



Resilience of an ancient tropical forest landscape to 7500 years of environmental change

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ABSTRACT

There is growing recognition that the fate of the world's terrestrial biodiversity depends on the management of human-dominated tropical forest landscapes. While global environmental change is transforming the ecology of tropical forests, a number of studies have also demonstrated that tropical forests are able to recover following disturbance. But are tropical forests resilient to environmental and anthropogenic disturbances over timescales of centuries or millennia? Here we examine the relationship between vegetation cover and variation in monsoon rainfall, soil erosion, and fire over 7500 years in an ancient tropical landscape in the Western Ghats of India. We collected two overlapping sediment sequences at one study site and analysed them with palaeoecological techniques to reconstruct vegetation cover. Results suggest that climate and land-use changes might have had synergistic effects on this forested landscape, although the relationship between these factors and vegetation cover has varied over time. Results also indicate that the weakening of monsoon around 5750 BP might have caused a threshold event altering this landscape to a low tree-cover state. Although anthropogenic fire has maintained this landscape in low tree cover state from 3500 BP, this degraded tree–grassland mosaic has remained relatively resilient to fluctuations in environmental and anthropogenic factors. Tree taxa present throughout the sequence have lighter seeds than those absent in parts of the sequence, suggesting that dispersal mode might be an important factor in their persistence. Despite maintaining a degraded and fragmented forest mosaic, however, this landscape has supported populations of heavy-seeded trees and a probable refuge to their dispersal agents. We suggest that retaining tree cover on this landscape, even if fragmented, is key to maintaining its ecological resilience to environmental and anthropogenic disturbance.

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1. Introduction

The extent to which human-dominated tropical forests are resilient to environmental and anthropogenic disturbances has been a major point of debate among tropical ecologists (Chazdon, 2003; Peres, 1999; Wright and Muller-Landau, 2006; Laurance, 2007; Lugo, 2009; Tabarelli, 2010). While there is evidence that global environmental change is transforming the ecology of tropical forests (Lewis et al., 2009), there is also a growing number of studies demonstrating that tropical forests are able to recover rapidly following environmental and anthropogenic disturbance (Chazdon, 2003; Ruiz et al., 2005; Phillips et al., 2006; Norden et al., 2009).

However, most of this evidence pertains to timescales of 10–50 years and very little is known about resilience of tropical forests to environmental and anthropogenic disturbance over longer time scales of centuries or millennia (but see Brncic et al., 2009; Virah-Sawmy et al., 2009; Figueroa-Rangel et al., 2010). Such understanding is particularly important because many of the remaining tropical forests are situated within highly human-dominated landscapes, making it necessary to find approaches to balance conservation goals and livelihood needs (Karanth and DeFries, 2010).

A fundamental question with respect to human-dominated tropical landscapes is: How resilient are these to climatic and anthropogenic influences? Resilience is the capacity of an ecosystem to tolerate disturbance without shifting to an alternative state (Holling, 1973; Carpenter et al., 2001; Gunderson, 2000). The literature distinguishes two types of resilience: *Ecological resilience* is the amount of disturbance a system can absorb without changing to another state (Walker, 1995; Holling, 1996). *Engineering resilience* is the return time of the system to equilibrium following

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disturbance (O'Neill et al., 1986; Holling, 1996). The concept of resilience therefore encompasses (a) *resistance*: the magnitude of disturbance that a system can tolerate without causing a change in the system; and (b) *recovery*: the speed of return of a system to its original structure (Côté and Darling, 2010). Here we examine the relationship between environmental and anthropogenic disturbance and vegetation cover in an ancient tropical landscape in order to understand the extent to which it has remained resilient to these changes.

The Western Ghats of India and Sri Lanka is a biodiversity hotspot with one of the highest human population densities recorded (Cincotta et al., 2000). Although the conservation network in the Western Ghats covers nearly 15% of land in 20 National Parks and 68 wildlife sanctuaries (Conservation International, 2012), a high demand for agricultural land has been responsible for fragmentation of forests (Giriraj et al., 2010). In Kodagu district of Karnataka state, the formal network of protected areas consists of three wildlife sanctuaries and one national park and occupies approximately 30% of the landscape. While protected areas provide continuous forest cover, the remaining 60% land is covered in shade-grown coffee plantations and about 10% of the total area is treeless, under land uses such as paddy cultivation (Bhagwat et al., 2005). However, the Western Ghats also have a long history of human occupation and the forests in this region are known to have been fragmented due to agriculture for at least 2000 years (Chandran, 1997; Ranganathan et al., 2008). This ancient human-modified landscape therefore provides an excellent opportunity to examine the relationship between environmental and anthropogenic disturbance and vegetation cover over time scales of centuries and millennia.

Here we ask: To what extent is this ancient landscape resilient to environmental and anthropogenic disturbance? We hypothesise that in a resilient system environmental or anthropogenic disturbance will have a weak or no relationship with vegetation cover and in a non-resilient system vegetation cover will decrease with disturbance (Fig. 1). Consequently a system with high resilience that starts at time T_1 will remain in a similar state at time T_2 and display tolerance to a wider range of disturbance regimes. On the other hand, a system with low resilience that starts at T_1 will return to a different state at time T_2 and display tolerance to a narrower range of disturbance regimes at any time period. With this conceptual framework, we address three questions with regards to an ancient tropical forest landscape in the Western Ghats: (1) What is the relationship of vegetation cover to different environmental and anthropogenic drivers of disturbance? (2) Is the relationship of vegetation cover with these drivers constant through time and at various levels of disturbance? (3) Are there differences in the relationship of different tree taxa to disturbance? By answering these questions, we examine the relationship between environmental and anthropogenic impacts and forest vegetation at a mid-elevation forest landscape in the Western Ghats over the last 7500 years.

2. Materials and methods

2.1. Study site

We reconstructed the vegetation dynamics of a tropical forest landscape in the Western Ghats of India (Fig. 2) using palaeoecological techniques. Two 172-cm long overlapping sediment sequences were collected from a small swamp (approximately 10-m diameter) situated at the confluence of two perennial streams in a coffee estate (latitude 12°17'16"N, longitude 75°13'26"E and altitude 910 m asl) surrounded by a mosaic of forest fragments and arable agriculture. We used GeoCore sediment coring system (<http://www.geo-core.com>). Each coring drive of this system yields

1-m long sediment sequence and therefore in basins which are deeper than 1-m, two overlapping replicate sequences are collected. At the site of sediment coring, coffee (*Coffea arabica* var. *robusta*) is planted in the understorey of open woodland composed of shade trees, spaced approximately 25-m apart, many of which are representative of native vegetation. Native trees are mixed with betel nut palm (*Areca catechu*), also used for shade. The plantation is spread over a hill slope and occupies an area of approximately 5 ha surrounding the coring site. The site is less than 10 km away from a native forest reserve currently under government protection. The ecological history of this site is not known, but the regional history of forest conversion to coffee suggests that this estate is less than 25 years old and the conversion from secondary forest to coffee plantations is relatively recent.

The location where we collected our sediment sequences is representative of the mid-elevation (500–1500 m asl) forest landscape, which occupies over 90% of the Western Ghats. The site is located within a typical agricultural landscape with a long history of human presence characterised by paddy cultivation in low-lying valleys and agroforestry systems on hill slopes, even though the conversion of traditional agroforestry systems to commercial coffee estates at this particular site is relatively recent. The site is situated at a remote location and adjacent to a forest reserve thereby preserving a relatively intact sequence of sediment. While such millennial time-scale studies have been carried out previously on sediment deposits at high altitudes (e.g. Sukumar et al., 1993, 1995; Premathilake, 2006), sites located within mid-elevation forest landscapes are rare. The studies at high altitudes (above 1500 m) have shown that these areas harbour natural forest–grassland mosaics even without anthropogenic management of landscape (Puyravaud et al., 1994, 2003; Caner et al., 2007), but such mosaics are absent at mid-elevations. At mid-elevations, grassland patches within forest landscapes are invariably shaped by anthropogenic activities, particularly fire for cultivation (e.g. Kodandapani et al., 2009). Therefore, this site provides an important insight into the dynamics of a tropical forest landscape that is affected by anthropogenic fire and environmental factors, and allows examination of their relationship with vegetation cover.

The data presented in this paper are derived from sediment sequences collected at one site. An ideal landscape–ecological study would have several replicate samples covering a latitudinal gradient, geological features, soil types, various lengths of wet-season and a wide range of anthropogenic disturbances (Sutherland, 2006). However, long-term ecological studies, particularly those in tropical landscapes, are compromised by the availability of 'intact' sediment sequences spanning such gradients. This is particularly true in anthropogenic landscapes, where sedimentary depositional environments such as low-lying valleys are susceptible to disturbance and anthropogenic alteration, making it hard to obtain continuous sediment sequences (Jacobson and Bradshaw, 1981; Overballe-Petersen and Bradshaw, 2011). Furthermore, certain soil types, factors such as aridity and geomorphological contexts such as hill slopes do not provide suitable depositional environments thus restricting the availability of sediment sequences even further. As such, many influential long-term ecological studies from the tropics have been based on interpretation of sediment sequences from one site (Hodell et al., 2001; Bakker et al., 2008, 2011). Our intact sequence from a tropical forest in the Western Ghats, therefore, affords a unique opportunity to understand the influence of environmental and anthropogenic factors on vegetation cover in this anthropogenic tropical forest landscape.

2.2. Sediment sequences

One of our two sediment sequences was sub-sampled for fossil pollen signatures at every 4-cm interval and a chronology of the

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