986, 4-Schwark et  
236 al 2002, 5- Ficken et al., 2000, 6-Nichols et al., 2006, 7-Andersson et al., 2011, 8-Zheng et al.,  
237 2007, 9-Jardé et al., 2007a, 10-Jardé et al., 2007b, 11- Derrien, Yang, and Hur 2017, 12-Grimalt  
238 et al., 1990)

239

240

241

242



	<b>Lipid biomarker ratio</b>	<b>Inference</b>	<b>Reference</b>
<i>n</i> -alkane index	$ACL = \frac{\sum_{n=25}^{31}(C_n * n)}{\sum_{n=25}^{31}(C_n)}$	In warmer climates vascular land plants develop longer chain wax lipids than in cooler climates in order to avoid loss of water during transpiration	1,2,3
	$\frac{C_{27}}{C_{31}}$	Elevated $C_{27}/C_{31}$ ratio indicates increased input from biomarkers related to tree-leaf origin while low $C_{27}/C_{31}$ indicate higher grass input.	4
	$P_{aq} = \frac{C_{23} + C_{25}}{C_{23} + C_{25} + C_{27} + C_{29}}$	Both ratios indicate the proportions of hydrocarbons from submerged and or floating aquatic macrophytes relative to the input from terrigenous and immersed plants.	5,6
	$\frac{C_{23}}{C_{27} + C_{31}}$	Higher value is an indicator of moisture availability in the peatland which can be inferred as <b>increased precipitation</b> .	7,8
Steroid Index	$R1 = \frac{\text{Campesterol} + \text{Sitosterol}}{\text{Cholesterol}}$	Higher proportion of sitosterol and campesterol indicates phytosterol-based diet, and <b>R1 &gt;2.5</b> is found in bovine faeces.	9,10,11
	$R2 = \frac{\text{Coprostanol}}{\text{Cholestanol} + \text{Coprostanol}}$	Coprostanol is a stanol found in higher proportion in human faeces and a ratio <b>R2 &gt;0.7</b> indicates human faecal presence in the sample	12

243

244

### 245 **3. Results**

246

#### 247 *3.1 Chronology*

248 AMS radiocarbon dating of peat samples from 7 depths of the Sandynallah pit were found to  
 249 be in sequence without inversions; both radiocarbon and calibrated dates along with uncertainty  
 250 estimates are given in Table 1. The uppermost sample in the profile near the surface (PS1) is  
 251 modern in age, PS3 is dated to 1320 cal BP, and the deepest sample in the profile is dated to  
 252 22,103 cal BP. We see a faster accumulation rate in the Holocene and slower rate in Late  
 253 Pleistocene sections of the profile.

254

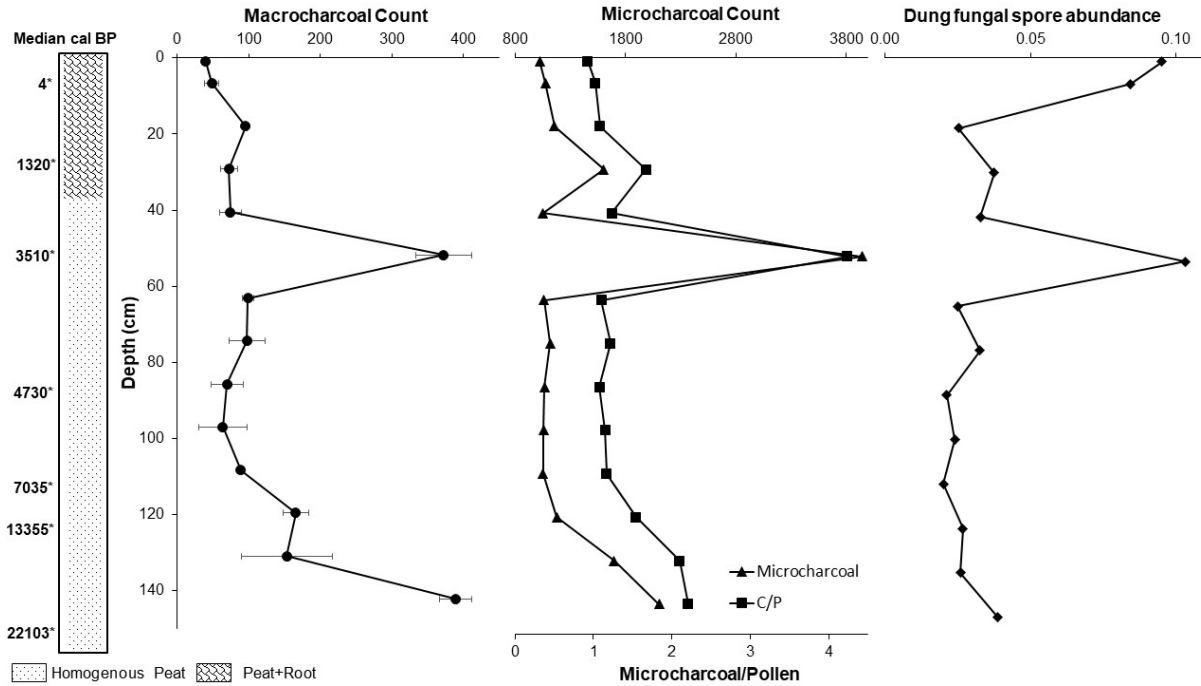
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#### 256 *3.2 Charcoal abundance and fire occurrence*

257 Macrocharcoal counts from the peat samples of Sandynallah are high at ~22,000 cal BP  
 258 indicative of fires; the microcharcoal counts and charcoal/pollen ratios at this time are also  
 259 enhanced though to a lesser extent than the macrocharcoal counts. On the other hand,

260 macrocharcoal shows a sharp peak ~3,500 cal BP along with corresponding peaks in  
 261 microcharcoal counts and microcharcoal/pollen ratio (Fig. 2), clearly indicating intensive fire  
 262 in the region at this time.

263



264

265 Fig 2. Macrocharcoal count, Microcharcoal count, Microcharcoal/Pollen ratio and the fungal  
 266 spore abundance plotted against depth for the 14 peat samples at Sandynallah.

267

### 268 3.3 Dung fungal spore abundance

269 Coprophilous fungal spores of the taxa *Sporormiella spp.*, *Sordaria spp.*, *Delitschia spp.*, and  
 270 *Trichodelitschia spp.* were found in the peat samples at different depths. The pollen-normalized  
 271 ratio of coprophilous fungal spore abundance showed two peaks, one in the modern samples  
 272 and another at ~3500 cal yr BP (Fig 2). Peaks in modern samples are consistent with the  
 273 increased presence of domestic livestock in the area, the peak at ~3500 cal yr BP coinciding  
 274 with the peak in micro- and macrocharcoal abundances, indicating a corresponding increase in  
 275 mammalian herbivore abundance around the time that intense fires were recorded.

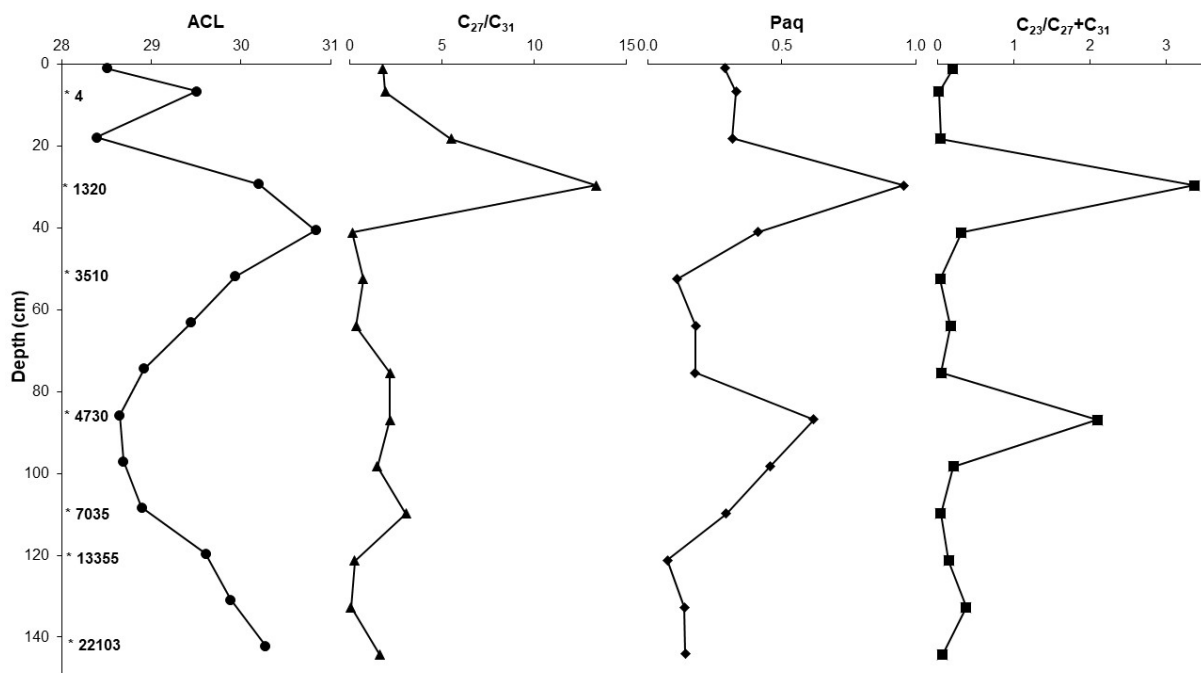
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### 277 3.4 Lipid biomarkers

278 The lipid biomarker proxies evaluated in the current study can be of three broad categories:  
 279 vegetation proxies (average chain length (ACL) and  $C_{27}/C_{31}$ , moisture proxies (Paq and  
 280  $C_{23}+C_{25}/C_{23}+C_{25}+C_{27}+C_{29}$ ) and steroid indices (R1 and R2) (Table 2). Total *n*-alkane content  
 281 of the samples ranged from 0.12 to 22.5  $\mu\text{g/g}$  of dry peat. Average chain length (ACL) in *n*-

282 alkanes varied between 28 to 31. ACL values peaked at 22,000 cal BP and shows an increasing  
283 from 4700 cal BP onward with a peak between 3500 and 1300 cal BP. The calculated  $P_{aq}$  ranged  
284 from 0.109 to 0.954 with the 3500 cal BP sample showing the lowest value  $P_{aq}$  value.  $nC_{27}/nC_{31}$   
285 ratio ranged from 0.13 to 5.57 in the peat samples with an average of 1.98 (Fig. 3). Changes in  
286  $nC_{23}/(nC_{27}+nC_{31})$  over time broadly correlated with the  $P_{aq}$  value, showing two peaks at ~4700  
287 and ~1300 cal BP. Two ratios of steroid compounds (see Table 2), one comprising sterols  
288 indicative of herbivore faecal presence and the other comprising stanols indicative of human  
289 faecal presence, from the peat samples are plotted in Figure 2. Peat sample dated at ~3500 cal  
290 yr BP showed the highest value for both ratios ( $R_1= 20.27$  and  $R_2= 0.98$ ) indicative of  
291 herbivore presence and human faecal presence. The sample at ~1300 cal yr BP also showed  
292 steroid ratios ( $R_1= 5.12$  and  $R_2= 0.94$ ) above threshold levels indicative of herbivore and  
293 human faeces. Modern samples also showed traces of herbivore faecal matter, though the  
294 steroid ratios were below the threshold of human faecal presence.

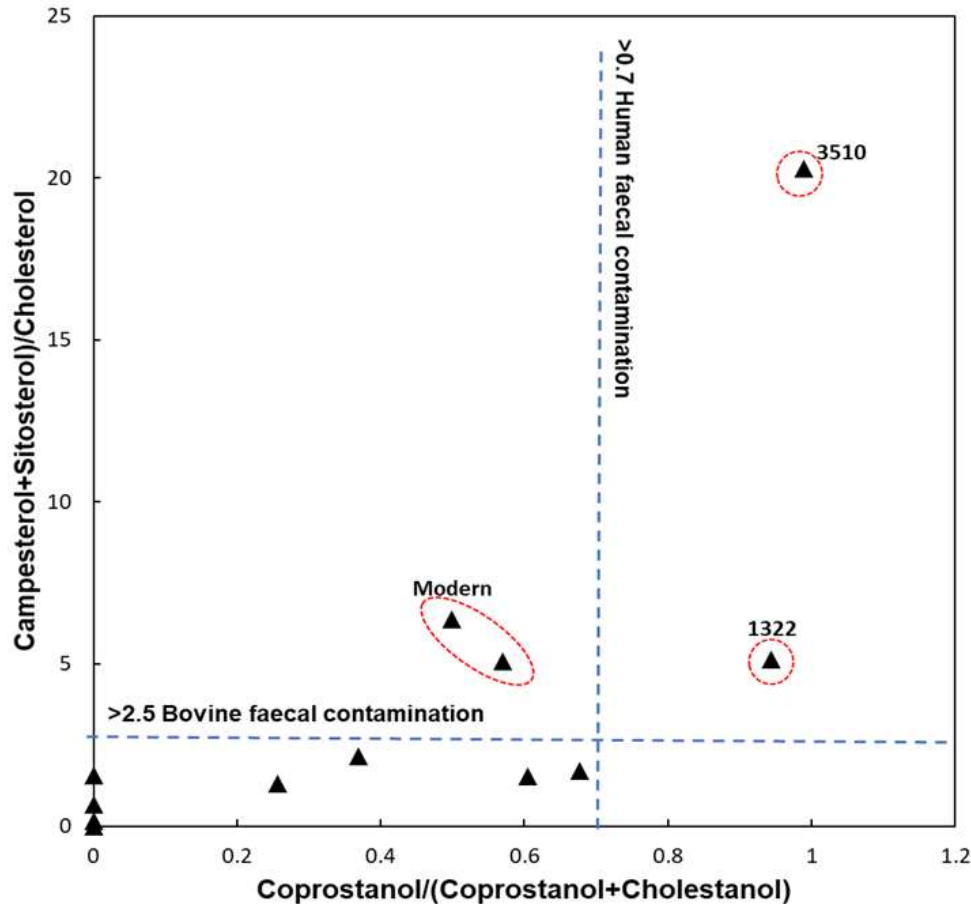
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296

297 Fig 3. n-alkane biomarker indices, ACL and  $nC_{27}/nC_{31}$  indicating vegetation shifts in the past,  
298 and  $P_{aq}$ ,  $nC_{23}/(nC_{27}+nC_{31})$  indices showing the contribution from lower chain length  
299 alkanes indicating peatland wetness (see text and Table 2 for details).

300



301

302 Fig 4. Plot of sterol biomarker ratio R1 versus R2 (see Table 2 for details), with human and  
303 bovine faecal contamination thresholds indicated by dotted lines. Biomarker ratios which are  
304 above the threshold values for bovine and human faeces are marked with a red circle along  
305 with their dates in cal BP.

306

#### 307 4. Discussion

308

309 We have shown through a combination of charcoal and pollen abundance, *n*-alkane  
310 concentration, coprophilous fungal spores and steroid lipid biomarkers in peat deposits  
311 (spanning the period ~ 22,000 cal. yr BP to the present) that intense fire activity at ~ 3500 cal.  
312 yr BP coincided with dominant grassland cover, abundance of herbivorous animals, and the  
313 presence of humans for the first time in a montane region (>2000m asl) of the Western Ghats,  
314 India. There are several questions which arise from these findings: were the fires in the  
315 extensive grasslands during this time the result of climatic desiccation or entirely due to  
316 deliberate human action?; does the abundance of herbivorous animals indicate populations of

317 wild mammals or domesticated mammals?; who were the people inhabiting the plateau at this  
318 time?

319

#### 320 *4.1 Fire history from the charcoal record*

321

322 The history of wildfire at a given location reflects both the prevailing climate as well as human  
323 activity and, hence, can provide valuable clues on human occupation of a site. Macrocharcoal  
324 (>125  $\mu\text{m}$ ) usually gets deposited close to the source of the fire making it a useful proxy for  
325 reconstructing fire history at a local scale, while microcharcoal (<125  $\mu\text{m}$ ) can have its origin  
326 over a much wider region, thus being a proxy for fire history over a broad spatial and temporal  
327 scale (Clark et al. 1998; Carcaillet et al. 2001; Whitlock and Larsen 2002).

328

329 Charcoal counts at Sandynallah depict two periods of enhanced fire activity, the first at ~  
330 22,000 cal yr BP and the second at ~3500 cal yr BP (Fig 2). The elevated levels of  
331 macrocharcoal in the sample from the deepest layer (142 cm) dated at ~22,000 cal yr BP are  
332 suggestive of burning of woody vegetation (shrubs and/or trees) (Fig 5). The sharply increased  
333 counts of microcharcoal and the high charcoal/pollen ratio clearly point to grassland fires  
334 during this period. This fire event is consistent with the expansion of C4 grasses and arid  
335 climatic conditions during the Last Glacial Maximum (LGM) recorded in paleovegetation and  
336 paleoclimate studies from the Nilgiri plateau (Sukumar et al. 1993; Caner et al. 2007). The Last  
337 Glacial Maximum dated variously across the globe at between 26-16 ka and characterized by  
338 lower temperatures and arid conditions worldwide (Clark et al. 2009; Hughes and Gibbard  
339 2015). The Indian summer (southwest) monsoon also weakened during the LGM (Prell and  
340 Kutzbach 1987; Kumaran et al. 2013; Saraswat, Nigam, and Correge 2014) including in the  
341 northern and central Western Ghats (Sukumar et al. 1993; Rajagopalan et al., 1997; Prabhu et  
342 al. 2004; Caner et al. 2007; Kumaran et al. 2013), and this would have increased the  
343 flammability of the vegetation including forest patches in the montane Nilgiris as seen in other  
344 tropical regions (Farrera et al. 1999; Bassinot et al. 1994; Prabhu et al. 2004; Caner et al. 2007).  
345 Greater fire activity during the Last Glacial Maximum (LGM) is also observed in charcoal  
346 records from tropical latitudes of Southeast Asia (Power et al. 2008).

347

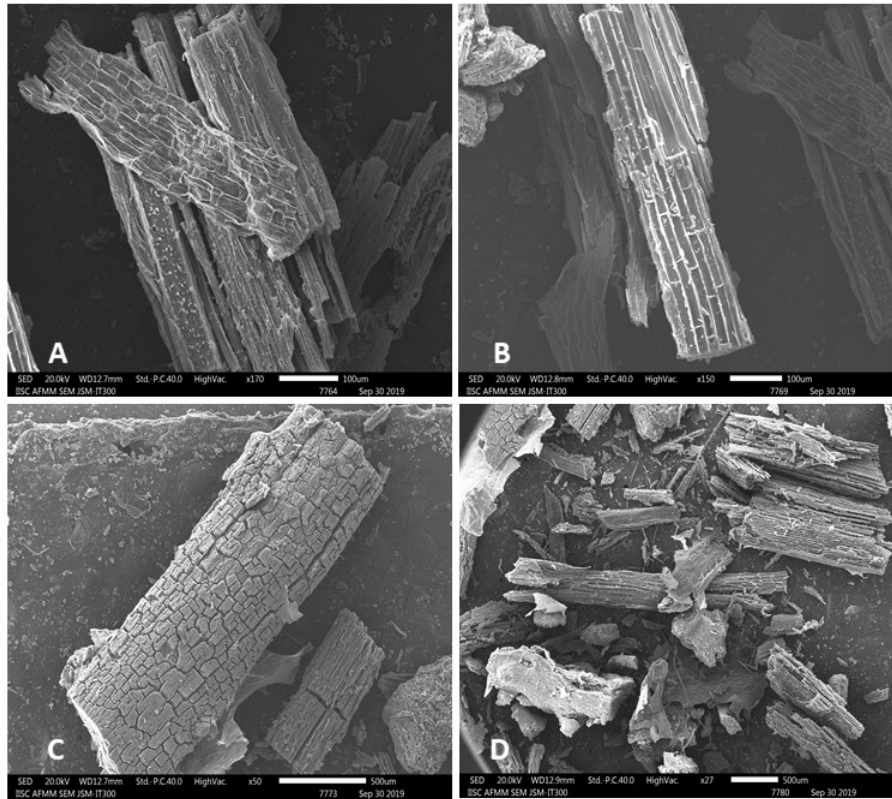
348 The sharp increase in macrocharcoal counts, microcharcoal counts and C/P ratio in the peat  
349 layer from ~ 3500 cal yr BP is indicative of an intense, local fire event (Fig 2). Climate is the  
350 primary driver of wildfires globally (Flannigan et al. 2009; Krawchuk and Moritz 2011) and at

351 local scales such as the Nilgiris (Mondal and Sukumar 2016), with successful ignition and  
352 spread of fire from human activity (as opposed to natural causes such as lightning) generally  
353 playing a secondary role (Bowman et al. 2011) It is entirely possible that an immigrant  
354 pastoralist people set fire to the natural grasslands in order to improve the pasture for their  
355 livestock, a very common practise around the world since historical times (Johansen 2004;  
356 Vuorio et al. 2014; Coughlan 2015). Paleo-ecological studies, based on stable carbon isotope  
357 ratios discriminating between C4 plants (tropical grasses) and C3 plants (trees, shrubs and other  
358 herbs), at this site have clearly pointed to an overall weakening of the monsoon resulting in  
359 expansion of grassland during ~5000-2000 cal. yr BP (Sukumar et al. 1993; Rajagopalan et al.,  
360 1997). The environmental conditions at ~3500 yr BP would have been favourable for wildfires.  
361 However, the sharp spike in both micro- and macro-charcoal abundance in the present study  
362 indicates that not only grassland but also the embedded montane forest patches burnt, thereby  
363 implying that extremely dry weather and possibly high ambient temperatures provided the  
364 conditions for an intense fire/s to spread. There would have been no necessity for a pastoralist  
365 community to set fire to forest especially when grasslands were already extensive; it is thus  
366 most likely that natural fires or anthropogenic fires in the grasslands spread to the forest patches  
367 under extremely favourable weather conditions.

368  
369 Changes in pollen assemblages are used to interpret human agricultural practices, but  
370 palynological evidence from the Nilgiri region shows no indication of active cultivation in the  
371 higher elevation region except in recent times (Vasanthy 1988; Sutra, Bonnefille, and Fontugne  
372 1997). The intense fire event ~3500 cal yr BP in the upper Nilgiri plateau featuring dominant  
373 grassland vegetation is also coincident to the abrupt transition of forest to woodland/grassland  
374 further north in the Western Ghats (North Kanara district (0-700m asl) of Karnataka state, about  
375 500 km northwest from our montane site in the Nilgiris) at precisely the same time as evidenced  
376 in sharply enhanced counts of grass pollen and reduction of tree pollen in a marine core from  
377 the estuary of the Kalinadi River on the Arabian Sea coast (Caratini et al. 1991; Caratini et al.  
378 1994). This remarkable match in dates of the vegetation shift in North Kanara and the large  
379 fire event in the Upper Nilgiris provides unambiguous evidence of regional aridification at  
380 ~3500 cal yr BP in peninsular India.

381  
382 Increased forest clearing, landscape burning and agricultural activity after the mid-Holocene  
383 dry conditions played a crucial role in the determining the extent of vegetation cover in the  
384 mid- and lower elevations of the Western Ghats (Bhagwat et al. 2012). A study from mid-

385 elevation (c. 900 m asl) region of Kodagu District (Karnataka State), located 170 km to the  
386 north of the Nilgiris, recorded fire activity beginning around 3500 yr BP (though peaking at a  
387 later time), lowering the tree cover state, possibly due to large-scale land use changes for settled  
388 agriculture (Bhagwat et al., 2012).



389  
390 Fig 5. Scanning electron microscope (SEM) images of macrocharcoal particles from two fire  
391 events recorded in pit profile; A and B are particles from the 3510 cal BP peat sample, while  
392 C and D are particles isolated from the 22103 cal BP peat sample

393

#### 394 *4.2 Lipid n-alkane biomarkers and vegetation change*

395

396 The main objective of the lipid *n*-alkane biomarker analysis was to look at the vegetation  
397 history of these natural montane forest-grassland mosaics and compare this to previous  
398 paleoecological studies from the region. Organic matter accumulated in the peat consists of  
399 above-ground plant material as well as secondary products from microbial alteration and  
400 diagenesis of the primary material. We used sedimentary *n*-alkane ratios as a proxy to  
401 understand the vegetation changes in general and, more specifically, the climate associated  
402 with the fire event dating back to ~3500 cal yr BP. *n*-alkane distributions are dominated by  
403 longer chain homologues, mainly *n*-C<sub>22-32</sub>, indicating higher input from epicuticular leaf waxes

404 of vascular plants and only minor contribution from algal and bacterial sources (Cranwell et  
405 al., 1987; Eglinton and Hamilton, 1967; Rieley et al., 1991; Rommerskirchen et al., 2006).  
406 Cranwell (1973) attributed elevated  $nC_{31}$  to grass input, whereas  $nC_{27}$  or  $nC_{29}$  predominance  
407 was related to a tree-leaf origin. Following this idea, we employed ACL and  $C_{27}/C_{31}$  as  
408 vegetation indices to elucidate the grassland-forest dynamics in the past. Since this is the first  
409 attempt to interpret vegetation abundance through  $n$ -alkanes at Sandynallah, we are aware of  
410 the limitations of not directly accounting for relative percentage contributions of biomass from  
411 grass and woody species. However, what is striking is that in both the major fire layers, i.e. at  
412  $\sim 22000$  cal BP and  $\sim 3500$  cal BP, higher ACL values and lower  $C_{27}/C_{31}$  point to a higher  
413 proportion of  $n$ - $C_{31}$  alkanes in the sediment, indicating a prevalence of grasslands (Cranwell,  
414 1973; Bi et al., 2005; Rommerskirchen et al., 2006). We also considered proxies of surface  
415 wetness in the peat bog since  $n$ -alkane distributions of submerged and floating plants maximize  
416 at  $C_{23}$  and  $C_{25}$  while land plants maximize at  $C_{27}$ ,  $C_{29}$  and  $C_{31}$  (Zheng et al. 2007). The moisture  
417 indices ( $P_{aq}$  ratio and  $nC_{23}/(nC_{27}+nC_{31})$ ) showed two peaks, one at  $\sim 4700$  cal BP and the other  
418 at  $\sim 1300$  cal BP, indicating wetter conditions; these indices however indicate very low surface  
419 wetness in the fire-impacted layers, consistent with the expectation of arid conditions during  
420 these periods (Fig 3). In past studies, the dominance of C4 plants (grasses and sedges) has been  
421 used as a proxy for dry and arid climatic conditions (Sukumar et al. 1993; Caner et al. 2007),  
422 consistent with our results of a grass-dominated, arid environment during the LGM, and the  
423 arid period at  $\sim 3500$  years BP supported by fluctuating monsoon conditions during mid-  
424 Holocene (Rajagopalan et al. 1997).

425

#### 426 *4.3 Coprophilous fungal spores and herbivore abundance*

427

428 Coprophilous fungal spores are used as a proxy for herbivore presence and abundance and to  
429 understand past pastoral activities (van Geel et al. 2011; Baker, Bhagwat, and Willis 2013;  
430 Dubois and Jacob 2016). Spores of coprophilous fungi such as *Coniochaeta*, *Sporormiella*,  
431 *Sordaria*, *Podospora*, *Delitschia* and *Trichodelitschia* are generally considered as reliable  
432 indicators of pastoralism (Cugny, Mazier, and Galop 2010; van Geel et al. 2011). The origin  
433 of the dung can be from livestock corralled at a site or from its use as manure, fuel and building  
434 materials (Linseele et al 2013). The spike in coprophilous fungal spores count at  $\sim 3500$  cal yr  
435 BP in the Nilgiri plateau indicates increased presence of herbivorous animals, which could be  
436 due to introduction of livestock by immigrant people (Fig 2). At the same time, the extensive  
437 grasslands at this time, possibly expanding over several hundred years (Rajagopalan et al.



438 1997), could also have facilitated an increase in the population of wild herbivores.  
439 Coprophilous fungal spores alone cannot distinguish between domestic and wild fauna  
440 (Giguët-Covex et al. 2014). One mammal species which could have benefitted from grassland  
441 expansion is the Nilgiri tahr (*Nilgiritragus hylocrius*), endemic to the higher elevation  
442 grasslands of the Western Ghats, but we cannot rule out the presence of other herbivorous  
443 mammals with more widespread distribution such as the gaur (*Bos gaurus*), a bovid, and the  
444 elephant (*Elephas maximus*), found in very low numbers presently at elevations >1500 m asl.  
445 However, a 5-fold spike in coprophilous fungal spores is unlikely to reflect an upsurge in wild  
446 herbivore populations but rather a corralled herd of domestic herbivores. Currently, sheep and  
447 other livestock are maintained at Sandynallah and this is accurately picked up in the increased  
448 coprophilous fungal spore abundance in the modern samples (Fig 2).

449

#### 450 *4.4 Lipid steroid biomarkers and human presence*

451

452 Faecal biomarkers are routinely used in archaeobotanical studies to understand anthropogenic  
453 inputs and to identify the origin of dung at a study site (Bull et al. 2001; Shillito et al. 2011;  
454 Bull et al. 2002; Bull et al. 1999). The relative ratio of two or more sterols and stanols can be  
455 used to discriminate the sources of faecal contamination (Derrien, Yang, and Hur 2017;  
456 Leeming et al. 1996). Herbivore faeces are expected to have higher proportion of sitosterol and  
457 campesterol due to their phytosterol-based diet, and the R1 >2.5 (see Table 2) is typical of  
458 faecal presence in a sample (Jardé et al. 2007a; Jardé et al. 2007b; Derrien, Yang, and Hur 2017).  
459 5 $\alpha$ -cholestanol is the diagenetic product of cholesterol indicative of source and preservation of  
460 stanol in the environment. We used R2 ratio (Table 1) to compare the 5 $\alpha$ -cholestanol with the  
461 coprostanol, which is a stanol found in higher proportion in human faeces to detect the presence  
462 of humans in the region (White et al. 2018; Bull et al. 2002). The 3500 cal yr. BP sample with  
463 higher R1 as well as R2 ratio indicate both human and herbivore faecal presence in the samples  
464 (Fig 4) (Derrien, Yang, and Hur 2017; Grimalt et al. 1990; Prost et al. 2017; Jardé et al. 2007a,  
465 Jardé et al. 2007b ). Modern samples showed traces of herbivore faecal contamination which  
466 is expected since the study site presently maintains stocks of sheep and is also visited by cattle  
467 (Fig 4). Interestingly, both R1 and R2 ratios are above the threshold levels in the 1300-year-  
468 old sample indicating the continued presence of livestock and humans.

469

470

471

472 *4.5 Who were the earliest inhabitants of the upper Nilgiri plateau?*

473

474 There are five traditional peoples or “tribes” in the Nilgiri hills – the Kurumbas, the Irulas, the  
475 Badagas, the Kotas and the Todas (Noble 1967).(Noble 1967) Of these, the Kurumbas and the  
476 Irulas inhabit the lower elevations (1600-600m asl) of the Nilgiris, practise subsistence  
477 agriculture or are hunter-gatherers and, thus, are unlikely to be the earliest inhabitants of the  
478 upper Nilgiri plateau. The Badagas are mainly cultivators inhabiting the upper plateau but are  
479 known to have migrated to the Nilgiris from the northern Karnataka region only during the late  
480 16th century CE following the defeat of the Vijayanagar Empire (Francis 1908; Hockings  
481 1980). The Kotas in the upper plateau are essentially artisans, musicians, and cultivators,  
482 though, like the Badagas, they may also tend some buffalo presently.

483

484

485 The most obvious candidates for the earliest inhabitants would be the Todas, a near-obligate  
486 pastoralist people believed to have inhabited the Nilgiri plateau around the 1st century CE and  
487 remained relatively isolated to the outside world until they were “discovered” during the early  
488 19th century by the erstwhile British administration (Rivers 1906; Emeneau 1997; Walker  
489 1997). Local legend also generally concedes that the Todas are the original inhabitants of the  
490 Nilgiri plateau. Based mainly on linguistic affinities of the Toda language with the common  
491 Dravidian languages of southern India, it has been suggested or even assumed that the Toda  
492 origin in the Nilgiris is not more than 2000 years old (Rivers 1906; Noble 1976; Emeneau  
493 1997; Zagarell 1997). Our study provides compelling evidence for the presence of people and  
494 livestock at Sandynallah in the higher elevations of the Nilgiris at 3500 cal BP coinciding with  
495 or subsequent to a changed climate and environment in peninsular India. This pastoralist people  
496 also probably managed the landscape through setting grassland fires whose spread was aided  
497 by favourable weather conditions. The most parsimonious interpretation would be that these  
498 people were indeed the Todas who had immigrated along with their buffaloes to this location  
499 by 3500 cal BP, or more than 1500 years prior to what has been believed so far. Genetic studies  
500 suggest that the Toda buffalo is most closely related to the buffaloes further north along the  
501 Western Ghats in the South Kanara district of Karnataka state (Kathiravan et al. 2011). It is of  
502 course entirely possible that the people and livestock recorded at 3500 cal BP represent an  
503 unknown tribe or even a failed immigration. In any case, the evidence opens up the  
504 interdisciplinary fields of paleoecology, archaeology, and human ecology during mid- to late

505 Holocene for further investigation not only in the montane Nilgiris but the broader region of  
506 peninsular India.

507

508

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