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

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Abstract

Identifying the impacts of anthropogenic fires on biodiversity is imperative for human-influenced tropical rainforests because – i) these ecosystems have been transformed by human-induced fires for millennia; and ii) their effective management is essential for protecting the world's terrestrial biodiversity in the face of global environmental change. While several short-term studies present the impacts of fires on local plant diversity, how tropical plant diversity responds to fire regimes over long time scales is a significant knowledge gap, posing substantial impediment to evidence-based management of social-ecological systems. Using wet evergreen forests of Western Ghats of India as a model system, we discuss the synergistic effects of anthropogenic fires and enhanced aridity on tropical plant diversity over the past 4000 years by examining fossil pollen-based diversity indices (e.g., pollen richness and evenness, and temporal β-diversity), past fire management, the intervals of enhanced aridity due to reduced monsoon rainfall, and land use history. By developing a historical perspective, our aim is to provide region-specific management information for biodiversity conservation in the Western Ghats. We observe that the Western Ghats agroforestry landscape switches between periods of no fires (4000-1800 yr BP, and 1400-400 yr BP) and fires (1800-1400 yr BP, and 400-0 yr BP), with both fire periods concomitant with intervals of enhanced aridity. We find synergistic impacts of anthropogenic fires and aridity on plant diversity uneven across time and suggest that this is potentially due to different land management strategies. For example, during 1800-1400 yr BP, diversity reduced in conjunction with a significant decrease in the canopy cover related to sustained use of fires, possibly linked to large-scale intensification of agriculture. On the contrary, the substantially reduced fires during 400-0 yr BP may be associated with the emergence of sacred forest groves, a cultural practice supporting the maintenance of plant diversity. Overall, notwithstanding apparent changes in fires, aridity, and land use over the past 4000 years, present-day plant diversity in the Western Ghats agroforestry landscape falls within the range of historical variability. Importantly, we find a strong correlation between plant diversity and canopy cover throughout the record, emphasising the crucial role of active fire management and maintaining tree cover for biodiversity conservation. Systematic tree management in tropical social-ecological systems is vital for livelihoods of billions of people, who depend on forested landscapes. In this context, we argue that agroforestry landscapes can deliver win-win solutions for biodiversity as well as people in the Western Ghats and wet topics at large.

Keywords

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

1. Introduction

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

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

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

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

2. Materials and methods

2.1 The study site in the Western Ghats

The Western Ghats is a mountain range running along the western coast of peninsular India (Fig. 1a). The mid-elevation (500–1500 m asl) terraces constitute over 90% of the Western Ghats, presenting a mosaic of wet evergreen rainforest and grasslands shaped by human activities, particularly fire (Premathilake, 2006; Kodandapani et al., 2009). Here we utilise one such mid-elevational sedimentary sequence (hereafter, Agroforest-1), derived from the Kodagu district of Karnataka i.e. the central part of the Western Ghats (Fig. 1). The region boasts the extensive network of wet evergreen rainforest reserves primarily of *Mesua-Palaquium* type (Ramesh and Pascal, 1997), occupying about 30% of the landscape (Fig. 1b; Bhagwat et al., 2005a). In addition to these formally protected forests, *c*. 60% of the landscape is managed as agroforestry with high tree-canopy shading coffee plantations while remaining 10% of the landscape is under rice cultivation (Bhagwat et al., 2005b). The Agroforest-1 sequence is extracted from a small swamp situated in a coffee estate (12° 9' 14''N, 75° 42' 47''E; 910 m asl) surrounded by a patchwork of arable land and forest fragments (Fig. 1b). At the site, coffee (*Coffea arabica* var. *robusta*) is planted in the understorey of shade trees (Fig. 1c), many of which are representative of native vegetation mixed with betel nut palm (*Areca catechu*; Bhagwat et al., 2012). The site is less than 10 km away from a forest reserve currently under government protection (Fig. 1b).

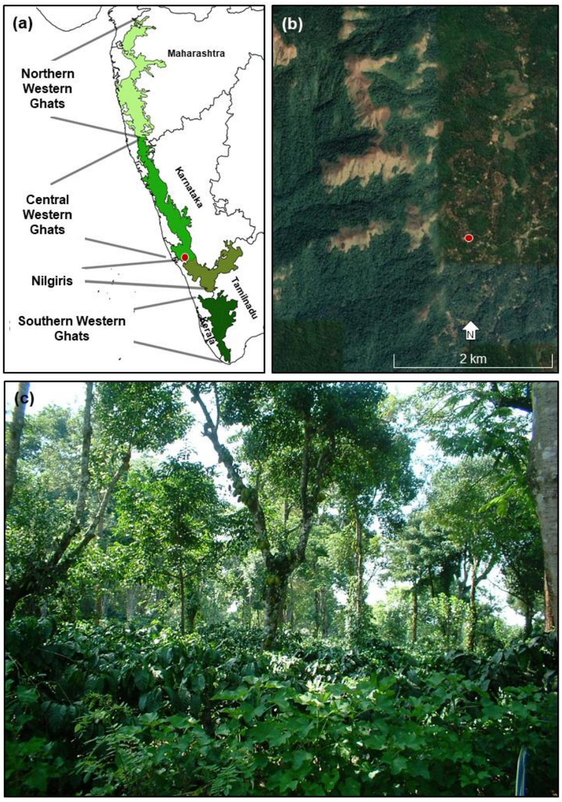

Figure 1: (a) The Western Ghats (WG) of India (after Mirza et al., 2014). The circle represents the location of the study site in the Central part of the WG, located in Kodagu District, Karnataka. (b) Google Image of the Kodagu region; the sedimentary sequence under study (12°9'14''N, 75°42'47''E; shown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

2.2 Extent and components of canopy cover

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

2.3 Plant diversity

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

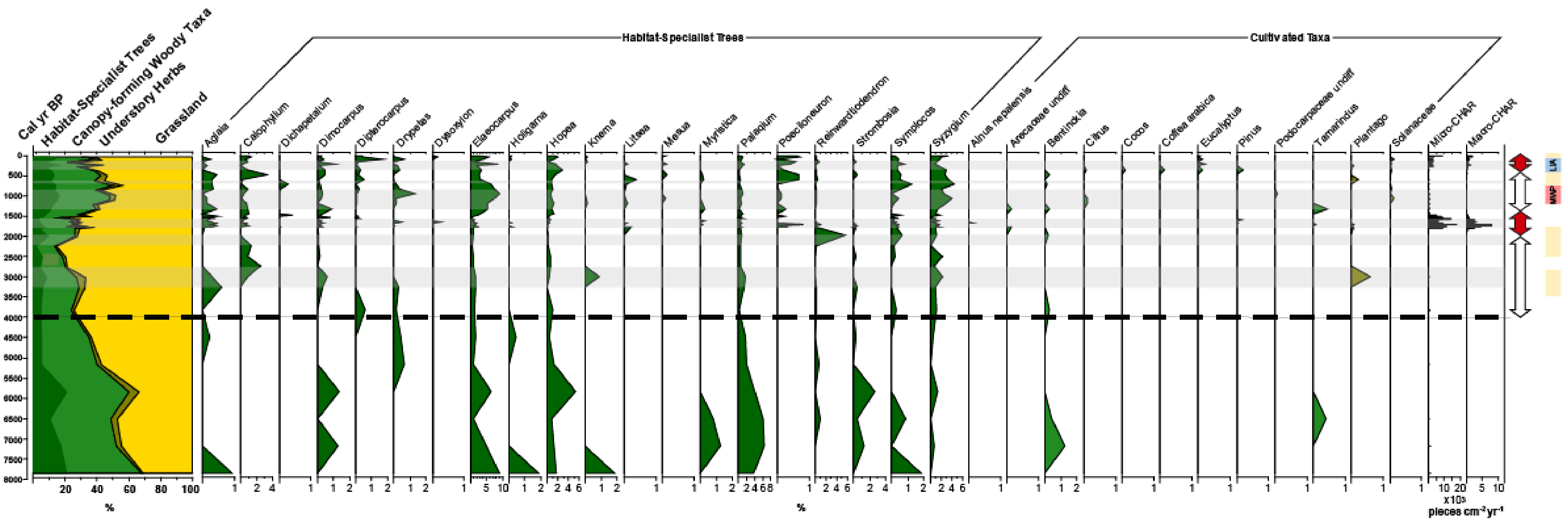

Figure 2: The relative abundances (%) of canopy-forming woody taxa, grassland, and understory herbaceous taxa are juxtaposed with those of individual habitat-specialist trees (indicative of low disturbance) and cultivated plant taxa including *Coffea arabica* (representing the present-day agroforestry landscape). Anthropogenic fires are represented by Micro-CHAR and Macro-CHAR (pieces cm^{-2}yr^{-1}) values. The years 1780±60 yr BP, 1436±60 yr BP, and 359±30 yr BP mark the switches among the no-fire and fire periods (white and red arrows respectively). Yellow bars highlight the intervals of enhanced aridity. Pink and blue bars indicate Medieval Warm Period (MWP) and Little Ice Age (LIA). Grey areas highlight periods of societal transitions i.e. changes in land management (see Fig. 3 and Sections 3-4 for details). The dotted line shows the period of the last 4000 years focused in this work.

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

2.4 Change in vegetation composition over time

In palaeoecological time series, temporal β-diversity is a measure of change in vegetation composition between adjacent samples using the rate-of-change metric (Birks, 2007). To estimate change in vegetation composition over time, we first linearly interpolated the pollen percentages on equal time intervals, and subsequently calculated the dissimilarity between adjacent samples using the chord distance of square-root transformed percentage values (Birks and Birks, 2008). Chord distance values range between zero (no change in vegetation composition) and two (complete change in vegetation composition, i.e. the two assemblages have no species in common). The trends are illustrated by a LOESS-smoothed curve (Cleveland and Devlin, 1988). Considering the varying sample resolution across the Agroforest-1 sequence (Fig. S1), we present two sets of temporal β-diversity records obtained with different interpolation-window widths – one for the entire 4000-yr period at 260-yr resolution while another for the last 2000 yr BP at 150-yr resolution (Fig. 3c). By employing a shorter interpolation-window width for the past 2000 years, we are able to visualise transformations in vegetation composition associated with intensified burning and land use change in the Western Ghats agroforestry landscape (Fig. 3c).

2.5 Past fire management

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

2.6 Monsoon variability and intervals of enhanced aridity

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

2.7 Land use history

The Western Ghats has a long history of human occupation and modification as early as 8,00,000 yr BP (Pappu and Deo, 1994; Gaillard et al., 2010). While the roots of agriculture-pastoralism in the region can be traced back to *c*. 5000 yr BP (Fuller et al., 2004), the agroforestry systems in particular is thought to be in existence for the past 2000 years (Krishna and Morrison, 2010). Based on the review of archaeological and environmental history literature (e.g., Rice, 1878; Chandran, 1997; Asouti and Fuller, 2008; Krishna and Morrison, 2010), we compiled a summary of land use history of the Kodagu region through notable ecological, social and political changes (Fig. 3, top panel). The key societal transitions i.e. changes in land management either through intensification of existing strategies and/or through introduction of new means help us explore the historic roots of fires in the Western Ghats.

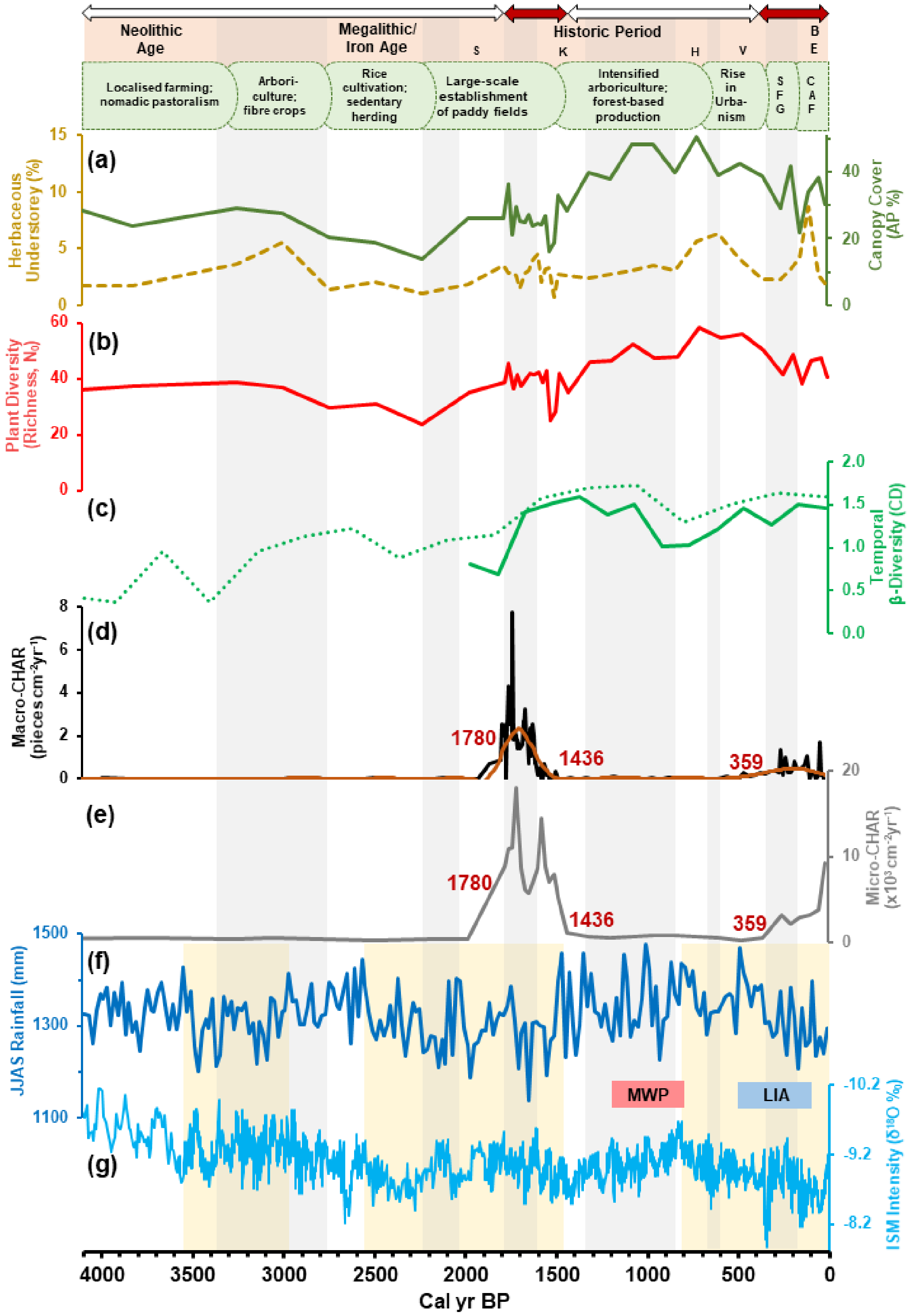

Figure 3: Temporal transformation of the Western Ghats agroforestry landscape over the past 4000 years:

(a) The extent (%) of the canopy cover (solid green) and the abundance of understory herbs (dashed);

(b) Plant diversity signified using the pollen richness (N_0) of all terrestrial taxa;

(c) Temporal β-diversity (expressed in chord distance) suggestive of the change in vegetation composition over time, calculated at 260-yr resolution (dotted) and 150-yr resolution;

(d-e) Anthropogenic fires based on macroscopic (CHAR; pieces $cm^{-2}yr^{-1}$) and microscopic (CHAR; $x10^3$ pieces $cm^{-2}yr^{-1}$) charcoal analysis; the thick brown line in macro-charcoal record is a 13-yr wide lowess-smoothing depicting charcoal background;

(f) Regional monsoonal months (JJAS) rainfall (mm) at 20-yr interval;

(h) $\delta^{18}O$ speleothem record from North India demonstrating Indian Summer Monsoon (ISM) intensity (after Kathayat et al. 2017).

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

3. Results

3.1 Trends in canopy cover and plant diversity

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

The pollen richness (N_0 = 24-58) and evenness (N_2/N_0 = 0.07-0.13) show largely analogous trends, collectively identifying plant diversity changes over time (Fig. 4). Starting from intermediate values (N_0 = 35-37), the pollen richness consistently declines reaching its minima (N_0 = 24) c. 2250 yr BP. The corresponding evenness values show modest fluctuations between 0.08 and 0.1. The period between 2250 and 1450 yr BP shows a dissonance between the two: the richness subsequently recovers to a stable state (N_0 = 35-42 except 25 c. 1550 yr BP) whereas the evenness decreases until 1550 yr BP before increasing to 0.1. A perpetual rise is visible in both richness and evenness during 1450 and 1050 yr BP; both reach the highest values (N_0 = 58 and N_2/N_0 = 0.13) in the sequence around 700 yr BP. While the richness remains high until 450 yr BP, the evenness starts to drop. Subsequently, there is an overall declining trend in both indices. The present-day pollen richness value (N_0= 41) is slightly lower than its immediate no-fire counterpart in the Historic Period but higher than its oldest, no-fire counterpart (Figs. 3 and 5). Importantly, except a visible setback *c.* 1550 yr BP, the number of canopy-forming woody taxa hardly varies over the past four millennia (see the oldest and present-day values in Fig. 5). Evidently, there is a strong correlation ($R^2 = 0.78$) between the plant diversity and the canopy cover in the Western Ghats agroforestry landscape (Fig. 6).

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

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

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

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

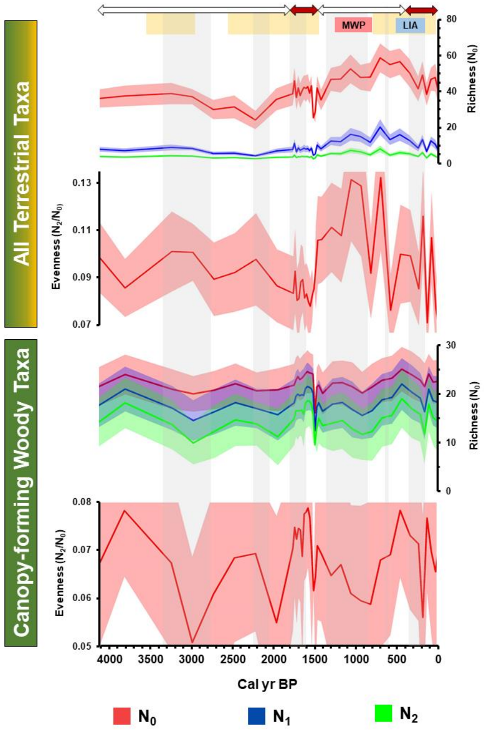

Figure 4: The pollen richness (N_0 = Total number of taxa present; N_1 = Total number of common taxa present; N_2 = Total number of dominant taxa present) and evenness (N_2/N_0) values of all terrestrial taxa and those of canopy-forming woody (AP) taxa from the Western Ghats. Shaded areas indicate the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

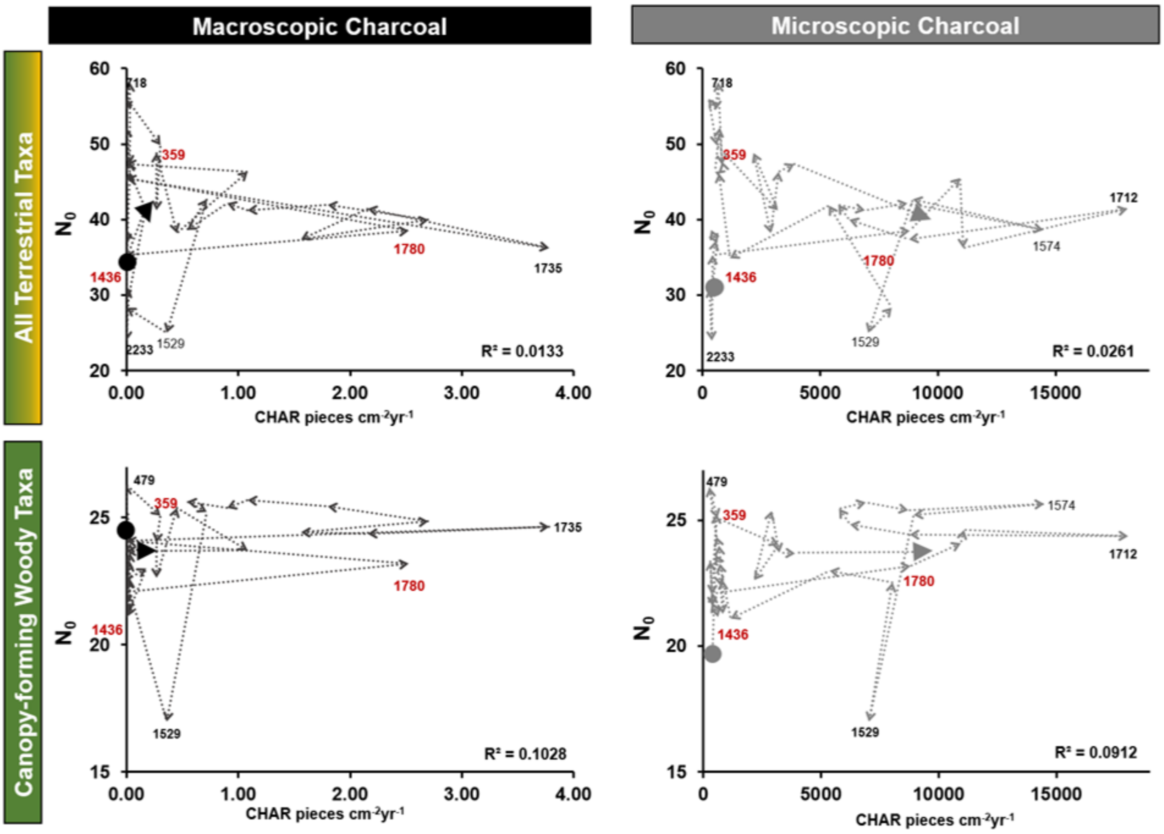

Figure 5: A relationship between plant diversity and anthropogenic fires in the Western Ghats agroforestry landscape. The pollen richness (N_0) values for all terrestrial taxa and canopy-forming woody taxa are plotted against macro- and micro-CHAR values (pieces $cm^{-2}yr^{-1}$) and the points are connected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

4. Discussion

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

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

We find a strong correlation between plant diversity and the canopy cover in the Western Ghats: higher the canopy cover, higher the number of taxa in the landscape (Figs. 3a-b and 6). In human-influenced tropical landscapes, high canopy cover would mean less fragmented landscape (Chazdon, 2003). Thus, the overall sustainability of plant diversity in this social-ecological system does seem to be closely linked with the extent of canopy cover. The changes in canopy cover have little effect on the diversity of canopy-forming woody taxa, which has remained steady over the course of past 4000 years (Figs. 3-4). Thus, high plant diversity in the Western Ghats agroforestry landscape is associated with the increased variety (and abundance) of herbaceous taxa i.e. understorey vegetation (Figs. 3a-b). Tree cover in the landscape is capable of reducing the severity of microclimatic changes including higher temperatures, increased wind speed, lower humidity, and lower soil moisture (Freidenburg, 1998; Kapos et al., 1997). As a result, there may be less edge-related disturbance and more habitat available for forest-dwelling understorey taxa (Bhagwat et al., 2005b; Muthuramkumar et al., 2006). The overall congruence between the extent of the herbaceous understorey and canopy cover in the Western Ghats (Fig. 3a) is indicative of the above ecological processes, thereby highlighting the significance of tree cover in sustaining plant diversity in tropical social-ecological systems.

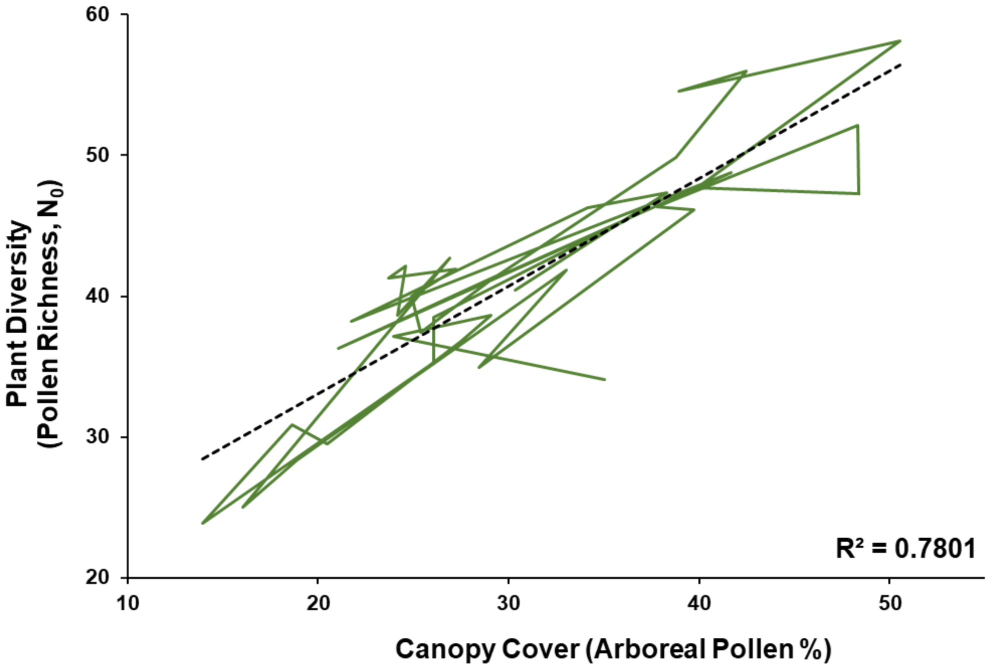

Figure 6: A relationship between plant diversity (based on pollen richness, N_0) and the canopy cover (Arboreal Pollen (AP) %) in the Western Ghats agroforestry landscape. The coefficient of determination (R^2) shows that the strength of association is high.

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

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

Overall, the loss in plant diversity, especially that of woody taxa, *c.* 1550 yr BP would have had serious implications for ecosystem services. In this context, the reduction in fires *c.* 1450 yr BP onwards and subsequent substantial upsurge in both woody taxa as well as overall plant diversity over the next 850 years is interesting (Figs. 3c-e). Moreover, during this period, several habitat-specialist trees also found their way back after long hiatuses (e.g. *Dipterocarpus*, *Myristica*) while some made their first appearance (e.g. *Dichapetalum*, *Poeciloneuron*) in this Western Ghats agroforestry sequence, indicating a post-disturbance transition towards a closed canopy evergreen forest (Figs. 2-3a). Interestingly, temporal β-diversity remained high until 1000 yr BP, *c.* 400 years after the end of the first fire period. This may suggest a long vegetation recovery time or that other factors (e.g. land use) had been critical in forest transformation. Overall, the increased plant diversity and canopy cover during the no-fire period (1400-400 yr BP) are more or less coterminous with organised slash-and-burn agriculture, intensification of arboriculture, and the onset of agroforestry during the warm-wet Medieval Warm Period (Fig. 3; Asouti and Fuller, 2008; Kathayat et al., 2017). A collective strategy for curtailing the use of fires (e.g., infrequent, very localised burns) and planting trees and shrubs on productive agricultural land could have played an important role in invigorating plant diversity in the region (Figs. 3 and 5). Such large-scale changes in land use may be achievable only due to paradigm shifts in local communities (e.g. Luoga et al., 2005; Dalle et al., 2006) i.e. changes in their attitude towards forests in recognising their value as a prime resource and provider of ecosystem services (Bhagwat et al., 2014). Appreciating the importance of forests, native trees, and their ability to foster biodiversity in connection with ecosystem services (Ellison et al., 2017) could have been a timely comprehension for predominantly agro-pastoral societies in the face of changing climate (i.e. the Medieval Warm Period). The subsequent reduction of canopy cover and loss of plant diversity over the course of Vijayanagara Empire (Fig. 3), however, could indicate deleterious impacts of intensified urbanism and consequent resource pressures on the Western Ghats forests (Morrison, 2013).

Lastly, the return of fires *c.* 400 yr BP is in concurrence with the emergence of sacred forest groves in the Kodagu region (Fig. 3; Bhagwat et al., 2014). Although created as dedicated places for worship, the formation of sacred forest patches could have led to unintentional protection and conservation of native trees (see the highest extent (16%) of habitat-specialist trees in Fig. 2; Bhagwat and Rutte, 2006). In maintaining sacred forest groves, a strict demarcation of forested and agricultural land parcels was implemented by the local dynasty and indigenous communities living under its rule (Belliappa, 2008), which could have effectively resulted into increased canopy cover in the region (Fig. 2). Thus, more coherent social-ecological systems in the Western Ghats can be attributed to the communities actively managing the landscape through a moderated use of fires and through maintenance as well as restoration of trees (Nogué et al., 2018), making positive influences on plant diversity during the Little Ice Age-induced aridity.

The British occupation of the Western Ghats over the past 150 years established commercial agroforestry as well as state forestry, setting the new tone for forestry operations and overall landscape management to date (Chandran, 1997). During this period, forest working plans, essentially modelled after European forestry systems, were adopted extensively in the Western Ghats (Rangarajan, 1996; Ribbentrop, 1900); forest management was centralised around the production of large timber volumes and generation of cash revenue from forest resources (Guha, 1983; Rajan, 1998). The overall colonial view of forests as a commodity resulted in complete banning of the slash-and-burn practice, which came in direct conflict with traditional forest management practices (Gadgil and Guha, 1993). Under such completely altered landscape management strategy, the Kodagu region experienced the establishment of commercial coffee estates *c.* 100 yr BP (1854 CE; Ambinakudige and Choi, 2009). Records indicate that when coffee was introduced, growers substantially cleared the forest to plant coffee but when coffee plants could not survive heavy monsoon rains, shade grown coffee became the cultivation practice in the area (Ambinakudige and Sathish, 2009). Both the phases of reduction and revival of the canopy cover and that of plant diversity are visible in the Western Ghats agroforestry sequence, so is the gradual rise in vegetation transformation (Figs. 3a-c). Despite the banning of slash-and-burn practice, fires continued to occur in the Western Ghats landscape, perhaps as a sign of resistance from indigenous communities to ‘formal’ forest management (Thekaekara et al., 2017). The overall degree of burning in this fire period, however, has been much lower than that of during the previous fire period (1800-1400 yr BP; Figs. 3d-e). From a historic perspective, the present-day plant diversity in the Western Ghats agroforestry landscape falls within the range of historical variability: while the present-day plant diversity values are slightly lower than those in the previous fire period, they are higher in comparison with their oldest (no-fire) counterparts (see Figs. 3 and 5). In other words, shade grown coffee cultivation in this part of Western Ghats somewhat reduced the overall plant diversity in merely 100 years (Fig. 3). However, with its ability to increase canopy cover through deliberate maintenance of trees, this cash-crop intensification also paved ways to revive plant diversity in the future. Today’s landscape under shade-grown coffee cultivation (over 60% of the landscape) where native shade trees constitute a major share of the evergreen forest canopies (Fig. 2), offers avenues for fostering biodiversity in the Western Ghats.

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

4.3.1 Importance of conservation beyond forest reserves

Alongside other long-term, pollen-based diversity studies in the tropics (e.g., Weng et al., 2006; Figueroa-Rangel et al., 2012; Palazzesi et al., 2014; Rodríguez-Zorro et al., 2018), this record echoes the unique ecological character of the tropics at large: the tree-covered landscape matrix is the most important determinant of sustaining biodiversity in the tropics. From a conservation point of view, our results further underline the need for maintaining trees in human-influenced tropical landscapes. While forest reserves in the tropics are strictly protected for biodiversity conservation, such areas might fall short in fulfilling their purpose without conservation management in the landscapes surrounding them (DeFries et al., 2010; Karanth and DeFries, 2010). Tree management in tropical landscapes under mounting anthropogenic pressures is quite challenging, calling for pragmatic solutions that support both biodiversity and people. As envisaged in India’s National Agroforestry Policy (Chavan et al., 2015), increasing area under agroforestry would be one of the most practical ways to do so – its potential in providing habitats outside formally protected land, connecting nature reserves, and alleviating resource-use pressure on conservation areas is already substantiated (Bhagwat et al., 2008; Schroth et al., 2004). Interestingly, positive canopy cover-biodiversity correlation is already visible in the modern-day coffee-dominated agroforestry landscapes in the Western Ghats (Kushalappa et al., 2019) and in other kinds of tropical agroforestry systems elsewhere (Tscharntke et al., 2011; Acabado and Martin, 2018; Ticktin et al., 2018), providing region-specific analogues for wider implementation.

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

4.3.2 Towards effective fire management

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

5. Conclusions

The synergistic impacts of anthropogenic fires and enhanced aridity on plant diversity in one of world's ancient social-ecological systems point out the non-linear relationship between plant diversity and human-induced fires. While there are examples of reduced plant diversity due to consistent fire coupled with enhanced aridity, our work also brings positive narratives where the limited, localised use of fires could have promoted the revival of plant diversity in the Western Ghats. Despite apparent changes in fires, aridity, and land use, the present-day plant diversity in the Western Ghats agroforestry landscape falls within the range of historical variability. Interestingly, the diversity of the canopy-forming woody taxa in this record remains almost constant over the course of past 4000 years and the variations in plant diversity in this tropical landscape are largely constituted by changes in herbaceous understorey. Furthermore, in accordance with other tropical records, our data demonstrate that the canopy cover is the most crucial determinant of sustaining plant diversity in a tropical landscape. Thus, the tree-covered matrix, even if fragmented, is one key landscape feature that needs to be conserved because of its role in providing refugia for important elements of tropical biodiversity (Bhagwat et al., 2012). Therefore, biodiversity conservation in the tropics needs to go beyond reserves; strictly protected areas might be inadequate to fulfil their purpose without conservation management in the landscapes surrounding them (Karanth and DeFries, 2010). Under mounting anthropogenic pressures, tree management in the tropical social-ecological systems calls for pragmatic solutions that support both ecological and social components of the landscape. Through the use of palaeoecological data from the Western Ghats, we show that people can play an active role in forest conservation and in sustaining plant diversity through reduced biomass burning and intentional woodland management. Thus, we argue that for the success of ecological management in this (and other) human-influenced tropical regions, it is important to recognise that people are part of the landscape. Conservation-restoration efforts for sustaining biodiversity in the face of future monsoon variability can succeed only if they are planned in tandem with careful, evidence-based incorporation of traditional land management practices. Our work demonstrates that ancient tropical agroforestry systems form a good practice example of such collaborative efforts and have the potential to benefit both biodiversity and people.

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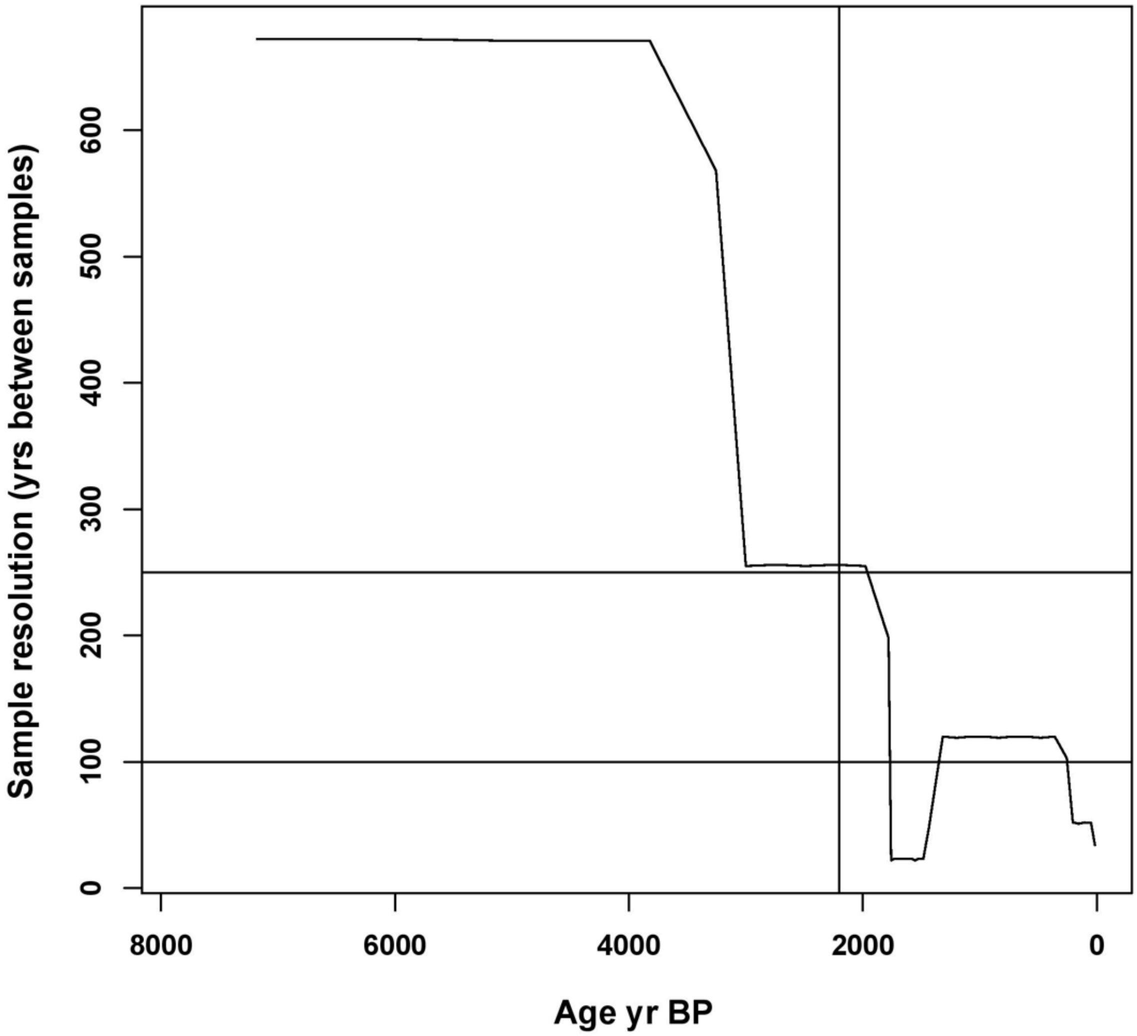

Supplementary Figure 1: Variation in the sample resolution across the Agroforest-1 sequence informing two interpolation-window widths of 260 and 150 years for calculating temporal β-diversity i.e. change in vegetation composition over time.