

1 **Synergistic impacts of anthropogenic fires and aridity on plant diversity in the Western**
2 **Ghats: Implications for management of ancient social-ecological systems**

3

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25 **Abstract**

26 Identifying the impacts of anthropogenic fires on biodiversity is imperative for human-
27 influenced tropical rainforests because – i) these ecosystems have been transformed by human-
28 induced fires for millennia; and ii) their effective management is essential for protecting the
29 world’s terrestrial biodiversity in the face of global environmental change. While several short-
30 term studies present the impacts of fires on local plant diversity, how tropical plant diversity
31 responds to fire regimes over long time scales is a significant knowledge gap, posing
32 substantial impediment to evidence-based management of social-ecological systems. Using
33 wet evergreen forests of Western Ghats of India as a model system, we discuss the synergistic
34 effects of anthropogenic fires and enhanced aridity on tropical plant diversity over the past
35 4000 years by examining fossil pollen-based diversity indices (e.g., pollen richness and
36 evenness, and temporal β -diversity), past fire management, the intervals of enhanced aridity
37 due to reduced monsoon rainfall, and land use history. By developing a historical perspective,
38 our aim is to provide region-specific management information for biodiversity conservation in
39 the Western Ghats. We observe that the Western Ghats agroforestry landscape switches
40 between periods of no fires (4000-1800 yr BP, and 1400-400 yr BP) and fires (1800-1400 yr
41 BP, and 400-0 yr BP), with both fire periods concomitant with intervals of enhanced aridity.
42 We find synergistic impacts of anthropogenic fires and aridity on plant diversity uneven across
43 time and suggest that this is potentially due to different land management strategies. For
44 example, during 1800-1400 yr BP, diversity reduced in conjunction with a significant decrease
45 in the canopy cover related to sustained use of fires, possibly linked to large-scale
46 intensification of agriculture. On the contrary, the substantially reduced fires during 400-0 yr
47 BP may be associated with the emergence of sacred forest groves, a cultural practice supporting
48 the maintenance of plant diversity. Overall, notwithstanding apparent changes in fires, aridity,
49 and land use over the past 4000 years, present-day plant diversity in the Western Ghats

50 agroforestry landscape falls within the range of historical variability. Importantly, we find a
51 strong correlation between plant diversity and canopy cover throughout the record,
52 emphasising the crucial role of active fire management and maintaining tree cover for
53 biodiversity conservation. Systematic tree management in tropical social-ecological systems is
54 vital for livelihoods of billions of people, who depend on forested landscapes. In this context,
55 we argue that agroforestry landscapes can deliver win-win solutions for biodiversity as well as
56 people in the Western Ghats and wet tropics at large.

57

58 **Keywords**

59 Agroforestry; biodiversity conservation; evidence-based policymaking; fire management;
60 social-ecological systems; wet tropics

61 **1. Introduction**

62 Conservation managers aim to mitigate past environmental degradation and simultaneously
63 strive to design resilient and self-sustaining future ecosystems (Society for Ecological
64 Restoration International Science & Policy Working Group, 2004). The value of
65 palaeoecological approach in conservation management has been widely recognised (Jackson,
66 2007; Froyd and Willis, 2008; Birks, 2012; Gillson, 2015; Whitlock et al., 2018) because of
67 the insights it can lend into past ecological information relevant to management frameworks
68 (e.g., baseline conditions, historic land management). For example, fires have often been
69 viewed as a damaging factor to forest ecosystems worldwide and, therefore, fire prevention is
70 routinely implemented as a mechanism for landscape restoration and biodiversity conservation
71 (Wright and Heinselman, 1973; Gadgil and Guha, 1993; Tacconni et al., 2007). However,
72 diverse lines of research on ecological history (e.g., Swain, 1973; Clark et al., 1989;
73 Dunwiddie, 2001; Burrows, 2008; Leys et al., 2014; Anderson and Keeley, 2018) demonstrate
74 that fires are a fundamental ecological process in most ecosystems and strict fire prevention
75 could be detrimental to biodiversity (Colombaroli et al., 2019; Słowiński et al., 2019;
76 McLauchlan et al., 2020). While such scientific understanding has led to comprehensive fire
77 management and conservation plans in some parts of the world (e.g., Brown et al., 1991;
78 Keeley, 2006), there currently is a shortfall in evidence-based policymaking for effective
79 biodiversity conservation in human-influenced tropical landscapes (Karanth and DeFries,
80 2010; Juárez-Orozco et al., 2017). Considering the close association between tropical
81 landscapes and fires since prehistoric times (Bowman et al., 2009; Cochrane, 2011; Roberts et
82 al., 2017), it is imperative to identify the impacts of fires on biodiversity in these ancient social-
83 ecological systems. How tropical plant diversity responds to fire regimes over long time scales
84 is a significant knowledge gap that needs to be addressed for sustainable management of these
85 human-influenced landscapes (Driscoll et al., 2010; Seddon et al., 2014).

86 Among human-influenced landscapes, agroforestry – a practice of planting crops under
87 or alongside native shade trees – holds special promise for biodiversity conservation (McNeely
88 and Schroth, 2006; Bhagwat et al., 2008). Agroforestry landscapes promote intentional
89 management of trees in productive agriculture and support the livelihoods of people including
90 those living in world’s biodiversity hotspots (Ashley et al., 2006; Miller and Nair, 2006; Fisher
91 and Christopher, 2007; Chavan et al., 2015). The Western Ghats of India (Fig. 1) is one such
92 biodiversity hotspot with ancient agroforestry systems and well-established fire management
93 practices (Asouti and Fuller, 2008; Krishna and Morrison, 2010). Notably, fires in the wet
94 evergreen forests of the Western Ghats are predominantly anthropogenic in nature because
95 fires caused by natural phenomena (e.g. lightning strikes) rarely spread beyond small areas in
96 moist evergreen forest ecosystems (Kodandapani et al., 2004, 2008). However, small-scale
97 farmers typically burn fallow land very locally and these fires may unintentionally spread over
98 wide areas during exceptionally hot and dry years (Bowman et al., 2011; Cochrane, 2011).
99 Such anthropogenic fires are particularly alarming in light of the projected weakening of the
100 Indian Summer Monsoon (henceforth, monsoon) and resultant rainfall irregularities in the
101 Subcontinent (Sinha et al., 2011; Roxy et al., 2015; Mishra et al., 2020). Thus, the most
102 significant consequence of future environmental change could be extended periods of aridity,
103 resulting into drier fuel loads and more frequent spread of anthropogenic fires beyond
104 agricultural land (Kodandapani et al., 2009). In this context, we examine the combined effects
105 of anthropogenic fires and aridity on plant diversity in the Western Ghats agroforestry
106 landscapes over the past 4000 years, a period known for incipient weakening of monsoon and
107 enhanced aridity in the Indian Subcontinent (Dixit et al., 2014; Kathayat et al., 2017). By
108 developing a historical perspective, our aim is to provide region-specific management
109 information for biodiversity conservation in the Western Ghats and wet tropical agroforestry
110 landscapes at large. Thus, we address the following questions:

- 111 1) How has the plant diversity changed over the past 4000 years?
112 2) What are the synergistic effects of anthropogenic fires and the weakening of monsoon
113 (enhanced aridity) on plant diversity and vegetation composition?
114 3) What are the potential implications of historical fire regimes in sustaining plant diversity in
115 a tropical social-ecological system?

116 These questions are relevant for understanding transformation of tropical forests into intricate
117 social-ecological systems, assessing the role of fire management and its effects on plant
118 diversity under current and future environmental change.

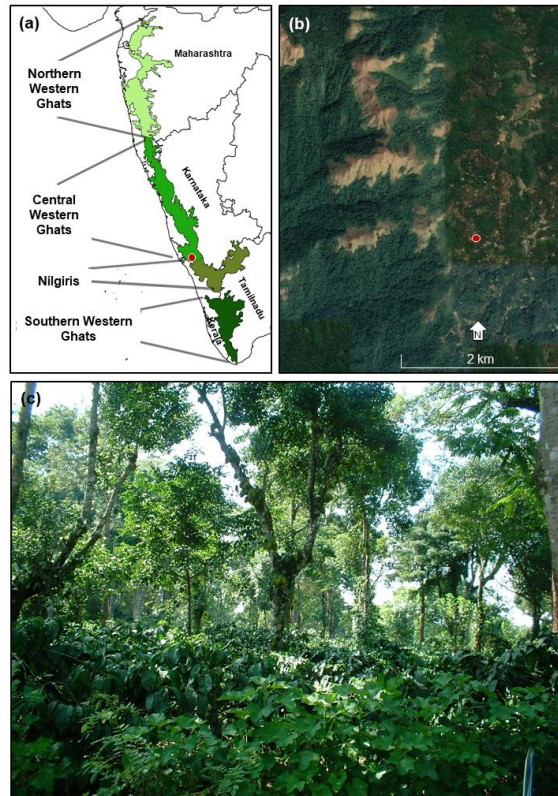
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120 **2. Materials and methods**

121 **2.1 The study site in the Western Ghats**

122 The Western Ghats is a mountain range running along the western coast of peninsular India
123 (Fig. 1a). The mid-elevation (500–1500 m asl) terraces constitute over 90% of the Western
124 Ghats, presenting a mosaic of wet evergreen rainforest and grasslands shaped by human
125 activities, particularly fire (Premathilake, 2006; Kodandapani et al., 2009). Here we utilise one
126 such mid-elevational sedimentary sequence (hereafter, Agroforest-1), derived from the Kodagu
127 district of Karnataka i.e. the central part of the Western Ghats (Fig. 1). The region boasts the
128 extensive network of wet evergreen rainforest reserves primarily of *Mesua-Palaquium* type
129 (Ramesh and Pascal, 1997), occupying about 30% of the landscape (Fig. 1b; Bhagwat et al.,
130 2005a). In addition to these formally protected forests, c. 60% of the landscape is managed as
131 agroforestry with high tree-canopy shading coffee plantations while remaining 10% of the
132 landscape is under rice cultivation (Bhagwat et al., 2005b). The Agroforest-1 sequence is
133 extracted from a small swamp situated in a coffee estate (12° 9' 14"N, 75° 42' 47"E; 910 m asl)
134 surrounded by a patchwork of arable land and forest fragments (Fig. 1b). At the site, coffee
135 (*Coffea arabica* var. *robusta*) is planted in the understorey of shade trees (Fig. 1c), many of

136 which are representative of native vegetation mixed with betel nut palm (*Areca catechu*;
137 Bhagwat et al., 2012). The site is less than 10 km away from a forest reserve currently under
138 government protection (Fig. 1b).



139 **Figure 1:** (a) The Western Ghats (WG) of India (after Mirza et al., 2014). The circle represents
140 the location of the study site in the Central part of the WG, located in Kodagu District,
141 Karnataka. (b) Google Image of the Kodagu region; the sedimentary sequence under study
142 ($12^{\circ}9'14''N$, $75^{\circ}42'47''E$; shown with a circle) is derived from a coffee agroforestry setting from
143 the middle reaches of the Western Ghats (Data source: <https://earth.google.com/>). (c) An
144 example of a coffee plantation grown under the shade of native trees in Kodagu, Western Ghats,
145 India. A layer of coffee bushes is seen in the understory and a canopy of native trees is seen
146 above this layer. Such plantations of shade-grown coffee in many tropical regions have canopy
147 structure similar to that of secondary forests. The shade of native trees provides habitat for
148 many forest-dwelling species in otherwise highly human-dominated landscapes (Image Credit:
149 Shonil A. Bhagwat).

150 **2.2 Extent and components of canopy cover**

151 Drawing upon a robust chronology and a high-resolution pollen record (Bhagwat et al., 2012;
152 Nogué et al., 2018), we classify Agroforest-1 fossil pollen taxa into three groups: canopy-
153 forming woody taxa (i.e. arboreal pollen (AP) types including trees, shrubs, lianas, climbers),
154 grassland taxa (Poaceae and Cyperaceae), and herbaceous understorey taxa (all other non-
155 arboreal pollen types; Fig. 2). The percentage (%) abundances of the above groups specify the
156 discrete extents of the canopy cover, grassland, and understorey vegetation in the Western
157 Ghats agroforestry landscape respectively (Figs. 2-3a). Additionally, we provide the individual
158 relative abundances of 20 habitat-specialist evergreen rainforest trees that are indicative of low
159 disturbance and closed-canopy forest (Laurance et al., 2007; Fig. 2). These long-lived
160 evergreen trees constitute the subsection of the Western Ghats rainforest exhibiting forest
161 structural changes (Nogué et al., 2018). We also juxtapose the individual relative abundances
162 of commonly cultivated plant taxa (e.g. *Coffea*) to differentiate the anthropogenic components
163 of the forest ecosystem (Fig. 2).

164

165 **2.3 Plant diversity**

166 It is long debated whether or not pollen-assemblage richness accurately reflects plant diversity
167 (see Birks et al., 2016), however, recent studies (e.g., Meltsov et al., 2011; Odgaard, 2013;
168 Felde et al., 2014) demonstrate that within one vegetation or climatic region, pollen richness
169 can give reliable estimates about the variation in plant richness and landscape structure.
170 Following this lead, we apply rarefaction analysis to the terrestrial pollen dataset of Agroforest-
171 1 to determine plant richness i.e. plant diversity. Using the ‘vegan’ package (Oksanen et al.,
172 2013) and a self-written computer code in the R environment (R Core Team, 2014), we estimate
173 richness as the effective number of taxa (N_0), the expected number of common taxa (N_1), and
174 the expected number of dominant taxa (N_2 ; Fig. 3b). These measures provide information at

176 different levels based on how rare and abundant taxa are weighted (Hill, 1973). Instead of
177 taking a classical rarefaction approach (Birks and Line, 1992), we resample randomly and
178 without replacement the pollen counts 1000 times to the smallest sample size (here $n=243$) to
179 calculate the mean and 95% confidence intervals for N_0 , N_1 , and N_2 (Felde et al., 2016;
180 Finsinger et al., 2017). We also calculate the evenness as N_2/N_0 (Fig. 4), which is thought to
181 be a reliable indicator of plant diversity (See Hill, 1973; Odgaard, 2008; Tuomisto, 2012).
182 However, considering the size of the swamp under study (<1 ha) and corresponding small-
183 intermediate pollen source area (~10-20 km; Prentice, 1985; Sugita, 1993), our record would
184 more likely show a high correlation between pollen-assemblage richness and evenness (e.g. in
185 Colombaroli et al., 2013). To estimate diversity of the canopy-forming woody taxa, we apply
186 the same method exclusively to the sum total of arboreal pollen (AP) types (including trees,
187 shrubs, lianas, climbers) in the Agroforest-1 record (Fig. 4).

188

189 **2.4 Change in vegetation composition over time**

190 In palaeoecological time series, temporal β -diversity is a measure of change in vegetation
191 composition between adjacent samples using the rate-of-change metric (Birks, 2007). To
192 estimate change in vegetation composition over time, we first linearly interpolated the pollen
193 percentages on equal time intervals, and subsequently calculated the dissimilarity between
194 adjacent samples using the chord distance of square-root transformed percentage values (Birks
195 and Birks, 2008). Chord distance values range between zero (no change in vegetation
196 composition) and two (complete change in vegetation composition, i.e. the two assemblages
197 have no species in common). The trends are illustrated by a LOESS-smoothed curve
198 (Cleveland and Devlin, 1988). Considering the varying sample resolution across the
199 Agroforest-1 sequence (Fig. S1), we present two sets of temporal β -diversity records obtained
200 with different interpolation-window widths – one for the entire 4000-yr period at 260-yr

201 resolution while another for the last 2000 yr BP at 150-yr resolution (Fig. 3c). By employing a
202 shorter interpolation-window width for the past 2000 years, we are able to visualise
203 transformations in vegetation composition associated with intensified burning and land use
204 change in the Western Ghats agroforestry landscape (Fig. 3c).

205

206 **2.5 Past fire management**

207 For reconstructing fire history, we perform high-resolution macroscopic charcoal analysis at
208 1-cm resolution (~28 yr per sample). Following Finsinger et al., (2014), 1 cm³ of sediments are
209 deflocculated and bleached overnight with a 10% Sodium hexametaphosphate + 5% Sodium
210 hypochloride mixture followed by wet sieving through a 150 µm mesh. Thereafter, samples
211 are suspended in 15% Hydrogen peroxide for 15-20 minutes, subsequently wet sieved and
212 manually counted under a binocular microscope. To ensure the consistency in data collection,
213 we re-analyse the macro-charcoal samples from 0-1197 yr BP utilised in Nogué et al., (2018b).
214 In addition, we utilise Agroforest-1 microscopic charcoal record by Bhagwat et al., (2012; Fig.
215 3e). All charcoal concentrations (number of pieces cm⁻³) are transformed to charcoal
216 accumulation rates (CHAR; pieces cm⁻²yr⁻¹) using the sediment accumulation-rate values in
217 Nogué et al., (2018; see Fig. S1 and Table S4). Overall, macroscopic charcoal (<600 µm) and
218 microscopic charcoal pieces can be dispersed over large distances (up to 30-50 km; Tinner et
219 al., 1998; Oris et al., 2014; Adolf et al., 2018). Thus, the low-frequency background component
220 of macroscopic charcoal (CHAR_{back}) and the microscopic charcoal trends are considered as
221 proxies for the fire activity at the landscape-scale (Marlon et al., 2008; Adolf et al., 2018). We
222 estimate the background component by interpolating the macro-charcoal record using a
223 constant temporal resolution of 13 years (i.e. the median sediment-accumulation rate), followed
224 by LOWESS smoothing (Fig. 3d).

225

226 **2.6 Monsoon variability and intervals of enhanced aridity**

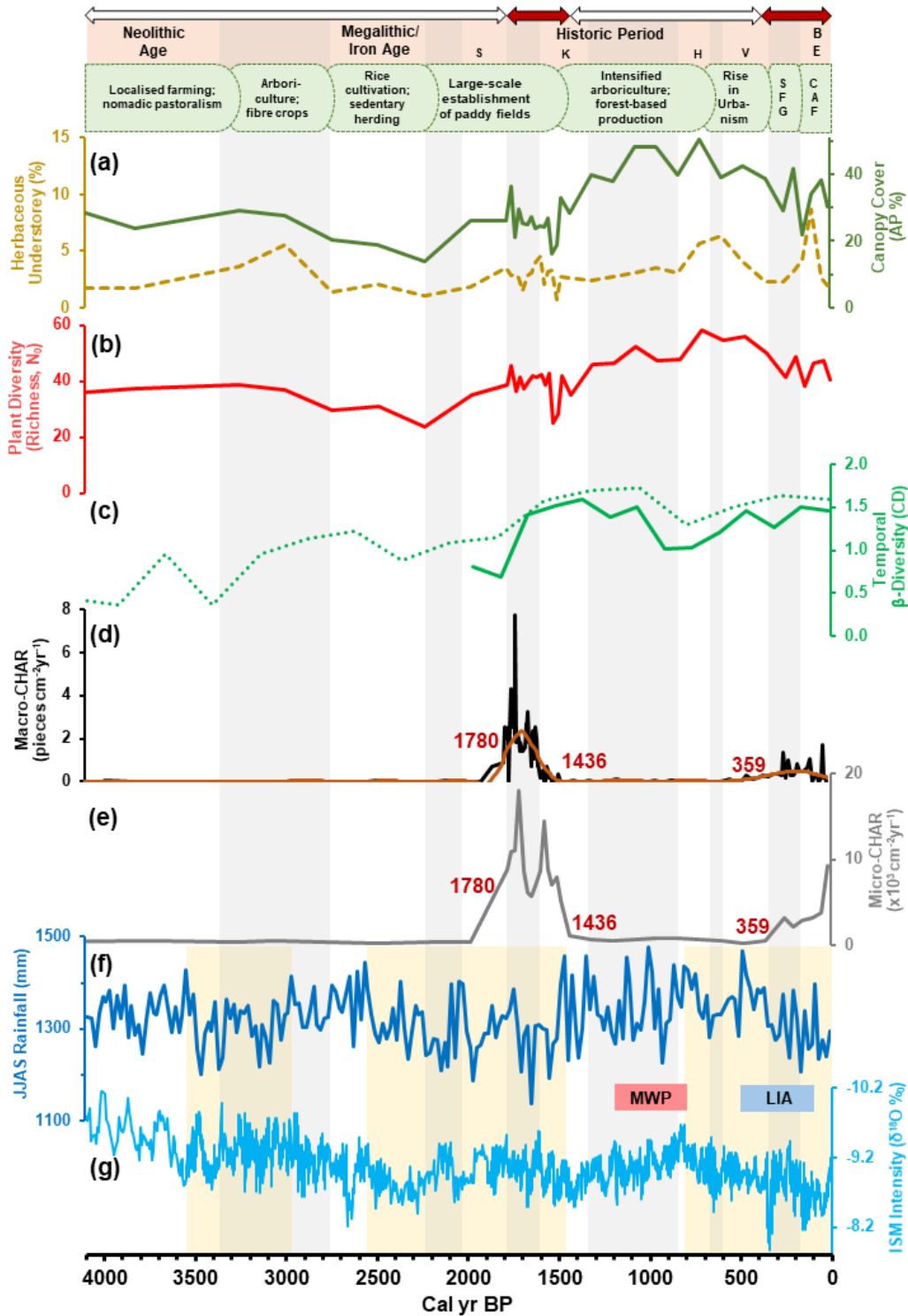
227 During the monsoonal months of June-September (JJAS), the Central Western Ghats receive
228 *c.* 2000 mm of average rainfall (Ambinakudige and Sathish, 2009). While February-March can
229 be the driest months with little to no rainfall, the pre-monsoon months of April-May bring
230 small amount of rainfall (*c.* 200 mm/month; Sukumar et al., 2004). Taking this rainfall pattern
231 into consideration, we bring two independent lines of evidence to detect the intervals of
232 enhanced aridity in response to reduced monsoon rainfall. First, using a Community Climate
233 System Model-based PaleoView (Fordham et al., 2017), we obtained mean JJAS rainfall for
234 the Kodagu region at 20-yr resolution (Fig. 3f). Although PaleoView provides substantially
235 lower JJAS rainfall values than the reported average (1300 vs. 2000 mm), it is the relative
236 changes in rainfall that we focus on for identifying intervals of enhanced aridity on the regional
237 scale. In addition, we employ an extremely high-resolution (*c.* 1.8 years on average) and well-
238 dated speleothem record from North India to identify the weakening of the monsoon in the
239 Indian subcontinent (Kathayat et al., 2017; Fig. 3g). Despite possible regional heterogeneities
240 within the subcontinent, we compare both records to identify common arid intervals across the
241 past 4000 years.

242

243 **2.7 Land use history**

244 The Western Ghats has a long history of human occupation and modification as early as
245 8,00,000 yr BP (Pappu and Deo, 1994; Gaillard et al., 2010). While the roots of agriculture-
246 pastoralism in the region can be traced back to *c.* 5000 yr BP (Fuller et al., 2004), the
247 agroforestry systems in particular is thought to be in existence for the past 2000 years (Krishna
248 and Morrison, 2010). Based on the review of archaeological and environmental history
249 literature (e.g., Rice, 1878; Chandran, 1997; Asouti and Fuller, 2008; Krishna and Morrison,
250 2010), we compiled a summary of land use history of the Kodagu region through notable

251 ecological, social and political changes (Fig. 3, top panel). The key societal transitions i.e.
 252 changes in land management either through intensification of existing strategies and/or through
 253 introduction of new means help us explore the historic roots of fires in the Western Ghats.



254 **Figure 3:** Temporal transformation of the Western Ghats agroforestry landscape over the past
 255 4000 years:

256 (a) The extent (%) of the canopy cover (solid green) and the abundance of understory herbs
257 (dashed);
258 (b) Plant diversity signified using the pollen richness (N_0) of all terrestrial taxa;
259 (c) Temporal β -diversity (expressed in chord distance) suggestive of the change in vegetation
260 composition over time, calculated at 260-yr resolution (dotted) and 150-yr resolution;
261 (d-e) Anthropogenic fires based on macroscopic (CHAR; pieces $\text{cm}^{-2}\text{yr}^{-1}$) and microscopic
262 (CHAR; $\times 10^3$ pieces $\text{cm}^{-2}\text{yr}^{-1}$) charcoal analysis; the thick brown line in macro-charcoal record
263 is a 13-yr wide lowess-smoothing depicting charcoal background;
264 (f) Regional monsoonal months (JJAS) rainfall (mm) at 20-yr interval;
265 (h) $\delta^{18}\text{O}$ speleothem record from North India demonstrating Indian Summer Monsoon (ISM)
266 intensity (after Kathayat et al. 2017).

267 Yellow bars highlight the intervals of increased aridity. Pink and blue bars indicate the
268 Medieval Warm Period (MWP) and Little Ice Age (LIA). The top panel shows the summary
269 of land use history of the Kodagu region through notable ecological, social and political
270 changes (based on Rice, 1878; Subash Chandran, 1997; Asouti and Fuller, 2008; Krishna and
271 Morrison, 2010). Within the Historic Period, S = Satavahana Dynasty (2050-1800 yr BP), K =
272 Kadamba Dynasty (1600-1350 yr BP), H = Hoyasala Kingdom (850-650 yr BP), V =
273 Vijayanagara Empire (600-350 yr BP), and BE = British Era (150-0 yr BP). SFG stands for
274 sacred forest groves while CAF stands for coffee agroforestry. Grey areas highlight periods of
275 societal transitions i.e. changes in land management either through intensification of existing
276 strategies and/or through introduction of new means. The years 1780 ± 60 yr BP, 1436 ± 60 yr
277 BP, and 359 ± 30 yr BP mark the switches between the no-fire and fire periods (white and red
278 arrows respectively) and are considered as points of major transformations in the system.

279

280 **3. Results**

281 **3.1 Trends in canopy cover and plant diversity**

282 The canopy cover exhibits considerable changes over the past 4000 years (Figs. 2-3a). The
283 canopy cover is initially stable (23-29%) but then significantly declines to its lowest (14%) *c.*
284 2250 yr BP. Subsequently, a notable increase is visible until 2000 yr BP (~28%), followed by
285 a series of fluctuations during 2000-1450 yr BP incorporating phases of both high canopy cover
286 (~36% *c.* 1750 yr BP) and high openness (e.g. 16% *c.* 1550 yr BP). Over the next 850 years,
287 the canopy cover substantially increases up to 48-51% (*c.* 1100-750 yr BP). From 600 yr BP
288 onwards, the canopy-forming woody taxa gradually shrink to constitute *c.* 30% of the present-
289 day landscape (Figs. 2-3a).

290 The pollen richness ($N_0 = 24-58$) and evenness ($N_2/N_0 = 0.07-0.13$) show largely
291 analogous trends, collectively identifying plant diversity changes over time (Fig. 4). Starting
292 from intermediate values ($N_0 = 35-37$), the pollen richness consistently declines reaching its
293 minima ($N_0 = 24$) *c.* 2250 yr BP. The corresponding evenness values show modest fluctuations
294 between 0.08 and 0.1. The period between 2250 and 1450 yr BP shows a dissonance between
295 the two: the richness subsequently recovers to a stable state ($N_0 = 35-42$ except 25 *c.* 1550 yr
296 BP) whereas the evenness decreases until 1550 yr BP before increasing to 0.1. A perpetual rise
297 is visible in both richness and evenness during 1450 and 1050 yr BP; both reach the highest
298 values ($N_0 = 58$ and $N_2/N_0 = 0.13$) in the sequence around 700 yr BP. While the richness
299 remains high until 450 yr BP, the evenness starts to drop. Subsequently, there is an overall
300 declining trend in both indices. The present-day pollen richness value ($N_0 = 41$) is slightly lower
301 than its immediate no-fire counterpart in the Historic Period but higher than its oldest, no-fire
302 counterpart (Figs. 3 and 5). Importantly, except a visible setback *c.* 1550 yr BP, the number of
303 canopy-forming woody taxa hardly varies over the past four millennia (see the oldest and

304 present-day values in Fig. 5). Evidently, there is a strong correlation ($R^2 = 0.78$) between the
305 plant diversity and the canopy cover in the Western Ghats agroforestry landscape (Fig. 6).

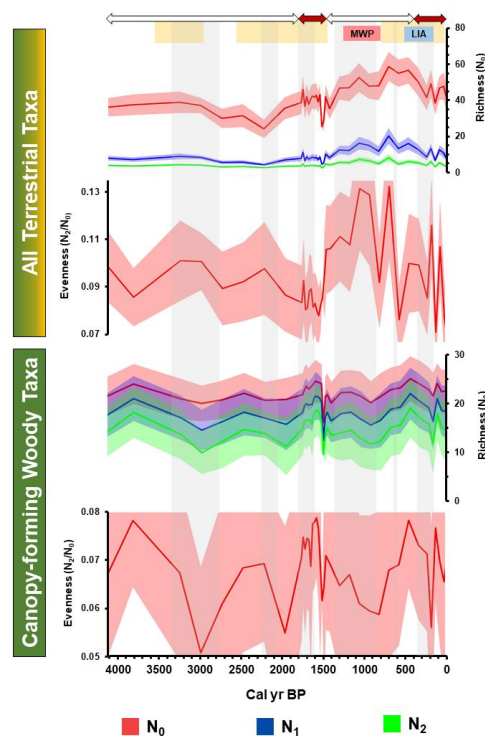
306 In case of vegetation composition over time (temporal β -diversity), there is an overall
307 increasing trend throughout the record (Fig. 3c). During 4000-2350 yr BP, the temporal β -
308 diversity increases and decreases between 0.4 to 1.22, followed by an upward trend until 1050
309 yr BP (visible in both curves; more peculiar the 2000-yr curve in Fig. 3c). There is a modest
310 drop in the temporal β -diversity during 1000-700 yr BP, however, it successively stabilises to
311 constitute the present-day value of 1.5.

312

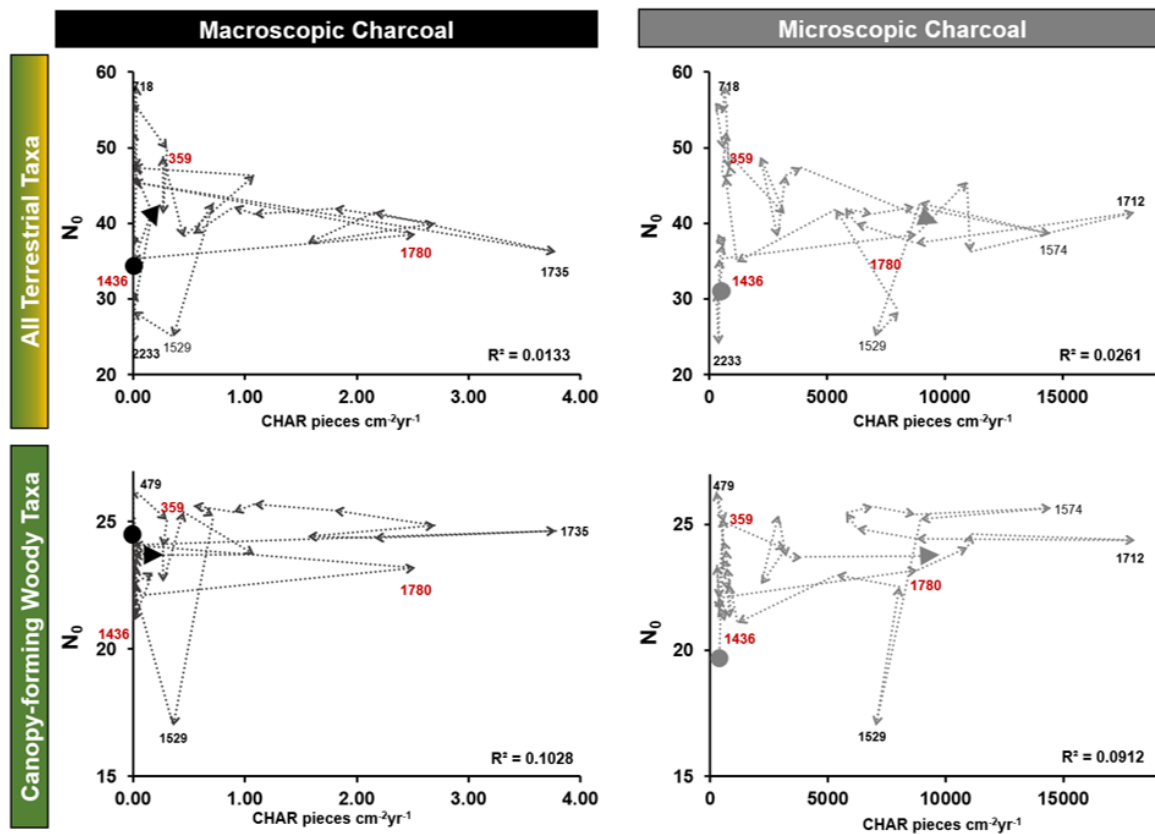
313 **3.2 Anthropogenic fires, land use changes and intervals of enhanced aridity**

314 We find no evidence of fire occurrence between 4000 and 1800 yr BP (Figs. 3d-e). This period
315 witnesses several changes in land use from localised agro-pastoral subsistence to beginnings
316 of arboriculture and subsequently, the onset of rice cultivation alongside sedentary herding
317 (Fig. 3; Asouti and Fuller, 2008). Fires first appear in the landscape *c.* 1800 yr BP and continue
318 until 1400 yr BP (Figs. 3d-e). This period coincides with the large-scale establishment of paddy
319 fields in the region, subsequently augmented with intensified arboriculture (Fig. 3; Chandran,
320 1997). Negligible fires are noted over the period of next \sim 1000 years, which is associated with
321 intensified arboriculture, onset of agroforestry as well as the first organised attempts of slash-
322 and-burn in the Western Ghats region (Krishna and Morrison, 2010). Fires reappear in the
323 landscape *c.* 400 yr BP, albeit at a much lower degree (Fig. 3d-e). This period coincides with
324 the emergence and maintenance of sacred forest groves in the Kodagu region (Bhagwat et al.,
325 2014). The last 150 years witness extensive logging followed by the development of coffee-
326 based commercial agroforestry in the Western Ghats and a near-complete ban on slash-and-
327 burn practice under the British rule (Ambinakudige and Sathish, 2009).

328 Comparing regional JJAS rainfall and the overall monsoon intensity, the three
 329 pronounced aridity intervals are observed: regional aridity during 3550-2950 yr BP and
 330 subcontinental aridity during 2550-1450 yr BP, and the last 800 yr BP (except a short, wet
 331 regional spell *c.* 500 yr BP; Figs. 3e-f). The warm interval of the Medieval Warm Period
 332 (MWP) is observed to be overall wet while the cooler Little Ice Age (LIA) conditions are
 333 coterminous with substantial aridity and extreme variability as seen through the weaker
 334 monsoon rainfall and deteriorating regional rainfall in the Central Western Ghats region.



335 **Figure 4:** The pollen richness (N_0 = Total number of taxa present; N_1 = Total number of
 336 common taxa present; N_2 = Total number of dominant taxa present) and evenness (N_2/N_0)
 337 values of all terrestrial taxa and those of canopy-forming woody (AP) taxa from the Western
 338 Ghats. Shaded areas indicate the width of the 95% confidence interval around estimates. The
 339 no-fire and fire periods are shown by white and red arrows, respectively. Yellow bars highlight
 340 the intervals of enhanced aridity. Pink and blue bars indicate Medieval Warm Period (MWP)
 341 and Little Ice Age (LIA). Grey areas highlight major periods of societal transitions i.e. changes
 342 in landscape management (see Fig. 3 and Sections 3-4 for details).



343 **Figure 5:** A relationship between plant diversity and anthropogenic fires in the Western Ghats
 344 agroforestry landscape. The pollen richness (N_0) values for all terrestrial taxa and canopy-
 345 forming woody taxa are plotted against macro- and micro-CHAR values ($\text{pieces cm}^{-2}\text{yr}^{-1}$) and
 346 the points are connected in a chronological sequence. The solid circle represents the initial
 347 (oldest) plant diversity value in the sequence while the triangle shows the present-day value.
 348 Two fire periods, 1800-1400 yr BP and 400-0 yr BP are visible in Figs. 2-4: the years 1780 ± 60
 349 yr BP, 1436 ± 60 yr BP, and 359 ± 30 yr BP mark the switches among the no-fire and fire periods.
 350 The years associated with highest and lowest points in plant diversity and significant biomass
 351 burning events are also shown. Note: The sample interval for pollen-based plant diversity
 352 indices and microscopic charcoal is 4-cm while that of for macroscopic charcoal is 1-cm. Thus,
 353 the corresponding macroscopic charcoal dataset in this comparative analysis resulted in a
 354 different CHAR ranges ($0\text{-}4 \text{ cm}^{-2}\text{yr}^{-1}$) as compared to the complete data range ($0\text{-}8 \text{ cm}^{-2}\text{yr}^{-1}$)
 355 seen in Figs. 2-3.

356 **4. Discussion**

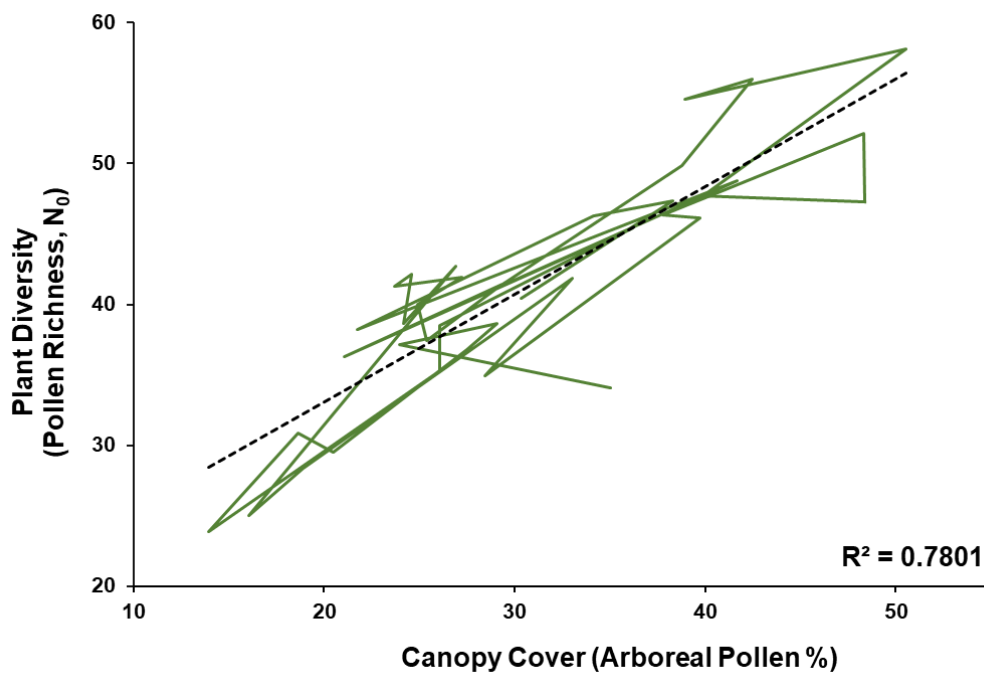
357 In the Western Ghats agroforestry landscapes, we find two distinct periods of fire – 1800-1400
358 yr BP and 400-0 yr BP – that are concomitant with enhanced aridity (Figs. 3-4). Extended
359 periods of aridity mean drier fuel loads and intensified fire frequency in the wet evergreen
360 Western Ghats forests (Kodandapani et al., 2004). The synergy between two environmental
361 stressors could exacerbate the drying of these wet tropical forests, making the forest canopy
362 more open and affecting plant diversity in the Western Ghats. We interpret the switches
363 between the fire and no-fire periods as points of major transformations in this tropical
364 landscape (Figs. 2-5) and explore their relationships with the overall plant diversity and
365 canopy-forming woody taxa. As land use patterns (agriculture, grazing, logging) further
366 influence the severity of disturbance events and the rate of recovery in and around tropical
367 rainforests, we subsequently interpret these results in the context of past landscape
368 management and future conservation strategies for the Western Ghats and human-influenced
369 wet tropical landscapes at large.

370

371 **4.1 Linkages between plant diversity and the canopy cover in the Western Ghats**

372 We find a strong correlation between plant diversity and the canopy cover in the Western
373 Ghats: higher the canopy cover, higher the number of taxa in the landscape (Figs. 3a-b and 6).
374 In human-influenced tropical landscapes, high canopy cover would mean less fragmented
375 landscape (Chazdon, 2003). Thus, the overall sustainability of plant diversity in this social-
376 ecological system does seem to be closely linked with the extent of canopy cover. The changes
377 in canopy cover have little effect on the diversity of canopy-forming woody taxa, which has
378 remained steady over the course of past 4000 years (Figs. 3-4). Thus, high plant diversity in
379 the Western Ghats agroforestry landscape is associated with the increased variety (and
380 abundance) of herbaceous taxa i.e. understorey vegetation (Figs. 3a-b). Tree cover in the

381 landscape is capable of reducing the severity of microclimatic changes including higher
382 temperatures, increased wind speed, lower humidity, and lower soil moisture (Freidenburg,
383 1998; Kapos et al., 1997). As a result, there may be less edge-related disturbance and more
384 habitat available for forest-dwelling understorey taxa (Bhagwat et al., 2005b; Muthuramkumar
385 et al., 2006). The overall congruence between the extent of the herbaceous understorey and
386 canopy cover in the Western Ghats (Fig. 3a) is indicative of the above ecological processes,
387 thereby highlighting the significance of tree cover in sustaining plant diversity in tropical
388 social-ecological systems.



389 **Figure 6:** A relationship between plant diversity (based on pollen richness, N_0) and the canopy
390 cover (Arboreal Pollen (AP) %) in the Western Ghats agroforestry landscape. The coefficient
391 of determination (R^2) shows that the strength of association is high.

392

393 **4.2 Synergistic effects of anthropogenic fires and enhanced aridity on plant diversity**

394 Plant diversity is very weakly correlated with anthropogenic fires (Fig. 5). Both highest and
395 lowest plant diversity are observed when fires were completely absent. At the same time,

396 neither of the fire periods (1800-1400 yr BP and 400-0 yr BP) resulted into the extensive loss
397 of taxa but shows their intermediate range (Figs. 4-5). The only significant decline in plant
398 diversity amid the first fire period (1800-1400 yr BP) is *c.* 1550 yr BP (1529±60 yr BP in Fig.
399 5). The decline in the canopy-forming woody taxa is also visible around this time, which
400 otherwise show no change across the past 4000 years (Figs. 4-5). These complexities highlight
401 the non-linear relationship between plant diversity and fires: the sustained burning coupled
402 with enhanced aridity seems to reduce plant diversity through increased canopy openings (Fig.
403 3). The prolonged use of fires can generate habitat heterogeneity by opening and increasing
404 gaps and creating snags and deadwood patches, resulting in increasing the number of potential
405 ecological niches (Pausas and Keeley, 2019). In keeping with this, we find a greater temporal
406 β -diversity (i.e. change in vegetation composition) during this fire period, indicating a higher
407 degree of ecological transformation in response to fires, increased seasonality, and land use
408 (e.g., the extensive establishment of rice cultivation; Fig. 3).

409 Overall, the loss in plant diversity, especially that of woody taxa, *c.* 1550 yr BP would
410 have had serious implications for ecosystem services. In this context, the reduction in fires *c.*
411 1450 yr BP onwards and subsequent substantial upsurge in both woody taxa as well as overall
412 plant diversity over the next 850 years is interesting (Figs. 3c-e). Moreover, during this period,
413 several habitat-specialist trees also found their way back after long hiatuses (e.g.
414 *Dipterocarpus*, *Myristica*) while some made their first appearance (e.g. *Dichapetalum*,
415 *Poeciloneuron*) in this Western Ghats agroforestry sequence, indicating a post-disturbance
416 transition towards a closed canopy evergreen forest (Figs. 2-3a). Interestingly, temporal β -
417 diversity remained high until 1000 yr BP, *c.* 400 years after the end of the first fire period. This
418 may suggest a long vegetation recovery time or that other factors (e.g. land use) had been
419 critical in forest transformation. Overall, the increased plant diversity and canopy cover during
420 the no-fire period (1400-400 yr BP) are more or less coterminous with organised slash-and-

421 burn agriculture, intensification of arboriculture, and the onset of agroforestry during the warm-
422 wet Medieval Warm Period (Fig. 3; Asouti and Fuller, 2008; Kathayat et al., 2017). A
423 collective strategy for curtailing the use of fires (e.g., infrequent, very localised burns) and
424 planting trees and shrubs on productive agricultural land could have played an important role
425 in invigorating plant diversity in the region (Figs. 3 and 5). Such large-scale changes in land
426 use may be achievable only due to paradigm shifts in local communities (e.g. Luoga et al.,
427 2005; Dalle et al., 2006) i.e. changes in their attitude towards forests in recognising their value
428 as a prime resource and provider of ecosystem services (Bhagwat et al., 2014). Appreciating
429 the importance of forests, native trees, and their ability to foster biodiversity in connection with
430 ecosystem services (Ellison et al., 2017) could have been a timely comprehension for
431 predominantly agro-pastoral societies in the face of changing climate (i.e. the Medieval Warm
432 Period). The subsequent reduction of canopy cover and loss of plant diversity over the course
433 of Vijayanagara Empire (Fig. 3), however, could indicate deleterious impacts of intensified
434 urbanism and consequent resource pressures on the Western Ghats forests (Morrison, 2013).

435 Lastly, the return of fires *c.* 400 yr BP is in concurrence with the emergence of sacred
436 forest groves in the Kodagu region (Fig. 3; Bhagwat et al., 2014). Although created as dedicated
437 places for worship, the formation of sacred forest patches could have led to unintentional
438 protection and conservation of native trees (see the highest extent (16%) of habitat-specialist
439 trees in Fig. 2; Bhagwat and Rutte, 2006). In maintaining sacred forest groves, a strict
440 demarcation of forested and agricultural land parcels was implemented by the local dynasty
441 and indigenous communities living under its rule (Belliappa, 2008), which could have
442 effectively resulted into increased canopy cover in the region (Fig. 2). Thus, more coherent
443 social-ecological systems in the Western Ghats can be attributed to the communities actively
444 managing the landscape through a moderated use of fires and through maintenance as well as

445 restoration of trees (Nogué et al., 2018), making positive influences on plant diversity during
446 the Little Ice Age-induced aridity.

447 The British occupation of the Western Ghats over the past 150 years established
448 commercial agroforestry as well as state forestry, setting the new tone for forestry operations
449 and overall landscape management to date (Chandran, 1997). During this period, forest
450 working plans, essentially modelled after European forestry systems, were adopted extensively
451 in the Western Ghats (Rangarajan, 1996; Ribbentrop, 1900); forest management was
452 centralised around the production of large timber volumes and generation of cash revenue from
453 forest resources (Guha, 1983; Rajan, 1998). The overall colonial view of forests as a
454 commodity resulted in complete banning of the slash-and-burn practice, which came in direct
455 conflict with traditional forest management practices (Gadgil and Guha, 1993). Under such
456 completely altered landscape management strategy, the Kodagu region experienced the
457 establishment of commercial coffee estates *c.* 100 yr BP (1854 CE; Ambinakudige and Choi,
458 2009). Records indicate that when coffee was introduced, growers substantially cleared the
459 forest to plant coffee but when coffee plants could not survive heavy monsoon rains, shade
460 grown coffee became the cultivation practice in the area (Ambinakudige and Sathish, 2009).
461 Both the phases of reduction and revival of the canopy cover and that of plant diversity are
462 visible in the Western Ghats agroforestry sequence, so is the gradual rise in vegetation
463 transformation (Figs. 3a-c). Despite the banning of slash-and-burn practice, fires continued to
464 occur in the Western Ghats landscape, perhaps as a sign of resistance from indigenous
465 communities to ‘formal’ forest management (Thekaekara et al., 2017). The overall degree of
466 burning in this fire period, however, has been much lower than that of during the previous fire
467 period (1800-1400 yr BP; Figs. 3d-e). From a historic perspective, the present-day plant
468 diversity in the Western Ghats agroforestry landscape falls within the range of historical
469 variability: while the present-day plant diversity values are slightly lower than those in the

470 previous fire period, they are higher in comparison with their oldest (no-fire) counterparts (see
471 Figs. 3 and 5). In other words, shade grown coffee cultivation in this part of Western Ghats
472 somewhat reduced the overall plant diversity in merely 100 years (Fig. 3). However, with its
473 ability to increase canopy cover through deliberate maintenance of trees, this cash-crop
474 intensification also paved ways to revive plant diversity in the future. Today's landscape under
475 shade-grown coffee cultivation (over 60% of the landscape) where native shade trees constitute
476 a major share of the evergreen forest canopies (Fig. 2), offers avenues for fostering biodiversity
477 in the Western Ghats.

478

479 **4.3 Implications for ecological management in the Western Ghats and tropical** 480 **agroforestry landscapes**

481 **4.3.1 Importance of conservation beyond forest reserves**

482 Alongside other long-term, pollen-based diversity studies in the tropics (e.g., Weng et al., 2006;
483 Figueroa-Rangel et al., 2012; Palazzesi et al., 2014; Rodríguez-Zorro et al., 2018), this record
484 echoes the unique ecological character of the tropics at large: the tree-covered landscape matrix
485 is the most important determinant of sustaining biodiversity in the tropics. From a conservation
486 point of view, our results further underline the need for maintaining trees in human-influenced
487 tropical landscapes. While forest reserves in the tropics are strictly protected for biodiversity
488 conservation, such areas might fall short in fulfilling their purpose without conservation
489 management in the landscapes surrounding them (DeFries et al., 2010; Karanth and DeFries,
490 2010). Tree management in tropical landscapes under mounting anthropogenic pressures is
491 quite challenging, calling for pragmatic solutions that support both biodiversity and people. As
492 envisaged in India's National Agroforestry Policy (Chavan et al., 2015), increasing area under
493 agroforestry would be one of the most practical ways to do so – its potential in providing
494 habitats outside formally protected land, connecting nature reserves, and alleviating resource-

495 use pressure on conservation areas is already substantiated (Bhagwat et al., 2008; Schroth et
496 al., 2004). Interestingly, positive canopy cover-biodiversity correlation is already visible in the
497 modern-day coffee-dominated agroforestry landscapes in the Western Ghats (Kushalappa et
498 al., 2019) and in other kinds of tropical agroforestry systems elsewhere (Tschardt et al., 2011;
499 Acabado and Martin, 2018; Ticktin et al., 2018), providing region-specific analogues for wider
500 implementation.

501 Furthermore, this record (Fig. 2) shows that habitat-specialist trees have persisted in the
502 Western Ghats landscape over the past 4000 years (e.g., *Eleocarpus*, *Syzygium*), reappeared at
503 <1000-yr intervals (e.g., *Holigarna*, *Myristica*, *Reinwardtiadendron*), or even “arrived” during
504 the first fire period (e.g., *Poeciloneuron*, *Litsea*). Throughout the record, these habitat-
505 specialist trees continue to constitute c. 25-33% of the Western Ghats wet evergreen forest
506 cover (Fig. 2), suggesting the resilience of old-growth trees towards varying degrees of land
507 use and management. While a few of them (e.g., *Dipterocarpus*, *Hopea*, and *Palaquium*) are
508 already part of historic baselines that conservationists valorise in planning and restoration of
509 the Western Ghats (Muthuramkumar et al., 2006), our long-term, pollen-based record provides
510 further, empirical support to this assumption. Patches of native trees on agroforestry landscapes
511 would, thus, be natural places to focus organised conservation and restoration efforts beyond
512 forest reserves. However, to sustain the conservation potential of agroforestry systems, a
513 balance between production and protection of natural features in the landscape is essential
514 (Bhagwat et al., 2008). Thus, keeping remnants of such forests within agroforestry plantations
515 and redesigning annual croplands to include features (e.g. hedgerows) of old-growth trees can
516 contribute to landscape-level connectivity, thereby making biodiversity conservation more
517 effective (Bobo et al., 2006; Morel and Nogu e, 2019).

518

519 **4.3.2 Towards effective fire management**

520 We find a weak correlation between anthropogenic fires and plant diversity in the wet
521 evergreen forests of the Western Ghats: a significant impact on the diversity of woody and
522 herbaceous taxa does seem to be associated with intensified canopy opening through continued,
523 extensive use of fires. Importantly, the relationship between fires and canopy-forming woody
524 taxa in the Western Ghats (Fig. 5) provides a new perspective to look at slash-and-burn
525 agriculture, which is a localised, short-term burning practice. In the Indian Subcontinent, it is
526 practiced as a fertilising process through destroying crop residues near the onset of the pre-
527 monsoon rainfall during the months of April and May (~20% of the annual rainfall; Sukumar
528 et al., 2004). While it is restricted to agricultural lands, the probability of spread of fire from
529 agricultural lands into forest lands increases with the fragmentation of the landscape and
530 dryness of fuels (Kodandapani et al., 2004). This often leads to conflict between rural,
531 indigenous communities and the Indian Forestry Departments (IFDs), resulting into
532 incendiarism, rapid fragmentation of landscape and loss of forests that IFDs hopes to avoid
533 (Singh, 2008; Thekaekara et al., 2017). Bringing past analogues of indigenous people's
534 practices to curb fires and subsequent revival of the Western Ghats rainforest and plant
535 diversity, we demonstrate that the limited, planned use of fires on agricultural land on localised
536 scales may not leave a negative impact on plant diversity including canopy-forming woody
537 taxa (see the discussion on sacred forest groves in Section 3.2). Since agroforestry landscapes
538 hold a promise of connecting nature reserves by increasing tree cover in the landscape
539 (Bhagwat et al., 2008), we propose that low intensity biomass burning on agricultural lands
540 would be a more practical solution, accommodating both traditional practice and avoidance of
541 fires into forest reserves in the Western Ghats. These could be considered as "prescribed burns"
542 on agroforestry landscapes, an evidence-based "middle ground" for a collective engagement
543 of two key actors in executing National Agroforestry Policy. We argue that such measures will

544 sincerely help facilitate the effective implementation of this economically and ecologically
545 important policy and its desired positive social-ecological outcomes.

546

547 **5. Conclusions**

548 The synergistic impacts of anthropogenic fires and enhanced aridity on plant diversity in one
549 of world's ancient social-ecological systems point out the non-linear relationship between plant
550 diversity and human-induced fires. While there are examples of reduced plant diversity due to
551 consistent fire coupled with enhanced aridity, our work also brings positive narratives where
552 the limited, localised use of fires could have promoted the revival of plant diversity in the
553 Western Ghats. Despite apparent changes in fires, aridity, and land use, the present-day plant
554 diversity in the Western Ghats agroforestry landscape falls within the range of historical
555 variability. Interestingly, the diversity of the canopy-forming woody taxa in this record remains
556 almost constant over the course of past 4000 years and the variations in plant diversity in this
557 tropical landscape are largely constituted by changes in herbaceous understorey. Furthermore,
558 in accordance with other tropical records, our data demonstrate that the canopy cover is the
559 most crucial determinant of sustaining plant diversity in a tropical landscape. Thus, the tree-
560 covered matrix, even if fragmented, is one key landscape feature that needs to be conserved
561 because of its role in providing refugia for important elements of tropical biodiversity
562 (Bhagwat et al., 2012). Therefore, biodiversity conservation in the tropics needs to go beyond
563 reserves; strictly protected areas might be inadequate to fulfil their purpose without
564 conservation management in the landscapes surrounding them (Karanth and DeFries, 2010).
565 Under mounting anthropogenic pressures, tree management in the tropical social-ecological
566 systems calls for pragmatic solutions that support both ecological and social components of the
567 landscape. Through the use of palaeoecological data from the Western Ghats, we show that
568 people can play an active role in forest conservation and in sustaining plant diversity through

569 reduced biomass burning and intentional woodland management. Thus, we argue that for the
570 success of ecological management in this (and other) human-influenced tropical regions, it is
571 important to recognise that people are part of the landscape. Conservation-restoration efforts
572 for sustaining biodiversity in the face of future monsoon variability can succeed only if they
573 are planned in tandem with careful, evidence-based incorporation of traditional land
574 management practices. Our work demonstrates that ancient tropical agroforestry systems form
575 a good practice example of such collaborative efforts and have the potential to benefit both
576 biodiversity and people.

577

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592

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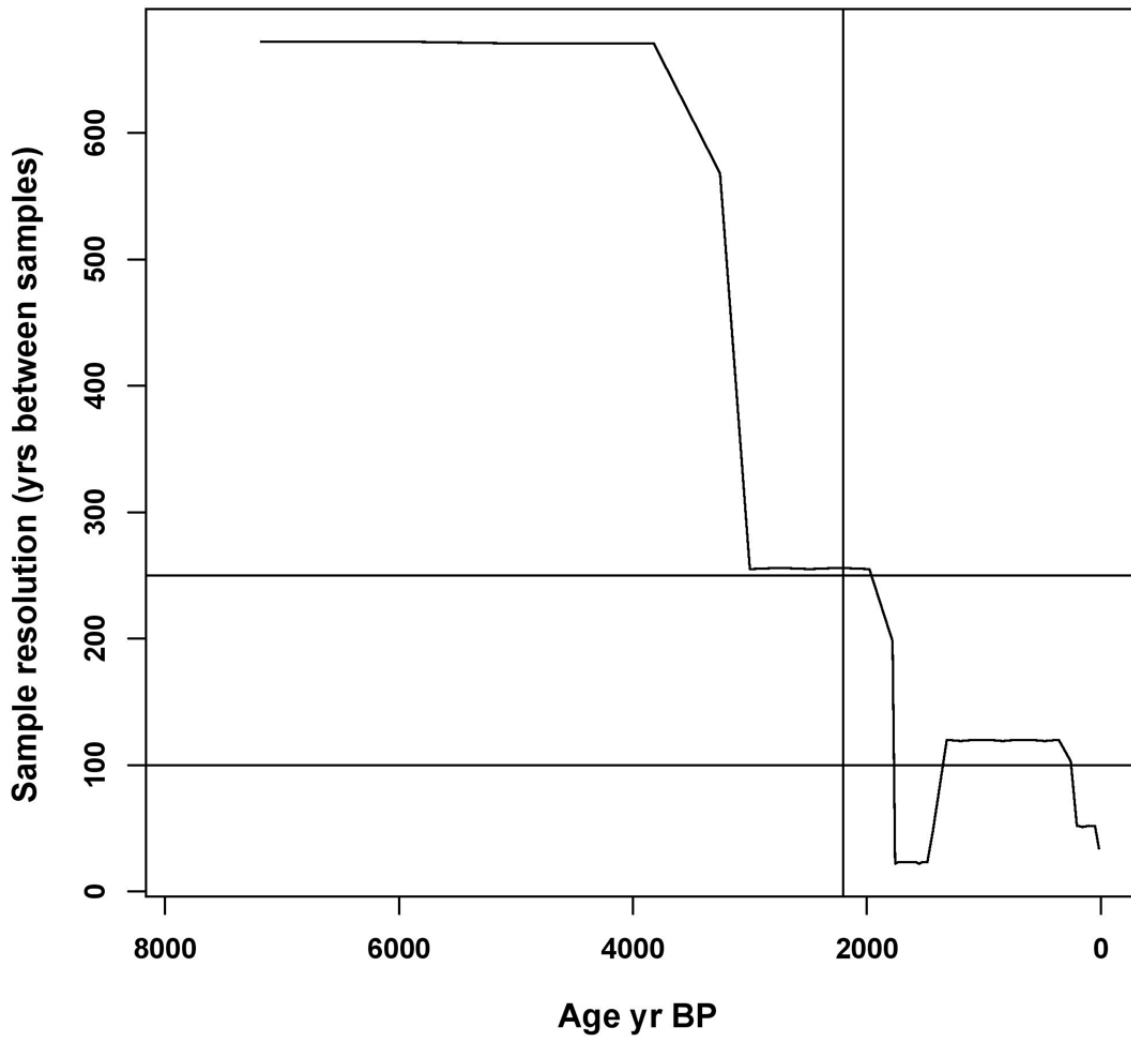
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977 **Supplementary Figure 1:** Variation in the sample resolution across the Agroforest-1 sequence
 978 informing two interpolation-window widths of 260 and 150 years for calculating temporal β -
 979 diversity i.e. change in vegetation composition over time.