The Fire-Lantana Cycle Hypothesis in Indian Forests

Ankila J. Hiremath and Bharath Sundaram

Abstract: *Anthropogenic fires in Indian forests probably date back to the arrival of the first hominids on the Indian subcontinent.However, with our continuing dependence on forests for a variety of resources, but with shrinking forested areas, forests are being subjected to more intensive use than before. As a result, fires are occurring more frequently today than at any time in the past. This altered fire regime is probably qualitatively different from historical fire regimes in its impact on forests at multiple spatial scales. Present-day fires have possibly led to forest degradation, increasing susceptibility to invasion by alien species such as lantana (*Lantana camara*). We hypothesise that there may be a positive feedback between present-day fires and invasion by lantana, leading to a firelantana cycle that can have deleterious compositional and functional consequences for forest ecosystems and the commodities and services that society derives from them. Despite the widespread nature of the problem, we lack good empirical information on the effects of varying fire frequency and severity in Indian dry forests. So also, we lack a sound understanding of the mechanistic underpinnings of lantana's success and barriers to its control in Indian forests. Without such information we have little hope of a way out of the fire-lantana cycle.*

Keywords: alien invasive species, fire, India, *Lantana camara*, tropical dry forests.

INTRODUCTION

"*BY JANUARY, the grass has all seeded and become dry, and it is then fired by the jungle-people. The hitherto impenetrable jungles are now reduced to clear forests*

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of trees, interspersed with separate evergreen thickets. Moving about in such forests is rendered easy, but warm work, the heat rising from the blackened earth under a tropical sun being very trying where the forest is not dense…The junglepeople burn the grass to admit of their gathering certain fruits and jungle-products, especially the gall-nut, used in tanning. This burning insures a supply of sweet grass as soon as showers fall on the fertilising ash."

Thus did G. P. Sanderson (1882: 9-10) describe the annual dry-season fires in the seasonally dry forests in and around the Biligiri Rangan Hills of southern India. Although Sanderson wrote these lines more than a century ago, they could as easily describe these same forests during the annual dry season today.

The history of human-caused fires in Indian forests is probably as old as the history of humans in the region. Regardless of whether or not fires were part of the natural disturbance regime, or whether their arrival coincided with the arrival of the first hominids, it is probably fair to say that, with shrinking forests and growing human populations, the frequency of fires in Indian forests today is far greater than at any time in the past. In the Mudumalai wildlife sanctuary in South India, for example, Kodandapani et al. (2004) estimate an average fire-return interval of <7 years, which represents a three-fold increase in the frequency of fires in these forests over the last century alone. Fire-return intervals are even shorter in Mendha, in Central India, where forests are burned annually to facilitate collection of two locally important non-timber products, *Madhuca longifolia* flowers and *Diospyros melanoxylon* leaves (Saha 2002). Such frequent fires can have profound implications for forest structure, composition, and functioning at multiple spatial scales.

The vast majority of fires occur in India's seasonally dry tropical forests, which account for ~40% of all forest in India (Wikramanayake et al. 1998; Rodgers et al. 2002). In India and elsewhere in the tropics, large areas of what were once tropical dry forests have already been converted to anthropogenic grasslands as a result of fire, as also to other uses (Murphy and Lugo 1986; Sagar and Singh 2004). It is critical, therefore, to try and understand the role of fire in the conservation and management of these endangered ecosystems (Janzen 1986a). We review the effects of fire at scales ranging from the species to the landscape, and suggest that altered fire regimes in Indian dry tropical forests have probably resulted in ecosystem degradation, increasing their susceptibility to invasion by exotic species. We hypothesise, further, that there may be positive feedback between fire and invasive species––especially *Lantana camara*––with detrimental consequences for these ecosystems and for human societies dependent upon them.

Fires in Indian Forests

In regions of the world where forest fires are part of the natural disturbance regime, lightning is the principal cause of forest fires (Brown and Smith 2000). Lightning is not, however, considered an important source of ignition in Indian forest fires. One

reason for this is India's monsoon climate. The suggestion is that lightning storms are invariably accompanied by rainfall, thereby reducing the possibility of lightningcaused fires spreading, even if started (Saha and Howe 2001). Others argue that lightning storms in India are qualitatively no different from elsewhere in the world; moreover, lightning-struck trees typically smoulder for several days, even through rain, igniting fires once the rain has passed and the fuel is dry again (Keeley and Bond 2001). These authors also provide evidence for a substantial number of lightning storms during the dry season in India, when forests are at their most flammable. Why, then, is lightning not considered an important source of ignition of fires in Indian forests? According to Keeley and Bond (2001), the answer is not the dearth of lightning storms; rather, it may be that the long history of conversion and fragmentation of these forests has altered fuel characteristics, reducing the likelihood of ignition and spread of lightning-caused fires.

Be that as it may, human activity is generally regarded as the principal cause of forest fires in India (Saha and Howe 2001). People have been clearing and burning forests for shifting cultivation for millennia (Gadgil and Meher-Homji 1985; Schule 1990), though this is now a dying practice in most parts of the country except in the northeast (Raman et al. 1998). Nonetheless, forest-dependent communities continue to burn forests to promote the growth of fresh fodder for grazing (Gadgil and Meher-Homji 1985), and to facilitate the collection of non timber forest products (Rodgers 1986; Saha 2002). For example, in a note on fire protection (Anon 1905: p. 584), the District Forest Officer of what was then North Coimbatore was quoted as attributing forest fires to three principal causes. According to him 60% of all fires resulted from "wilful incendiarism by graziers in order to obtain new grass;" 30% of fires were set by hill tribes ("the *Sholagar*s") for "enabling them to find out minor forest produce;" and the remaining 10% were due to the "carelessness of travellers and bandymen passing along cart-tracks, paths or streams in the jungle." These remain the principal causes of fires, although, to a much smaller extent, arson and acts of retaliation against Forest Department policies also account for some human-caused fires in Indian forests today (Saberwal et al. 2000).

The role of fires in Indian forests––whether natural or anthropogenic, beneficial or detrimental––has been debated for at least a century (see Walker 1903, 1910; Sengupta 1910; Fischer 1912). Yet, the issue remains as polarised, and as uninformed by good empirical information, alas, as it has always been. Presentday opponents of fire maintain that fires are detrimental and must be prevented at all costs (Ministry of Environment and Forests 2001). Proponents of fire, on the other hand, fall back on its use as part of age-old traditional forest management practices (Saberwal et al. 2000), and on the more contemporary theory of disturbance as an intrinsic part of ecosystem dynamics (e.g., Pickett and White 1985), to support their argument for the beneficial effects of fire. A fundamental concern gets lost in this debate: one cannot assume that anthropogenic disturbances are necessarily

equivalent to natural disturbances in their effects on ecosystem processes. For anthropogenic disturbances to mimic natural disturbances, they must also occur at the same spatial and temporal scales as natural disturbances (Roberts and Gilliam 1995). With evidence pointing to increasing frequency of anthropogenic fires today, it is more than likely that these fires are qualitatively different in their effect on ecosystems from fires in the past.

Changing Fire Regimes, Changing Forests

In ecosystems that burn only infrequently, even very low-intensity fires can have profound consequences for forest structure and composition. For example, in the Amazon, a region that has not experienced frequent burning over evolutionary time, forests are extremely vulnerable to damage from fire. In such forests, even very low-intensity ground fires can cause mortality of thin-barked adult trees (Cochrane and Schultz 1998; Barlow et al. 2003). There is some observational evidence from Indian forests to suggest that the higher relative abundance of certain thick-barked species, or species that are able to resprout vegetatively (e.g., *Boswellia serrata, Dalbergia paniculata,* and *Sterculia sp.*; Brandis 1882), may in fact be a legacy of increased burn frequencies (coupled with indiscriminate felling of the more valuable timber species). This is bolstered by recent empirical evidence that fires preferentially select for species that are able to resprout clonally over species that rely solely on regeneration from seed (Saha and Howe 2003). Over repeated burn cycles, forests are depleted of species that can neither resist fires (due to their thin bark) nor tolerate fires (due to their inability to resprout following damage). Increased burn frequencies can therefore progressively weed out the more fire-vulnerable components of biodiversity. The result is significantly altered, and reduced, species composition.

Another aspect of increased burn frequencies and reduced fire return times is the direct impact on young, regenerating vegetation. We know, for instance, that tree seedlings are more vulnerable to fire than saplings and trees (Saha and Howe 2003). Couple the greater fire-vulnerability of regenerating vegetation with the shortened time for vegetation recovery between fires, and the result is species' populations that are depauperate in the smaller size classes. Such an absence of smaller individuals in the present can constitute a potential population bottleneck in the future (e.g., populations of the important non-timber forest product species, *Phyllanthus emblica,* in the Biligiri Rangan Hills of South India; Ganesan and Setty 2004). Even for more fire-resistant thick-barked species, bark thickness––and the protection this affords the vulnerable cambial layer from lethal fire temperatures ––scales with tree size (Pinard and Huffman 1997). Thus frequent fires may cause mortality of smaller trees, opening up the canopy and leading to the gradual conversion of once-closed forests to woodland savannas with low tree density and a grassy understory (Stott et al. 1990; Puyravaud et al. 1994; Barlow and Peres 2004). The result is significantly altered forest structure.

Frequent fires are generally less severe in their effect on ecosystem functioning than infrequent fires, but there may be exceptions to this. Frequent fires, which allow less time for fuel to accumulate between successive burns, tend to burn cooler. Such low-intensity fires can lead to short-term pulses in nutrient availability, benefitting regenerating seedlings as well as grass that resprouts after burning; this increased nutrient availability is due to deposition of cation-rich ash on the soil surface, and to increased mineralisation of soil organic matter resulting from elevated temperature, pH, and moisture. Infrequent fires, on the other hand, allow for greater fuel accumulation between successive burns, and therefore burn hotter. Such high-intensity fires can result in soil nitrogen volatilisation and a reduction in soil organic matter. The result is reduced soil nutrient availability, accompanied by increased bulk density and decreased porosity and soil waterholding capacity (Neary et al. 1999). Nonetheless, even low-intensity fires, if they occur frequently enough, and do not allow for soil recovery between successive disturbances, can result in progressive soil degradation (DeBano 2000a). Declining soil fertility increasingly jeopardises ecosystem productivity and resilience (DeBano 2000b). Over time, repeated fires may therefore result in the conversion of relatively productive deciduous forests to degraded scrub or thorn woodland (Johnsingh 1986; Brown and Lugo 1990). For example, Beddome (1878: 190) described the effects of increased burn frequencies (as often as once in 8-10 years, compared to once in 40-50 years, previously) under slash-and-burn *podu* cultivation in the South and East Indian States of Andhra Pradesh and Orissa. According to him, the forests "....have a wretched and stunted appearance, are very dry and more or less inpenetrable from a tangled rank undergrowth, and there are no seedlings; nothing, in fact, but the coppice growth generally of only the quicker growing but poorer sorts of timber."

Fires in a Cultural Landscape

There are additional reasons why the traditional practice of burning may have historically affected forests very differently than it does today. Possibly more than at any time in the past, the landscape we inhabit today is a cultural one – one that is a mosaic of land-use practices, both past and present, shaped by a variety of cultural and socio-economic factors. A hallmark of this landscape is a high degree of forest fragmentation. Fragmentation results in a greater ratio of edge-to-interior environments, leading to altered microclimates and consequently greater forest drying (Janzen 1986b; Laurance and Williamson 2001).

Not only are forests more fragmented today, they have also experienced a history of more intensive management over the past century than they had previously (e.g., the management of forests for revenue generation from timber; Gadgil and Guha 2000). Management practices such as selective logging open up

the canopy, resulting in more rapid drying of understory fuels, as is happening in parts of the neotropics today (Kauffman and Uhl 1990). The likely combined legacy of fragmentation and management history is greater forest flammability than in the past. So fires, when they occur, probably burn more intensely, with more severe consequences for ecosystem processes.

Ecosystem Invasibility and Species' Invasive Ability

Invasive alien species are increasingly being regarded as among the principal threats to global biodiversity along with land-use change, climate change, anthropogenic nitrogen deposition, and increasing atmospheric carbon dioxide (Sala et al. 2000). A recent article in the widely-read popular science and environment fortnightly, *Down to Earth* (Sethi 2004), attests to the growing recognition of this problem by civil society, and to its no longer being a concern of the scientific community alone.

A number of theories have been proposed to explain the success of alien invasive species in non-native habitats. It has been suggested that many invasive species defy classic life-history theory, embodying contrasting traits: many are good colonisers as well as good persisters (D'Antonio and Meyerson 2002). The former is characterised by an ample supply of well-dispersed propagules to opportunistically take advantage of disturbances; the latter by the ability to compete effectively with native species for available resources (see also Denslow 2003). Invasive species also benefit from their homoclimatic origins (Di Castri 1989) and from the scarcity of natural enemies in the areas they invade (Colautti et al. 2004).

But it is not the ecological traits of invasive species alone that necessarily determine invasions: the presence of invasive species may merely be a "symptom," the underlying cause being ecosystem invasibility (Ewel 1986). There is evidence linking ecosystem invasibility to disturbance: more disturbed ecosystems are more vulnerable to invasions by alien species than less disturbed ones (e.g., Myers 1983; Hobbs 1989; Larson et al. 2001).

Ecosystem invasibility has also been related to species diversity. It is thought that species-poor biotas (e.g., on oceanic islands; Elton 1958) are especially invasible––that these less diverse systems have "empty niches," making them vulnerable to colonisation by alien species. There is some evidence from experimental systems that supports this idea (Kennedy et al. 2002), but the resistance to invasion could be related to more complete use of resources than to diversity per se (Stachowicz et al. 2002). This theory of vacant niches applies equally well to increasingly isolated mainland habitats, especially as they become more depauperate, with missing species and functional groups, as can happen under scenarios of intensified disturbance (e.g., increased fire frequencies). But though the inverse diversity-invasibility relationship appears to apply at small

spatial scales, at landscape and biome scales it may be soil fertility rather than species diversity that determines ecosystem invasibility. Thus, unrelated to native species diversity, habitats with more resource availability show greater invasion by non-native species than low-resource habitats (Stohlgren et al. 1999).

Fire and Invasive Species

Given the evolutionary link between fire and native savannas the world over, it is not surprising that fire as a disturbance is particularly implicated in the success and persistence of invading grasses. This phenomenon of the invasive grass-fire cycle has been especially well documented for the Americas, and on the Hawaiian Islands (D'Antonio and Vitousek 1992; D'Antonio 2000; Lippincott 2000). Many of these grasses originate in Africa and Eurasia, where they have had a long evolutionary history in conjunction with hominids (and associated fires and grazing). The grass lifeform is particularly well adapted to fires, with perennating belowground organs and basal meristems that enable rapid resprouting in response to defoliation (D'Antonio and Vitousek 1992). In the Hawaiian Islands, and in parts of the southeastern United States and Mexico, fire has followed introduced pasture grasses into forests. Grasses fuel fires; fires encourage the regeneration of grasses in preference to woody perennials; the result is a grass-fire cycle that feeds on itself, to the detriment of the native ecosystem (Mack and D'Antonio 1998). This can have profound implications for native biodiversity, clearly, but also for ecosystem structure and functioning, and for the services that society derives from these ecosystems.

But grasses are not the only invasive lifeform that is favoured by fire. Some woody perennial invasive species are also associated with fire as a disturbance. An example is that of exotic pines (*Pinus pinaster* from Europe) and hakeas (*Hakea* spp. from Australia) invading the unique *fynbos* vegetation of South Africa. What is remarkable in this case is that fire is part of the natural disturbance regime in the *fynbos*. Nonetheless, these invading woody perennials have a demographic advantage over the native fire-adapted *fynbos* vegetation: they have short juvenile periods and produce copious quantities of seeds, both of which give them a headstart over native species in pre-empting resources made available following fire (Holmes and Cowling 1997).

One of the few well-documented examples of the link between fire and invasive species in India comes from the northeast, where shifting cultivation, or *jhum,* continues to be the primary form of cultivation (Raman et al. 1998). Ramakrishnan and Vitousek (1989) reviewed the impacts of shortened intervals between *jhum* cycles (down to 4-5 years from the earlier $>$ 20-30 years) on species regeneration. Their review shows that the greatly shortened *jhum* interval resulted in soil degradation due to nutrient leaching, coupled with insufficient time between successive cycles for the soil to recover its nutrient status. In addition, the shortened

interval was not long enough for slow-growing native vegetation to grow and produce seeds, thus leading to a paucity of propagules for recolonisation. The result was regenerating vegetation that was dominated by invasive weeds, both natives (*Imperata cylindrica*, *Pteridium aquilinium*, and *Saccharum spontaneum*) and exotics (*Eupatorium odoratum*, *Eupatorium adenophorum*, and *Mikania micrantha*). The native weeds were distinguished by their ability to resprout in response to fire. The alien weeds were distinguished by their high reproductive potential and by their greater efficiency at sequestering scarce resources from these degraded soils; the former affording them a demographic advantage, and the latter giving them a competitive edge over the native vegetation.

Fire and Lantana in India's Dry Forests: The Fire-Lantana Cycle Hypothesis

An alien invasive species that is widespread in Indian dry forests is *Lantana camara* (Verbenaceae; hereafter, lantana). Originally a native of South and Central America, lantana was introduced as an ornamental into many parts of the tropical and subtropical world during the nineteenth and early twentieth century (Mack et al. 2000). It has since established and spread in its introduced range—from the islands of Oceania to mainland Asia and Africa—at a cost to native species and habitats; so much so that the IUCN-World Conservation Union considers it amongst the world's 100 most invasive species (Lowe et al. 2004).

In India, lantana is amongst the most widespread terrestrial invasive species today, particularly in dry-to-moist deciduous forests. The documented history of lantana in India goes back to at least the nineteenth century. It was probably introduced into the country on multiple occasions; at least two separate accounts talk of its introduction as a garden ornamental in Coorg in the 1860s (Anon 1895), and as a hedge plant in Calcutta in the early nineteenth century (Hakimuddin 1929). Hakimuddin (1929) goes on to provide an interesting early account of lantana's invasiveness, following its introduction to Kathgodam in Nainital district c. 1905. According to him, in 1911, lantana was still confined largely to hedges and did not occur more than a few miles from its place of introduction, being relatively sparse where it did occur. Within two decades, however, it had spread in a thick continuous mass to a distance of about 25 miles (40 km) in all directions, indiscriminately taking over farm and pasture, fallow land and forest.

There are similar records of lantana as a problem weed from other regions of the country around the same time (Pereira 1919). Today, lantana continues to be regarded as one of the principal threats to native biodiversity by forest-dwelling communities and researchers alike. For example, the Soligas in the Biligiri Rangan Hills of South India consider lantana a threat to biodiversity largely due to its extreme flammability. Climbing stems of lantana can reach up to >20 metres, getting into the forest canopy and resulting in devastating crown fires when they burn (Tireman 1916). Lantana also suppresses regeneration (Ganesan and Bawa,

unpublished), which affects biodiversity and has an economic impact on people who harvest non-timber forest products (Hegde et al. 1996).

Lantana apparently embodies several of the advantageous characteristics of other fire-enabled or fire-adapted invasive species. It resprouts readily on being burnt (Pereira 1919; Hakimuddin 1929); and it flowers and fruits year round, producing copious quantities of seeds that are readily dispersed by frugivores (Hakimuddin 1929). Surprisingly, there are few empirical studies in India that look at lantana and its invasive ability, especially in response to fire, despite its pervasive distribution. We propose that lantana invasion may be facilitated by fire. Further, we suggest that lantana, once established, fuels further fires, setting up a selffeeding fire-lantana cycle (see Figure 1). We draw largely on anecdotal information, and on descriptive observations of the species, to support our hypothesis of a fire-lantana cycle. We hope, nonetheless, to demonstrate that there may, in fact, be a strong link between fire and the occurrence of lantana in India's tropical and subtropical deciduous forests.

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The hypothesised fire-lantana cycle

Notes: The hypothesised fire-lantana cycle: forest fragmentation, coupled with intensified anthropogenic disturbances—especially fires—have resulted in degradation of ecosystems, making them more vulnerable to invasion by alien species; some invasive species (e.g., lantana), in turn, fuel further fires. The resultant positive feedback has deleterious compositional and functional consequences for ecosystems and the goods and services that society derives from them.

Recent findings from other parts of the tropics confirm that lantana may be favoured by disturbances such as fire and grazing (Duggin and Gentle 1998; Gentle

and Duggin 1998). There is also some evidence from northern India to suggest that it is capable of colonising sites on very degraded soils (Bhatt et al. 1994; Rawat et al. 1994). Observations and anecdotal evidence provide further support to this idea. For example, in the Biligiri Rangan Hills, there is some indication that high lantana density may be associated with areas that have been managed either for shifting cultivation or selective logging in the last hundred years (R. Ganesan, unpublished data). Furthermore, according to the local Soliga elders, the initial spread of lantana in these dry forests coincided with the last mass-flowering and die-back of bamboo, which was followed by widespread fires (V. Gogi, *pers. comm.*), presumably resulting in a vacant understory.

What are the ecological mechanisms underlying the success and persistence of lantana? One potential mechanism relates to its tolerance to being burnt. Early records of attempted lantana control underscore the importance of completely uprooting lantana after cutting and burning aboveground biomass to prevent it recolonising from the rootstock (Tireman 1916; Pereira 1919). In fact, recent evidence suggests that lantana actually regrows more densely in response to being burnt (Gentle and Duggin 1998). Moreover, the high productivity of lantana rapidly yields large quantities of biomass, which can fuel further fires (Bingelli et al. 1998). Thus, forests once colonised by lantana can well fall victim to a fire-lantana cycle, perpetuating lantana to the detriment of other vegetation.

A second potential mechanism underlying the success of lantana is its ability to compete for scarce nutrients. Lantana is exceedingly efficient at nutrient uptake and use, enabling it to grow on highly impoverished soils (Bhatt et al. 1994; Rawat et al. 1994). Such an ability to extract and use nutrients efficiently would give it a competitive advantage over other species in low-fertility environments (Tilman et al. 1997), for example, in forests already degraded by frequent burning.

Finally, a third potential mechanism underlying the success of lantana is its colonising ability. Lantana's abundant perennially available flowers and fruit make it a good host for pollinators and frugivores, respectively, and ensure a year-round supply of well-dispersed propagules. Even in places where lantana is completely uprooted, it regenerates profusely from seeds in the soil seed bank for several years following its removal. Thus, a complete eradication of lantana requires repeated uprooting of successive crops for several consecutive years (Tireman 1916). Other invasive species (e.g., *Mimosa pigra* in Australia; Lonsdale et al. 1988) have been known to enrich the soil with their own seeds (up to 12,000 seeds/ m², a number that is several times greater than seed densities recorded under other tropical secondary vegetation); lantana may be an example of a similar successful coloniser.

The Effects of Lantana in Indian Forests

Despite the widespread concern about invasive species and their effects on biodiversity worldwide, there is no holistic picture of the biodiversity effects of lantana in India. Though lantana is known to enhance diversity of certain taxa, such as butterflies (R. Borges, *pers. comm.*), the locally enhanced richness of a few pollinator species attracted by a rich nectar reward may, be a high price to pay for

suppressed regeneration and potential habitat loss, accompanied by increasing landscape homogenisation in the long term.

As damaging as the compositional changes are the functional changes wrought by invasive alien species. People have attempted to quantify the loss of essential ecosystem services from species invasions and the resultant societal costs that such losses entail (e.g., Zavaleta 2000). Examples of functional consequences of species invasions can range from the loss of pollinators (Ghazoul 2004) to the loss of hydrological services (Le Maitre et al. 2001; van Wilgen et al. 2001) and that of economically important land uses such as pasture and cropland (Pimentel et al. 2000).

Lantana is known to produce secondary compounds that are toxic to ungulates (Sharma et al. 1981). However, the reduction in forage availability to domestic and wild herbivores as a result of lantana invasion into degraded forests and pastures has not been quantified. Lantana is also known to suppress regeneration of other vegetation (Ganesan and Bawa, unpublished). Thus, another effect of lantana invasion likely to manifest in the very near future is the reduced availability of non-timber products that people derive from forests. But other than these tangible impacts of lantana invasion, and a passing reference to lantana "affect[ing] water supply injuriously" (Anon 1895; though there is no elaboration of the statement), we know next to nothing about the functional effects of lantana invasion in Indian forests, let alone the economic burden that society will have to bear as a result thereof.

The Fire-lantana Cycle in India: Is there a Way Out?

Although we lack specific information regarding historical fire regimes in Indian forests, there is good reason to infer that present-day fire regimes are qualitatively different. Such an alteration in fire regimes, as we have demonstrated, can have wide-ranging consequences for forest structure, composition, and functioning. One outcome of these fire-driven changes is the increased invasibility of these forests, and their invasion by fire-tolerant or fire-resistant alien species. Recorded observations about lantana, and experimental studies of invasive species from other parts of the world, strongly suggest that lantana in India is analogous to other fire-maintaining and fire-maintained invasive species elsewhere in the tropics. This hypothesised synergy between anthropogenic fires and lantana invasion in Indian forests has potentially damaging consequences for sustaining these forests and the ecosystem services they provide. What, then, is the way out of the firelantana cycle?

Not only are fires a critical management tool for forest-dependent communities to meet their non-timber product and grazing requirements, but keeping fires out of certain ecosystems may even be detrimental to those ecosystems. For example, fires (and frost; Meher-Homji 1967) are essential to maintain the unique sholagrassland ecosystem in the upper reaches of the Western Ghats. These sholagrasslands provide a critical hydrological service for the upper Nilgiris (Sikka et al. 2003), and are important habitat for the endemic Nilgiri *tahr* and locally diverse plant genera such as the *Impatiens* and *Strobilathus*. So also, fires are essential to maintain the flood-plain grasslands of India's northeast. With flood control, and

without the fires that maintain them in lieu of the frequent flooding they have historically experienced, these grasslands would very quickly undergo succession to forest (Deb Roy 1986); this could be devastating for endemics like the Indian rhinoceros, pygmy hog, and hispid hare, for whom these grasslands are the last remaining habitat.

Anthropogenic fires have been an integral part of India's forest landscape and are likely to remain so in the foreseeable future, opponents of such fires notwithstanding. The debate on fires in Indian forests thus needs to move away from whether fires are natural or anthropogenic, beneficial or detrimental. We should focus, instead, on what the specific management objectives of burning are in a given forest. We should focus, also, on the effects a prevailing burn regime may be having on that forest, since not all ecosystems respond the same way to fire; nor do all fires have the same effect on ecosystems. There is an urgent need to put in place large-scale monitoring of fires and invasive species across the landscape to better gauge the spatial and temporal patterns of one, and the spatial extent of the other. There is, as well, an urgent need to empirically understand the effects of fires at multiple spatial scales; so also a need to understand the ecological mechanisms of invasive species success, and the barriers these pose for native species restoration. It is only with such information in hand that we can hope to attempt restoration and management to meet the varied objectives of multiple stakeholders, be they local forest-dependent communities, wildlife conservationists, forest managers, or civil society at large.

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REFERENCES

Anon. 1895. Is Lantana a friend or an enemy? *Indian Forester* 21:454-460.

- Anon. 1905. Fire protection in Madras. Extracts from official papers. *Indian Forester* 31:584-596.
- Barlow, J. and C.A. Peres. 2004. Ecological responses to El Nino-induced surface fires in central Brazilian Amazonia: Management implications for flammable tropical forests. *Philosophical Transactions: Biological Sciences* 359:367- 380.
- Barlow, J., C.A. Peres, B.O. Lagan and T. Haugaasen. 2003. Large tree mortality and the decline of biomass following Amazonian wildfires. *Ecology Letters* 6:6.

Beddome, R.H. 1878. The Jeypore forests. *Indian Forester* 3:188-205.

Bhatt, Y.D., Y.S. Rawat and S.P. Singh. 1994. Changes in ecosystem functioning after replacement of forest by Lantana shrubland in Kumaon Himalaya. *Journal of Vegetation Science* 5:67-70.

- Bingelli, P., J.B. Hall and J.R. Healey. 1998. *An Overview of Invasive Woody Plants in the Tropics*. School of Agriculture and Forest Sciences Publication Number 13. University of Wales, Bangor, UK.
- Brandis, D. 1882. The forests of South India. *Indian Forester* 7:363-369.
- Brown, J.K. and J.K. Smith. 2000. *Wildland Fire in Ecosystems: Effects on Flora*. General technical report, USDA, Forest Service, Rocky Mountain Research Station.
- Brown, S. and A.E. Lugo. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6:1-32.
- Cochrane, M.A. and M.D. Schulze. 1998. Forest fires in the Brazilian Amazon. *Conservation Biology* 12:948-950.
- Colautti, R.I., A. Ricciardi, I.A. Grigorovich and H.J. Macisaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721-773.
- D' Antonio, C.M. 2000. Fire, Plant Invasions, and Global Change. In: *Invasive Species in a Changing World* (eds. H.A. Mooney and R.J. Hobbs), pp. 65-93. Island Press, Washington DC.
- D' Antonio, C.M. and P.M. Vitousek. 1992. Biological invasion by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
- D' Antonio, C.M. and L.A. Meyerson. 2002. Exotic plant species as problems and solutions in ecological restoration: A synthesis. *Restoration Ecology* 10:703-713.
- Deb Roy, S. 1986. Fire in wet grassland habitats of Assam. *Indian Forester* 112:914-918.
- DeBano, L.F. 2000a. The role of fires and soil heating on water repellency in wildland environments: A review. *Journal of Hydrology* 231:195-206.
- DeBano, L.F. 2000b. Water repellency in soils: A historical overview. *Journal of Hydrology* 231:4-32.
- Denslow, J.S. 2003. Weeds in paradise: Thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden* 90:119-127.
- Di Castri, F. 1989. Histories of Biological Invasions with Special Emphasis on the Old World. In: *Biological Invasions: A Global Perspective* (eds. J. A. Drake, H.A. Mooney, F. Di Castri, R.H. Grove, K.J. Kruger, M. Rejmanek and M. Williamson), pp. 1-30. SCOPE 37. Wiley and Sons, Chichester, United Kingdom.
- Duggin, J.A. and C.B. Gentle. 1998. Experimental evidence on the importance of disturbance intensity for invasion of *Lantana camara* L. in dry rainforestopen forest ecotones in north-east NSW, Australia. *Forest Ecology and Management* 109:279-292.
- Elton, C.S. 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London, UK.
- Ewel, J.J. 1986. Invasibility: Lessons from South Florida. In: *Ecology of Biological Invasions of North America and Hawaii* (eds. H.A. Mooney and J.A. Drake), pp. 214-230. Ecological Studies Volume 58. Springer-Verlag, New York.

- Fischer, C.E.C. 1912. The need of fire protection in the tropics. *Indian Forester* 38:191-221.
- Gadgil, M. and R. Guha. 2000. *The Use and Abuse of Nature: Omnibus of This Fissured Land and Ecology and Equity*. Oxford University Press.
- Gadgil, M. and V.M. Meher-Homji. 1985. Land Use and Productive Potential of Indian Savannas. In: *Ecology and Management of the World's Savannas* (eds. J.C. Tothill, and J.J. Mott), pp. 107-113. Australian Academy of Science, Canberra.
- Ganesan, R. and R.S. Setty. 2004. Regeneration of amla (*Phyllanthus emblica* and *P. indofischeri*), an important NTFP from southern India. *Conservation and Society* 2:365-375.
- Gentle, C.B. and J.A. Duggin. 1998. Interference of *Choricarpia leptopetala* by *Lantana camara* with nutrient enrichment in mesic forests on the Central Coast of NSW. *Plant Ecology* 136:205-211.
- Ghazoul, J. 2004. Alien abduction: Disruption of native plant-pollinator interactions by invasive species. *Biotropica* 36:156-164.
- Hakimuddin, M. 1929. Lantana in northern India as a pest and its probable utility in solving the cowdung problem. *Indian Forester* 56:405-410.
- Hegde, R., S. Suryaprakash, L. Achoth and K.S. Bawa. 1996. Extraction of nontimber forest products in the forests of the Biligiri Rangan Hills, India. 1. Contribution to rural incomes. *Economic Botany* 50:243-251.
- Hobbs, R.J. 1989. The Nature and Effects of Disturbance Relative to Invasions. In: *Biological Invasions: A Global Perspective* (eds. J.A. Drake, H.A. Mooney, F. Di Castri, R.H. Grove, K.J. Kruger, M. Rejmanek and M. Williamson), pp. 389- 405. SCOPE 37. Wiley and Sons, Chichester, United Kingdom.
- Holmes, P.M., and R.M. Cowling. 1997. Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. *Plant Ecology* 133:107-122.
- Janzen, D.H. 1986a. The future of tropical ecology. *Annual Review of Ecology and Systematics* 17:305-324.
- Janzen, D.H. 1986b. The Eternal External Threat. In: *Conservation Biology: the Science of Scarcity and Diversity* (ed. M.E. Soulé), pp. 286-303. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Johnsingh A.J.T. 1986. Impact of fire on wildlife ecology in two dry deciduous forests in south India. *Indian Forester* 112:933-938.
- Kauffman, J.B. and C. Uhl. 1990. Interactions of Anthropogenic Activities, Fire, and Rainforests in the Amazon basin. In: *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges* (ed. J.G. Goldammer)*,* pp. 117-134. Ecological Studies 84, Springer-Verlag, Berlin.
- Keeley, J. E. and W. J. Bond. 2001. On incorporating fire into our thinking about natural ecosystems: A response to Saha and Howe. *American Naturalist* 158:664-670.
- Kennedy, T.A., S. Naeem, K.M. Howe, J.M.H. Knops, D. Tilman and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636-638.

- Kodandapani, N., M.A. Cochrane and R. Sukumar. 2004. Conservation threat of increasing fire frequencies in the Western Ghats, India. *Conservation Biology* 18:1553-1561.
- Larson, D.L., P.J. Anderson and W. Newton. 2001. Alien plant invasion in mixedgrass prairie: Effects of vegetation type and anthropogenic disturbance. *Ecological Applications* 11:128-141.
- Laurance, W.F. and G.B. Williamson. 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conservation Biology* 15:1529-1535.
- Le Maitre D.C., B.W. van Wilgen, C.M. Gelderblom, C. Bailey, R.A. Chapman and J.A. Nel. 2001. Invasive alien trees and water resources in South Africa: Case studies of the costs and benefits of management. *Forest Ecology and Management* 160:143-159
- Lippincott, C.L. 2000. Effects of *Imperata cylindrica* (L.) Beauv. (cogon grass) invasion on fire regime in Florida Sandhill (USA). *Natural Areas Journal* 20:140-149.
- Lonsdale, W.M., K.L.S. Harley and J.D. Gillett. 1988. Seed bank dynamics in *Mimosa pigra*, an invasive tropical shrub. *Journal of Applied Ecology* 25:963-976.
- Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2004. Hundred of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database. Invasive Species Specialist Group of the IUCN-World Conservation Union. URL:http//www.issg.org/booklet.pdf.
- Mack, M.C. and C.M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195-198.
- Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout and F.A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689-710.
- Meher-Homji, V.M. 1967. Phytogeography of the South Indian hill stations. *Bulletin of the Torrey Botanical Club* 94:230-342.
- Ministry of Environment and Forests, India. 2001. The Coimbatore Charter on Environment and Forests. Available online: http://envfor.nic.in/misc/ coimchar.html
- Murphy, P.G. and A.E. Lugo 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17:67-88.
- Myers, R.L. 1983. Site susceptibility to invasion by the exotic tree *Melaleuca quinquenervia* in southern Florida. *Journal of Applied Ecology* 20:645-658.
- Neary, D.G., C.C. Klopatek, L.F. DeBano and P.F. Ffolliott. 1999. Fire effects on belowground sustainability: A review and synthesis. *Forest Ecology and Management* 122:51-71.
- Pereira, W.E. 1919. Lantana in the Math working circle in Savantavadi state forest. *Indian Forester* 46:188-193.
- Pickett, S.T.A. and P.S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.

- Pimentel, D., L. Lach, R. Zuniga and D. Morrison. 2000. Environmental and economic costs of non-indigenous species in the United States. *Bioscience* 50:53-65.
- Pinard, M.A., and J. Huffman. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in Eastern Bolivia. *Journal of Tropical Ecology* 13:727-740.
- Puyravaud, J.P., J.P. Pascal and C. Dufour. 1994. Ecotone structure as an indicator of changing forest-savanna boundaries (Linganamakki region, southern India). *Journal of Biogeography* 21:581-593.
- Ramakrishnan, P.S. and P.M. Vitousek. 1989. Ecosystem Level Processes and the Consequences of Biological Invasion. In: *Biological Invasions: A Global Perspective* (eds. J.A. Drake, H.A. Mooney, F. Di Castri, R.H. Grove, K.J. Kruger, M. Rejmanek and M. Williamson), pp. 281-300. SCOPE 37. Wiley and Sons, Chichester, United Kingdom.
- Raman, T.R.S., G.S. Rawat and A.J.T. Johnsingh. 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, North-East India. *Journal of Applied Ecology* 35:214-231.
- Rawat, Y.S., Y.D. Bhatt, P. Pande and S.P. Singh. 1994. Production and nutrient cycling in *Arundinaria falcata* and *Lantana camara*: The two converted ecosystems in Central Himalaya. *Tropical Ecology* 35:53-67.
- Roberts, M.R. and F.S. Gilliam. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecological Applications* 5:969-977.
- Rodgers, W.A. 1986. The role of fire in the management of wildlife habitats: A review. *Indian Forester* 112:845-857.
- Rodgers, W.A., H.S. Panwar and V.B. Mathur. 2002. *Wildlife Protected Area Network in India - A Review: Executive Summary*, pp. 44. Wildlife Institute of India, Dehradun.
- Saberwal, V., M. Rangarajan and A. Kothari. 2000. *People, Parks, and Wildlife*. Orient Longman, India.
- Sagar, R. and J.S. Singh. 2004. Local plant species depletion in a tropical deciduous forest of northern India. *Environmental Conservation* 31:55-62.
- Saha, S. 2002. Anthropogenic fire regime in a deciduous forest of central India. *Current Science* 82:101-104.
- Saha, S. and H.F. Howe. 2001. The bamboo fire cycle hypothesis: A comment. *American Naturalist* 158:659-663.
- Saha, S. and H.F. Howe. 2003. Species composition and fire in a dry deciduous forest. *Ecology* 84:3118-3123.
- Sala, O.E., F.S. Chapin III, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker and D.H. Wall. 2000. Global biodiversity scenarios for the year 2001. *Science* 287:1770-1774.

- Sanderson, G.P. 1882. *Thirteen Years Among the Wild Beasts of India: Their Haunts and Habits from Personal Observation; With an Account of the Modes of Capturing and Taming Elephants*. First Published: London, 1882. Reprint: Asian Educational Services, New Delhi, 2000.
- Schule, W. 1990. Landscapes and Climate in Prehistory: Interactions of Wildlife, Man, and Fire. In: *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges* (ed. J.G. Goldammer), pp. 273-318. Ecological Studies 84, Springer-Verlag, Berlin.
- Sengupta, B. 1910. Fire conservancy in Indian forests. *Indian Forester* 36:130-145.
- Sethi, N. 2004. The war of species. *Down to Earth* 12:27-34.
- Sharma, O.P., H.P. Makkar, R.K. Dawra and S. S. Negi. 1981. A review of the toxicity of *Lantana camara* (Linn) in animals. *Clinical Toxicology* 18:1077-1094.
- Sikka A.K., J.S. Samra, V.N. Sharda, P. Samraj and V. Lakshmanan. 2003. Low flow and high flow responses to converting natural grassland into bluegum (*Eucalyptus globulus*) in Nilgiris watersheds of South India. *Journal of Hydrology* 270:12–26.
- Stachowicz J.J., H. Fried, R.W. Osman and R.B. Whitlatch. 2002. Biodiversity, invasive resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology* 83:2575-2590.
- Stohlgren, T. J., D. Binkley, G.W. Chong, M.A. Kalkhan, L D. Schell, K.A. Bull, Y. Otsuki, G. Newman, M. Bashkin and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25-46.
- Stott, P.A., J.G. Goldammer and W.L. Werner. 1990. The Role of Fire in the Tropical Lowlands Deciduous Forests of Asia. In: *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges* (ed. J.G. Goldammer), pp. 32-44. Ecological Studies 84, Springer-Verlag, Berlin.
- Tilman, D., C.L. Lehman and K.T. Thomas. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the National Academy of Sciences* 94:1857-1861.
- Tireman, H. 1916. Lantana in the forests of Coorg. *Indian Forester* 42:384-392.
- van Wilgen, B.W., D.M. Richardson, D.C. Le Maitre, C. Marais and D. Magadlela. 2001. The economic consequences of alien plant invasions: Examples of impacts and approaches to sustainable management in South Africa. *Environment, Development and Sustainability* 3:145-168.
- Walker, H.C. 1903. Fire protection in the teak forests of lower Burma. *Indian Forester* 29:554-562.
- Walker, H.C. 1910. Fire conservancy in Indian forests. *Indian Forester* 36:679-686.
- Wikramanayake, E.D., E. Dinerstein, J.G. Robinson, K.U. Karanth, A. Rabinowitz, D. Olson, T. Mathew, P. Hedao, M. Conner, G. Hemley and D. Bolze. 1998. An ecology-based method for defining priorities for large mammal conservation: the tiger as case study. *Conservation Biology* 12:865-878.
- Zavaleta, E. 2000. Valuing Ecosystem Services Lost to *Tamarix* Invasion in the United States. In: *Invasive Species in a Changing World* (eds. H.A. Mooney and R.J. Hobbs), pp. 261-300. Island Press, Washington DC, USA.