Exploring the ecological history of a tropical agroforestry landscape using fossil pollen and charcoal analysis from four sites in Western Ghats, India.

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Abstract

Contrary to expectations, some human modified landscapes are considered to sustain both human activities and biodiversity over the long-term. Agroforestry systems are among these landscapes where crops are planted under native shade trees. In this context, ancient agroforestry systems can provide insight into how farmers managed the landscape over time. Such insight can help to quantify the extent to which tropical forests (especially habitat-specialist trees) are responding to local and landscape level management. Here, we extracted fossil pollen (indicator of past vegetation changes) and macroscopic charcoal (indicator of biomass burning) from four forest hollows' sedimentary sequences in an ancient agroforestry system in Western Ghats, India. We used a mixed-modelling approach and a Principal Components Analysis (PCA) to determine past trajectories of forest change and species composition dynamics for the last 900 years. In addition, we reconstructed the long-term forest canopy dynamics and examined the persistence of habitat-specialist trees over time. Our results show that the four sites diverged to a surprising degree in both taxa composition and dynamics. However, despite these differences, forest has persisted over 900 years under agricultural activities within agroforestry systems. This long-term analysis highlights the importance of different land-use legacies as a framework to increase the effectiveness of management across tropical agricultural lands.

Keywords: agroforestry, charcoal, ecological history, fossil pollen, India, mixed-modelling, tropical forest.

Introduction

In many tropical countries, agroforestry (i.e. the practice of planting crops under shade trees) is an important strategy for forest management (McNeely & Schroth, 2006; Bhagwat and others 2008). However, there are still significant knowledge gaps regarding the ability of agroforestry systems to maintain biodiversity across space and time (Foster and others 2003; Ranganathan and others 2008; Bhagwat and others 2008, 2012). Especially, given that recent results suggest that tropical forest systems seem to be recovering faster following larger infrequent events such as cyclones and earthquakes than following small-scale human-induced impacts such as burning (Cole and others 2014). These findings are particularly relevant in the old tropics where agricultural activities are thought to have started approximately 11000 years ago and potentially leaving a historical legacy of past human impacts (e.g. Pimm and Raven 2000; Ellis and others 2010).

Palaeoecological research has provided fundamental insights on the impacts of land-use change on forest ecosystems (Dearing and other 2012; Willis and Birks 2006). For example, studies have suggested that after the introduction of a new land-cover type there is often an increase in canopy opening, a decline in tree abundance, introduction of new taxa, community turnover, and/or local extinctions (e.g. Denham and others 2003; de Nascimento and others 2015). However, not all palaeoecological records reported large changes in the composition of forest taxa. For example, there is evidence that retention of tree cover under low intensity land-use change can retain forests in human-modified landscapes over hundreds of years (Ranganathan and others 2008).

In addition, palaeoecological records have also provided information on the replacement of certain tree taxa in favour of trees important for: timber production (e.g. New Forest, UK), ornamentation (e.g. Poor Knights islands, New Zealand), and for daily household needs like the "forest gardens" of the Maya peoples (e.g. Mesoamerican forest, Belize) (Grant and Edwards 2008; Ewers and other 2013; Wilmshurst and others 2014). Hence, the ability of forest cover to persist over long-time scales when human activities have been dominant over hundreds of years deserves more attention. In particular, it is important to understand whether policies that encourage the development of agroforestry systems, such as shade-grown coffee plantations, are good strategies to maintain biodiversity across space and time (Gordon and others 2006; Bhagwat and other 2005b; Garcia and others 2010; Tscharntke and other 2011).

Many ideas about agroforestry systems as refuges of biodiversity have been discussed in the literature (e.g. Bhagwat and others (2008). For example, agroforests are often very small in size (<10 ha) and resemble forest patches and they have drawn attention from the conservationists as reservoirs of biodiversity (FAO & JRC, 2012). It has also been documented that the effective conservation of agroforests is assisting to protect important habitats where fauna could act as dispersal agents and ensure seed rain, and in turn, forest regeneration (Ricketts and others 2008). However, degradation of these forest patches has also been reported (e.g. Laurance and others 2007, 2011). For example, by excessive removal of tree cover and repeated use of fire, the forest structure, function, and dynamics might be altered beyond the capacity of these agroforests to fully recover. There are therefore many questions pertaining to the sustainability of agroforestry techniques to maintain biodiversity over time and understanding the relationship between agroforestry, cultural landscapes, and long-term biodiversity remains an important knowledge gap.

In order to address this knowledge gap we reconstructed the long-term vegetation dynamics of tree-covered landscapes in the Kodagu region in the Western Ghats of India. This is a region characterised by a mixture of extensive agroforestry plantations and forest patches. Shade-grown coffee plantations occupy much of the landscape but this region also has a high density of sacred groves. These sacred groves are an example of community-based conservation and they serve as refugia for many forest-dwelling species over the timescales of hundreds of years (Bhagwat and others 2014; Nogué and others 2016). The sacred groves are surrounded by coffee plantations where coffee is planted under shade trees (Bhagwat and others 2008; Garcia and others 2010; Tscharntke and others 2011). Therefore, it represents an excellent region to test agroforestry systems dynamics over multi-centennial time scales and its ability to sustain biodiversity in the landscape over time. We used a palaeoecological approach to analyse four sites in this tree-covered landscape to obtain information about past land-use change, canopy dynamics, composition of taxa, and trajectories of forest change. To do this we extracted fossil pollen (indicator of past vegetation changes) and macroscopic charcoal (indicator of biomass burning) from four forest hollows' sedimentary sequences covering the last 900 years. We have two specific objectives to determine:

1) To examine the rate of temporal change in the composition of plant taxa in ancient agroforestry systems, we reconstructed trajectories of vegetation change to test whether forest taxa have been sustained in the presence of agricultural activities over the past 900 years.

2) To reconstruct patterns of structural change in forest over time we used two measures obtained from the palaeoecological data: i) canopy dynamics to measure canopy closure over time, and ii) long-term presence of habitat-specialist evergreen rainforest trees (particularly long-lived trees) that are indicators of low disturbance (Lowmand and Schowalter 2007).

Methods

Site location

Four sedimentary sequences were collected from small swamps at an altitude of 900 m a.s.l. within agroforestry landscapes on the eastern side of the Kodagu district, Karnataka, India (Figure 1, Table S1). We collected sedimentary sequences from two forest patches also known as sacred groves (sacred grove-1, and -2) and two from agroforests (agroforest-1 and -2). More information about the four study sites is included in Table S1. We selected these sites in an area of 30x40 km^2 with a minimum distance between them of 5.3 km and a maximum of 31km. Given their close proximity and based on previous studies, we made the assumption that the four forest sites have been subjected to the same climatic conditions at least over the last 1000 years (Gupta and others 2006).

Determining age chronology of section: Radiocarbon and Lead 210 dating

A total of eleven samples were radiocarbon dated to determine the age-depth relationships for each sedimentary sequence (Figure S1). More detail can be found in Bhagwat and others (2012, 2014) and in Table S4. In addition, the sections comprising the uppermost 8 cm of each sequence were dated using ^{210}Pb at the University of Oxford (School of Geography and Environment) and the sediment surfaces were given the age AD 2005, corresponding to the collection date (Table S4). Radiocarbon ages where calibrated using the IntCal13 dataset (Reimer and others 2013) to years before present (cal yr BP). Age-depth relationships where established using Clam (Blaauw 2010).

Reconstructing vegetation and fire dynamics over time: Fossil pollen, spores, and charcoal analysis

Fossil pollen was extracted from samples taken at 4-cm intervals from each of the four sedimentary sequences following standard methodologies (Bennett & Willis, 2002). Relative abundance of pollen taxa (%) was calculated as a proportion of the individual sum divided by the total land pollen sum (ΣTLP) (Figure S2, S3). Pollen influx (grains/cm^2/year) was calculated for each taxon in order to demonstrate the relationship between pollen counts and past vegetation abundance taking into account variations in sedimentation rates (more details in Figure S2). We grouped the fossil taxa into four plant functional groups: evergreen forest (including e.g. trees, shrubs, and lianas), Poaceae and Cyperaceae (hereinafter referred to as grasslands), herbaceous (understory taxa, excluding Poaceae and Cyperaceae), and crop taxa (such as e.g. *Bentinckia, Coriandrium, Tamarindus*). We separated grasses into two different functional groups to differentiate grassland vegetation (Caratini and others, 1994) from grasses from the forest understory. Full list of taxa is provided in supplementary information.

To trace the variation in biomass burning through time, we estimated the rate of charcoal accumulation (i.e. the ‘charcoal influx’, denoted CHAR, charcoal particles/cm^3/year), which accounts for changes in sedimentation rate and sediment compaction down-core (Whitlock and Larsen 2001). Contiguous sediment samples were processed and analysed following Finsinger and others (2014). Because it is highly likely that current fire-return intervals in the Western Ghats are significantly smaller (< 15 years; Kodandapani and others 2004) than the temporal resolution of our charcoal records, the variation in charcoal influx values we aimed to capture were those related to fire frequency and amount of biomass burned (Colombaroli and others 2014).

Patterns of forest structural changes

Landscape changes are difficult to define and measure and present a significant challenge to test using palaeoecological data. In our work we therefore approached their measurement using two indices to help tracking over time changes in habitat-specialist trees indicators of low disturbance, and canopy closure.

First, to analyse the long-term changes of local habitat-specialist trees we used the list of species that were surveyed during the period 1999-2001 on the study sites (Bhagwat and others 2005a,b). According to these surveys and the following published literature we selected habitat-specialist trees indicators of sites with low disturbance (Table 1) (Daniels and others 1995; Ayyappan and Parthasarathy 1999; Muthuramkumar and others 2006). We then grouped the habitat-specialist tree species into 24 types where their pollen is identifiable to genus level: *Aglaia, Artocarpus, Calophyllum, Cullenia, Dichapetalum, Dimocarpus, Dimorphocalyx, Dipterocarpus, Drypetes, Dysoxylon, Elaeocarpus, Holigarna, Hopea, Knema, Litsea, Mesua, Murraya, Myristica, Pallaquium, Poeciloneuron, Reinwardtiodendron, Strombosia, Symplocos,* and *Syzygium* (Table 1). Within the tree genera such *Artocarpus*, while *Artocarpus heterophyllus* is commonly cultivated around human settlements for its edible fruits, the species that is commonly found in tree-covered landscapes are *Artocarpus hirsuta.* Although it is not possible to distinguish between the pollen of different species of *Artocarpus* under the light microscope, previous tree surveys from the study sites (Bhagwat and others 2005a,b) provide a robust basis for classifying *Artocarpus* as habitat-specialist tree taxa.

Second, to determine the degree of canopy closure, we calculated the relative proportion of arboreal pollen (AP) to nonarboreal pollen (NAP). This ratio has been demonstrated a reasonable index to assess the degree of canopy closure/opening and therefore canopy cover (Svenning 2002).

Forest trajectories of change

To analyse trajectories of forest change, we analysed evergreen forest change through time using generalized mixed models (GAMM). We chose this approach to extract the main trend through time. We used evergreen forest influx as a dependent variable while: age, charcoal influx, grasslands (Poaceae and Cyperaceae), herbaceous taxa, crop taxa influx, and the ratio between arboreal and non-arboreal pollen influx (AP:NAP ratio) were used as independent variables. To incorporate data from the four sites into the model we averaged the pollen and charcoal influx within 50-year-bins to make the data comparable. Transformations were applied when necessary to meet the normality assumption. We performed a linear regression, and given that we detected non-linearity of the residuals against time we used a GAMM where age was treated as a smooth term and site as a random term. Given the heterogeneity of variance found in the residuals we incorporated into the model a variance structure per current land management type (sacred groves *vs* agroforests). The selection of the most adequate variance structure was based on its best performance using AIC values (Table S2). No temporal autocorrelation was found in the data. Models were performed in R using the mgcv package (Table S2).

Changes in trajectories of composition of taxa though time were analysed performing a Principal Components Analysis (PCA) in CANOCO 4.5 (ter Braak 1986). Pollen percentages were square-root-transformed and centred by taxa (functional groups). We performed ordination biplots showing the trajectory of change (series of samples) where the initial composition is represented by a circle and the present composition represented by an arrow.

Results

Pollen community composition

Our results indicated that agroforest-1 displayed a decrease in forest influx between 900 years ago until around 400 (<10000 grains/cm2/year) when a slight recovery can be observed towards the present time (maxima of 25000 grains/cm^2/year). On the contrary, the influx of tropical forest pollen taxa showed an increase at 800 years in the agroforest-2 site (from 200 to 25000 grains/cm^2/year) while the two sacred sites displayed low influx until 300 years ago when pollen influx increased (from 100 to 30000 grains/cm^2/year). In addition, pollen taxa indicative of agricultural activities (e.g. *Coffea*, *Plantago*) appeared in three sites (agroforests and sacred grove-1) (Figure 1, Figure S3). Agroforest-1 is the only site where cultivated species were present continuously, albeit at low abundance, over the last 900 years. At agroforest-2 and sacred grove-1 the abundance of cultivated pollen peaked twice: about 600 years ago and during the past 1-2 centuries. At the sacred grove-2 there was no presence of cultivated taxa. Grassland pollen (Poaceae and Cyperaceae) was abundant at both agroforests. Other herbaceous pollen taxa displayed a low abundance at three sites (agroforest-1, and sacred groves) and an increasing trend in agroforest-2.

Forest structural change

The relative proportion of arboreal pollen (AP) to non-arboreal pollen (NAP) known as the index of canopy closure showed a shift from an open landscape to a forested habitat in sacred groves during the past 300 years (Figure 2). In contrast, both agroforests experienced either no major canopy change (agroforest-1) or only a slight canopy closing before 600 years ago (agroforest-2).

Pollen influx of habitat-specialists trees, indicative of sites with low disturbance, showed a steep increase in both sacred groves at around 300-400 years ago (Table 1, Figure 2). In agroforests, abundance of these pollen taxa was either high for the last 700 years (agroforest-2) or low throughout the record (agroforest-1).

Fire history

Charcoal influx records did not show a general common pattern suggesting that periods of high biomass burning occurred at different times (Figure 1). For example, agroforest-1 displayed high biomass burning during the last 400 years (0.25 grains/cm^2/year) while agroforest-2 displayed two peaks at 800 and 450 cal. years BP (1 charcoal /cm^2/year) and another peak recently in the last 100-50 years (0.60 charcoal/cm^2/year). Charcoal influx values in sacred groves were overall lower than in agroforests. The sacred grove-1 remained virtually protected from burning at least until 50 years ago when cultivated pollen taxa first appeared, while sacred grove-2 burned mostly when the canopy was open, i.e. before about 700 years ago (0.25 charcoal/cm^2/year).

Forest trajectories of change

The additive model showed that forest taxa experienced two contrasting types of trajectories of change between sites over the last 900 years: significant linear and non-linear relationship with time (Figure 3a and Table 2). First, both agroforests showed non-linear trends between forest influx and time. In agroforest-1 a U-shaped pattern was observed with a decrease at around 400 years ago and then a recovery, while in agroforest-2 we observed a hump-shaped pattern with an increase around 400 years ago and then a decline (Figure 3a). On the contrary, sacred groves showed a positive linear relationship between time and the abundance of forest pollen influx. This indicates an increasing trend of forest through present times. Only sacred grove-2 showed a statistically significant positive linear relationship. In addition, we found a significant negative relationship between charcoal and evergreen forest pollen influx, suggesting that a decrease in biomass burning leads to an increase of evergreen forest (Table 2). Finally, we also found a positive relationship between the pollen influx of forest and other functional groups (Table 2).

Second, the analysis of change in taxa composition using the ordination PCA biplot showed different patterns for each site (Figure 3b). Axis 1 represents a gradient from Poaceae and Cyperaceae grasslands on the left (correlation coefficient = -0.9976) to forest taxa on the right (correlation coefficient = 0.9846), while Axis 2 has a high positive correlation with herbaceous taxa (correlation coefficient = 0.9764). Main results showed that while agroforest-1 remained mainly constant over time, agroforest-2 revealed a highly dynamic trajectory, moving from grasslands to evergreen forest and herbaceous taxa over this time. The two current sacred grove forest patches displayed a clear gradual change from grassland towards evergreen taxa.

Discussion

1. Land management and patterns of forest structural change

The current rate of deforestation in tropical regions constitutes a major global biodiversity crisis (Lamb and others, 2005). Here, we have analysed 900 years of ecological history in one of the most densely populated biodiversity hotspots where the expansion of conservation areas is limited by the competing pressures from other more productive land uses (Myers and others, 2000, Cincotta and others 2000; Jha and others 2000; Newbold and others, 2015).

Studies dealing with the quantification of human impacts over the recent past show that between 1920 and 1990 the Western Ghats experienced 40% decline in forest cover and 83% reduction in average of patch area (Menon and Bawa 1997). In addition, a study analysing the spatial data on fire occurrence between 1989 and 2002 suggests that the increasing occurrence of fires in the Western Ghats poses a severe and persistent conservation threat to forests both within and outside protected areas (e.g. Kodandapani and others 2004). In this context, it has been suggested that agroforestry systems have recently emerged as one of the most promising approaches to reducing deforestation in the tropics while enhancing rural livelihoods (Bhagwat and others 2008).

Our charcoal and pollen analysis suggests that during the last 900 years fire was commonly used in this region (Figure 1). For example, we found the irregular occurrence of pollen taxa indicator of agricultural activities such as *Plantago, Tamarindus*, and *Coffea* together with the presence of charcoal. We interpret the variations of charcoal influx as an indicator of burning as part of agricultural activities. However, a relevant result is that even when the landscape was showing strong signs of mixed shifting cultivation, trees were still present in the landscape but in low abundance (Figs. 1 and 2). To further analyse the implications of these results and to provide more detail on forest structural change we selected two indexes: 1) the closeness of the forest canopy (AP: NAP ratio), and 2) the abundance of habitat-specialists trees from the genera e.g. *Dipterocarpus*, *Diospyros*, *Hopea*, and *Palaquium* (Table 1) which are considered good indicators of sites with low disturbance and are a priority in the conservation planning of the region (Muthuramkumar and others 2006). Our results showed that 900 years ago the landscape was open with low canopy closure index values (<1 in all four sites, Figure 2), and 2) low abundance of habitat-specialists trees (<2000 grains/cm^2 year). However, the source of the tree pollen found during this period might be attributed to both potential nearby, large forest masses beyond the agricultural lands and from the smaller and fragmented forest patches within the agricultural landscape. A recent phytolith analysis (i.e. the opaline silica bodies from plant tissues) carried out in two of the study sites (agroforest-1 and sacred grove-1), is useful in the interpretation of this result (Nogué and others 2016). Phytoliths are known to be an excellent proxy to investigate the presence of vegetation, especially grasses, at a local scale (Barboni and others, 2010). This paper showed that the local presence of tree taxa concur (with a slight temporal delay) with the tree pollen time-series (Bhagwat and others, 2012; Bhagwat and others 2014). Such concurrence between these two different palaeoecological proxies makes us confident that the pollen signal we are recovering from the sedimentary cores is from the forest patch remaining in the agricultural land.

The period of low presence of trees in the landscape lasted approximately 250 years when there was an increase of both forest canopy and habitat-specialist trees. Finally, we found that in sacred groves habitat-specialist trees displayed an increasing trend during the last 200 years, in parallel to canopy closure index. These results suggest that the current landscape configuration of forest patches (some of them sacred groves), and paddy cultivation fields, is truly ancient (e.g. 400 years) and that farmers have actively managed the landscape by reducing but also by maintaining the number of trees in the landscape. One example is the establishment of sacred groves that are known to be protecting trees dedicated to the worship (Bhagwat and Rutte 2006). The long-term history of sacred groves could be indicating that farmers may have protected habitat-specialist trees from fires and other major disturbances associated with the change of land-use from forest to agriculture (Chazdon 2003; Bhagwat and others 2014). In addition, an examination of socio-cultural drivers of forest recovery in the past have suggested that forest recovery may have taken place due to the values attached to tree-covered landscapes (particularly ecosystem service provision from forests; Bhagwat et al. 2014). The high tree cover in the present-day landscape (over 60% of the landscape is under shade-grown coffee cultivation; see Bhagwat et al. 2005 a,b) is also indicative of the value attached to trees in shade-grown coffee cultivation today.

2. Temporal change in taxa composition in ancient agroforestry systems

This palaeoecological study shows that the landscape in this region are highly dynamic displaying strongly divergent trends at local scale in terms of taxa composition and trajectories of forest change (Figures 1-3). By using the smooth term of the GAMM we were able to extract the main trend of the trajectories of change and we found both non-linear trajectories (agroforests) and linear trajectories (sacred groves) of forest change over time. For example, the agroforest-1 site (with a non-linear trajectory) has remained as a mixed shifting cultivation fallow with small changes in taxa composition during the whole time-period (excluding the last 10 years), presumably due to the influence of frequent burning activities (Figure 1, 3). In contrast, the sacred grove-2 site (with a linear trajectory), displays a gradual change from grassland towards evergreen forest with the highest increase occurring during the last 400 years (Figure 1, 3).

Changes in taxa composition also support the trajectories of forest change (Figure 2b). With the ordination PCA biplot we show that while vegetation composition of agroforest-1 remains mainly constant over time, composition of agroforest-2 reveals a highly dynamic trajectory of change, moving from Poaceae and Cyperaceae grasses (grasslands) to evergreen forest and other herbaceous taxa over time. On the contrary, the two current sacred groves display a clear gradual change from grassland towards evergreen taxa. As such, high dynamism and divergence are likely to be common features of tropical agroforestry systems where human intervention could promote both linear and non-linear trajectories of forest change i.e. by actively removing and/or maintaining trees. Although further progress is required to determine a consistent global trend across tropical agroforestry systems, our results suggest that the divergent trajectories of change might have promoted the maintenance of biodiversity within the agroforestry at the landscape (Penne and others 2010; Ewers and others 2013).

A limitation encountered in this study is that although we found a negative relation between forest and charcoal which shows the negative effect of burning related to agricultural activities on forest (Table 2), our analysis does not capture other land-clearing mechanisms. For example, in sacred grove-1 we found grassland dominance in the absence of fire, thus making the role of human protection less obvious. An alternative hypothesis such as logging and protection of forest patches could explain the initial grassland dominance followed by tree dominance in sacred groves. However, this type of data is difficult to obtain from the long-term records. What we can confirm however is a strong evidence for the historical maintenance of both agroforests and sacred groves (and potentially other forest patches) for 900 years in this region despite widespread use of fire by ancient farmers (Figure 1).

3. Conclusions

We have shown that humans might have actively removed but also maintained trees both in agricultural landscapes and in sacred groves in the Western Ghats during the last 900 years and thus the sustainability of its biodiversity. In addition, human activities and disturbances over the last 900 years were insufficient to prevent long-term forest recovery and regeneration, following cessation of cultivation activities and grassland burning. However, the results suggest that natural forest recovery processes may have been aided by fire suppression and protection of nearby evergreen forest patches by humans. Our study showed that the Western Ghats landscape is an appropriate model system to study the historical management of agroforestry lands over time.

Although we cannot draw general conclusions about global historical land use changes of tropical agroforestry landscapes our study does provide an initial glimpse of trajectories of forest change. For example, while providing new evidence on the temporal dynamics of agricultural lands, we have shown that agroforests are responding differently to local disturbances. Finally, studies like this provide frameworks for increasing the effectiveness of forest management in tropical countries (Swetham and others 1999).

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Supporting Information captions

Figure S1: Age-depth model for the four sites

Figure S2: (a,b,c): detailed % pollen diagrams for the four sites

Figure S3: summary % pollen diagram

Table S1: Sites information

Table S2: Details of the additive model

Table S3: taxa included in the study

Table S4: Dating

Figure 1

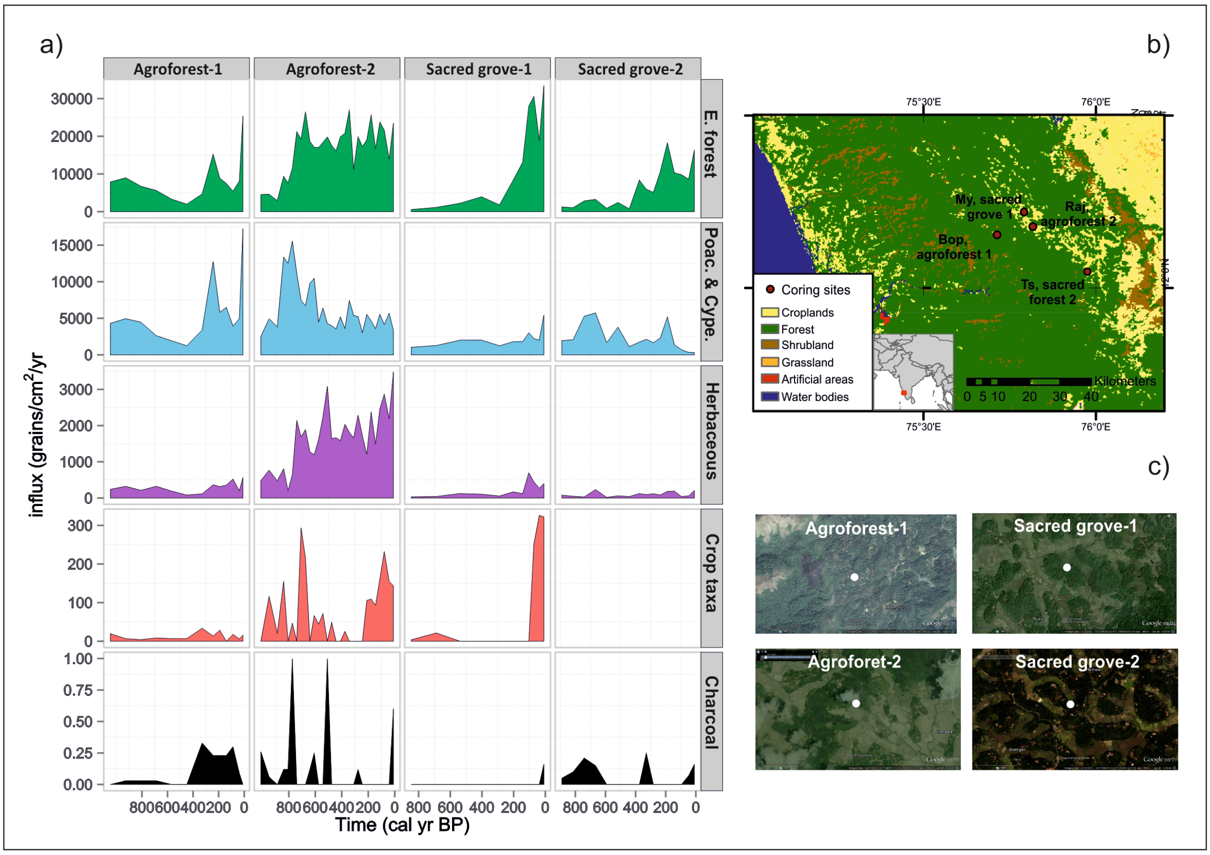
a)
Agroforest-1
Agroforest-2
Sacred grove-1
Sacred grove-2
E. forest
Poac. & Cype.
Herbaceous
Crop taxa
Charcoal
influx (grains/cm^2/yr)
30000
20000
10000
0
15000
10000
5000
3000
2000
1000
300
200
100
1.00
0.75
0.50
0.25
0.00
800 600 400 200 0
Time (cal yr BP)
b)
75°30'E
76°0'E
12°0'N
My, sacred grove 1
Raj, agroforest 2
Bop, agroforest 1
Ts, sacred forest 2
● Coring sites
🟨 Croplands
🟩 Forest
🟫 Shrubland
🟧 Grassland
🟥 Artificial areas
🟦 Water bodies
Kilometers
0 5 10 20 30 40
c)
Agroforest-1
Sacred grove-1
Agroforet-2
Sacred grove-2

Figure 2

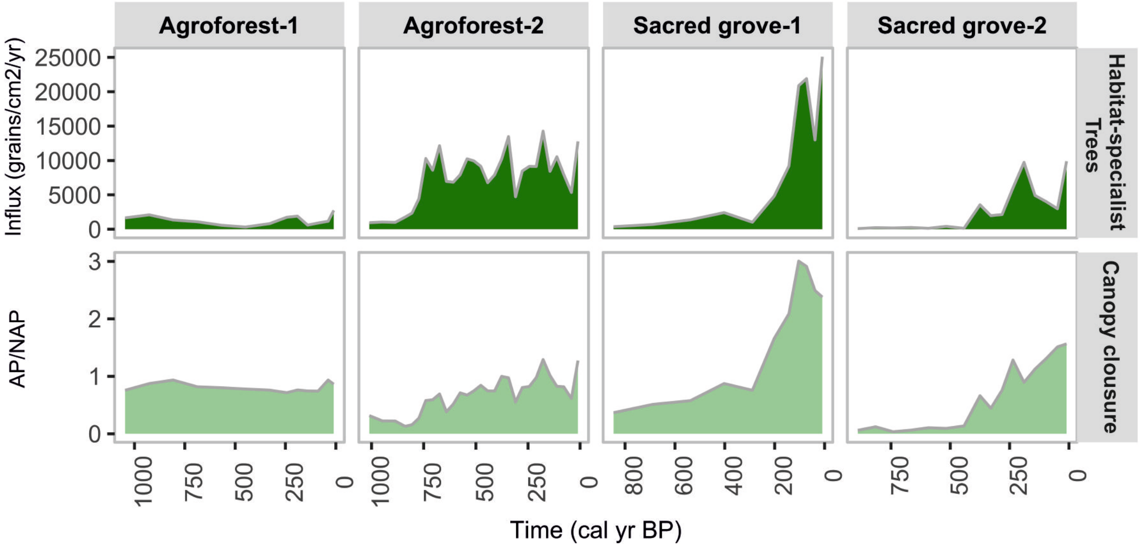
Agroforest-1
Agroforest-2
Sacred grove-1
Sacred grove-2
Influx (grains/cm2/yr)
25000
20000
15000
10000
5000
0
Habitat-specialist Trees
AP/NAP
3
2
1
0
Canopy clousure
1000
750
500
250
0
1000
750
500
250
0
800
600
400
200
0
750
500
250
0
Time (cal yr BP)

Figure 3

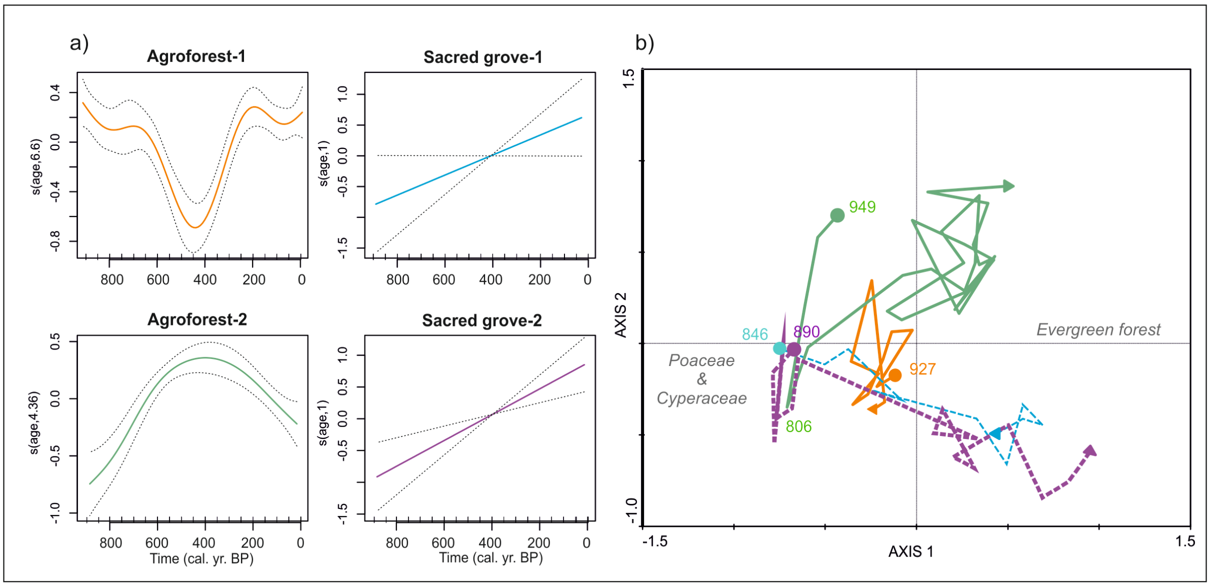
a)
Agroforest-1
s(age,6.6)
0.4
0.0
-0.4
-0.8
800
600
400
200
0
Sacred grove-1
s(age,1)
1.0
0.5
0.0
-0.5
-1.5
Agroforest-2
s(age,4.36)
0.5
0.0
-0.5
-1.0
Time (cal. yr. BP)
Sacred grove-2
s(age,1)
1.0
0.5
0.0
-0.5
-1.5
Time (cal. yr. BP)
b)
1.5
AXIS 2
-1.0
-1.5
AXIS 1
1.5
949
846
890
927
806
Evergreen forest
Poaceae
&
Cyperaceae

Figure 1: a) Changes in Influx of four vegetation types (crop taxa, evergreen forest, Poaceae and Cyperaceae, and other herbaceous). Charcoal influx values represented by particles/cm^2/year. E. forest: Evergreen forest; Poac. and Cype: Poaceae and Cyperaceae (Grassland). b) Location of the four sites: two located in current agroforestry plantations (Agroforest-1 and -2) and two in current sacred grove forest (Sacred grove-1 and -2). c) Google map location of the 4 sites (scale, 1km).

Figure 2: a) Pollen influx of habitat specialist tree taxa corresponding with local pollen taxa indicative of low disturbance at each site (details in Supplementary Information); b) changes in canopy closure index (AP:NAP ratio). For the AP:NAP ratio values closer to 0 represent a very open canopy, values around 1 represent about 50% of open canopy while values above 1 represent greater canopy closure.

Figure 3: a) GAMM model for forest over time showing the different trajectories of change for each site. b) Ordination biplot of the PCA showing the trajectories of change in taxa composition of the two current sacred groves (dashed lines) and the two current agroforests (solid lines). The solid circle represents the initial taxa composition where the date (cal. years BP) is noted. Additionally, the date when the taxa composition of agroforest-2 is similar to that of the sacred groves is also noted. Axis 1 explains 84% of the species composition while Axis 2 explains 12%. Axis 1 represents a gradient from grassland taxa (left) to evergreen forest

Table 1: Habitat-specialist tree species corresponding with local pollen taxa indicative of low disturbance at the four study sites in the Western Ghats ancient tropical landscape (corresponding tree species are based on ecological surveys at the study sites conducted between 1999 and 2001 and reported in Bhagwat et al. 2005a,b as sites Topaij39 (agroforest-1; Pllsge08 (agroforest-2); Hglsge16 (sacred grove-1); Tslsg58 (sacred grove-2)). *Present-day tree inventories suggest that the species of *Artocarpus* cultivated around human settlements (*A. heterophyllus*) for its edible fruit is different to the one more commonly found in tree-covered landscapes (*A. hirsuta*). Although there are taxonomical limitations in pollen analysis, the present-day tree surveys from the study sites provide a robust basis for classifying *Artocarpus* as habitat-specialist tree taxa.

Pollen taxon	**Corresponding tree species**
Aglaia	*Aglaia anamallayana*; *Aglaia jainii*; *Aglaia simplicifolia*
*Artocarpus**	*Artocarpus heterophyllus*; *Artocarpus hirsuta*
Calophyllum	*Calophyllum polyanthum*
Cullenia	*Cullenia exarillata*
Dichapetalum	*Dichapetalum gelonioides*
Dimocarpus	*Dimocarpus longan*
Dimorphocalyx	*Dimorphocalyx lawianus*
Dipterocarpus	*Dipterocarpus indicus*
Drypetes	*Drypetes elata*
Dysoxylon	*Dysoxylum malabaricum*
Elaeocarpus	*Elaeocarpus serratus*; *Elaeocarpus tuberculatus*
Holigarna	*Holigarna arnottiana*; *Holigarna beddomei*; *Holigarna grahamii; Holigarna nigra*
Hopea	*Hopea ponga*
Knema	*Knema attenuata*
Litsea	*Litsea mysorensis*; *Litsea oleoides*; *Litsea stocksii*
Mesua	*Mesua ferrea*
Murraya	*Murraya koenigii*
Myristica	*Myristica dactyloides*
Pallaqium	*Palaquium ellipticum*
Poeciloneuron	*Poeciloneuron indicum*
Reinwardtiodendron	*Reinwardtiodendron anamalaiense*
Strombosia	*Strombosia ceylanica*
Symplocos	*Symplocos macrophylla*
Syzygium	*Syzygium gardnerii*; *Syzygium hemisphericum*; *Syzygium heyneanum*; *Syzygium mundagam*; *Syzygium munronii*; *Syzygium*

	phyllareoides; *Syzygium zeylanicum*

Table 2. Results of the best GAMM model for evergreen forest influx against charcoal influx (Charcoal), Poaceae and Cyperaceae influx, other herbaceous influx, crop taxa, and canopy clousure index (AP:NAP ratio) as fixed variables and time (50-year bin) per site as smooth terms.

Parametric coefficients:				
	Estimate	Std.Error	t value	Pr(>|t|)
(Intercept)	7.56E+00	2.42E-01	31.275	<2e-16
Charcoal	-3.01E-01	1.20E-01	-2.507	0.01697
Poaceae and Cyperacea	9.91E-05	1.03E-05	9.649	2.12E-11
Herbaceous taxa	2.22E-04	6.76E-05	3.28	0.002351
Crop taxa	2.23E-03	5.97E-04	3.735	0.000665
AP:NAP ratio	7.32E-01	1.67E-01	4.391	9.91E-05
Approximate significance of smooth terms (s(age):site):				
	edf	Ref.df	F	p-value
Agoforest -1	6.602	6.602	9.242	7.30E-07
Sacred site -1	1	1	3.943	0.054803
Agroforest -2	4.356	4.356	16.877	3.61E-09
Sacred site -2	1	1	13.315	0.000817
R-sq.(adj) = 0.707 Scale est. = 0.0079189 n = 54				