Tree community change in a tropical dry forest: the role of roads and exotic plant invasion

AYESHA E. PRASAD[1,2]*

[1]*Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, Mysore 570002, India and* [2]*Department of Environmental and Forest Biology, State University of New York, College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA*

SUMMARY

Among the most endangered tropical ecosystems, tropical dry forests are threatened by degradation that includes edge effects arising from perturbations such as the creation and maintenance of roads and other clearings. While much is known about these adverse effects on tree communities in tropical moist forests, similar effects in tropical dry forests are little understood. This paper examines the relationship between roads, road-related exotic plant invasion and tree community change in a tropical dry forest in southern India. Forty pairs of roadside and interior plots across four factorial combinations of road width (wide and narrow) and understorey type (native and exotic) were sampled. Tree death and extant tree community composition were compared using generalized linear models and similarity analyses. Tree death near roads was more than double that away from them, suggesting that roads may increase tree death in these forests. The interactive effect of understorey type (exotic or native) and road width on tree death was significant, with highest tree death near wide roads bordered by exotic understorey. Conversely, tree community composition was influenced by road width and understorey type, but not by proximity to roads. Creation and maintenance of roads for forest management may have serious implications for tree communities in tropical dry forests and should thus be minimized. Exotic plants may also be important contributors to increasing tree death, and further research on their impacts, particularly into underlying mechanisms, is critical to the long-term conservation of tropical dry forest communities.

Keywords: community composition, degradation, generalized linear model, *Lantana camara*, non-metric multi-dimensional scaling, tree death

*Correspondence: Dr A. E. Prasad e-mail: ayesha@ncf-india.org

INTRODUCTION

Dry forests are considered among the world's most endangered tropical ecosystems (Janzen 1988). Yet, little is known about the structure and dynamics of tropical dry forests compared to those of tropical moist forests. The survival of tropical dry forest ecosystems is undermined by two broad classes of threats: loss of forest cover and degradation. While forest cover loss consists of episodic events of conversion of forest to alternative land-uses such as agriculture and development, forest degradation is manifest in a chronic gradual manner in forest remnants and is often rampant even within protected forests (Liu *et al*. 2001). One process associated with forest degradation is the creation of edges, the effects of which are a well-known and important threat to forest ecosystems (Gascon *et al*. 2000).

Since roads are clearings and form a distinct edge with the surrounding forest, their impacts can include increased tree mortality via microclimatic change (Kapos 1989; Williams-Linera 1990), mechanical damage (Chen *et al*. 1992) and high infestation rates by pathogens (Dickie & Reich 2005) resulting from edge creation. Although considerable research has addressed edge-related increases in tree mortality in tropical moist forest ecosystems, these effects are poorly understood in dry forests, which due to their strong seasonality may be particularly susceptible to alterations in microclimate (Kapos 1989; Williams-Linera 1990). The primary objective of this study was to assess the effects of the creation and maintenance of roads on tree death (defined as the ratio of dead trees to live trees) and tree community composition change in a tropical dry forest which is protected from loss of forest cover.

Facilitation of exotic plant invasion is also well documented among the varied effects of roads and other linear forest clearings and openings (see for example Lugo & Gucinski 2000; Honnay *et al*. 2008). Specifically, roads have been shown to act as conduits of exotic plants (Gelbard & Belnap 2003). Fragmented seasonal forests are particularly prone to colonization by invasive plants (Fensham *et al*. 1994; Laurance 1997), as such disturbance may promote exotic plant invasion (Davis *et al*. 2000). In the fragmented seasonal dry forests of southern India, intensive habitat management together with forest biomass harvest by local and indigenous communities (Silori & Mishra 2001) and fire (Kodandapani *et al*. 2004), appear to have facilitated invasion by exotic

plants, including the Neotropical shrub *Lantana camara* Linn. (Verbenaceae; hereafter *Lantana*). *Lantana* is widespread, and particularly abundant along roads and other clearings where it grows in dense thickets (often exceeding 5 kg m^{-2} dry weight, and comprising over 75% of the understorey biomass; A. E. Prasad & M. D. Madhusudan, unpublished data 2007; Appendix 1, see Supplementary material at URL http://www.ncl.ac.uk/icef/EC_Supplement.htm). Although in these tropical dry deciduous forests, exotic plants such as *Lantana* grow in close association with clearings such as roads, and roads may be at least partially responsible for these invasions, very little is known about whether such road-related invasion is associated with tree community change. My second objective was to determine whether tree death and community composition change were associated with the presence of *Lantana* along roads.

First, in order to test whether proximity to roads increases tree death and alters tree community composition, I compared tree death and extant tree community composition between roadsides and forest interiors. Based on studies that have shown the distinct effects of clearings on tree mortality (Esseen 1994; Ferreira & Laurance 1997; Harper *et al.* 2005), I predicted that there would be greater tree death near roads and roadsides than in forest interiors. Further, since a rise in tree mortality can fundamentally alter forest composition and diversity (Hubbell & Foster 1986), I predicted that the composition of the tree community should vary systematically between roads and forest interiors. Second, in order to determine whether road-related exotic plant invasion is associated with these tree community changes, I compared tree death and tree community composition between roads bordered by exotic understorey (dominated by *Lantana*) and those bordered by native forest understorey. While *Lantana* is known to have serious adverse impacts on native vegetation (see Gentle & Duggin 1997; Sharma & Raghubanshi 2007), these impacts are on forest understorey species and tree regeneration, and the nature of its impacts on adult trees is relatively unknown. Therefore, in keeping with the adverse effects of *Lantana* on other vegetation strata, I predicted that *Lantana*-invaded forest would be associated with greater tree death and, accordingly, different forest tree composition than forest with native understorey. I conducted this study in Bandipur Tiger Reserve (BTR), a protected tropical dry deciduous forest in the Western Ghats biodiversity hotspot in southern India (Myers *et al.* 2000), where an existing natural experiment allowed me to test my predictions under a fully factorial combination of treatments.

METHODS

Study area

BTR (880 km^2; 11°57′ N, 76°12′ E–11°35′ N, 76°51′ E) in the Western Ghats of southern India (Fig. 1) has temperatures ranging from 10° to 35°C and has an average annual rainfall of 800–1600 mm, most of which occurs during the monsoon season (June–October). BTR is predominantly
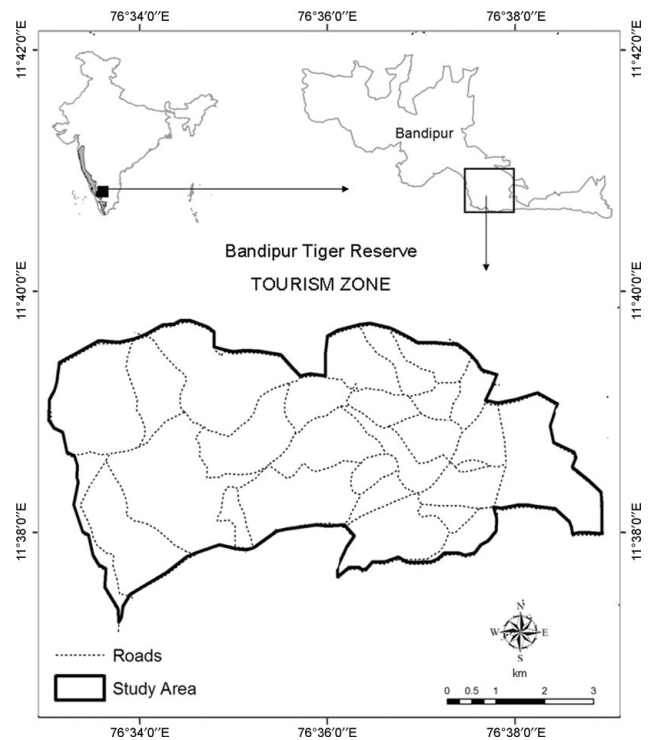

Figure 1 Diagrammatic map and location of the tourism zone of the Bandipur Tiger Reserve.

tropical deciduous forest dominated by *Anogeissus latifolia*, *Tectona grandis* and *Terminalia* spp. (Prasad & Sharatchandra 1984). The native understorey consists mainly of the tall grass *Themeda cymbaria*, along with shrubs such as *Helicteres isora*, *Holorrhaena pubescens*, *Zizyphus* spp. and *Grewia* spp. BTR and adjacent forests have been invaded by several exotic plants, such as *Lantana*, *Chromalaena odorata* and *Parthenium hysterophorus* (Murali & Sidappa Shetty 2001), the occurrence of which is thought to be associated with anthropogenic disturbances (Silori & Mishra 2001; Kodandapani *et al.* 2004).

Protected dry forests across the Western Ghats landscape, including BTR, are intensively managed for wildlife tourism and biodiversity conservation via small-scale forest clearing for the construction and maintenance of roads, waterholes and firebreaks. The study area (32 km^2) coincided with the assigned tourism area located in the south-eastern part of BTR. It has 72 km of roads, some of which are tourism roads, others being management roads (Fig. 1). Tourism roads are bordered by view-lines, which are clearings that run along both sides of roads and increase visibility for viewing wildlife, and are 30–40 m wide (wide roads). View-lines are maintained by cutting and burning understorey vegetation at least once a year, but sometimes more often depending upon how quickly the clearing is overgrown by *Lantana*; trees are left standing. Management roads are not bordered by view-line clearings and are 10–12 m wide (narrow roads). While most roads and clearings are bordered by *Lantana*, others have native understorey (Appendix 1, see Supplementary material at URL http://www.ncl.ac.uk/icef/EC_Supplement.htm).

Thus, management practices in BTR that maintain roads and view-lines, along with variation in understorey, offer an experimental set up within which to document tree death and tree community composition with respect to road, road width and road-associated exotic plants. Comparisons of tree death and tree community composition between roadside and forest interior were nested within comparisons across factorial combinations of understorey type (two levels, namely native and exotic) and road width (two levels, namely wide and narrow).

Data collection

Within this factorial experimental design, I counted trees in paired plots (road and interior, i.e. 50 m distant from the road) at 10 random locations in each of the factorial combinations of road width and understorey type (narrow-narrow, wide-native, narrow-exotic, wide-exotic). If view-lines were present (wide roads) then road plots were located within them; where view-lines did not border roads (narrow roads), road plots were placed immediately adjacent to the road within the edge. In each plot (10 m radius; $n = 80$ plots overall) I noted the total number and species of trees (>15 cm girth at breast height) and the number of dead trees (including snags, stumps and fallen trees). I used bark, leaf and flower characteristics to identify tree species. Dead trees without bark, or with damaged bark, for example by fire, could not be identified; consequently the species of 47 out of 573 sampled trees (approximately 8%) could not be determined. Data collection occurred between October 2006 and January 2007.

Statistical analyses

For tree death, I first tested for systematic variation in overall tree density across factors using a generalized linear model (GLM) with Poisson distribution (log-link) because these are count data (McCullagh & Nelder 1989). Since overall tree density varied systematically across factors, I used the ratio of dead to live trees per plot as a measure of tree death. This ratio was the response variable in a GLM for testing the effects of road, road width and understorey type on tree death. To neutralize inherent under-dispersion in these data ($\Phi = 0.24$), I used a quasi-likelihood distribution for this GLM (McCullagh & Nelder 1989; Crawley 2007). Additive effects of road (location), understorey type, road width, and road width × understorey type interaction on tree death were analysed sequentially. All analyses using generalized linear models were conducted in R 2.6.1 (R Core Development Team 2007).

For tree community composition, I first used a non-metric multi-dimensional scaling (NMDS) ordination to visualize compositional differences between tree communities in the various factorial treatment combinations. I used Bray-Curtis dissimilarity indices to estimate differences in composition of live trees between all pairs of plots. To determine whether compositional dissimilarities in live tree communities varied systematically among the different levels of road (location), road width and understorey type, I used an analysis

of similarities (ANOSIM). ANOSIM is analogous to the parametric analysis of variance, and tests for similarities or differences between groups of community samples (defined a priori) using permutation/randomization methods on a similarity/dissimilarity matrix (Primer-E 2001). A similarity or dissimilarity matrix consists of similarity/dissimilarity (distance) indices (such as Bray-Curtis or Euclidean) for all pairs of data points, distributed across all factors, in the community samples. The present ANOSIM would show whether location with respect to road, road width and understorey type were associated with compositional differences in the extant tree community. Finally, I used similarity percentage (SIMPER) to determine what species contributed to the compositional dissimilarity between groups or factors and whether certain species contributed disproportionately. I used PRIMER 5 software for the NMDS and ANOSIM.

RESULTS

I counted a total of 573 trees from 51 species during sampling. Total tree density (individuals per plot) ranged from 3 to 17, and live tree density varied between 1 and 16. Seventy per cent of plots (56 out of 80) contained at least one dead tree. The highest live tree density occurred in plots away from narrow roads, bordered by native understorey, whereas the highest dead tree density, which also coincided with the lowest live tree density, occurred in roadside plots associated with wide roads and exotic (*Lantana*-dominated) understorey (Fig. 2)

Tree death

Variation in tree death (ratio of dead to live trees per plot) was best explained by location with respect to road ($F_{1,78} = 5.75$, $p < 0.02$; Fig. 3) with road plots (0.44 ± 0.08 SE) having
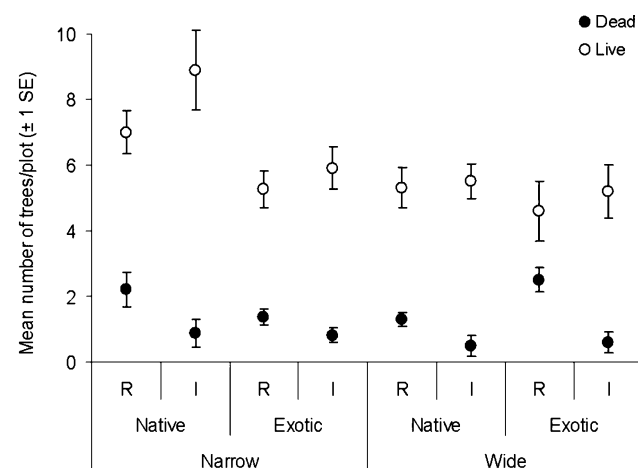
Figure 2 Mean density of live (○) and dead trees (●), measured by number of individuals in paired roadside (R) and interior (I; 50 m distant from road) 10 m radius plots, distributed across factorial combinations of road width (narrow and wide) and understorey type (native and exotic).
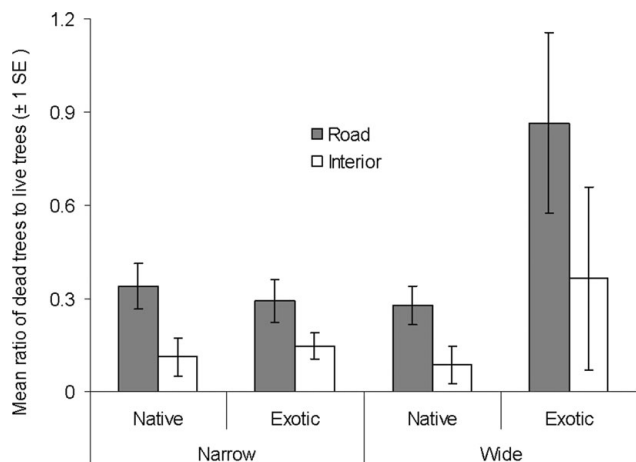
Figure 3 Mean tree death (ratio of dead to live trees per 10 m radius plot, $n = 80$) in tree communities near roads (road) and 50 m distant from roads (interior), distributed across factorial combinations of road width (narrow and wide) and understorey type (native and exotic), Bandipur Tiger Reserve.

145% greater tree death than interior plots (0.18 ± 0.08 SE). The main effect of road width on tree death was not significant ($F_{1,77} = 2.5$, $p = 0.11$). Further, although plots associated with exotic understorey (0.41 ± 0.11) had over twice as much tree death as plots associated with native understorey (0.20 ± 0.04), the relationship between tree death and understorey was not significant ($F_{1,76} = 3.74$, $p = 0.056$). However, the interaction between road width and understorey type was significant ($F_{1,73} = 3.94$, $p = 0.05$).

Tree community composition

Plots did not differ in composition of extant tree community between roadsides and interior forest (Fig. 4*a*). The ANOSIM showed that plot location (road versus interior) did not influence extant tree community composition (Global R = 0.009, $p = 0.22$). However, NMDS and ANOSIM showed that plots with *Lantana* had a significantly different composition of live trees relative to plots with native understorey (Global R = 0.135, $p = 0.001$; Fig. 4*b*). SIMPER showed that plots with native understorey had within-group dissimilarity of 37.6%, while those with *Lantana* understorey had average within-group dissimilarity of 40.1%. However, average dissimilarity between native and exotic understorey groups was 62.7%. While *Anogeissus latifolia* and *Terminalia alata* were more abundant in plots with native understorey, *Tectona grandis* and *Phyllanthus emblica* were more abundant in plots with *Lantana*. Similarly, plots associated with different road widths also differed significantly in composition (Global R = 0.152, $p = 0.001$; Fig. 4*c*). Plots associated with narrow roads were 43.6% dissimilar within group, and those associated with wide roads were 34.4% dissimilar within group, while plots were 62.7% dissimilar between narrow and wide road groups. Plots associated with wide roads had
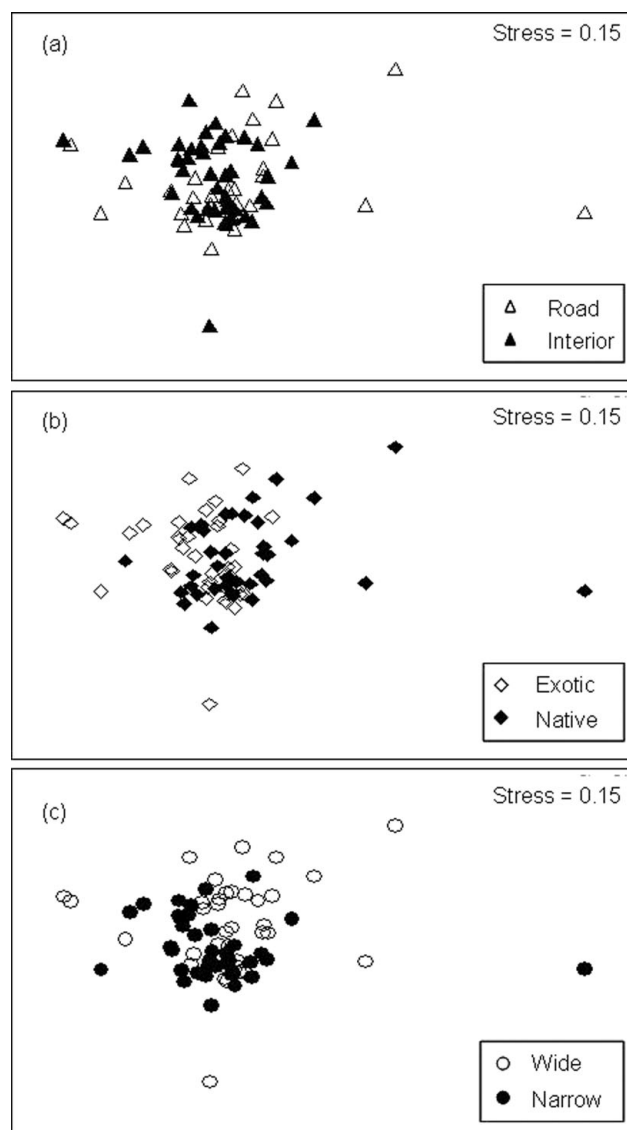
Figure 4 Non-metric multidimensional scaling (MDS) plots comparing species composition of extant tree community in two levels each of three factors: (*a*) plots located near roads (road) and distant from them (interior), data pooled across road width and understorey type; (*b*) plots associated with native versus exotic understorey, data pooled across road width and proximity to road; (*c*) plots associated with wide and narrow roads, data pooled understorey type as well as proximity to road.

relatively lower representation of *A. latifolia*, *T. grandis*, *T. alata* and *P. emblica*, four species which explain over 50% of the dissimilarity.

DISCUSSION

Tree death

Roads and their view-lines appear to be strongly contributing to increased tree death in these endangered ecosystems (*sensu* Janzen 1988), with tree death within and along roads being

two and a half times greater than that away from them. A variety of forest ecosystems also show greater tree mortality in association with clearings compared to interiors (temperate forest, Chen *et al.* 1992; boreal forest, Esseen 1994; tropical rainforest, Ferreira & Laurance 1997). Such clearing-related increases in tree mortality are likely to result in greater numbers of dead trees (and greater tree death) as documented by this study. While the negative impacts of clearings on trees are not novel in a global context, the implications for disturbed and fragmented tracts of forest, particularly insular patches of forest which are protected for biodiversity conservation, are especially serious. This dataset highlights that even management for conservation and tourism can have adverse effects on tree communities, which in turn may affect various animal taxa (for example invertebrates, Klein 1989; mammals, Stevens & Husband 1998; birds, Laurance & Gomez 2005). These indirect effects are in addition to the potential direct effects of roads on natural systems and species (Forman & Alexander 1998). Further, by acting as corridors or agents for dispersal, providing suitable environmental conditions and holding reservoirs of propagules for future episodes of invasion, roads may promote exotic species invasions (Parendes & Jones 2000) which have their own ecological fallout (Levine *et al.* 2003).

The occurrence of the highest dead tree density, together with the lowest live tree density in plots associated with an exotic understorey (Fig. 2), in addition to the 100% higher tree death in plots associated with exotic understorey compared to plots associated with native understorey (Fig. 3), clearly shows that here greater tree death is associated with the presence of exotic plants. These data highlight an association which cannot be interpreted as a causal mechanism. It is known that canopy gaps, which could arise due to clearing or tree death, promote *Lantana* (Fensham *et al.* 1994; Day *et al.* 2003). Thus, it is likely that forests where tree death due to roads and other perturbations is higher could be more 'invasible' by *Lantana* compared to forest with intact tree communities, resulting in the association indicated by this dataset. However, whether this association between tree death and exotic plants in turn leads to exotic plant-induced tree death remains to be investigated.

Tree community composition

Long-term anthropogenic forest disturbance is known to result in tree community composition change (Whitmore & Burslem 1998). However, this dataset does not indicate that proximity to road influences composition of the extant tree community since communities both adjacent to and distant from roads had similar composition (Fig. 4*a*). The lack of evidence for roads altering tree community composition may be owing to several reasons, of which I discuss two. Firstly, many roads in the study area have probably existed for several decades since these forests began to be exploited for game and timber. It is unclear as to what time scale is required for composition changes to manifest, and whether

the last few decades during which roads have existed suffice to precipitate community composition differences. Long-term studies on tree communities, such as those in Neotropical forests (see Condit 1995; Laurance *et al.* 2002), particularly those that monitor individual trees and the environmental and anthropogenic processes that they are exposed to, are essential in order to further understand mechanisms of tree community change in these dry forests. Secondly, it is also possible that a spatial separation of 40–50 m between road and interior plots was insufficient for community composition changes to be apparent. However, since the density of roads in the study area was very high (72 km of roads for a 32 km^2 area; 2.25 km. km^{-2}), a distance of >50 m from one road was, in several places, <50 m from another. Consequently, I could not compare composition in roadside plots with that in plots further than 50 m from roads. Comparison of tree composition between plots further from roads may elucidate the effects of distance from roads on composition.

Although road width was not associated with increased tree death, it was associated with significant differences in community composition of live trees, with wide roads having fewer individuals of the four dominant species, namely *A. latifolia*, *T. grandis*, *T. spp.* and *P. emblica*, than plots associated with narrow roads. The difference appears to be owing to changes in the abundance of dominant species rather than replacement or loss of species. The data also showed that *Lantana* was associated with changes in tree species composition. *P. emblica* and *T. grandis* were more abundant in invaded forest, while *A. latifolia* and *T.* spp. were more abundant in *Lantana*-free forest. Yet, I cannot conclude that *Lantana* causes tree composition change. As in the case of tree death, existing differences in tree community composition resulting from factors such as varying fire and management histories, as well as differential herbivory in the regeneration stage, could render these communities differently 'invasible' by *Lantana*. Given that we currently know very little about the ecology of these tree species, the mechanistic underpinnings of differences in composition associated with wide roads and exotic understorey remain unclear.

Conservation and management implications

These data highlight that tropical dry forest tree communities are linked to the creation and maintenance of roads. Furthermore, even management for conservation and tourism can be interwoven with patterns of forest degradation. Thus, in addition to other potential drivers of degradation, such as anthropogenic pressures for forest-biomass and fire, the creation and maintenance of roads within protected forest islands could be detrimental to these endangered forest ecosystems.

Although roads are essential for management, conservation and monitoring, as well as tourism, the creation and maintenance of roads and other clearings must be minimized, and when necessary, must be only as small as needed (Lugo & Gucinski 2000). Moreover, management planning and

implementation for the protection of dry forests, in India and elsewhere, must be based on sound science, and concomitant with rigorous monitoring. Additionally, there is an urgent need to better understand impacts of exotic plant invasions, particularly in edges bordering roads and other clearings, together with mechanisms of impacts and methods to combat them.

Trees largely determine forest architecture and micro-climate, and hence changes in tree community dynamics may strongly affect other forest species (Klein 1989) and ecological processes (Didham *et al.* 1996). The dry forests of the Western Ghats are critical habitat for globally important populations of endangered species such as the tiger *Panthera tigris* (Wikramanayake *et al.* 1998), gaur *Bos gaurus* and Asian elephant *Elephas maximus*. Thus, the long-term protection and conservation of these dry forest habitats is crucial not only for the forests themselves, but for a range of wildlife whose survival is closely tied to them. Understanding the drivers of tree community change, and forest degradation in general, is critical to the conservation of tropical dry forest ecosystems and their biodiversity.

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