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LETTER

Factors associated with long-term species composition in dry tropical forests of Central India

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Abstract

The long-term future of species composition in forests depends on regeneration. Many factors can affect regeneration, including human use, environmental conditions, and species' traits. This study examines the influence of these factors in a tropical deciduous forest of Central India, which is heavily used by local, forest-dependent residents for livestock grazing, fuel-wood extraction, construction and other livelihood needs. We measure size-class proportions (the ratio of abundance of a species at a site in a higher size class to total abundance in both lower and higher size classes) for 39 tree species across 20 transects at different intensities of human use. The size-class proportions for medium to large trees and for small to medium-sized trees were negatively associated with species that are used for local construction, while size class proportions for saplings to small trees were positively associated with those species that are fire resistant and negatively associated with livestock density. Results indicate that grazing and fire prevent non-fire resistant species from reaching reproductive age, which can alter the long term composition and future availability of species that are important for local use and ecosystem services. Management efforts to reduce fire and forest grazing could reverse these impacts on long-term forest composition.

1. Introduction

Tropical dry forests constitute 17% of currently standing tropical forests (UNEP-WCMC Forest Programme 2011), support large populations of forest dependent people (Miles et al 2006), and provide important ecosystem services such as watershed protection, biodiversity, climate regulation, soil fertility, flood control, and provision resources such as timber and fodder (for example: Maass et al 2005). Biophysical conditions such as climate and fire regime, and human use of different species potentially alter the long-term composition of these forests. Already, a long history of human habitation and management of tropical dry forests suggests that humans influence structure and community composition even in forests considered 'natural' (Heywood and Iriondo 2003).

The ability of these forests to provide ecosystem services may change with altered forest composition. For instance, conversion of tropical dry forests to scrub is associated with poor soil characteristics (Mehta et al 2008) and different species composition in the same area is associated with lower infiltration and evapotranspiration (Krishnaswamy et al 2013). Variables such as soil nutrients (Siebert 1987), vegetation structure, and species diversity (Kumar and Shahabuddin 2005, Lefevre et al 2012, Nagendra 2012) have been used to assess whether a forest has been altered so that it can no longer provide ecosystem-services or support livelihoods (Garcia-Fernandez et al 2008). Yet, forests that appear sustainable using these metrics may not be able to provide similar services in the future either due to catastrophic tipping points or trends of slow decline (Scheffer et al 2001,



Heywood and Iriondo 2003). Human use may have led to some changes (for example, reduced shade) that could lead to a catastrophic tipping point (as species that require shade during early growth cannot grow to adulthood) or a slow decline (as the proportion of shade bearer species that regenerate becomes lower). Thus, the long-term composition of the forest may already be altered due to impacts on regeneration and demographics of different tree species. Consequently, future forest composition may be very different from the present.

This study assesses plant traits and human uses of tree species associated with regeneration of forest species in dry tropical forests in a study area in Central India. We compare abundances of tree species in different size classes in sites with varying rates of human use and similar environmental conditions and species pool (Schmidt et al 2011). Agarwala et al (2016) concluded that human pressure in the study area alters forest biomass, composition and relative abundance of species. This study examines which factors, including site characteristics (e.g. population densities, livestock density, distance to market), types of human use (e.g. species part used, whether species is used consumptively, and whether a species is used for subsistence or for commercial purposes), and plant traits (e.g. shade tolerance, fire resistance) are associated with transition of species from lower size class to higher size class.

2. Methods and materials

2.1. Study area

The study was located in highly seasonal dry tropical forests around Kanha Tiger Reserve in Mandla, Balaghat and Seoni districts in India (figure 1). These forests are representative of dry tropical forests as they are highly heterogeneous with leaf fall concentrated in the summer months. Dominant trees include sal (*Shorea robusta*) and *Terminalia* species. Further, these forests protect the upper reaches of the watershed as they form the headwaters of the River Narmada (the 7th largest river system in India), provide important migration routes for wildlife (Sharma *et al* 2013, Yumnam *et al* 2014) and support the livelihoods of local populations (Saigal 2008).

2.2. Sample selection

From this landscape, we selected six representative villages for sampling based on population density, livestock density, available forest area, and distance to town. We used cluster analysis to identify clusters of villages which had similar values for these parameters, and then randomly selected two villages to serve as replicates from each of the three largest clusters (details in Agarwala *et al* 2016). In each cluster, we selected two villages that were located close to each other and shared the same forest (see figure 1 as an

example). The clusters had different population densities, forest cover, and distance to major towns (see appendix A for values), but population density was the most important predictor for differences in forest biomass (Agarwala et al 2016). In selecting villages, we also excluded those villages where the neighboring forest compartment (where a compartment is a welldefined forest management unit ranging in size from 0.1 to 5.3 km², and with a mean size of 2.3 \pm 1.06 km²) had a history of logging and silviculture by the Forest Department, to retain only those villages where changes in forests would be natural or due to villagelevel human use. We quantified forest use around these six selected villages by tracking people and cattle in the forest across two seasons in 2012, and used these data to identify forest patches around the three village clusters that had high use (used by both cattle and people in both seasons), intermediate use (used by either cattle or people in one season), or no known use (no documented use by either people or livestock) (figure 1; detailed methods in Agarwala et al 2016). We then surveyed forest vegetation in twenty sample plots (each plot consisted of five 20 m \times 20 m subplots) across the three village clusters where we placed plots in patches of high use, intermediate use and no known use (see appendix A for distribution of plots across village clusters).

2.3. Field surveys

For estimating tree population structure, we identified all floral species in four size classes: large trees (>10 cm DBH), medium-sized trees (4–10 cm DBH), small trees (4 cm DBH and height >2.1 m), and saplings (height <2.1 m) in five 20 m \times 20 m subplots in each plot. In this design, four subplots were located 100 m away from the central subplot in opposite directions. We also measured understory biomass and canopy cover using a spherical densiometer at two randomly located 1 m quadrats within each subplot. Species were identified using a plant identification key (Brandeis 2007) and local residents with forest experience. Finally, we recorded species with visual signs of browsing in each sample (Seidl *et al* 2011).

2.4. Method to assess long-term forest composition

Long-term sampling required for calculating species regeneration (Hall and Bawa 1993, Caswell 2001, Heywood and Iriondo 2003, Schmidt *et al* 2011) is not always possible (Feeley *et al* 2007). The coefficient of skewness calculated from size distribution of trees (Wright *et al* 2003) can predict the direction of change for most species (Feeley *et al* 2007), but gives an average value for the entire distribution of a species and masks the impact on individual size classes at which the drivers may operate. It also requires at least 25 individuals per site (Feeley *et al* 2007), which limits the number of species that can be examined (appendix B). Our study modified this method by



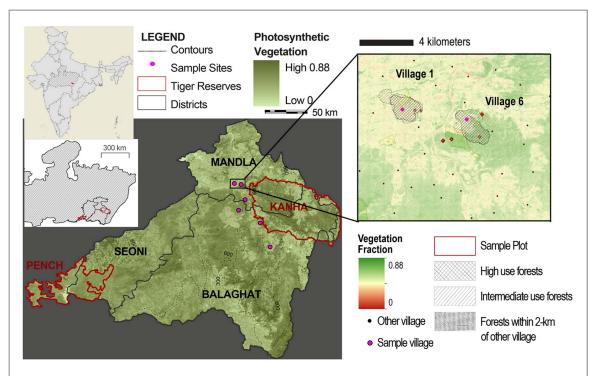


Figure 1. Study Area: six representative villages (three replicates) in study area. Inset shows layout of plots in a village replicate. For more details, see Agarwala et al (2016).

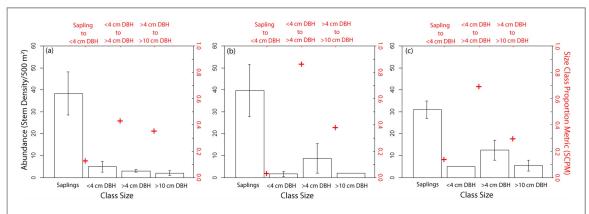


Figure 2. Abundances (black bars) and size class proportion metric SCPMs (red crosses) for *Terminalia alata* at (a) low frequency of use, (b) intermediate-use frequency, and (c) high frequency of use.

collecting species abundance at size class intervals (Herrero-Jáuregui *et al* 2012). We then calculated a size-class proportion metric (henceforth referred to as SCPM) separately for every species in each transect. This is defined as the ratio of abundance of a species at a site in a given size class to total abundance in that size class and the size class below it. We calculate SCPM as:

$$C_{ijk} = \frac{F_{ij(k+1)}}{F_{ijk} + F_{ij(k+1)}},\tag{1}$$

where F_{ijk} is the abundance of species i at site j at size class k.

SCPM quantifies the proportion of individuals in a species that are present in a higher size class, which represents the slope of the population distribution in the size-class intervals between lower size class and higher size class (figure 2). SCPM varies from zero (present in lower size class but absent in higher size class at a sample site) to a maximum value of one (present in higher size class but absent in lower size class). Significantly different SCPM values at sites used at a higher frequency than at comparable sites with lower frequency of use where environmental factors are constant would suggest that human use is altering the proportion in higher size class, although causality can only be inferred. Over the long term, differences in SCPM would lead to differences in species composition in heavily used forests, compared with comparable sites used at lower frequency.

Unlike static life table methods that examine sizeclass distributions at a single site (Wright *et al* 2003),



this study reduces the impact of variations in size distributions due to past events such as logging, pathogen outbreaks, and droughts, by comparing size-class distributions at heavily used sites with locally situated comparable sites with lower frequency of use within the same village cluster. Although population density was associated with differences in biomass and forest structure in the study area, frequency of use was associated with changes in species diversity and relative abundance of species (Agarwala et al 2016). By comparing SCPM within and across clusters, we can identify factors within and across clusters that are associated with species and trait-level changes in the forest. Further, some species are necessarily absent in certain size classes due to their natural growth form. For grasses such as bamboo (Dendrocalamus sp.), we only recorded survival in the lower two size classes (height <2.1 m; height >2.1 m). Similarly, for species that do not reach large sizes (>10 cm DBH), presence for that size class was excluded from the analysis. This method is limited because it does not account for seedling germination and does not provide information on direction of change, as a higher SCPM than the control could be a result of both the higher proportion of higher size class and lower abundance of lower size class. Yet, given the presence of a germinated seedling (if a species is present in lowest size class) and given similar species pool, comparing SCPMs across different sites allows us to identify and understand change. Using SCPM may also bias analysis as uncertainty will be higher for SCPMs of those species with lower abundances, but we addressed this by removing observations where total abundance of species in a transect for a size class and the size class above it was less than one standard deviation below the mean. Because our previous study examined factors associated with differences in relative abundance of species (Agarwala et al 2016), we could remove abundance-related information to focus on factors associated with transitions of species to higher size classes.

2.5. Identification of factors associated with size class transitions

We used Generalized Linear Mixed Models (GLMM) to identify which factors are associated with differences in size class transitions based on a sample of 20 plots representing 39 species (see below). The response variable was SCPM and predictor variables included plant traits, biophysical conditions, and human use characteristics (table 1).

2.5.1. Data for predictor variables

We collected data on factors associated with the site that could impact regeneration due to human use (livestock and human population per forest area, distance to market and frequency of use) and sitespecific characteristics (canopy and understory cover, species diversity, mean fire radiative power, precipitation, temperature, elevation and slope) (table 1). We also collected data on soil nutrients and pH but there were no differences in these factors across sites (Agarwala *et al* 2016).

Plant traits included in the model are those known to influence size-class distribution (Wright et al 2003). These traits are: shade tolerance, wood density, resistance to fire and trampling, tolerance to planting density, and growth form (table 1). Shade tolerance has been identified as the most important plant trait in determining size-class distribution, and wood density is used as a proxy for physiological and morphological traits (Wright et al 2003). Particularly, wood density represents the growth strategy of a species, where species with lighter wood grow faster (Wright et al 2003). Data on plant traits were collected for as many species as possible from existing literature (Troup 1983, Brandeis 2007). Overall, we collected information on 39 species out of 84 for most categories (see detailed data sources in table 1 and detailed information for each species in table S1 of supporting information). These represent 91% of individuals in the sample plots.

We also included predictor variables for human uses known to impact regeneration rates. Data were compiled from field surveys, literature reviews and 250 interviews conducted in the study area (Agarwala et al 2016). For example, predictors from interviews included whether local people considered the species to be important (percentage of time that respondents recalled a species as important when asked about the uses of the forest: Agarwala et al 2016), whether the species was browsed (percentage of time that a species was browsed relative to the number of times it was present in the plot: Agarwala et al 2016), which species part was used, whether use was consumptive, whether the species was used for subsistence or for the market, and the specific use of every species part (table 1; table S1 in supporting information).

2.5.2. Model

We used GLMM to test which site-specific conditions, species-specific plant traits and use characteristics were significant in explaining differences in SCPM for saplings to small trees (n=208), small trees to medium-sized trees (n=190), and medium-sized to large trees (n=96). The GLMMs were run separately for each size class. The response variable was SCPM for 39 species. The model included species identity and village cluster as random effects and interactions that we hypothesized as plausible, for example, interaction of fire resistant species and fire radiative power at the site (complete list of interactions tested in table S2 in supporting information). The global model for this analysis was:



Table 1. Variables used as predictors in generalized linear models to predict size class proportion metric (SCPM).

Predictor	Source				
Species traits:					
Shade tolerance (categories: light demanding, light demanding but	Literature review (Troup 1983, Brandeis 2007)				
some shade tolerated, requires shade when young, shade bearer)	The state of the s				
Growth form (categories: tall tree with a crooked trunk, tall tree with a	Literature review (Troup 1983, Brandeis 2007)				
short trunk, tall tree with a straight trunk, moderate sized tree with a crooked trunk, moderate sized tree with a straight trunk, small					
tree, shrub, other)					
Resistance to fire (categories: no, somewhat, yes, yes when the plant is	Literature review (Troup 1983, Brandeis 2007)				
older)	•				
Resistance to trampling/cattle (categories: none, not at high inten-	Literature review (Troup 1983, Brandeis 2007)				
sity, yes)					
Resistance to planting density (categories: species grows well despite	Literature review (Troup 1983, Brandeis 2007)				
competitions, species growth is improved with ground weeding,					
species growth is improved by removal of overhanging vegetation					
or local canopy competition) Wood density (kg/cubic feet)	Literature review (Troup 1983, Brandeis 2007)				
Site Characteristics (values averaged for each plot; continuous variables sta	ndardized to the mean: $\sum (xi - \bar{x})/sd$):				
Frequency of use (categories: no recorded use $= 0$, intermediate	Field surveys (details in: Agarwala et al 2016)				
use = 1, high use = 2)					
Livestock per Forest Area (livestock populations per 30 m × 30 m	Census data (Department of Animal Husbandry 2012) and remote				
pixel) Population per Forest Area (human populations per 30 m $ imes$ 30 m	sensing for forest cover (details in: Agarwala <i>et al</i> 2016) Census data (Wildlife Institute of India 2011a) and remote sensing				
pixel)	for forest cover (details in: Agarwala et al 2016)				
Distance to market (km)	Village Census (Wildlife Institute of India 2011a)				
Canopy cover (proportion of canopy closure)	Field surveys				
Understory biomass (kg m $^{-2}$)	Field surveys				
Elevation (m) (30 m \times 30 m resolution)	ASTER-DEM (reverb.echo.nasa.gov)				
Slope (m ⁻¹)	Calculated from elevation				
Species diversity indices (Shannon and Simpson diversity indices)	Field surveys				
Fire radiative power (mW m $^{-2}$) (resampled from 1 km resolution)	MODIS 14A1 (reverb.echo.nasa.gov) mean (January–June:				
	2002–2012)				
Precipitation (mm h ⁻¹ converted to mm yr ⁻¹) (resampled from	TRMM 3B43 (trmm.gsfc.nasa.gov) mean (January–June:				
$0.25^{\circ} \times 0.25^{\circ})$	2002–2012)				
Temperature (Kelvin) (resampled from 1 km resolution)	MODIS 11A1 (reverb.echo.nasa.gov) mean (February–June: 2002–2012)				
Human use characteristics:					
Species browsed (proportion)	Field surveys (Agarwala et al 2016)				
Species named as important (proportion)	Interviews (Agarwala et al 2016)				
Species part used (categories: bole, branch and leaves, bark, sap, fruit, flower)	Interviews (Agarwala <i>et al</i> 2016), literature review (Brandeis 2007)				
Species use (categories: food, market, fodder, fuel-wood, construc- tion, implements, other)	Interviews (Agarwala et al 2016), literature review (Brandeis 2007)				

$$Y(\text{SCPM}) = B_0 + \sum (B_i \times (\text{site condition } [i]))$$

$$+ \sum (B_j \times (\text{species use } [j]))$$

$$+ \sum (B_k \times (\text{plant trait } [k]))$$

$$+ \sum (B_{ijk} \times \text{interaction}$$

$$\times (\text{site condition } [i],$$

$$\text{species use } [j], \text{plant trait } [k]))$$

$$+ (1| \text{Species}) + ((1| \text{Village Cluster}),$$

where B_0 = intercept, B_i = beta-coefficient for predictors representing *i*th site condition, B_i = beta-

coefficient for predictors representing jth species use, B_k = beta-coefficient for predictors representing kth plant trait, B_{ijk} = beta-coefficients for interaction terms where interaction may be between two or more predictors.

To account for collinearity, only predictors with correlations less than 0.3 were retained (correlation matrices in table S3 in supporting information) and used to construct alternative global models (table S2 in supporting information). Each of our global models included all the predictors that could be included

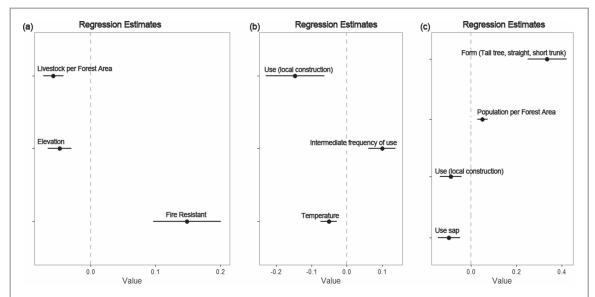


Figure 3. β -coefficient estimates and 95% confidence intervals (bars) for factors associated with change in SCPM from (a) saplings to small trees, (b) small to medium-sized trees, and (c) medium-sized trees to large trees.

without adding correlated predictors. Our alternative global models used correlated predictors separately. For example, if one global model included livestock density, which is highly correlated with population density, the other global model included population density and not livestock density. Our other alternative models modified the global models by deleting predictors. For models with interaction terms, we did not include any other correlated predictors, but the GLMM necessarily includes the individual predictors in an interaction term as predictors in the model. We used least AIC score to select the best model for each analysis (Burnham and Anderson 2002) and used ANOVA to test whether inclusion of interaction term or predictor was significant. We also calculated pvalues for predictors in models by using R package nlme (Pinheiro et al 2016). We used the same response and predictor variables in a regression-tree (R package randomForest: Liaw and Wiener 2002). Because randomForest bootstraps the analysis by selecting a random subsample of the dataset for each run of the analysis, we expect that similar results might provide a secondary check on the results.

3. Results

The variation explained (R^2 values) by the best model for SCPM from saplings to small trees was 0.36, for SCPM from small to medium size trees was 0.49 and from medium sized trees to large trees was 0.26. Analysis using a regression tree (randomForest) provided similar significant predictors as the least AIC method (figure C1, figure 3 shows only significant predictors). Because regression tree analysis

bootstraps the observations, it reduces the impact of influencing variables, and may be considered a complementary analysis yielding similar results. However, regression tree analysis does not allow inclusion of interaction terms or random effects, and thus can also be considered very different from GLMMs. Although some predictors performed poorly in randomForest (figure C1) and may be considered less dependable than other predictors—such as use as sap for transitions from medium-sized trees to large trees—the fact that the most important predictors using both analyses were similar (fire resistant species and livestock density for transitions from saplings to small trees, and growth form and use for local construction for transitions from medium-sized trees to large trees) lends further credence to the results.

For SCPM of species from saplings to small trees, higher SCPM was associated with fire resistance and lower SCPM was associated with livestock per forest area (figure 3, table C1, table S2 in supporting information). From small to mediumsized trees, site conditions (intermediate frequency of use and temperature) and species use (for local construction) were associated with differences in SCPM (figure 3). From medium-sized trees to large trees, higher SCPM was associated with higher human population density. Species that were tall but had a short trunk (and were thus not ideal for local construction) were also associated with higher SCPM in comparison with tall trees with tall trunks (ideal for local construction) and small and medium-sized trees. Species that were used for local construction and sap were also associated with lower SCPM (figure 3).



Overall, SCPM from saplings to small trees is lower with increasing livestock density. This trend of negative influences of human activities is reversed for transitions from medium-sized to large trees, for which increasing human population density is associated with higher SCPMs.

Human use of plant species is also significant, from small to medium-sized trees and from medium-sized to large trees. Consumptive use (where use necessitates the extraction of the individual tree from the forest) such as use of wood for local construction is associated with lower SCPM, while non-consumptive use of species for fuel-wood, fruit (for non-food purposes such as sale or local uses such as poison) are not associated with changes in SCPM. However, almost all site conditions that are included in the final models are influenced by human use (livestock and human populations, frequency of use), which suggests that alteration of site conditions due to human management is also responsible for changes in species composition.

The plant trait of fire resistance is the most important variable explaining transitions from saplings to small trees in the regression tree (figure C1). Consequently, non-fire resistant species at sites with high human pressures may be unable to propagate from saplings to small trees.

Overall, these results suggest that direct human use in the form of use for local construction as well as changes in site conditions due to human use in the form of livestock intensity are associated with changes in long-term forest composition, and that some species traits (lack of fire resistance) may be particularly vulnerable to these changes.

4. Discussion

Human management of forests alters forest composition either because disturbances create conditions that cause increases in abundance of some species or because forest users increase abundance of species that provide useful products by selectively removing other species (Crook and Clapp 1998). This study supports both of these pathways of human impacts on forest composition, as both direct and indirect uses were associated with changes in SCPM. For direct use, differences in SCPM occur for those species with direct consumptive use for local construction but not for those species for which only specific parts are harvested (e.g. where Diospyros melanoxylon leaves are extracted for the market, or Madhuca indica flowers are extracted for the market or for local consumption). For indirect use, this study provides evidence that the distribution of some species is influenced by disturbance. In particular, SCPM for saplings to small trees is higher for fire resistant species. Increase in survival

of species that are resistant to fire may be an indirect impact of disturbance such as burning forest understory to augment production of non-timber forest produce. Livestock populations are also negatively associated with transitions from sapling to small trees. Both cattle use and fire can damage saplings, alter rates of tree establishment and change the successional stage of the forest. Species that may be able to defend themselves via specific traits such as their phenology, resistance to disturbance or sapling defences against browsing (Seidl et al 2011) will grow at the expense of others. Since cattle grazing and fire prevent affected species from growing past sapling stage and reaching reproductive age, these species may be most vulnerable to local extinction, and may be potentially more harmful than impacts at higher size classes.

Overall, this study demonstrates that human activities can create disturbances that may alter long-term forest composition, as species that are resistant to human use may increase their proportion in the forest. Over the long term, other species may further reduce in frequency, become extinct locally and lead to shortages for local people. These changes could also reduce species and ecosystem diversity (Crook and Clapp 1998).

The study also highlights the importance of multispecies analysis to examine the long-term impact of human use on forest composition. Most research on impact of harvest and forest use for sustainable forestry is restricted to a few species that are known for their commercial value (Schmidt *et al* 2011). This study extends the analysis to other forest species by incorporating plant traits as a factor affecting long-term forest composition (Amatangelo *et al* 2014). Given the species diversity and heterogeneity in tropical deciduous forests, examining a large number of species better represents the forest than examining only the most abundant species (>25 individuals per site).

5. Conclusions

This study suggests that direct human use of tree species as well as indirect human alterations of the forest are altering long-term forest composition in the study region's tropical dry forests. For instance, fire and livestock grazing may have greater long-term impact, as they alter transition from saplings to small trees and change the probability of reaching reproductive age, than direct human use for fuel-wood, construction and commerce. While changes in the composition of large tree species suggest changes in forest structure and function, they do not alter the reproductive potential of species.



Table A1. Details on villages selected, based on data collected by Wildlife Institute of India (total population, distance to town), Department of Animal Husbandry (cattle and buffalo populations) and GIS (Agarwala *et al* 2016).

Village cluster	Village ID	Total population	Cattle + buffalo	Dist. to town (km)	Forest cover (km ² within 2 km radius)
DH	Village1	1007	500	7	1.75
DH	Village6	846	519	12	4.53
HA	Village5	881	373	15	2.40
HA	Village3	781	588	14	4.42
DU	Village2	403	737	21	7.94
DU	Village4	755	670	41	8.41

Table A2. Number of plots at different intensities of use in different village clusters.

Village cluster	No known use	Intermediate use	High use
DH	1	2	3
DU	3	3	2
HA	1	2	3

Results suggest possible interventions that may prevent local extinctions or reduced abundance of some species. For instance, managing fire and cattle grazing would maintain present forest composition more effectively than restricting use for fuel-wood, which does not appear to impact size class transitions, or construction, which only impacts size class transitions to large trees.

This study has implications over a broader geographical area, particularly dry tropical forests in Asia and Africa, which comprise a highly threatened ecosystem due to high human population densities and continuous use. An understanding of the patterns and impacts of human use and their interactions with environmental conditions, as demonstrated in this paper, will be important to understand the future of forests and the services they provide as human use may reduce abundance of certain species over long time scales. This study utilizes an approach to identify processes that lead to change in forest composition in these forests that can be applied in other forests similar to the study area.

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Appendix A

Details of population densities, distance to town and forest cover in sample villages in the study's village clusters are listed in table A1. Distribution of plots in forest patches that had high, intermediate and no recorded use intensity across three village clusters in the study area is given in table A2. Village cluster names are coded to protect the identity of villagers who provided sensitive information in return for confidentiality. Multiple attempts were made to increase number of plots with no known use, but it was not logistically possible.

Appendix B

Eighty-four total species (including trees, shrubs, climbers and grasses) were recorded in the study region in which 105 species have been recorded previously (Wildlife Institute of India 2011b). Of these, details on plant traits and human use characteristics could be collected for 39 species, which represented 91% of individuals. For comparison with methods using coefficient of skewness, we calculated how many species we could have examined using coefficient of skewness. One pre-condition for analysis using coefficient of skewness is a minimum of 25 individuals per plot (Feeley et al 2007), which left us with 16 species of which only five species occurred more than twice (figure B1). Further, comparison across sites required that the species be present at multiple sites within a cluster (which had the same species pool). This meant only four species could be compared in two clusters, and two species could be compared in one cluster (table B1).



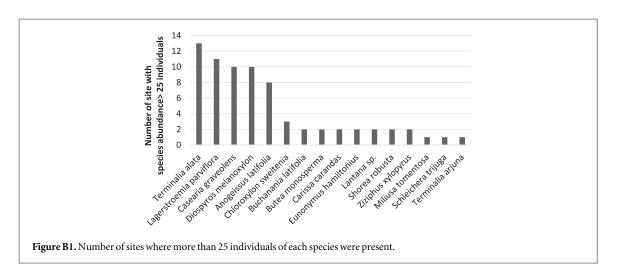


Table B1. Site conditions for which more than 25 individuals per species were present. Bold represents those species where species were present at multiple sites within a village cluster.

				-					
Village cluster	DH			DU		HA			
Frequency of use	0	1	2	0	1	2	0	1	2
Anogeissus latifolia	1	1	1	2	1	1	0	0	1
Chloroxylon	0	0	0	2	1	0	0	0	0
sweitenia									
Buchanania latifolia	0	1	0	0	0	0	0	0	1
Butea monosperma	0	1	0	0	0	0	0	0	1
Carissa carandas	0	1	0	0	0	0	0	0	1
Casearia graveolens	0	2	0	1	2	2	0	2	1
Diospyros	0	2	0	1	3	2	0	0	2
melanoxylon									
Eunonymus	0	1	1	0	0	0	0	0	0
hamiltonius									
Miliusa tomentosa	0	0	0	0	0	0	0	1	0
Lagerstroemia	0	0	1	3	3	1	0	1	2
parviflora									
Lantana sp.	0	0	0	0	0	2	0	0	0
Schleichera trijuga	0	0	0	0	0	0	0	1	0
Shorea robusta	0	0	0	0	0	0	1	1	0
Terminalia arjuna	0	0	0	0	0	0	0	0	1
Terminalia alata	1	2	1	3	2	2	0	0	2
Ziziphus xylopyrus	0	1	0	0	1	0	0	0	0

Appendix C

 ${\bf Table \, C1.} \, {\bf Significance} \, (p\text{-values}) \, {\bf of} \, {\bf predictors}.$

Factor	p-value where models were compared using ANOVA	p-value using nlme	
Saplings to small trees			
Interaction (fire	0.14	0.13	
$resistance \times frequency of use)$			
Fire resistance	0.007	0.0016	
Frequency of use	0.21	0.12	
Elevation	0.02	0.009	
Livestock per Forest Area	0.0001	0.0003	
Small trees to medium-sized trees			
Temperature	0.02	0.001	
Intermediate frequency of use	0.009	0.008	
Use for local construction	0.05	0.05	
Medium-sized trees to large trees			
Use sap	0.02	0.05	
Use for local construction	0.05	0.05	
Population per Forest Area	0.03	0.04	
Growth form	0.0003	0.0025	

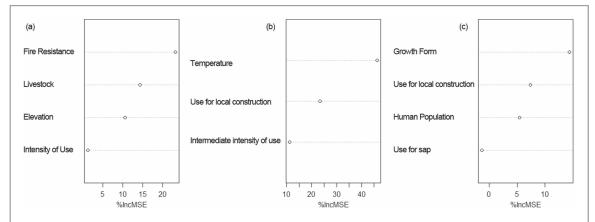


Figure C1. Importance of predictors for SCPM from (a) sapling to small trees, (b) small trees to medium-sized trees, and (c) medium-sized trees to large trees. Results obtained using randomForest's regression tree.



References

- Agarwala M, DeFries R S, Qureshi Q and Jhala Y V 2016 Changes in the dry tropical forests in Central India with human use *Reg. Environ. Chang.* 16 5–15
- Amatangelo K L, Johnson S E, Rogers D A and Waller D M 2014
 Trait-environment relationships remain strong despite 50
 years of trait compositional change in temperate forests *Ecology* 95 1780–91
- Brandeis D 2007 Forest Flora of North-West and Central India: A Handbook of the Indigenous Trees and Shrubs of Those Countries (Dehradun: Bishen Singh Mahendra Pal Singh)
- Burnham K P and Anderson D R 2002 Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach (New York: Springer)
- Caswell H 2001 Matrix Population Models-Construction, Analysis, and Interpretation (Sundarland, Massachussetts: Sinauer)
- Crook C and Clapp R A 1998 Is market-oriented forest conservation a contradiction in terms? *Environ. Conserv.* 25 131–45
- Department of Animal Husbandry 2012 18th Livestock Census, 2007 Ministry of Agriculture, Government of India
- Feeley K J, Davies S J, Noor M N S, Kassim A R and Tan S 2007 Do current stem size distributions predict future population changes? An empirical test of intraspecific patterns in tropical trees at two spatial scales J. Trop. Ecol. 23 191–8
- Garcia-Fernandez C, Ruiz-perez M and Wunder S 2008 Is multipleuse forest management widely implementable in the tropics? For. Ecol. Manage. 256 1468–76
- Hall P and Bawa K 1993 Methods to assess the impact of extraction of non-timber tropical forest products on plant populations *Econ. Bot.* 47 234–47
- Herrero-Jáuregui C, Sist P and Casado M A 2012 Population structure of two low-density neotropical tree species under different management systems For. Ecol. Manage. 280 31–9
- Heywood V H and Iriondo J M 2003 Plant conservation: old problems, new perspectives *Biol. Conserv.* 113 321–35
- Krishnaswamy J, Bonell M, Venkatesh B, Purandara B K,
 Rakesh K N, Lele S, Kiran M C, Reddy V and Badiger S 2013
 The groundwater recharge response and hydrologic services
 of tropical humid forest ecosystems to use and reforestation:
 support for the 'infiltration-evapotranspiration trade-off
 hypothesis' J. Hydrol. 498 191–209
- Kumar R and Shahabuddin G 2005 Effects of biomass extraction on vegetation structure, diversity and composition of forests in Sariska Tiger Reserve, India *Environ. Conserv.* 32 248–59
- Lefevre K L, Sharma S and Rodd F H 2012 Moderate human disturbance of rain forest alters composition of fruiting plant and bird communities *Biotropica* 44 427–36
- Liaw A and Wiener M 2002 Classification and Regression by RandomForest R News 2/3 18–22

- Maass J M *et al* 2005 Ecosystem services of tropical dry forests: insights from long-term ecological and social research on the pacific coast of Mexico *Ecol. Soc.* **10** 17 (www. ecologyandsociety.org/vol10/iss1/art17/)
- Mehta V K, Sullivan P J, Walter M T, Krishnaswamy J and DeGloria S D 2008 Ecosystem impacts of disturbance in a dry tropical forests in southern India *Ecohydrology* 1 149–60
- Miles L, Newton A, DeFries R, Ravilious C, May I, Blyth S, Kapos V and Gordon J E 2006 A global overview of the conservation status of tropical dry forests *J. Biogeogr.* **33** 491–505
- Nagendra H 2012 Assessing relatedness and redundancy of forest monitoring and change indicators *J. Environ. Manage.* 95 108–13
- Pinheiro J, Bates D, DebRoy S, Sarkar D and Core Team R 2016 nlme: Linear and Nonlinear Mixed Effects ModelsOnline: (http://cran.r-project.org/package=nlme)
- Saigal S 2008 Non-Timber Forest Products and Forest Governance: Synthesis Report Based on Three State-Level Studies Carried out During 2006–2007 (India: Forest Governance Learning Group)
- Scheffer M, Carpenter S, Foley J A, Folke C and Walker B 2001 Catastrophic shifts in ecosystems *Nature* 413 591–6
- Schmidt I B, Mandle L, Ticktin T and Gaoue O G 2011 What do matrix population models reveal about the sustainability of non-timber forest product harvest? *J. Appl. Ecol.* 48 815–26
- Seidl R et al 2011 Modelling natural disturbances in forest ecosystems: a review Ecol. Modell. 222 903–24
- Sharma S, Dutta T, Maldonado J E, Wood T C, Panwar H S and Seidensticker J 2013 Forest corridors maintain historic gene flow in a tiger metapopulation in the highlands of central India *Proc. R. Soc.* 280 20131506
- Siebert SF 1987 Land use intensification in tropical uplands: effects on vegetation, soil fertility and erosion *For. Ecol. Manage.* 21 37–56
- Troup R S 1983 Silviculture of Indian Trees vol 1–6 (Dehradun: Forest Research Institute)
- UNEP-WCMC Forest Programme 2011 Global statistics (www. unep-wcmc.org)
- Wildlife Institute of India 2011a Census of India for Critical Wildlife Habitats. This is a 2001 Census Based Village-Level Data Attached to a Shapefile of Villages. Data Used with Permission (Dehradun: Wildlife Institute of India)
- Wildlife Institute of India 2011b *Vegetation Plot Data* Madhya Pradesh Forest Department, Dehradun
- Wright S J, Muller-Landau H C, Condit R and Hubbell S P 2003 Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees *Ecology* 84 3174–85
- Yumnam B, Jhala Y V, Qureshi Q, Maldonado J E, Gopal R, Saini S, Srinivas Y and Fleischer R C 2014 Prioritizing tiger conservation through landscape genetics and habitat linkages PLoS One 9 e111207