Influence of anthropogenic factors on woody species composition, structure and demography in Eastern Ghats, India

Dissertation

zur Erlangung des Doktorgrades der Naturwissenschaften (Dr. rer. nat.)

der
Naturwissenschaftlichen Fakultät I – Biowissenschaften –
der Martin-Luther-Universität
Halle-Wittenberg

vorgelegt von
Neeraja Venkataraman

Gutachter:
Prof. Dr. Tiffany Marie Knight
Prof. Dr. Stan Harpole
Dr. Orou G. Gaoue

Datum der Verteidigung: 29.02.2024

Dedication

To my mother,

the wind beneath my wings

Gloriosa superba

Table of contents

Summary

Almost a third of the world’s population lives in dry tropical forest and savanna ecosystems and there is high human dependency for resources from these ecosystems, such as food, fuelwood, non-timber forest products and livestock grazing. Dry tropical ecosystems are being lost or degraded at an alarming rate due to changes in land use and climate. These dry tropical ecosystems cover a significant portion of the country of India and provide significant services to the human populations. Despite their ecological and socio-economic significances, dry tropical ecosystems are underrepresented in protected areas and receive less research focus than other ecosystem types. In the Eastern Ghats of India, woody plants in dry ecosystems are important for livestock grazing and fuelwood extraction, however the anthropogenic activities of burning to provide a flush of palatable grasses for grazing animals and harvesting of branches and stems for fuelwood and other purposes might threaten the long-term sustainability of these resources. My thesis examines the effect of harvesting and burning on woody plant community composition and population dynamics.

This dissertation is structured into five chapters to address this general theme. Chapter 1 broadly introduces the topics of forest community composition and structure and how anthropogenic activities alter this composition and structure. I present background on the context of the Eastern Ghats and the current state of our knowledge on the effects of fire and harvesting on woody plant composition and population dynamics. I set up the knowledge gaps that motivated the dissertation research.

Chapters 2-4 present my original research, and are stand-alone studies that have been published or submitted for publication in peer-reviewed scientific journals. In Chapter 2, I analyzed plots in the Eswaramala Reserve Forest to compare areas affected by recent fire with those not affected by recent fire. My results showed that burned areas experience an increase in stem density, but a decrease in species richness as fire-resistant and tolerant species became more dominant in the community. These species possess traits such as thick bark and clonal sprouting. Moreover, the presence of fire caused a shift in the size structure, favoring smaller, resprouting individuals.

In Chapter 3, I examined the vital rates and population growth rates of three dry tropical tree species under different conditions of harvesting. Using integral projection models, I found variations in demographic rates among the species. Harvesting led to reduced growth rates in two of the species. One species that was subjected to both branch and main stem harvesting experienced a significant decline in population growth rate. Analysis through life table response experiments indicated that this decline was primarily attributed to harvested individuals having to regrow from their base. Seed recruitment was limited for all species, possibly due to the presence of additional threats like fire.

In Chapter 4, I sampled more than 600 individual trees and compared the composition and structure of wooded savanna and open savanna habitats. Results showed significant differences in tree composition due to species turnover, likely influenced by soil, land use history, and current practices. Important tree species varied between the habitats. Both habitats had a right-skewed size distribution, likely attributed to different anthropogenic factors: fire in wooded savannas and grazing/harvesting in open savannas.

In Chapter 5, I discuss the overall findings of the dissertation, its limitations, and its utility to contribute to conservation. My research provides new knowledge on the effect of anthropogenic factors on community composition and demography in the Eastern Ghats and provides a baseline for future research in this understudied region.

Keywords: fire; harvesting; species composition; species diversity; size structure; demography; population growth rate; dry forest; savanna; Eastern Ghats; Deccan Plateau

Zusammenfassung

Fast ein Drittel der Weltbevölkerung lebt in trockenen tropischen Wald- und Savannenökosystemen, und der Mensch ist in hohem Maße von den Ressourcen dieser Ökosysteme abhängig, z. B. von Nahrungsmitteln, Brennholz, Nichtholzprodukten aus dem Wald und Viehweiden. Trockene tropische Ökosysteme gehen aufgrund von Veränderungen der Landnutzung und des Klimas in alarmierendem Tempo verloren oder werden degradiert. Diese trockenen tropischen Ökosysteme bedecken einen großen Teil des indischen Staatsgebiets und erbringen bedeutende Leistungen für die menschliche Bevölkerung. Trotz ihrer ökologischen und sozioökonomischen Bedeutung sind die trockenen tropischen Ökosysteme in Schutzgebieten unterrepräsentiert und werden weniger erforscht als andere Ökosystemtypen. In den östlichen Ghats Indiens sind Gehölze in trockenen Ökosystemen wichtig für die Weidehaltung des Viehs und die Gewinnung von Brennholz. Die anthropogenen Aktivitäten des Abbrennens, um die Weidetiere mit schmackhaften Gräsern zu versorgen, und des Erntens von Ästen und Stämmen für Brennholz und andere Zwecke könnten jedoch die langfristige Nachhaltigkeit dieser Ressourcen gefährden. In meiner Dissertation untersuche ich die Auswirkungen der Ernte und des Abbrennens auf die Zusammensetzung von Gehölzgemeinschaften und die Populationsdynamik.

Diese Dissertation ist in fünf Kapitel gegliedert, um dieses allgemeine Thema zu behandeln. Kapitel 1 gibt eine allgemeine Einführung in die Zusammensetzung und Struktur von Waldgemeinschaften und in die Frage, wie anthropogene Aktivitäten diese Zusammensetzung und Struktur verändern. Ich präsentiere Hintergrundinformationen über den Kontext der Eastern Ghats und den aktuellen Stand unseres Wissens über die Auswirkungen von Feuer und Holzernte auf die Zusammensetzung von Gehölzbeständen und die Populationsdynamik. Ich zeige die Wissenslücken auf, die mich zu meiner Dissertation motiviert haben.

Die Kapitel 2 bis 4 stellen meine ursprüngliche Forschung dar und sind eigenständige Studien, die in wissenschaftlichen Fachzeitschriften mit Peer-Review veröffentlicht oder zur Veröffentlichung eingereicht wurden. In Kapitel 2 analysierte ich Parzellen im Eswaramala Reserve Forest, um Gebiete, die in letzter Zeit von Bränden betroffen waren, mit solchen zu vergleichen, die nicht von Bränden betroffen waren. Meine Ergebnisse zeigten, dass in den verbrannten Gebieten die Stammdichte zunahm, der Artenreichtum jedoch abnahm, da feuerresistente und -tolerante Arten in der Gemeinschaft dominierten. Diese Arten weisen Merkmale wie dicke Rinde und klonale Vermehrung auf. Darüber hinaus führte die

Anwesenheit von Feuer zu einer Verschiebung in der Größenstruktur zugunsten kleinerer, wieder austreibender Individuen.

In Kapitel 3 untersuchte ich die Vitalitäts- und Populationswachstumsraten von drei trockenen tropischen Baumarten unter verschiedenen Erntebedingungen. Mithilfe von integralen Projektionsmodellen fand ich Unterschiede in den demografischen Raten der einzelnen Arten. Bei zwei der Arten führte die Ernte zu reduzierten Wachstumsraten. Bei einer Art, bei der sowohl die Äste als auch der Hauptstamm geerntet wurden, kam es zu einem erheblichen Rückgang der Wachstumsrate der Population. Eine Analyse anhand von Experimenten zur Lebenszyklusanalyse ergab, dass dieser Rückgang in erster Linie darauf zurückzuführen ist, dass die geernteten Individuen von ihrer Basis aus nachwachsen müssen. Die Samenrekrutierung war bei allen Arten begrenzt, was möglicherweise auf das Vorhandensein zusätzlicher Bedrohungen wie Feuer zurückzuführen ist.

In Kapitel 4 habe ich mehr als 600 Einzelbäume beprobt und die Zusammensetzung und Struktur von bewaldeten Savannen und offenen Savannenlebensräumen verglichen. Die Ergebnisse zeigten signifikante Unterschiede in der Baumzusammensetzung aufgrund des Artenwechsels, der wahrscheinlich durch den Boden, die historische Landnutzung und aktuelle Praktiken beeinflusst wird. Wichtige Baumarten variierten zwischen den beiden Lebensräumen. Beide Lebensräume wiesen eine rechtsschiefe Größenverteilung auf, die wahrscheinlich auf unterschiedliche anthropogene Faktoren zurückzuführen ist: Feuer in bewaldeten Savannen und Beweidung/Ernte in offenen Savannen.

In Kapitel 5 erörtere ich die Gesamtergebnisse der Dissertation, ihre Grenzen und ihren Nutzen für den Naturschutz. Meine Forschungsarbeit liefert neue Erkenntnisse über die Auswirkungen anthropogener Faktoren auf die Zusammensetzung und Demografie von Lebensgemeinschaften in den Eastern Ghats und bildet eine Grundlage für künftige Forschungen in dieser wenig erforschten Region.

Schlüsselwörter: Feuer; Holzeinschlag; Artenzusammensetzung; Artenvielfalt; Demographie; Bevölkerungswachstumsrate; Trockenwald; Savanne; Eastern Ghats; Deccan Plateau

Chapter 1

General Introduction

1.1 Human land use and forest structure and dynamics

Forests account for approximately 30% of the total Earth's terrestrial area (FAO 2020). Forests are an important component of terrestrial ecosystems, as they harbor much of the biodiversity of the world and provide many valuable goods and ecosystems services such as timber, fodder and non-timber forest products (IPCC 2020). Forests also provide important ecosystem functions such as heat and water balance regulation on a local level and carbon sequestration that mitigates global climate change (IPCC 2020).

Due to the growing demand of land and resources, forests are threatened directly by human activities, such as land use change and indirectly through climate change. Land use change by humans has affected about two thirds of the total global terrestrial area (Winkler 2021). Land use change affects forest ecosystems via habitat loss, modification, fragmentation, degradation of soil and water resources, extinction of native species, and introduction of exotic species (Vitousek 1994, Foley et al. 2005). Climate and land use change are interrelated problems, as deforestation is a primary contributor to climate change (Bennett et al. 2017). At local scales, human activities such as logging and fire can alter the microclimate by increasing surface warming and decreasing precipitation (Laurance 2004, Blonder et al. 2018).

Deforestation and agricultural expansion in the global south are the main causes of land use change (Lambin and Meyfroidt 2011, Winkler 2021). The nature of land use change varies geographically and are influenced by socioeconomic attributes. As human and livestock populations grow, future land use has even more potential to threaten biodiversity. Finding sustainable human land use options are therefore necessary to maintain species diversity, abundances and habitat structure thus ensuring ecosystem services (Godfray et al 2010, Martin et al. 2020).

1.2 Forest structure and dynamics

The structure of a forest ecosystem is described by the relative abundances of and diversity of woody species, and the size structure of woody stems. Disturbance is an important factor shaping woody plant community structure (Caswell and Cohen 1991, Bond and Midgley 2003, Kumi et al. 2021). Successional dynamics occur over a long time period, with pioneer species and small stems that are present immediately after disturbance being gradually replaced by shade-tolerant species and larger canopy trees. The dynamics of woody plant communities are governed by the survival, growth and reproduction of individuals in different environments (Easterling et al. 2000, Svenning et al. 2004). Structured population models can project the dynamics of each species under different environmental conditions. These models are particularly useful for forest species, as dynamics are difficult to observe due to the long time period over which they are realized (Barlow et al. 2016, Needham et al. 2018).

Community studies in different environmental contexts provide information on the effects of environmental factors on the composition of species and the size structure of the woody stems.

For example, analyses of community composition indicate whether species in one environmental context are a nested subset of the species present in another, or rather if different species occur in the different environments, potentially indicating different environmental preferences (Baeten et al. 2012, da Silva et al. 2018). Combining information on species composition with information about functional traits can help explain why species these environmental preferences (Wright and Reeves 1992, Carvalho et al. 2012). Size structure of woody stems provides hints to population dynamics (Crawley 1990). For example, populations composed of all large stems might indicate low recruitment rates and a path towards extinction.

The persistence of a species in a given location depends on its demography, and current presence of a species does not ensure long-term persistence (Hoffmann 1999, Bertuzzo et al. 2011, Hilde et al. 2020). Structure population models allow the projection of future populations in each environmental context based on current demographic vital rates (Easterling et al. 2000). For example, if trees are subjected to harvesting, the structured population model can be used to project future population size if the conditions and pattern of human use remain (Mandle and Ticktin 2012, Grogan et al. 2014). Understanding human land use on forests is best achieved by considering community patterns, functional traits and population demography.

1.3. Tropical dry forests

Dry forests account for almost half of the world's tropical forests (Murphy and Lugo 1986, Sunderland et al. 2015). These forests occur globally in Central and South America, Africa, South East Asia, India and Australia, and occur in the same climate as savannas (Pennington et al 2004). Tropical dry forests constitute about 17% of the global forests and support a large population of forest dependent people (Miles et al. 2006). They are comprised of woody plants that grow in a pronounced rainfall seasonality, and have an understory of C_3 and/or C_4 grasses. The favorable growing period in this forest is narrow rainy season (Pennington et al. 2018), and increasing length of the dry period can limit regeneration.

The dry tropics are home to one third of the global human population (Murphy and Lugo 1986, Pennington et al. 2018), and are thus threatened by human activities more than moist forests. Local human activities include land use conversion (e.g., agricultural expansion, pastures), commercial logging, resource extraction such as wood products and non-wood forest products, introduction of exotic species, and alteration of disturbance regimes (Siyum et al. 2020). Dry tropical forests are also threatened by global climate change, which is projected to increase the length of the dry season in many regions (Allen et al. 2017).

Compared to tropical rainforests, dry tropical forests have received less research attention, and thus there is less known about how human activities influence the structure, composition and dynamics of the dry tropical forests (Ticktin 2005, Sunderland et al. 2015, Pennington et al. 2021). A long history of human habitation in dry forests suggest that humans might sustainably use the forest resources that are currently present and have persisted (Setty et al. 2008, Hernández-Barrios et al. 2015).

Proper management of dry tropical biomes requires properly characterizing the ecosystem and understanding of the factors that are important to maintaining these ecosystems. Environmental factors such as soil properties, temperature, precipitation, fire and herbivory distinguish dry tropical forests from savanna ecosystems (Pennington et al. 2018). This is important in India, where recent literature suggests that the dry forests are actually savannas (Ratnam et al. 2016, Nerlekar et al. 2021, Stevens et al. 2022) due to the presence of continuous grassy layer in the understory. Devaluing grassy ecosystems is common worldwide and in India, and can lead to improper management (Parr et al. 2014, Silveria et al. 2020).

1.4 Eastern Ghats

The Eastern Ghats are discontinuous hill ranges in the East coast of India. This region is composed of dry evergreen, dry mixed deciduous, dry savanna, scrub and thorn forests (Champion and Seth 1968, Mani 1974, Reddy and Parthasarathy 2008). The majority of the forests in Eastern Ghats are composed of dry deciduous, savanna, scrub and thorn vegetation (Mani 1974, Reddy and Parthasarathy 2008). The Eastern Ghats and Deccan Plateau act as monsoon break of North East and South West monsoons (Rao 1976, Ponton et al. 2012). Due to the poor soil conditions, dryland farming is possible only with a few crop species, such as peanuts and millets (Singh 2013). The Eastern Ghats has a high population of economically disadvantaged tribal communities that depend on the forests for livelihood. Hence, conservation actions/efforts must consider humans as an integral part of the system (Rawat 1997, Reddy et al. 2004, Yadama et al. 2010). The Eastern Ghats have had loss of forest cover, with approximately 16% of forest cover lost across a span of 100 years (Ramachandran et al. 2015). Often, this is due to forests being converted to agricultural and fallow lands. The remaining forest is now quite fragmented (Ramachandran et al. 2015).

Documenting how environmental and anthropogenic factors influence forest composition in the Eastern Ghats is important because shifts in species composition would affect the ecosystem services that they provide, including provisioning services such as fuelwood, fodder and NTFPs, and regulating services such as soil protection (Rawat 1997, Aditya and Ganesh 2019). The colonial timber centric view of the forests has led to large scale felling of native and endemic species, which have been replaced by plantations of exotic species (e.g., *Eucalyptus* spp. in Chittoor district, Simon et al. 2019). The Eastern Ghats and Deccan Plateau is currently a patchwork of forests and interspersed with village commons, agricultural lands, grazing lands and rural settlements (FES 2003, FES 2011). Although Eastern Ghats and Deccan Plateau harbour many endemic species, they are currently absent in the conservation discourse in India (Reddy et al. 2008, Nerlerkar et al. 2021). The grasslands in the Eastern Ghats are often referred to as degraded and are marked as areas for potential afforestation. The degree to which such afforestation would benefit or harm the endemic flora and fauna in landscape is unknown.

People in the Eastern Ghats depend on forests for fuelwood, non-timber forest products and livestock grazing (Schmerbeck 2011, Shackleton and Pandey 2014). In addition, small timber harvested from the forests are used to make agricultural implements, fences and thatches (Adolf et al. 2001). Non-timber forest products include fruits, gum, resin and tanning material (Reddy et al. 2016). Harvesting branches of trees for fuelwood was a common activity until recently. Conservation efforts that increase household assets (gas stoves, houses) decreased the collection of branches for fuelwood in dry tropical forests of Central India (Agarwala et al. 2016, Ruth de Fries et al. 2022). People also cut branches of trees to provide fodder for livestock, and populations of livestock have increased through time (FES 2011).

While the above activities might threaten the forest species, especially as human populations grow, the larger threats to these forests come from more commercial activities that local people do not profit from. These include commercial logging activities, forest clearing for solar/wind power plants, and conversion of forests to agricultural lands or plantations (Ramesh and Kalpana 2015). More recently there has been large-scale harvesting and collection of woody species for brickmaking (FES 2011).

In order to understand the structure and dynamics of woody plant communities in the Eastern Ghats and Deccan Plateau, three primary factors are important: (1) the role of fire, (2) the effect of harvesting for local uses, and (3) the potential for open savanna or grasslands to support unique species. I will discuss each of these in turn.

<u>Fire</u>: Forest fires in this region are anthropogenic in nature, set mainly to promote new flush of grasses for grazers, or to clear land for agricultural fields (FES 2011, Reddy et al. 2012). Due to the increasing livestock populations, extended dry seasons and low availability of woody fodder, the number of fires set per year are increasing at a subcontinent scale (Kondandapani et al. 2004, Kale et al. 2017). Sometimes multiple fires occur in a single year at a location (Reddy et al. 201). Once set, these fires follow a mosaic like pattern of spread depending on the weather conditions on that day and the grass cover in the understory. Fires are expected to increase in the Deccan Peninsula (Kale et al. 2017). Change in climate and El Niño have increased the dryness in the subcontinent, exacerbating the intensity and extent of anthropogenic fires (Jolly et al. 2015).

Fires are known to have many effects on woody plant communities in other regions of the world, including tropical dry forests in the Western Ghats (Mondal and Sukumar 2015, Verma et al. 2017) and Central India (Saha and Howe 2003). Specifically, increases in the intensity and/or frequency of fires from historic rates typically favors one or only a few species, decreasing the evenness of the community (Tubbessing et al. 2020). The effects of grass presence, fire and browsing are interactive and are often difficult to disentangle in many systems. For example, the presence of fire-tolerant grasses provides fuel for fire. In the Eastern Ghats, the dominant grass is native species in the genus *Cymbopogon* (Elangovan et al. 2012). These grasses can resprout and grow rapidly post fire (Sankaran 2005). It is a tall native grass and when areas are not burned for long periods, there is high grass biomass and fuel load causing larger fires. Fire has been used a management tool in the Eastern Ghats historically (Thekaekara et al. 2017).

Repeated fires can cause strong environmental filtering for species with certain functional traits (Bond and Midgley 2001). Species with functional traits such as thick bark and multiple strategies of resprouting via below ground bud banks are known to be adapted to fire (Khan and Tripathi 1989, Saha and Howe 2003). Fires can also create conditions that allow fire tolerant and/or disturbance tolerant exotic species to invade and spread. In the Eastern Ghats and Deccan Plateau, exotic woody plants include *Prosophis juliflora* and *Lantana camara.*

<u>Harvesting</u>: In the Eastern Ghats, woody plants are harvested for fuelwood, making agricultural implements, non-timber forest products (Jegenathan et al 2008, Naidu et al. 2019). Studies on harvesting in other regions show that the sustainability of harvesting depends on the part of the plant harvested and the intensity of the harvesting (Ticktin 2005). Harvesting is known to affect physiological processes, vital rates, population growth rates, and alter community and ecosystem patterns and processes (Ticktin and Shackleton 2011, Gaoue et al. 2013).

In the Eastern Ghats, the introduction of government programs that provide household fuels and brick/cement for the building of homes has caused harvesting of woody species to shift from fuelwood and building materials to fodder and small timber use (Mundoli 2011). It is important to understand the current levels of harvesting and if these levels are sustainable for the woody plant populations. Some species in the Eastern Ghats are reported to have declined overtime, and this might be due to harvesting pressure. These include *Hardwickia binata, Anogesiuss latifolia, Chloroxylon swietenia,* and *Albizia amara* (FES 2011).

<u>Grasslands:</u> Studies have reported that grasslands in the Eastern Ghats are ancient and are maintained by climate rather than new and the result of deforestation (Riedel et al. 2021). Globally, grasslands and savanna ecosystems are threatened by afforestation schemes aimed to

improve their carbon services (Veldman et al. 2019, Madhusudan and Vanak 2021). Other compounding threats includes expansion of agriculture and conversion to renewable energy projects (Ramachandran et al. 2020). While the composition of woody species in the Eastern Ghats is known to depend on the bioclimatic and topographic variables (Jayakumar et al. 2002, Reddy et al. 2011), it is currently not known if the woody species present in the grasslands are a nested subset of the woody plants found in forests or a unique assemblage of species.

1.5 Thesis scope and chapter outline

Several studies have been conducted on the effects of human activities on forests, but little is known about the effects of human activities on the population dynamics and community structures of forests in Eastern Ghats. This is evident not only from a literature search, but also from an absence of demographic life history information of plants from this region in global databases such as COMPADRE (Salguero-Gomez et al. 2015), from the lack of vegetative plot data from this region in sPLOT (Sabatini et al. 2021), and from the absence of long-term monitoring plots in ForestGEO (Davies et al. 2021). The Eastern Ghats and Deccan Plateau have unique species and threats and high socioeconomic importance to the surrounding rural communities. These knowledge gaps motivated my doctoral research. In all chapters, I worked in the Sadhukonda Reserve Forest and Eswaramala Reserve Forest, located in the South-Central Eastern Ghats at the intersection of Eastern Ghats and Deccan Plateau.

In Chapter 2, I asked how recent fire influences the woody community composition and size structure in tropical dry forest in the Eastern Ghats. I hypothesized that fire presence would shift composition towards more fire tolerant species with functional traits such as those with resprouting ability and thick bark. I hypothesized that large trees that could survive fires and that these large individuals combined with small resprouting individuals would become dominant size classes. My collaborators and I sampled plots with and without evidence of recent fire and recorded the identity and size of woody plant species. Chapter 2 is published in *Ecology and Evolution*.

In Chapter 3, I asked how the current levels of harvesting influence the demography and population dynamics of the woody species? I hypothesized that higher harvesting rate and particularly harvesting at the main stem would decrease demographic vital rates and population growth rate. My collaborators collected demographic data of woody stems consisting of seedlings, saplings, adult trees and resprouting individuals for three dry forest tree species. We measured the tagged individuals across a 7-year study period, and recorded the presence and absence of harvesting. Chapter 3 is published in *Biotropica.*

In Chapter 4, I asked how woody plant composition differed between forest (wooded savanna) and grasslands (open savanna) sites and whether differences were due to nestedness or turnover of species? I hypothesize that the two habitats have an overall compositional dissimilarity. I hypothesize that this is due to woody species turnover between the two habitat types. My collaborators and I sampled plots within the reserve forest and grasslands and recorded the identity and sizes of woody plant species.

In Chapter 5, I synthesize the key findings in the dissertation. I discuss (1) summary of results (2) the relevance and potential application of my results to the conservation of woody plants in the Eastern Ghats and Deccan Plateau, (3) the limitations of my approach and specific needs for future experimental studies and long-term monitoring studies.

Chapter 2

Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats.

This chapter has been published in Ecology and Evolution as

Neeraja, U.V., Rajendrakumar, S., Saneesh, C.S., Dyda, V. and Knight, T.M., 2021. Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats. *Ecology and Evolution*, 11(11), pp.6593-6603. https://doi.org/10.1002/ece3.7514

Received: 5 March 2021 | Accepted: 12 March 2021
DOI: 10.1002/ece3.7514

ORIGINAL RESEARCH

Ecology and Evolution Open Access WILEY

Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats

U. V. Neeraja[1,2] | **S. Rajendrakumar**[4] | **C. S. Saneesh**[3,5] | **Venkat Dyda**[5] | **Tiffany M. Knight**[1,2,3]

[1]Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany
[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[3]Department of Community Ecology, Helmholtz Centre for Environmental Research- UFZ, Halle (Saale), Germany
[4]Centre for Sustainable Future, Department of Chemical Engineering and Materials Science, Amrita Vishwa Vidyapeetham, Coimbatore, India
[5]Foundation for Ecological Security, Madanapalle, India

Correspondence
German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
Email: neeraja.venkataraman@idiv.de

Funding information
Alexander von Humboldt Foundation; Helmholtz Association; German Research Foundation, Grant/Award Number: FZT-118-202548816

Abstract

Fire is known to have dramatic consequences on forest ecosystems around the world and on the livelihoods of forest-dependent people. While the Eastern Ghats of India have high abundances of fire-prone dry tropical forests, little is known about how fire influences the diversity, composition, and structure of these communities. Our study aimed to fill this knowledge gap by examining the effects of the presence and the absence of recent fire on tropical dry forest communities within the Kadiri watershed, Eastern Ghats. We sampled plots with and without evidence of recent fire in the Eswaramala Reserve Forest in 2008 and 2018. Our results indicate that even though stem density increases in the recently burned areas, species richness is lower because communities become dominated by a few species with fire resistance and tolerance traits, such as thick bark and clonal sprouting. Further, in the presence of fire, the size structure of these fire-tolerant species shifts toward smaller-sized, resprouting individuals. Our results demonstrate that conservation actions are needed to prevent further degradation of forests in this region and the ecosystem services they provide.

KEYWORDS
Eastern ghats, forest fire, species composition, species diversity, tropical dry forest

1 | INTRODUCTION

Species richness and composition are important indicators of forest biodiversity and are known to change across natural and anthropogenic environmental gradients (Barlow et al., 2016; Husch et al., 2002). Fire is an important disturbance factor that alters forest ecosystems around the world (Condé et al., 2019; De Andrade et al., 2020; He et al., 2019). Globally, more than 90% of forest fires are linked to human activity (FAO 2007). Fire is used for agricultural activities, maintaining grasslands for livestock, extracting forest products, cultivation, and hunting (FAO 2007). Annually, fires burn up to 500 million hectares of woodland, open forests, tropical and subtropical savannas, 10–15 million hectares of boreal and temperate forest, and 20–40 million hectares of tropical forests (Bunk, 2004). In recent years, there is an increase in the number of forest fires and burned area in several ecosystems worldwide (Chuvieco et al., 2004; Cochrane, 2003; Dimitrakopoulous et al., 2011; Kodandapani et al., 2004; Westerling, 2016). Tropical dry forests are especially prone to human-mediated fires because they have a distinct dry season in which dry vegetation such as grasses provides natural fuel for fires (Janzen, 1988a; Murphy & Lugo, 1986).

Fire is known to reduce the abundance and diversity of species in forests (Barlow et al., 2016; Condé et al., 2019; De Andrade et al., 2020), by influencing demographic processes such as survivorship, flowering, seed dispersal, and recruitment (De Luis et al., 2005; Prestes et al., 2020; Verma et al., 2017; Walters et al., 2004). Fire alters species composition, stage structure, and successional patterns through its varying effects across species (Syaufina & Nuruddin, 2011). Nonsprouting woody species with thin bark are especially sensitive to fire (Gosper et al., 2012; Hoffman et al., 2012; Keeley, 1986). The effects of fire on forest communities depend on the frequency and intensity of the fires (Bond & Keeley, 2005; He et al., 2019; Lewis & Debuse, 2012).

The Indian subcontinent is spatially diverse in its climate, forest vegetation types, flammability, and human impact (Champion & Seth, 1968; Ravindranath & Sukumar, 1998). Tropical dry forests account for 40.86% of the total forest cover (FSI, 2019). Fires are most common in this forest type and are increasing in their frequency and spatial extend through time (FSI, 2012; Reddy et al., 2017; Srivastava & Garg, 2013). Many people live in and around dry forest areas and rely largely on forest resources for their livelihood (Kothari et al., 1995; Schmerbeck & Fiener, 2015). Ecosystem services provided by these forests include timber and nontimber forest products, fuelwood, fodder, and places for worship (Sagar et al., 2003; Saha, 2002; Schmerbeck & Fiener, 2015; Singh & Singh, 2011). Fires in India are mainly anthropogenic, caused intentionally (e.g., because resprouting grasses are palatable to livestock) or negligently (Joseph et al., 2009; Roy, 2003; Saha, 2002). Forest fires occur during the dry season from February to June, and these are typically ground fires (Joseph et al., 2009) that spread due to fuel from the accumulation of dry litter, and dry grasses or herbaceous groundcover. Weather conditions during the dry season, such as strong winds, low humidity, and high temperature, also influence burning (Giriraj et al., 2010; Kodandapani et al., 2008). With enough fuel, wildfires can develop that go to treetops. Fires in Indian dry tropical forests have been shown to reduce recruitment, decrease forest diversity, and alter species composition (Chaturvedi et al., 2017; Mondal & Sukumar, 2015; Saha & Howe, 2003; Verma et al., 2017), especially if fires are frequent and intense (Jhariva et al., 2012; Kodandapani et al., 2008; Sathya & Jayakumar 2017; Verma & Jayakumar, 2015). Tree species that can persist have functional traits that allow them to resist or tolerate fire, such as thick bark and resprouting ability (Khan & Tripathi, 1989; Saha & Howe, 2003).

There is limited knowledge on the effects of fire on dry tropical forests in the Eastern Ghats of India. Approximately 14% of forest fires in India occur in Andhra Pradesh (Eastern Ghats; Reddy et al., 2017; Vadrevu, 2006), and there is concern that these fires may have increased in frequency across the past decade in response to changes in livestock practices toward more fodder-dependent species (FES, 2011; FES social survey 2018 unpublished). Dry tropical forests are the most common habitat type in Andhra Pradesh. An increase in burnt area (from 6,369 km^2 in 2009 to 8,593.5 km^2 in 2012) in Andhra Pradesh has been reported, with the Eastern Ghats and Deccan Plateau being the most affected geographical regions within the state (Reddy et al., 2012). The Eastern Ghats are spread across ~75,000 square kilometers covering the states of Orissa, Andhra Pradesh, southern Tamil Nadu and Karnataka, and have high biodiversity and many species that are endemic to the region (Sandhyarani et al., 2007). This region is home to a large human population with high forest dependency. The growth in human and livestock density has increased the demand for forest products (Bahuguna & Singh, 2002; Krishna & Reddy, 2012). However, forests in the Eastern Ghats have received little scientific attention, and as a result, little is known about the effects of fire on these forests. It is important to understand the drivers of tree species abundance, diversity, composition, and structure for conservation and management of biodiversity and to provide local livelihood needs (Davidar et al., 2010; Singh & Singh, 2011).

Our study evaluates (a) whether there has been an increase in the frequency of fires in forests in the state of Andhra Pradesh from 2001 to 2018, (b) tree species diversity and composition in recently burned and not burned plots in the southcentral Eastern Ghats in 2008 and 2018, and (c) stem density and stage structure of common tree species in burned and not burned plots and whether this depends on their fire tolerance traits in 2018. We expect that fire might have increased in its frequency across the past two decades and between our sampling periods of 2008 and 2018. We expect that fire presence has an influence on the density, diversity, composition, and stage structure of tree communities. In particular, we expect that fire-tolerant species will become more abundant and that these species will be present in smaller stage classes in plots with recent fire presence, indicative of recent resprouting.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area, the Eswaramala Reserve, is located in the Kadiri watershed in the southcentral Eastern Ghats within the Anantapur District, Andhra Pradesh (Figure 1). The Anantapur district is the second driest region in India (Rao et al., 2013), and the Kadiri watershed lies between 13°56'20" and 14°7'20" North and 78°19'30" and 78°27'20" East. The Eastern Ghats are known to have a wide range of topographical and physical features and to harbor rich and diverse flora (Reddy et al., 2008). The main river that drains the Kadiri watershed is Papagni, a tributary of River Pennar. The geographical extent of the watershed is ~185 km^2. Topography is undulating with elevations ranging from 300m to 1300m. The climate is tropical arid, with a mean annual temperature of 33.7°C and a mean annual rainfall of 553 mm (FES, 2011). The Kadiri watershed falls under the dry rain shadow area of the southern Deccan plateau. The rainfall is unevenly distributed in time, with long periods of drought being common. The soil types are classified as red and black sandy, clay, and red loamy. The main rock types in the study area are peninsular gneisses, younger granites, Dharwar schist belt rocks with

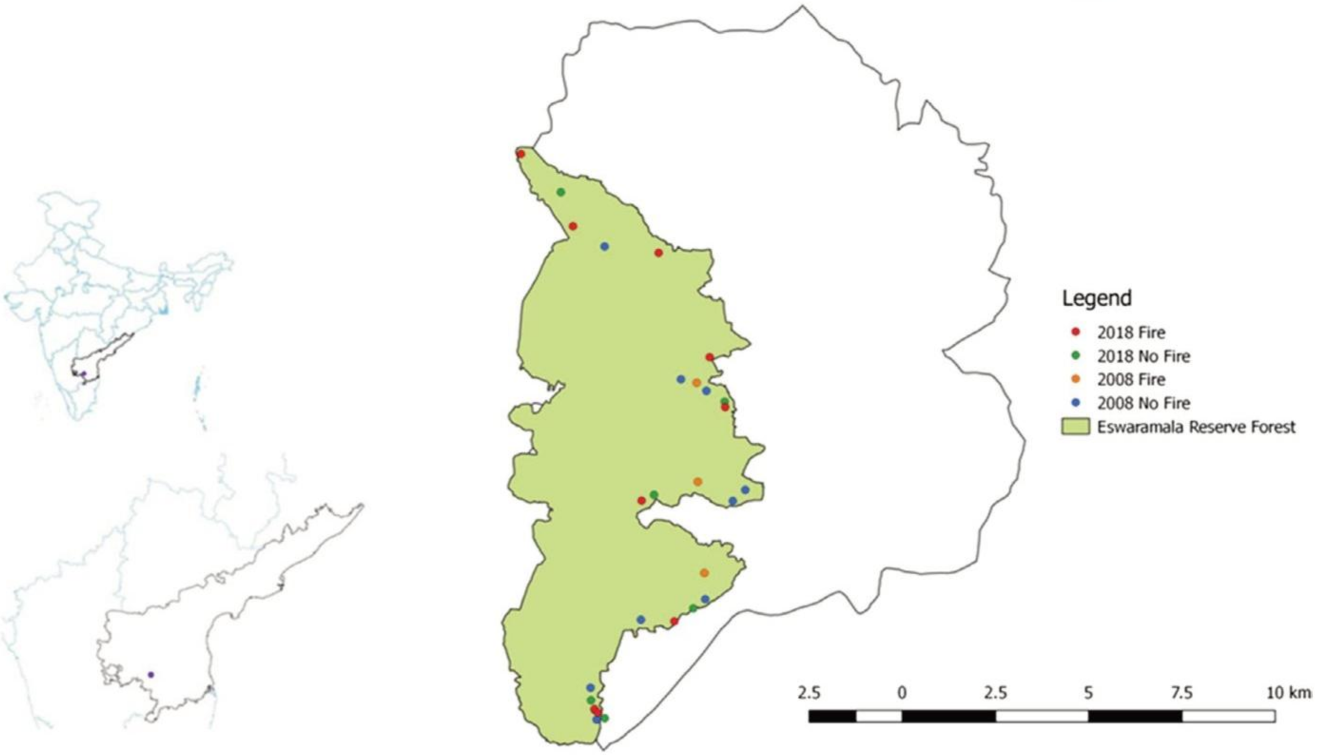


FIGURE 1 Maps showing the study location. Maps on the left show this study area within the context of the country (India) and state (Andhra Pradesh). The map on the right shows the Kadiri watershed. Our sampling locations (points) are within the Eswaramala Reserve Forest. Sampling locations are color-coded based on the year of study and whether or not recent fire occurred

secondary intrusives such as dykes, and quartz and pegmatite veins (FES, 2011).

Land use in the Kadiri watershed is classified as forest, agriculture, grassland, and open barren. Forest is the second largest land use and occupies over 62.23 km^2 (FES, 2011). Our study focuses on forests, which are situated within the Eswaramala Reserve Forest in the western side of the Kadiri watershed. These forests are best described as tropical dry deciduous and tropical thorny–scrub vegetation (Champion & Seth, 1968; Gadgil & Meher-Homji, 1986). Perennial tall C4 grasses, mainly *Cymbopogon coloratus*, dominate the forest floor (FES, 2011; Rajendrakumar, 2014). The high human density results in high dependency on forests to support rural livelihoods and economy. The forest experiences anthropogenic disturbances, including cutting and lopping of trees for fodder, fuelwood, brick making, timber and nontimber forest products, grazing by sheep and goats, and fires (FES, 2011; FES social survey 2018; Rajendrakumar, 2014). Soil erosion is often a consequence of these anthropogenic disturbances (Krishnaiah, 2013).

In the Eswaramala Reserve, fires occur in the dry season (between February and April) in patches across the forest (FES, 2011). The most common reason for start of fires in this system is burning to promote new flush of grasses for grazing livestock during the dry season. Fires do not seem to be set strategically but are rather set at random locations. Once started, fires spread naturally, the spread is governed by understory grasses (in the form of tall C4 grasses) and the local weather conditions (i.e., wind) on that day. There are natural firebreaks, which can prevent fires from spreading such as regular paths created by grazing livestock and shepherds, rockiness, and contour trenches. Some fires are stopped by forest department or village institution members that are trained to put out fires, to prevent fires from spreading over larger areas. Due to the frequent occurrence of fire, fire protection methods such as fire lines and basal area clearing (0.5m radius) around younger trees are prepared in advance by community members to prevent fires from burning large areas. Fires typically burn standing grass and younger woody plant biomass, and high-intensity crown fires are less common.

2.2 | Frequency of fire through time

To test whether the frequency of fire is increasing across time for forests in our region, we examined annual satellite samples of fire presence from 2001 to 2018 in the forested regions within the state of Andhra Pradesh. Data were obtained from the Forest Survey of India Forest fire portal (http://117.239.115.41/smsalerts/index.phpFSI). Detected forest fire points (1-km^2 resolution) are from MODIS satellites (Terra and Aqua). These include fresh and repeated detections of active fire at two time points in each day as the satellites pass over the region. From 2001 to 2018, the methods used by MODIS are consistent, allowing a test of whether the frequency of fire increases with time. We tested for a relationship between fire frequency through time by fitting a generalized additive model using the function *gam* from the package "mgcv" in R.

2.3 | Data collection

To quantify the richness and composition of trees in 2008 and 2018, we sampled circular plots with a 10 m radius. We focus on tree species (not herbs, shrubs) in this study and define a tree as either a woody plant capable of a height of at least two meters (for single-stemmed woody plants) or capable of having at least one of the stems with a girth of more than five centimeters (for multistemmed woody plants) (IUCN Global Tree Specialist Group; Beech et al., 2017). In 2008, plots were selected to represent the entire range of topography and disturbance regimes, while allowing for accessibility. In 2018, plots were selected to be in the same approximate locations as the 2008 plots, to capture the same range of topography and disturbance regimes. At each plot, all individual trees with greater than 2-cm basal girth were identified and counted, including young stage classes, such as saplings and small resprouting individuals. All the individuals were identified using the guide to the regional flora, viz. Flora of Andhra Pradesh vol I, II, and III (Pullaiah, 1997; Pullaiah & Ali Mouali, 1997; Pullaiah & Chennaiah, 1997). We measured girth at breast height (GBH) of stems above 20 cm in 2008, and GBH (or collar girth when GBH was not possible) of all stems in 2018. At each plot, we document the distance to nearest human habitation (distance to village center), and only plots that were at least 500 m away from these were considered in our analysis. In addition, we removed plots that contained less than two individual tree stems. We therefore included 38 plots in 2008 and 48 plots in 2018. We document evidence of recent fires by visual estimation of plots (see pictures in Figure 2). Eight of the 38 plots in 2008 and 29 of the 48 plots in 2018 had evidence of recent fire (i.e., fire marks on trees, lack of ground vegetation).

In 2008, there were 9 sampling locations with 2–6 plots in each location, each plot separated by a minimum of 100 m (Figure 1). In 2018, there were 10 locations, each with 2–8 plots separated by a minimum of 100 m (Figure 1). In both 2008 and 2018, we find that there is a weak relationship between pairwise geographical distance between plots and pairwise community dissimilarity (see Appendix S1A), likely because of both natural (slope, aspect, soil features) and anthropogenic (fire) factor turnovers at small spatial scales. For this reason, we treat each plot as an independent replicate.

2.4 | Richness and composition

We quantified whether richness and community composition of trees differ between four categories (2008 fire, 2008 no fire, 2018 fire, and 2018 no fire). Richness was assessed using individual-based rarefaction curves for each category, and their 95% confidence intervals generated from resampling using *iNext* package in R (Chao et al., 2014; Hsieh, 2016). Rarefaction curves with nonoverlapping 95% confidence interval were considered significantly different. We used nonmetric multidimensional scaling (NMDS) to visualize composition between the four categories. We performed NMDS using the *metaMDS* function and the Bray–Curtis dissimilarity matrix in *vegan* package (Oksanen et al., 2015) and used the *ggplot2* package for graphical representation. We used ANOSIM (analysis of similarities) from the *vegan* package to test whether categories differed in their community composition (Bray–Curtis). We removed eight plots from visualizations and analyses that included only one tree species, as two of these plots were clear outliers (Appendix S1B). All statistical analyses and visualizations were conducted in R programming version 3.6.2 (R Core Team, 2017).

FIGURE 2 Picture of a plot with no fire (top) and with fire (bottom). In the absence of fire, ground vegetation is present. After a fire, ground vegetation is absent and trees show fire marks

2.5 | Stem density and size structure

We used the more detailed data collection in 2018, for which the size of every stem was measured, to assess how the fire categories influence the density of stems per plot across all individual and the size structure of stems for 10 species with adequate sample size. We used the Kruskal–Wallis test to test for effects of fire category (presence, absence) on stems per plot. To visualize and test for differences in size structure across plots with and without fire, we considered 10 species that are present in both fire categories. These

10 species were sorted categorically based on their bark thickness (thick or thin) and resprouting ability (cannot resprout, basal sprouters, clonal sprouters) (see Appendix S1C for details). Basal sprouters are capable of resprouting from their root collar, and clonal sprouters are capable of resprouting of producing root sprouts and root collar sprouts (Clarke et al., 2013). We used a chi-square analysis to determine whether the fire presence influences the proportion of stems in four GBH size classes (<10 cm, 10-20 cm, >20-<50 cm, and >50 cm) for three functional categories of trees (basal sprouters with thin bark, basal sprouters with thick bark, and clonal resprouters with thick bark). We could not statistically consider all combinations of functional categories, as several had too few individuals in one of the treatments (e.g., species not capable of resprouting were rare in treatments with fire presence). While the sample size is inadequate for statistical analyses, the size structure of each of the 10 species is visualized in Appendix S1D.

3 | RESULTS

In our region, fires have increased in frequency from 2001 to 2018 in an asymptotic pattern ($p < .001$; Figure 3). Thus, the frequency of fire was similarly high during our two sampling years.

Our individual-based rarefaction curves show that the presence of fire dramatically reduced the number of species observed in both 2008 and 2018 (Figure 4). Across plots without fire, the 95% confidence intervals of the years overlapped with each other, indicating that tree diversity remains constant across the decade of sampling in this forest reserve in the absence of fire threats. In the presence of fire, tree diversity is similarly low in both 2008 and 2018.

There was a significant effect of category (all four combinations of years and fire) on tree species composition (ANOSIM, $R = 0.1505$, $p = .001$; Figure 5) and significant pairwise differences between 2018 fire and 2018 no fire (ANOSIM, R = 0.2976, $p = .001$) and 2008 fire and 2018 fire (ANOSIM, $R = 0.2978$, $p = .005$), but no significant pairwise differences between 2008 fire and 2008 no fire (ANOSIM, $R = 0.08436$, $p = .16$) and 2008 no fire and 2018 no fire (ANOSIM, $R = 0.06967$, $p = .053$).

Tree species such as *Dolichandrone atrovirens*, *Cassia fistula*, *Chloroxylon swetenia*, and *Anogeissus latifolia* are relatively common in the presence of recent fire (Figure 6). Species such as *Dalbergia paniculata*, *Premna tomentosa*, *Acacia nilotica*, *Albizia amara*, and *Erythroxylum monogynum* are relatively common in plots without recent fire incidence. Species such as *Wrightia tinctoria* are relatively common in both plots with and without recent fire incidence.

The density of stems was higher in plots with recent fire compared to those with no fire in 2018 (Kruskal–Wallis test, $p = .0017$). For the more common species for which we could assess size structure, there was a significant change in structure for the three categories of functional groupings. Specifically, the two most fire-tolerant functional groups of species have relatively more individuals in the second smallest size class in plots with recent fire (10-20 cm) (Table 1, Figure 7), whereas the least fire-tolerant functional group (basal sprouting and thin bark) has more individuals in the two largest size classes in the presence of fire.

4 | DISCUSSION

Our study finds strong effects of fire presence on tree abundance, diversity, and composition. While fire-affected areas have greater stem density, they have lower species diversity due to increased dominance of just a few species. Similar to other studies (e.g., Saha & Howe, 2003; Sukumar et al., 2005; Verma & Jayakumar, 2015), species with fire-tolerant traits such as thick bark and resprouting mechanisms have higher relative abundance in plots with fire. Further, fire shifts the size structure of the forest toward small resprouting individuals of species with fire-tolerant traits.

Our decadal sampling of the Eswaramala Reserve Forest indicates rapid changes. Fires have become more frequent in the region over the past two decades. Locally, residents report that fires also occur over larger areas (FES social survey 2018 unpublished). There

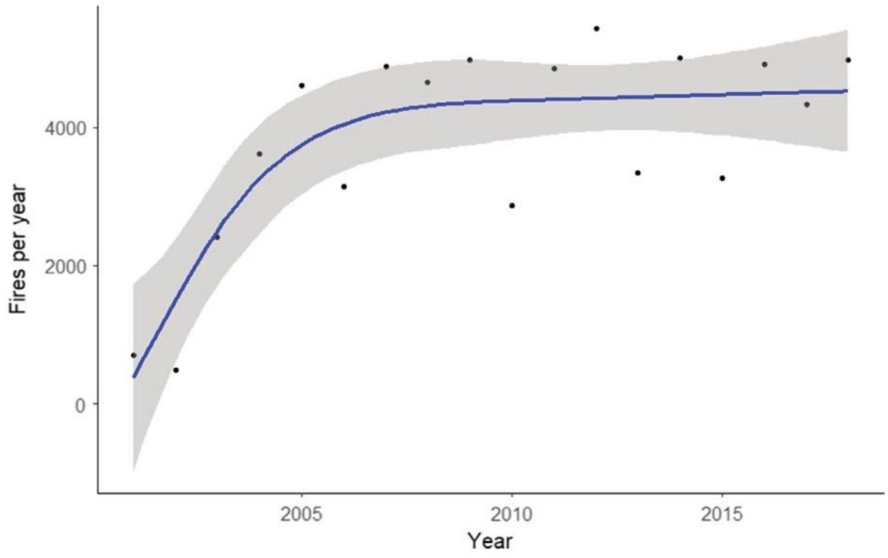


FIGURE 3 Fires per year detected from MODIS satellites from 2001 to 2018. The blue line shows the fit from a GAM with 95% confidence intervals

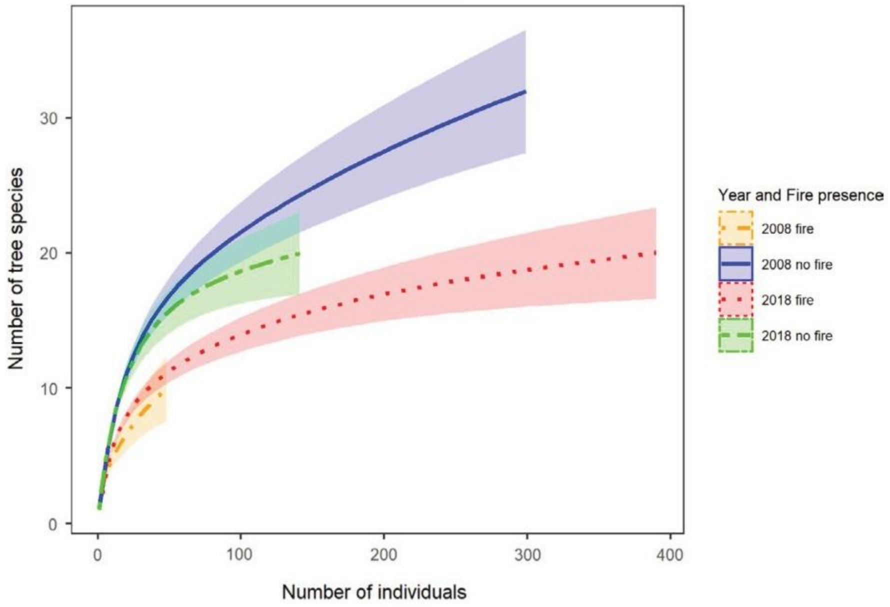


FIGURE 4 Individual-based rarefaction curves (and 95% confidence intervals) showing tree species richness across all sample plots in four categories representing different sampling years and the presence and absence of fire

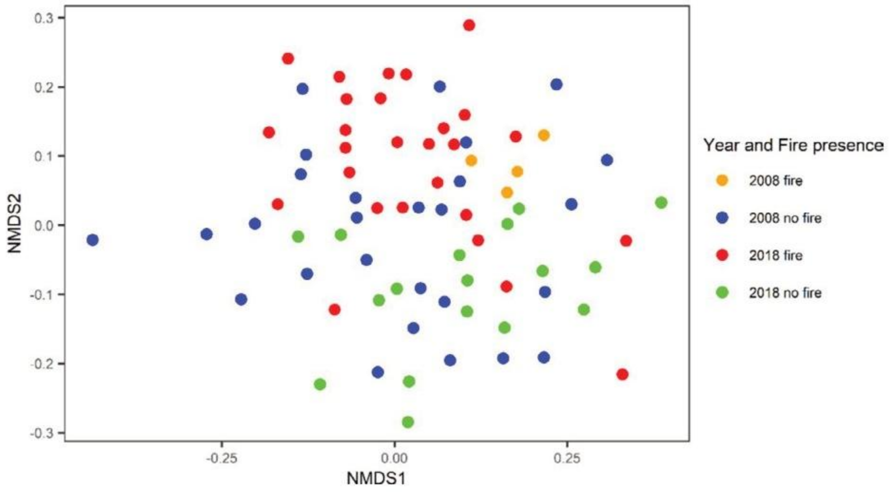


FIGURE 5 NMDS ordination of tree species composition (Bray–Curtis, stress=0.158) showing 78 sampling plots in four categories representing different sampling years and the presence and absence of fire

are reports of increased dominance of C4 grasses in the understory, especially the highly flammable *Cymbopogon coloratus*, in the forest understory (Rajendrakumar, 2014). Together, these observations suggest a grass–fire cycle, in which grasses that can tolerate fire provide fuel that can increase the frequency and/or extent of future fires (Bowman & Murphy, 2010; D'Antonio & Vitousek, 1992; Hiremath & Sundaram, 2005). In the long term, frequent fires convert forests into scrub vegetation and grasslands (Barlow & Peres, 2004; Cochrane, 2003; Kraus & Goldammer, 2007; Puyravaud et al., 1994) and cause soil erosion (Santin & Doerr, 2016). Frequently burned forests might also be more vulnerable to invasion by exotic fire-adapted species, such as *Prosopis juliflora*, *Lantana camara*, and *Parthenium histophorus* (Hiremath & Sundaram, 2005; Saha & Hiremath, 2003). For example, *Prosopis juliflora* now occurs in our study region, but was not present 25 years ago when fires were less common (FES, 2011).

Species that have the best fire tolerance and resistance traits (i.e., capable of producing basal and root resprouts and high bark thickness), such as *Dolichandrone atrovirens*, *Cassia fistula* and *Chloroxylon swietenia*, dominate in the presence of fire. In particular, we noticed that *Dolichandrone atrovirens* resprouts quickly and grows fast, which could explain its high abundance, especially of individuals in the 10–20 cm size class, in recently burned plots. Species with thin bark, such as *Premna tomentosa*, *Erythroxylum monogynum*, and *Gyrocarpus americanus*, have higher relative abundance in the absence of fire and have proportionately more individuals in larger size classes in the presence of fire. *Gyrocarpus americanus* is known to not have any clonal sprouting mechanisms (Otterstorm et al., 2006), and we noticed that *Premna tomentosa*, *Erythroxylum monogynum*, and *Acacia chundra* do not resprout as quickly as species in the most fire-tolerant functional group.

Local people cite frequent fire, along with fuelwood extraction and unregulated cutting for brickmaking, as important reasons for the reduced availability of forest resources in recent years, such as fodder, fuelwood, and nontimber forest products (FES, 2011; FES social survey, 2018 unpublished). Shifts in the abundance, size structure, and composition of trees in response to fire will affect

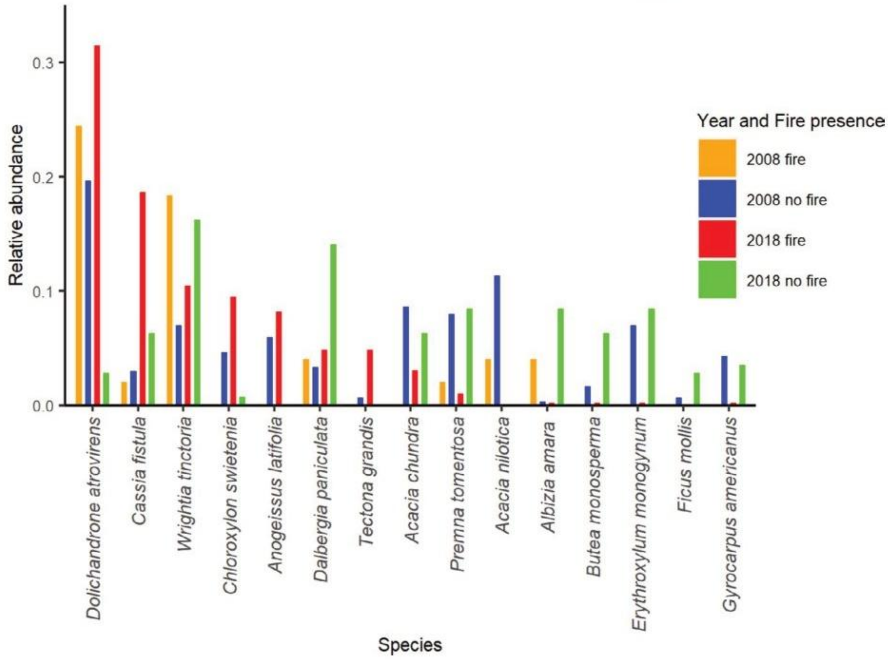


FIGURE 6 Relative abundance of tree species in four categories representing different sampling years and the presence and absence of fire. This visualization includes the 15 most common species across all sampling plots

TABLE 1 Chi-square results testing whether there are differences in size structure in the presence and absence of fire for each functional group. Individuals were pooled across species within each functional group category

Functional group and species	*p* value
Basal sprouting +Thin bark	
Albizia amara	.03554
Premna tomentosa	
Erythroxylum monogynum	
Dalbergia paniculata	
Acacia chundra	
Basal sprouting +Thick bark	
Wrightia tinctoria	.04259
Clonal sprouting +Thick bark	
Cassia fistula	.003327
Chloroxylon swietenia	
Dolichandrone atrovirens	

local livelihoods and regulating ecosystem services in our region. Shepherds in this region require fodder resources for livestock that mainly comprised of sheep and goats (FES social survey, 2018 unpublished). After a fire, if there is also precipitation due to summer rains, resprouting C4 grasses are palatable for a short time period and provide fodder resources to grazing animals in the dry season (FES social survey 2018 unpublished). Preferred fodder species for goats are *Dolichandrone atrovirens*, *Acacia chundra*, *Albizia amara*, *Azadirachta indica*, *Hardwickia binata*, and *Premna tomentosa*. Of these, only *Dolichandrone atrovirens* is common and abundant in the presence of fire. Sheep prefer *Azadirachta indica* and *Hardwickia binata*, which are already rare species at our site. Further, several species that provide valuable timber and nontimber forest products (i.e., ethnomedical uses) are rare in all plots or are particularly rare in plots with recent fire, such as *Dalbergia paniculata*, *Premna tomentosa*, *Gyrocarpus americanus*, *Erythroxylum monogynum*, *Ficus mollis*, and *Butea monosperma* (FES, 2011; FES social survey, 2018 unpublished).

A multistakeholder approach is already underway in this region to activate broad-base, community-led conservation action. The Foundation for Ecological Security (FES) is a local conservation NGO that is promoting protection of resources by collaborating with forest-dependent communities. FES engages in strengthening democratic village institutions for collective governance through helping communities secure tenure over them and undertake measures for the restoration of forest resources. FES has been engaging the rural community members to understand the effects of fire through campaigns and exercises on taking precautions to prevent forest fires and also on the measures of dousing fire.

We suggest that future research should experimentally exclude fire and follow permanently tagged individuals and plots, to allow opportunities to quantify demographic vital rates and project future population and community dynamics. While we believe the short-term results from our observational study would match those of an experimental study, as the spatial locations of burned versus. unburned sites are more likely to be random than due to differences in their physical and biological characters, it would be useful to have an experimental system that was designed for the long-term exclusion of fire. Further, while the presence of small, resprouting individuals of fire-tolerant species such as *Dolichandrone atrovirens* can maintain the size of a population in the intermediate future, recruitment is necessary for long-term viability (Bond & Midgley, 2001; Clark et al., 2013). Compared with nonsprouters, resprouters allocate more biomass to roots,

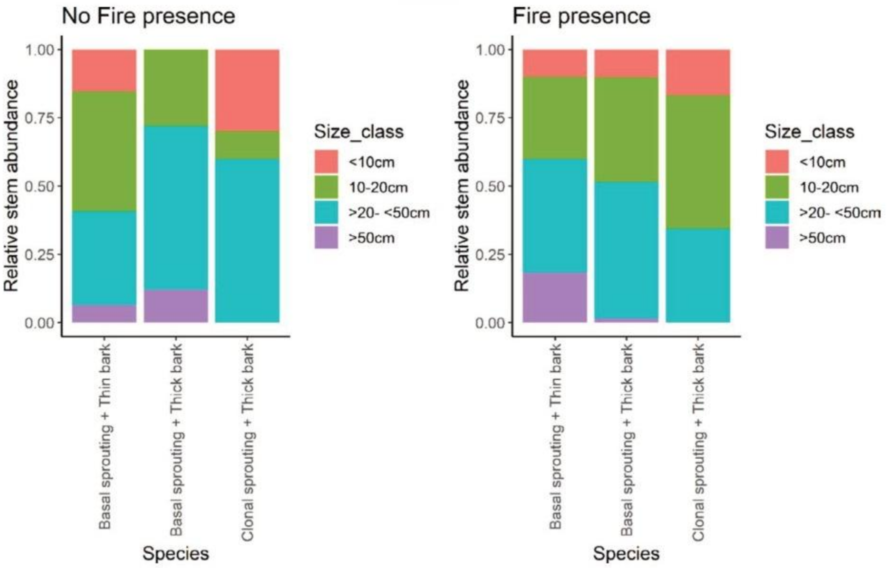


FIGURE 7 Relative number of stems for each functional group of species (considers common species in three functional group categories) that are in each size class in plots with no fire presence (left) and in plots with fire presence (right) in 2018

have lower seed output and seedling establishment, and take longer to reach a reproductive stage (Bond & Midgley, 2001; Clark et al., 2013). Thus, by favoring resprouting species, fire changes the functional composition of forests.

The dry forests in the Deccan Peninsula and Eastern Ghats face a serious threat from climate change (Das & Behera, 2019; Remya et al., 2015), which may extend the length of the dry season. These changes could directly cause the loss of species in our system, which cannot tolerate these new conditions. Currently, there is a lack of species distribution models for species in the Eastern Ghats, and this is an important topic for future research. Further, climate could also extend the fire season, and/or change the frequency, extent, or intensity of fires (Kale et al., 2017). Currently, the long dry season makes it difficult for many tree species to recover from fire. The interactive threats of fire and climate change could cause the local extinction of species that might otherwise be present in the presence of either threat.

5 | CONCLUSIONS

In our region, fire has increased in frequency across the past two decades. Fire poses an urgent threat to forests, as it results in the dominance of a few, fire-tolerant tree species, and a shift in the size structure toward smaller, resprouting individuals. These results demonstrate that conservation actions are needed to prevent further degradation of forests in this region that support local livelihood and other valuable ecosystem services.

ACKNOWLEDGEMENTS

This work was funded by the Alexander von Humboldt Foundation under the framework of the Humboldt Professorship, and by the Helmholtz Recruitment Initiative of the Helmholtz Association (both to TMK). NV and TMK gratefully acknowledge the support of iDiv funded by the German Research Foundation (FZT-118-202548816). We thank the staff of the Foundation for Ecological Security for support in the field and valuable discussions. We also thank members of Knight's research group for useful discussions. We thank Kyle Tomlinson and an anonymous reviewer for comments that have improved this manuscript.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

Neeraja U.V: Data curation (equal); Formal analysis (lead); Investigation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **S Rajendrakumar:** Data curation (equal); Investigation (equal); Methodology (supporting); Writing-review & editing (equal). **CS Saneesh:** Investigation (equal); Writing-review & editing (equal). **Venkat Dyda:** Funding acquisition (supporting); Supervision (supporting); Writing-review & editing (equal). **Tiffany M Knight:** Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Project administration (lead); Resources (lead); Supervision (lead); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (equal).

AUTHOR CONTRIBUTIONS

Neeraja U.V: Data curation (equal); formal analysis (lead); investigation (lead); visualization (lead); writing—original draft (lead); writing—review and editing (equal). **S. Rajendrakumar:** Data curation (equal); investigation (equal); writing—review and editing (equal). **C.S. Saneesh:** Investigation (equal); writing—review and editing (equal). **Venkat Dyda:** Supervision (supporting); writing—review and editing (equal); funding acquisition (supporting). **Tiffany M. Knight:** Conceptualization (lead); formal analysis (supporting); funding acquisition (lead); project administration (lead); resources (lead); supervision (lead); visualization (supporting); writing—original draft (supporting); writing—review and editing (equal).

DATA AVAILABILITY STATEMENT

Tree species abundance data for both sampling years and size structure data for 2018 are available on Dryad https://doi.org/10.5061/dryad.p2ngf1vq8

ORCID

U. V. Neeraja https://orcid.org/0000-0002-9749-3870
C. S. Saneesh https://orcid.org/0000-0002-9461-2272
Tiffany M. Knight https://orcid.org/0000-0003-0318-1567

REFERENCES

Bahuguna, V. K., & Singh, S. (2002). Fire situation in India. *Int. for. Fire News*, *26*, 23–27.

Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R. M., Thomson, J. R., Frosini, S., Ferraz, D. B., Louzada, J., Hugo, V., Oliveira, F., Parry, L., Ribeiro, R., Solar, D. C., Vieira, I. C. G., Aragão, L. E. O. C., Begotti, R. A., & Braga, R. F. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, *535*, 144–147. https://doi.org/10.1038/nature18326

Barlow, J., & Peres, C. A. (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.

Beech, E., Rivers, M., Oldfield, S., & Smith, P. P. (2017). GlobalTreeSearch: The first complete global database of tree species and country distributions. *Journal of Sustainable Forestry*, *36*(5). https://doi.org/10.1080/10549811.2017.1310049

Bond, W. J., & Keeley, J. E. (2005). Fire as a global "herbivore": The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*, 387–394. https://doi.org/10.1016/j.tree.2005.04.025

Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology and Evolution*, *16*, 45–51. https://doi.org/10.1016/S0169-5347(00)02033-4

Bowman, D. M. J. S., & Murphy, B. P. (2010). Fire and biodiversity. In N. S. Sodhi, P. R. Ehrlich (Eds.), *Conservation Biology For All* (pp. 163–180). Oxford: Oxford University Press.

Bunk, S. (2004). World on fire. *PLoS Biology*, *2*, 154–159. https://doi.org/10.1371/journal.pbio.0020054

Champion, H. G., & Seth, S. K. (1968). *A revised survey of the forest types of India*. Government of India Publication.

Chao, A., Hsieh, T. C., & Colwell, R. K. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*, 45–67. https://doi.org/10.1890/13-0133.1

Chaturvedi, R. K., Raghubanshi, A. S., Tomlinson, K. W., & Singh, J. S. (2017). Impacts of human disturbance in tropical dry forests increase with soil moisture stress. *Journal of Vegetation Science*, *28*, 997–1007. https://doi.org/10.1111/jvs.12547

Chuvieco, E., Cocero, D., Riaño, D., Martin, P., Martínez-Vega, J., De La Riva, J., & Pérez, F. (2004). Combining NDVI and surface temperature for the estimation of live fuel moisture content in forest fire danger rating. *Remote Sensing of Environment*, *92*, 322–331. https://doi.org/10.1016/j.rse.2004.01.019

Clarke, P. J., Burrows, G. E., Enright, N. J., & Knox, K. J. E. (2013). Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *The New Phytologist*, *197*, https://doi.org/10.1111/nph.12001

Cochrane, M. A. (2003). Fire science for rainforests. *Nature*, *421*, 913–919. https://doi.org/10.1038/nature01437

Condé, T. M., Higuchi, N., & Lima, A. J. N. (2019). Illegal selective logging and forest fires in the northern Brazilian Amazon. *Forests*, *10*(1), 61. https://doi.org/10.3390/f10010061

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological Invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology Evolution and Systematics*, *23*, 63–87. https://doi.org/10.1146/annurev.es.23.110192.00043

Das, P., & Behera, M. D. (2019). Can the forest cover in India withstand large climate alterations? *Biodiversity and Conservation*, https://doi.org/10.1007/s10531-019-01759-y

Davidar, P., Sahoo, S., Mammen, P. C., Acharya, P., Puyravaud, J. P., Arjunan, M., Garrigues, J. P., & Roessingh, P. (2010). Assessing the extent and causes of forest degradation in India: Where do we stand? *Biological Conservation*, *143*, 2937–2944. https://doi.org/10.1016/j.biocon.2010.04.032

De Andrade, D. F. C., Roberto, A., Schwartz, G., Olegário, J., Carvalho, P. D., Humphries, S., Ricardo, J., & Gama, V. (2020). Forest resilience to fire in eastern Amazon depends on the intensity of pre fire disturbance. *Forest Ecology and Management*, *472*, 118258. https://doi.org/10.1016/j.foreco.2020.118258

De Luis, M., Raventós, J., & González-Hidalgo, J. C. (2005). Factors controlling seedling germination after fire in Mediterranean gorse shrublands. Implications for fire prescription. *Journal of Environmental Management*, *76*, 159–166. https://doi.org/10.1016/j.jenvman.2005.01.014

Dimitrakopoulos, A. P., Vlahou, M., Anagnostopoulou, C. G., & Mitsopoulos, I. D. (2011). Impact of drought on wildland fires in Greece: Implications of climatic change? *Climatic Change*, *109*, 331–347. https://doi.org/10.1007/s10584-011-0026-8

Fire management global assessment 2006. (2007). *FAO Forestry Paper 151* (p. 119). FAO. http://www.fao.org/docrep/009/a0969e/a0969e00.htm

Forest Survey of India (FSI) (2012). Vulnerability of India's Forests to Fires. Ministry of Environment and Forest, Government of India.

Forest Survey of India FSI. (2019). Chapter 4: Forest types and Biodiversity. pp. 66–85. India State of Forest Report. Ministry of Environment and Forests Government of India. Retrieved from https://fsi.nic.in/forest-report-2019

Foundation for Ecological Security (FES). (2011). Ecological Baseline Assessment of Kadiri watershed Anantapur District in Andhra Pradesh. Retrieved from http://fes.org.in/studies/ecological-baseline-assessment-of-kadiri-watershed.pdf

Gadgil, M., & Meher-Homji, V. M. (1986). Localities of great significance to conservation of India's biological diversity. *Proceedings of Indian Academy of Sciences (Animal Sciences/Plant Sciences)*, 165–180. http://repository.ias.ac.in/64126/1/4_pub.pdf

Giriraj, A., Babar, S., Jentsch, A., Sudhakar, S., & Murthy, M. S. R. (2010). Tracking fires in India using advanced Along Track Scanning Radiometer (A) ATSR data. *Remote Sensing*, *2*, 591–610. https://doi.org/10.3390/rs2020591

Gosper, C. R., Yates, C. J., Prober, S. M., & Parsons, B. C. (2012). Contrasting changes in vegetation structure and diversity with time since fire in two Australian Mediterranean-climate plant communities. *Austral Ecology*, *37*, 164–174. https://doi.org/10.1111/j.1442-9993.2011.02259.x

He, T., Lamont, B. B., & Pausas, J. G. (2019). Fire as a key driver of Earth's biodiversity. *Biological Reviews*, *94*, 1983–2010. https://doi.org/10.1111/brv.12544

Hiremath, A. J., & Sundaram, B. (2005). The fire-lantana cycle hypothesis in Indian forests. *Conservation and Society*, *3*, 26–42.

Hoffmann, W. A., Geiger, E. L., Gotsch, S. G., Rossatto, D. R., Silva, L. C., Lau, O. L., Haridasan, M., & Franco, A. C. (2012). Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters*, *15*, 759–768. https://doi.org/10.1111/j.1461-0248.2012.01789.x

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*, 1451–1456. https://doi.org/10.1111/2041-210X.12613

Husch, B., Beers, T. W., & Kershaw, J. A. Jr (2002). *Forest mensuration*. John Wiley & Sons.

Janzen, D. (1988a). Tropical dry forests: The most endangered major tropical ecosystem. In E. O. Wilson (Ed.), *Biodiversity*, (pp. 24–36). : National Academic Press.

Jhariya, M. K., Bargali, S. S., Swamy, S. L., & Kittur, B. (2012). Vegetational structure, diversity and fuel load in fire affected areas of tropical dry deciduous forests in Chhattisgarh. *Vegetos*, *25*, 210–224.

Joseph, S. (2009). Forest fire in India: A review of the knowledge base. *Journal of Forest Research*, *14*(3), 127–134. https://doi.org/10.1007/s10310-009-0116-x

Kale, M. P., Ramachandran, R. M., Pardeshi, S. N., Chavan, M., Joshi, P. K., Pai, D. S., Bhavani, P., Ashok, K., & Roy, P. S. (2017). Are climate extremities changing forest fire regimes in India? An analysis using MODIS fire locations during 2003–2013 and gridded climate data of India meteorological department. *Proceedings of the National Academy of Sciences, India Section A: Physical Sciences*, *87*, 827–843. https://doi.org/10.1007/s40010-017-0452-8

Keeley, J. E. (1986). Resilience of Mediterranean shrub communities to fires. In B. Dell, A. J. M. Hopkins, & B. B. Lamont (eds.), *Resilience in Mediterranean-type ecosystems* (pp. 95–112.). W Junk.

Khan, M. L., & Tripathi, R. S. (1989). Effects of stump diameter, stump height and sprout density on the sprout growth of four tree species in burnt and unburnt forest plots. *Acta Oecologica*, *10*(4), 303–316.

Kodandapani, N., Cochrane, M. A., & Sukumar, R. (2004). Conservation threat of increasing fire frequencies in the Western Ghats, India. *Conservation Biology*, *18*(6), 1553–1561. https://doi.org/10.1111/j.1523-1739.2004.00433.x

Kodandapani, N., Cochrane, M. A., & Sukumar, R. (2008). A comparative analysis of spatial, temporal, and ecological characteristics of forest fires in seasonally dry tropical ecosystems in the Western Ghats, India. *Forest Ecology and Management*, *256*, 607–617. https://doi.org/10.1016/j.foreco.2008.05.006

Kothari, A., Suri, S., & Singh, N. (1995). Conservation in India: A new direction. *Economic and Political Weekly*, *30*, 2755–2766.

Kraus, D., & Goldammer, J. G. (2007). *Fire regimes and ecosystems: an overview of fire ecology in tropical ecosystems. Forest fires in India – workshop proceedings* (Edited by J. Schmerbeck, A. Hiremath, & C. Ravichandran, pp. 9–13). ATREE, Bangalore, India and Institute of Silviculture.

Krishna, P. H., & Reddy, C. S. (2012). Assessment of increasing threat of forest fires in Rajasthan, India using multi-temporal remote sensing data (2005–2010). *Current Science*, *102*, 1288.

Krishnaiah, Y. V. (2013). Landuse pattern and Landuse Efficiency of the Papagni River Basin. *India. Indian Journal of Spatial Science*, *4*(1), 59–68.

Lewis, T., & Debuse, V. J. (2012). Resilience of a eucalypt forest woody understorey to long term (34–55 years) repeated burning in subtropical Australia. *International Journal of Wildland Fire*, *21*, 980–991. https://doi.org/10.1071/WF11003

Mondal, N., & Sukumar, R. (2015). Regeneration of juvenile woody plants after fire in a seasonally dry tropical Forest of Southern India. *Biotropica*, *47*, 330–338. https://doi.org/10.1111/btp.12219

Murphy, P. G., & Lugo, A. E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology and Systematics*, *17*(17), 67–88. https://doi.org/10.1146/annurev.es.17.110186.000435

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B. et al (2015). The vegan package. Community ecology package. R package version 2.3-2. Available at: http://CRAN.R-project.org/package=vegan

Otterstrom, S. M., Schwartz, M. W., & Velazquez-Rocha, I. (2006). Responses to Fire in selected tropical dry forest trees. *Biotropica*, *38*, 592–598.

Prestes, N. C. C. S., Massi, K. G., Silva, E. A., Nogueira, D. S., de Oliveira, E. A., Freita, R., Marimon, B. S., Marimon-Junior, B. H., Keller, M., & Feldpausch, T. R. (2020). Fire Effects on Understory Forest Regeneration in Southern Amazonia. *Frontiers in Forests and Global Change*, *3*, 10. https://doi.org/10.3389/ffgc.2020.00010

Pullaiah, T. (1997). *Flora of Andhra Pradesh (India) Vol III* (pp. 922–1349). Scientific Publishers.

Pullaiah, T., & Ali Mouali, D. (1997). *Flora of Andhra Pradesh (India) Vol. II* (pp. 464–921). Scientific Publishers.

Pullaiah, T., & Chennaiah, E. (1997). *Flora of Andhra Pradesh (India) Vol. I* (pp. 1–463). Scientific Publishers.

Puyravaud, J. P., Pascal, J. P., & Dufour, C. (1994). Ecotone structure as an indicator of changing forest-savanna boundaries (Linganamakki region, southern India). *Journal of Biogeography*, *21*(6), 581–593. https://doi.org/10.2307/2846033

Rajendrakumar, S. (2014). Floristic Richness in catchment areas of Papagini River-A tributary of river Pennar, Andhra Pradesh. *India. International Journal of Environment*, *3*(1), 177–204. https://doi.org/10.3126/ije.v3i1.9953

Rao, V. U. M., Bapuji Rao, B., & Venkateswarlu, B. (2013). Agroclimatic Atlas of Andhra Pradesh, Central Research Institute for Dryland Agriculture, Hyderabad - 500 059, 270 pp

Ravindranath, N. H., & Sukumar, R. (1998). *Climate change and tropical forests in India*. Change. https://doi.org/10.1007/978-94-017-2730-3_21

R Core Team. (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reddy, C. S., Jha, C., Ganjam, M., Alekhya, V. V. L., Shaik, V., Koppineedi, S., Diwakar, P., & Dadhwal, V. (2017). Nationwide assessment of forest burnt area in India using Resourcesat-2 AWiFS data. *Current Science*, *112*, 10–2017. https://doi.org/10.18520/cs/v112/i07/1521-1532

Reddy, C. S., Krishna, P. H., Anitha, K., & Joseph, S. (2012). Mapping and inventory of forest fires in Andhra Pradesh, India: Current status and conservation needs. *ISRN Forestry*, *2012*, 1–10. https://doi.org/10.5402/2012/380412

Reddy, C. S., Varma, Y., Brahmam, M., & Raju, V. (2008). Prioritisation of endemic plants of Eastern Ghats for Biological conservation. *Proceedings of the National Seminar on Conservation of Eastern Ghats. EPTRI, Hyderabad*, pp. 3–13.

Remya, K., Ramachandran, A., & Jayakumar, S. (2015). Predicting the current and future suitable habitat distribution of *Myristica dactyloides* Gaertn. using MaxEnt model in the Eastern Ghats India. *Ecological Engineering*, *82*, 184–188. https://doi.org/10.1016/j.ecoleng.2015.04.053

Roy, P. S. (2003). Forest fire and degradation assessment using satellite remote sensing and geographic information system. *Satell. Remote Sens. GIS Appl. Agric. Meteorol*. pp. 361–400.

Sagar, R., Raghubanshi, A. S., & Singh, J. S. (2003). Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. *Forest Ecology and Management*, *186*, 61–71. https://doi.org/10.1016/S0378-1127(03)00235-4

Saha, S. (2002). Anthropogenic fire regime in deciduous forests of central India. *Current Science*, *82*, 101–104.

Saha, S., & Hiremath, A. (2003). Anthropogenic Fires in India: A Tale of Two Forests. *Arid Lands Newsletter*, 54.

Saha, S., & Howe, H. F. (2003). Species composition and fire in a dry deciduous forest. *Ecology*, *84*(12), 3118–3123. https://doi.org/10.1890/02-3051

Sandhyarani, S., Murthy, S. R., & Pullaiah, T. (2007). Tree Flora in Eastern Ghats of Southern Peninsular India. *Res. J. Bot.*, *2*, 176–185. https://doi.org/10.3923/rjb.2007.176.185

Santín, C., & Doerr, S. H. (2016). Fire effects on soils: The human dimension. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *371*(1696), 20150171. https://doi.org/10.1098/rstb.2015.0171

Sathya, M., & Jayakumar, S. (2017). Post-fire regeneration status of tree species in a tropical dry deciduous forest of Southern India. *Journal for Tropical Forest Science*, *29*(3), 305–317.

Schmerbeck, J., & Fiener, P. (2015). Wildfires, ecosystem services, and biodiversity in tropical dry forest in India. *Environmental Management*, *56*, 355–372. https://doi.org/10.1007/s00267-015-0502-4

Singh, J. S., & Singh, K. D. (2011). Silviculture of dry deciduous forests, India. In S. Günter, M. Weber, B. Stimm, & R. Mosandl (Eds.), *Silviculture in the tropics* (pp. 273–283). Springer.

Srivastava, P., & Garg, A. (2013). Forest fires in India: Regional and temporal analyses. *J. Trop. for. Sci.*, *25*, 228–239.

Sukumar, R., Suresh, H. S., Dattaraja, H. S., Srinidhi, S., & Nath, C. (2005). The dynamics of a tropical dry forest in India: Climate, fire, elephants and the evolution of life-history strategies. In S. Hartley (Ed.), *Biotic Interactions in the Tropics: Their role in the maintenance of species diversity* (pp. 510–529). Cambridge University Press.

Syaufina, L., & Ainuddin, A. N. (2011). Impacts of Forest Fire in Southeast Asia. *Asian Journal of Plant Sciences*, *10*(4), 238–244. https://doi.org/10.3923/ajps.2011.238.244

Vadrevu, K. P., Eaturu, A., & Badarinath, K. V. S. (2006). Spatial distribution of forest fires and controlling factors in Andhra Pradesh, India Using Spot satellite datasets. *Environmental Monitoring and Assessment*, *123*, 75–96. https://doi.org/10.1007/s10661-005-9122-4

Verma, S., & Jayakumar, S. (2015). Post-fire regeneration dynamics of tree species in a tropical dry deciduous forest, Western Ghats, India. *Forest Ecology and Management*, *341*, 75–82. https://doi.org/10.1016/j.foreco.2015.01.005

Verma, S., Singh, D., Mani, S., & Jayakumar, S. (2017). Effect of forest fire on tree diversity and regeneration potential in a tropical dry deciduous forest of Mudumalai Tiger Reserve, Western Ghats, India. *Ecological Processes*, *6*, 4–11. https://doi.org/10.1186/s13717-017-0098-0

Walters, M., Midgley, J. J., & Somers, M. J. (2004). *Dichrostachys cinerea* in the field. *BMC Ecology*, *4*, 1–13. https://doi.org/10.1186/1472-6785-4-3

Westerling, A. L. R. (2016). Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1696), 20150178, https://doi.org/10.1098/rstb.2015.0178

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Neeraja UV, Rajendrakumar S, Saneesh CS, Dyda V, Knight TM. Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats. *Ecol Evol*. 2021;00:1–11. https://doi.org/10.1002/ece3.7514

Chapter 3

Harvesting has variable effects on demographic rates and population growth across three dry forest species

This chapter has been published in Biotropica as

Neeraja, U.V., Saneesh, C.S., Dyda, V., Reddy, H., Yadama, G.N. and Knight, T.M., 2022. Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. Biotropica, 54(6), pp.1376-1389. https://doi.org/10.1111/btp.13135

Received: 15 October 2021 | Revised: 13 May 2022 | Accepted: 28 May 2022
DOI: 10.1111/btp.13135

ORIGINAL ARTICLE

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

Harvesting has variable effects on demographic rates and population growth across three dry forest tree species

U. V. Neeraja[1,2] | C. S. Saneesh[2,3] | Venkat Dyda[4] | Hemalatha Reddy[4] | Gautam N. Yadama[5] | Tiffany M. Knight[1,2,3]

[1]Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany
[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[3]Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle (Saale), Germany
[4]Foundation for Ecological Security, Madanapalle, Andhra Pradesh, India
[5]Boston College School of Social Work, Chestnut Hill, Massachusetts, USA

Correspondence
U. V. Neeraja, Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany.
Email: neeraja.venkataraman@idiv.de

Funding information
Washington University's I-CARES research award; Alexander von Humboldt Foundation; Helmholtz Recruitment Initiative of the Helmholtz Association

Associate Editor: Jennifer Powers

Handling Editor: Alvaro Duque.

Abstract

Understanding how anthropogenic activities, such as harvesting, influence plant populations is important to quantify sustainable practices that conserve species of socio-economic importance. There is limited knowledge on how harvesting of branches and non-timber forest products affect populations of trees in the dry tropics. We measure demographic vital rates of three dry tropical tree species in the presence and absence of harvesting and apply integral projection models to quantify population growth rates, which represent the mean fitness across the life cycle. Our results show that the three species vary in their demographic rates and life history. Harvesting significantly decreases the growth of two species. Current levels of harvesting only significantly decreased the population growth rate of one species that experienced both branch and main stem harvesting. Life table response experiments reveal that the negative effect of harvesting on the population growth rate of this species is primarily due to individuals being forced to re-sprout from their base. Few individuals were observed recruiting from seed, and this might be due to the presence of other threats, such as fire, soil erosion, and grazing. Our results provide knowledge on the demography and the effects of harvesting on endemic tree species of the Eastern Ghats, a region for which few demographic studies are available. These results are relevant to conserving forest biodiversity for the benefits of people and can contribute to quantitative threat assessment for IUCN red listing.

KEYWORDS
demography, eastern Ghats, harvesting, integral projection models, trees, tropical dry forest

1 | INTRODUCTION

In order to manage forest ecosystems for conservation and human livelihoods, it is important to understand the effects of anthropogenic activities on plant populations of economic, cultural, and conservation concern (Grogan et al., 2014; Kaye et al., 2001). Harvesting and use of plant products, especially non-timber forest products (NTFPs), account for a large proportion of the livelihoods of people living adjacent to forests (Ticktin, 2005). Overexploitation of timber and NTFPs is a concern, as 40% of plant species in the world are at risk of extinction (Nic Lughadha et al., 2020), and unsustainable harvesting practices are major drivers of plant loss (Brummitt et al., 2015). However, traditional harvesting practices by indigenous people can often be sustainable (Shackleton et al. 2015). Further, conservation

---

practices that separate people from nature, such as the creation of exclusionary protected areas, can have devastating consequences for rural communities (Endress et al., 2006; Robbins, 2012). This is increasingly recognized, as recent global strategies have focused on conserving biodiversity for the benefit of planet and people (CBD, 2021) and sustainably sourcing wild-harvested plant products (CBD, 2018).

The demographic vital rates (i.e., survival, reproduction) of trees depend on the size and stage of individuals, and these vital rates contribute unequally to the growth rate of the population. Thus, structured population models are necessary to assess the effects of factors such as harvesting on vital rates and population growth rates of trees (Tuljapurkar & Caswell, 1997). Structured population models are standard tools used to examine how different types and intensities of harvesting activities influence the growth rate and persistence of populations (e.g., Crouse et al., 1987; Gaoue, 2015; Isaza et al., 2017; Ticktin, 2004; Zuidema & Boot, 2002). There are many different types of harvesting practices that remove parts of plants, and these include forest products that require cutting branches or parts of trees for firewood, fodder, and construction timber and NTFPs such as fruits, foliage, bark, and root exudates which are used as medicine, food and sources of income for local people (Bawa et al., 2004; Gaoue et al., 2013; Shackleton et al. 2015; Shahabuddin & Prasad, 2004). The sustainability of the harvesting depends on several factors, such as the life history of harvested plant species, the part of the plant that is harvested, and the intensity of harvest (Peres et al., 2003; Schmidt et al., 2011; Ticktin, 2004). In addition, harvesting often takes place in the presence of other stressors such as fires, habitat loss, soil erosion, and erratic rainfall (Gaoue & Ticktin, 2007; Mandle & Ticktin, 2012).

By altering demographic vital rates, harvesting can influence both the population growth rate and population structure (i.e., the size distribution of individuals) of trees (e.g., Isaza et al., 2017; Martínez-Ballesté & Martorell, 2015). Both the number of individuals and the population structure influence the physical structure of the forest and the products that the forest provides to humans. Individuals in the largest size classes typically produce more forest resources, such as timber, bark, fruits, and leaves. However, these individuals are often also the target of harvesting. While large individuals might not die from harvesting, they might have reduced growth, or be forced to re-sprout in order to recover from the damage.

The effects of harvesting NTFPs on the demography and populations dynamics have been primarily studied in tropical forest ecosystems and on short-lived and fast-growing plant species such as shrubs and palms (Schmidt et al., 2011; Zuidema et al., 2007). However, examples of demographic studies on longer-lived trees include bark harvesting of *Prunus africana* in Africa (Cunningham & Mbenkum, 1993; Stewart, 2009), harvesting of Brazil nuts (*Bertholletia excelsa*) in South America (Peres et al., 2003), and harvesting of baobab fruits in African savannahs (Venter & Witkowski, 2013). The research that has been conducted on dry tropical forest trees so far suggests that the harvested effects are different from moist forests. In a notable example, Gaoue and Horvitz (2019) examined populations of African mahogany (*Khaya senegalensis*) along a moisture gradient and found that climate had a stronger effect on population dynamics than harvesting of leaves and bark by indigenous people in drier forests.

Little is known about the demography and life history of endemic tree species in India, and to our knowledge, there are very few studies on the effects of harvesting on tree population dynamics using structured population models. However, this is an important topic, as many people in India significantly rely on forest products for their local household incomes (Bawa et al., 2004; Davidar et al., 2010; Kothari et al., 1995). Growing human populations and populations of livestock add pressure on these forests in terms of grazing, annual fires, forest clearing for agricultural activities, and harvesting timber and NTFPs for energy, charcoal making, and income generation (Davidar et al., 2010). These anthropogenic activities are known to alter forest structure and composition (Bhuyan et al., 2003; Neeraja et al., 2021).

Our study area, the Sadhukonda Reserve forest, is a tropical dry forest in the Eastern Ghats surrounded with rural communities that depend on the forest for fuelwood, fodder, and NTFPs (FES, 2003). Extracted timber is used for household purposes (cooking, fencing, and making agricultural implements) and is sold in local markets (Chalise & Yadama, 2011; Yadama et al., 2010). Fruits and other forest products support household needs and also have local market value (FES, 2003, FES social survey 2018 unpublished). These harvesting activities take place in the context of other threats, such as fire and climate change (Neeraja et al., 2021; Shahabuddin & Prasad, 2004). Fire is used primarily to maintaining understory grasses for livestock (FAO, 2006) and has increased in frequency in the region in the past two decades (Neeraja et al., 2021). Climate change is already increasing the frequency and intensity of drought in this region (Sharma & Mujumdar, 2017; Remya et al., 2015; Ramachandran et al., 2018). While our study focuses on a particular forest, we note that the focal species and the techniques used to harvest them are similar across the region.

We measured demography and used an integral projection model (IPM, Ellner et al., 2016) to quantify fitness of three tree species across their life cycles. Our goal was to understand if current harvesting levels are sustainable, supporting both local livelihoods and species conservation. The three species, *Chloroxylon swietenia* (Rutaceae), *Gardenia gummifera* (Rubiaceae), and *Acacia chundra* (Fabaceae), are harvested for different purposes, which include fuelwood, fodder, and fruits. We addressed the following questions in our study: (1) What is the current intensity and type of harvesting? (2) How does harvesting influence the three demographic vital rates: survival, transition to sprout and growth of trees? (3) What are the vital rates and growth rates of these populations under ambient harvesting and what would these rates be in the absence of harvesting? (4) Which change in vital rates is the population growth rate most sensitive to, and which vital rates contribute most to the observed differences in population growth rate between harvesting and absence thereof? We hypothesized that stem harvesting and higher harvesting rate would decrease demographic vital rates and population growth rate.

2 | METHODS

2.1 | Study site

Our study area, the Sadhukonda Reserve Forest (SRF), is located between 13°46'N-13°54'N and 78°25′E-75°30′E at the junction of the Central Deccan Plateau and Eastern Ghats in the state of Andhra Pradesh. Our study area includes 224 ha within the 6331 ha of the SRF (Figure 1), which is accessible from nearby villages and for which active harvesting for forest products occurs (Yadama et al., 2010). Local communities have high dependency on biomass extraction from SRF for fuelwood, timber, fodder, and other NTFPs (Peipert et al., 2008). The SRF terrain is hilly, with elevation ranging from 470 to 1128 m. The annual average rainfall is 650 mm, and temperature ranges between 15°C and 45°C. Although the climate is influenced by South-West and North-East monsoons, the SRF is rather dry because the site falls under a rain shadow area. Annual fires are a common occurrence in this region (FES, 2003; Neeraja et al., 2021; Schmerbeck & Fiener, 2015). SRF is comprised of tropical dry deciduous, scrub, and savanna habitats. C_4 grasses such as *Cymbopogon* spp. are dominant in the understory.

2.2 | Study species

Chloroxylon swietenia (Family: Rutaceae; Common name: Indian Satinwood; and Local name: Billu) is a deciduous tree found in drier tracts of tropical dry deciduous forests. It is endemic to the Indian peninsula and Sri Lanka. It has characteristic thick, furrowed and ridged bark that is composed of corky tissue that confers fire tolerance (Sankara Rao et al., 2019). It is a valuable timber species, and NTFPs include the bark (used as an astringent) and the leaves (used as mosquito repellant) (Survase & Raut, 2011). It is listed as "Vulnerable" by IUCN red list owing to population decline due to overexploitation for timber (Asia Regional Workshop, 1998). Individuals shed leaves in February–March, flower in March–April, and release winged seeds in May–August. At the SRF, the branches and main stem of *Chloroxylon swietenia* are lopped for use as small construction poles, for agricultural tools, fodder, and fuelwood (See Figure S1 for photographs of main stem harvesting).

Gardenia gummifera (Family name: Rubiaceae; Common name: Cumbi-gum tree; and Local name: Bikki) is a small deciduous tree found in dry deciduous and scrub forests (Pullaiah et al. 2007). It is endemic to Peninsular India and is found in the states of Andhra Pradesh, Karnataka, Odisha, Kerala, and Tamil Nadu. It is harvested for gum-resin and fruits (FES, 2003). It was listed as "Least Concern" by IUCN in 1998, but was flagged as a species in need of future research on population trends (CAMP Workshops on Medicinal Plants, India, 1998). Individuals flower from January to April and produce fruits between April–August (Khare, 2007). At the SRF, branches of trees are cut for fodder and fruit harvest.

Acacia chundra (Family: Fabaceae; Common name: Red Cutch; and Local name: Sandra) is a deciduous tree with rough bark found in drier regions of India, Sri Lanka, and Myanmar (Sankara Rao et al., 2019). Timber is harvested to make agricultural implements and for firewood/charcoal, but this species is not preferred because the wood is heavy to carry. NTFPs include the bark and leaves (used medicinally). This species is not assessed by the IUCN red list. Flowering is during May–June and fruiting is in until October. At the SRF, branches with seeds and fruits are cut for fodder during the dry season, and timber is harvested on individuals for fuelwood and making of traditional mortar and pestle that are located in close proximity to villages (FES, 2003) (See Figure S2 for photographs of branch harvesting).

Individuals of all three species can re-sprout basally (or rarely, can re-sprout from the sides of the main stem) when the main stem

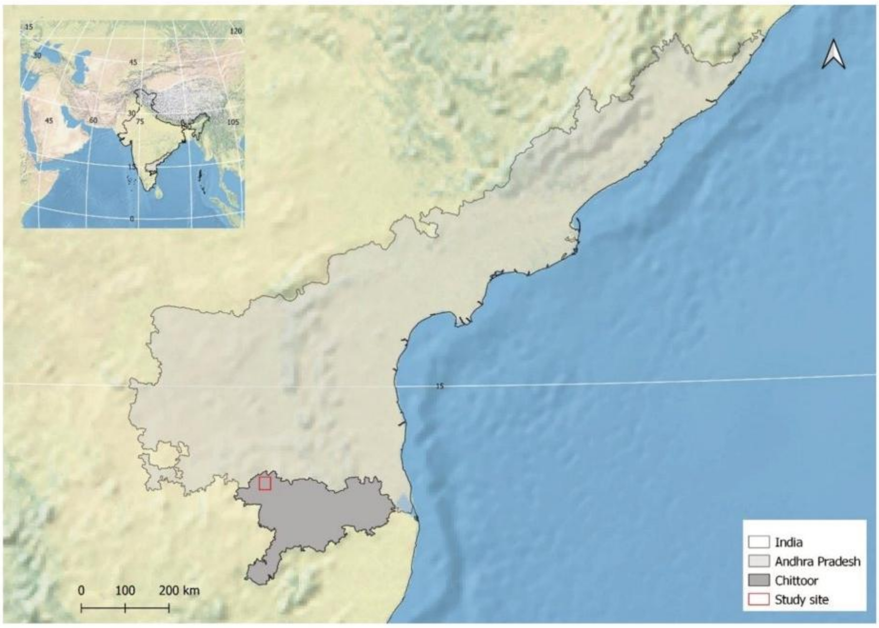


FIGURE 1 Map of the 224 ha study site located in the Chittoor district within the state of Andhra Pradesh in India

is lost from a disturbance (e.g., top kill from fire, main stem harvesting). In this manuscript, we refer to these resprouting individuals as "sprouts" (see Figure S3 for a photograph of a sprout). Sprouts have multiple small stems that emerge from the base of the individual (all stems are smaller than 0.64 collar diameter). In the absence of repeated disturbances, sprouts can re-enter the tree state by growing to have at least one stem with a minimum collar diameter of 0.64 cm. For all three species, very little is known about the recruitment dynamics from seed, such as longevity in the seedbank and requirements for germination.

2.3 | Data collection

Demographic data were collected during post-monsoon period in 2009 and 2016. Our search area for individuals of the three species spanned the entire 224 ha study area. We aimed to sample at least 200 trees per species and we aimed to also avoid aggregation in our sampling of individuals (McMahon et al., 2019). Mortality of large-sized trees is difficult to detect and is often spatial aggregated, but small changes in mortality are known to have large effects on the changes in the population size over time. Thus, an adequate sample size of trees is necessary to distinguish mortality effects of harvesting from stochasticity (McMahon et al., 2019).

Despite our best efforts, the three focal species were present across this large sampling area in relatively small clusters of individuals. We placed nine permanent rectangular plots around these clusters, which ranged in size from 0.2 ha to 1.2 ha, and mapped and tagged individuals of the three study species. We observed that *Acacia chundra* individuals were mostly likely to occur at lower slopes of our study site and *Chloroxylon swietenia* individuals at higher slopes. In total, we sampled 63, 83, and 98 stems with a diameter of at least 0.64 cm for *Acacia chundra*, *Chloroxylon swietenia*, and *Gardenia gummifera*, respectively (Table 1). We aimed to sample at least 50 and up to 100 resprouting individuals (i.e., sprouts) for each species. We were able to do so for *Chloroxylon swietenia*, and *Gardenia gummifera*. However, sprout is a rare stage class for *Acacia chundra*, and only 10 individual sprouts were found (Table 1).

Similarly, we aimed to sample at least 50 and up to 100 seedlings for each species. In 2009, ten researchers extensively searched the entire 224 ha study area searching for seedlings of these three species, and only found a total of three seedlings, two belonging to *Gardenia gummifera* and one to *Acacia chundra*. No seedlings of *Chloroxylon swietenia* were found in either 2009 or 2016. There were reproductive individuals present of all three species in the study site that appeared to be producing viable seeds, and yet we found very few individuals recruiting from seed in our broad search. This lack of recruitment is therefore a real result that we discuss more later (see Section 4).

During both censuses, we measured girth at breast height (GBH) or collar girth when GBH was not possible. If an individual had multiple stems, we calculated total girth as the square root of sum of squares of GBH of each stem (Vaz Monteiro et al., 2016). We

TABLE 1 Sample sizes of plots and number of individuals for each species time *t* (2009) and *t* + 1 (2016). Individuals are shown separately for the two state classes: *Trees* and *sprouts*

Species	No. of plots	*Trees* at *t*	*Trees* dead at *t* + 1	*Trees* transitioned to *sprouts* state at *t* + 1	*Trees* harvested	*Sprouts* at *t*	*Sprouts* dead at *t* + 1	*Sprouts* transitioned to *trees* state at *t* + 1	*Sprouts* Harvested
Acacia chundra	2	63	7	6	8	10	10	0	0
Chloroxylon swietenia	4	83	1	6	19	55	3	4	0
Gardenia gummifera	5	98	4	2	21	80	33	10	0

converted GBH into diameter for our data analysis (i.e., divide girth by π to get diameter). For each individual, we documented presence or absence of harvesting damage on each tree, and whether the damage was on the main stem or branches. When branch harvesting occurred, it typically involved a large proportion (between 33% and 100%) of the branches being cut, which was visible on the tree (it was possible to observe the cut branches on the tree; see photographs in the Appendix S1). None of the resprouting individuals “sprouts” were harvested.

All three seedlings from 2009 were dead in the 2016 census, and we had similar difficulties finding seedlings of all three species in 2016. During our census, recruitment of new individuals from seed was effectively non-existent and thus recruitment dynamics cannot be explicitly modeled at this time. Our integral projection model (see below) considers the current situation in which population dynamics are determined by survival and growth of existing individuals. Without recruitment, it is impossible for these populations to grow, and thus, the maximum possible population growth rate is 1.0 (which would occur if all existing individuals survive during the census period).

2.4 | Life cycle and vital rates

The life-cycle of all three species was considered across a seven-year time interval using one continuous (tree) and one discrete (sprout) state class (Figure 2). The vital rates of trees include probability of survival (s_1), the probability that surviving trees move to the discrete sprout stage class (a), and growth of surviving trees (g). These vital rates may be significantly affected by tree size (log-transformed diameter) and/or harvesting (presence or absence). To test for the effects of harvesting and size on s_1 and a, we used logistic regression with binomial error distributions. Some species did not show significant effects of individual size on either s_1 or a; in these cases, s_1 and a are modeled as constants in the integral projection model IPM (see below). The growth of surviving trees (g) was modeled as a linear regression, with log size at time step $t+1$ as a function of log size in time t and harvesting as a factor. Because our trees have multiple stems, it is possible for trees to lose a stem and decrease in size even in the absence of harvesting for a variety of reasons (fire, drought, pests).

The vital rates of the discrete state, sprouts, are constants that summarize the proportion of sprouts that survive from one time step to the next (s_2) and the proportion of surviving sprouts that enter the continuous tree state (b). The size of individual trees re-entering the tree state from the sprout state (d) is described by the mean and standard deviation of a normal distribution of the log size of those individuals.

2.5 | Integral projection models

We used integral projection models (IPMs) to determine the population growth rate (λ) of the three focal tree species under two scenarios that are relevant to management: ambient and no harvesting. Population growth rate (λ) provides a summary of demographic vital rates across the life cycle of the plants and can be interpreted as lifetime fitness of individuals in the population under different harvesting scenarios. The ambient scenario considered vital rates and population growth rates for each species in the presence of harvesting at the current (i.e., ambient) levels. The no harvesting scenario quantifies the vital rates and population growth rates of each species under the management scenario in which harvesting would cease to occur. For the ambient scenario, vital rates were calculated using all individuals sampled (both harvested and not harvested individuals). For the no harvesting scenario, vital rates were calculated using only individuals with no observed harvesting damage in 2009 or 2016. Sample sizes for each species are shown in Table 1.

We implemented density independent and deterministic IPM. IPMs describe individuals as either belonging to a discrete state, or as driven by a continuous trait such as size (Easterling et al., 2000; Ellner et al., 2016). IPMs were thus ideal to describe our species,

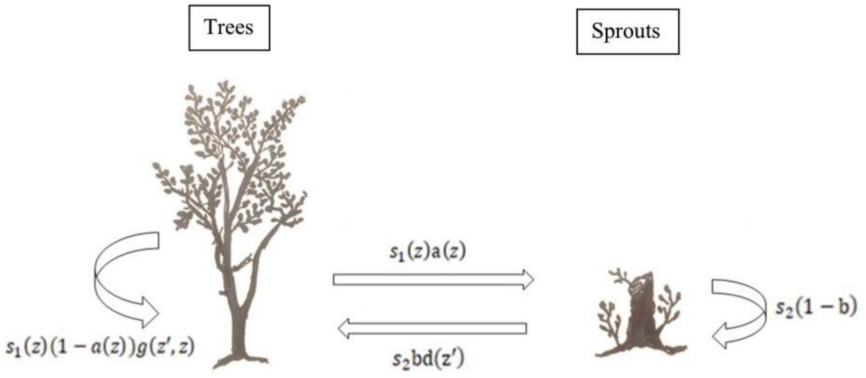


FIGURE 2 Life cycle graph of the study species. All three species are modeled with one continuous and one discrete state, trees and sprouts, respectively. The vital rates are incorporated in an integral projection model (IPM) that describes how the size of individuals changes across one time step (see equation [1]). Size of trees at time t is z, and size at time $t+1$ is z'. Vital rates are as follows: Survival of trees (s_1), survival of sprouts (s_2), growth of trees (g), probability of transitioning from tree to sprout (a) and from sprout to tree (b), and size of sprouts when they re-enter the tree state (d)

whose populations were comprised of sprouts (a discrete state) and trees (individuals described by a continuous trait, size). The change in the number of trees from one seven-year time step (t) to the next ($t+1$) was described by

$$n(z',t+1) = C(t)s_2\mathrm{b}d(z') + \int_L^U s_1(z)(1-a(z))g(z',z)n(z,t)dz \tag{1}$$

The vector $n(z', t+1)$ describes the number of trees at size z at time $t+1$. The first term describes sprouts entering the tree state, which is the product of the number of sprouts at time t, $C(t)$, sprout survival (s_2), the proportion of surviving sprouts that enter the continuous tree state (b), and the size distribution of new trees $d(z')$. The second term refers to individuals that remain trees from one time step to the next. This is a two-dimensional kernel that describes the probability of all possible transitions from size z at time t, size z' at time $t+1$. These transitions depend on size-dependent tree survival $s_1(z)$, probability that surviving trees remain in the tree state (1-a), and tree growth $g(z', z)$. The kernel and the $n(z,t)$ function were defined between the lowest, L, and upper, U, size observed in our three populations. These IPMs represent the kernel and $n(z,t)$ function using 100 discrete states. These discrete states allowed us to approximate the integral of the kernel using the midpoint rule.

The discrete state of the population, sprouts, is described by

$$C(t+1) = C(t)s_2(1-\mathrm{b}) + \int_L^U s_1(z)a(z)n(z,t)dz \tag{2}$$

The first term describes sprouts surviving and remaining in the sprout state, and the second term describes trees surviving and entering the sprout state. We implemented these IPMs using the *ipmr* package (Levin et al., 2021).

We used IPMs to calculate population growth rate (λ) for each species in ambient harvesting and no harvesting scenarios (Ellner et al., 2016). The species *Chloroxylon swietenia* experiences both branch and main stem harvesting. We considered an additional scenario just for this species to disentangle the importance of the different harvesting types. Specifically, the "exclude stem harvesting" scenario includes the presences of not harvested and branch harvested individuals, and excludes stem harvested individuals.

To quantify uncertainty in our data for each species and scenario, we resampled individuals with replacement 1000 times, refit all vital rates, and computed λ. We report our point estimate of λ and the 95% confidence intervals from the bootstrapping procedure. Non-overlapping 95% confidence intervals in λ between scenarios for a species are interpreted as evidence that the presence of harvesting significantly decreases λ.

We evaluated the sensitivity of λ to changes in vital rates under the ambient harvesting scenario for all three species. Sensitivities were estimated numerically by applying a uniform perturbation (0.001) to each model parameter and quantifying the difference in λ. To decompose the contribution of different vital rates to the observed difference in λ between the ambient and no harvesting scenarios, we conducted a life table response experiment (LTRE, Caswell 2000, 2001). The contribution of each of the ten model parameters is calculated as

$$\sum_i^{10} \left(\alpha_i^{\text{no harvesting}} - \alpha_i^{\text{ambient harvesting}}\right) \frac{\partial \lambda}{\partial \alpha_i} \tag{3}$$

where α_i is one of the model parameters, and $\frac{\partial \lambda}{\partial \alpha_i}$ is the sensitivity of λ to changes in α_i. A vital rate will have a large contribution to the observed difference in λ between the ambient and no harvesting scenarios if it changes dramatically between those scenarios and/or if λ is sensitive to changes in that vital rate. We report sensitivities and LTRE results with respect to six vital rates: survival of trees, growth of trees, transition from tree to sprout, survival of sprouts, transition from sprout to tree, and sprout size distribution. These vital rates often combine the effects of multiple model parameters (e.g., survival of trees is described by the slope and intercept of a logistic regression for some species).

All analyses and visualizations were performed in R (version 3.5.1; R Core Team 2018).

3 | RESULTS

3.1 | Harvesting

All three species experienced branch harvesting (Figure 3). *Chloroxylon swietenia* individuals were the only ones observed to have harvesting of their main stem (Figure 3). *Chloroxylon swietenia* experienced the highest and *Acacia chundra* experienced the lowest harvesting rates (Figure 3).

3.2 | Vital rates

Survival was overall highest in *C. swietenia* (only one individual was observed to die). Survival was not predicted by size in *C. swietenia* and *A. chundra* and was therefore modeled as a constant (Table 2, Figure 4). Survival significantly increased with size in *G. gummifera* (Table 2, Figure 4). Harvesting did not influence survival of any species (Table 2).

The proportion of surviving trees that transitioned to the sprout state decreased with tree size for *G. gummifera* and *A. chundra*, but did not depend on tree size for *C. swietenia* (Table 2, Figure 4). Harvesting did not influence proportion of trees that transitioned to the sprout state for any species (Table 2). However, we note that all six of the *C. swietenia* trees that transitioned to sprout experienced main stem harvesting. Two of the 94 surviving trees of *G. gummifera* and six of the 56 surviving trees of *A. chundra* transitioned to sprout.

Growth was significantly reduced by harvesting for *G. gummifera* and *C. swietenia*, but not for *A. chundra* (Table 2, Figure 5).

Sprouts of *C. swietenia* had high survival (94.5%), but only 9.6% of the surviving sprouts transitioned to tree state (Table 3). In contrast,

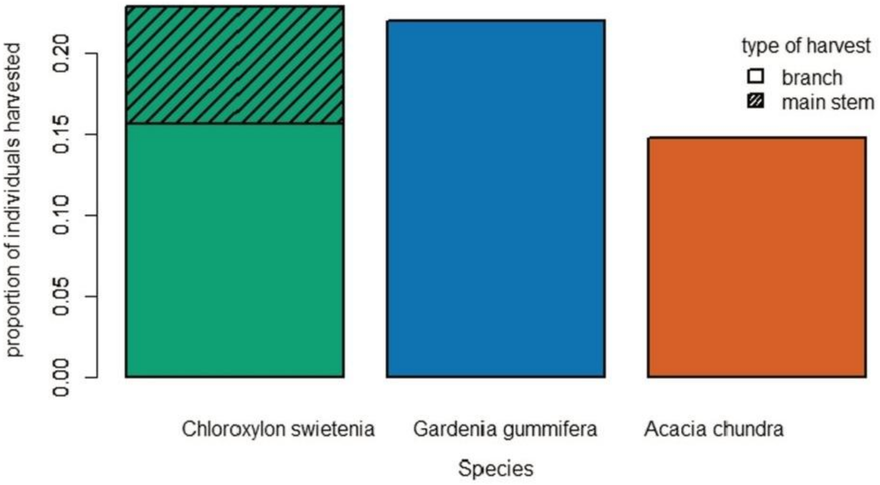


FIGURE 3 Proportion of trees harvested for each species and whether the harvesting is on the main stem or branches of the tree

only 58.7% of the sprouts of *G. gummifera* survived, but 21.2% of the surviving sprouts transitioned to tree state. None of the sprouts of *A. chundra* survived.

3.3 | Population growth rates

Harvesting significantly decreased the population growth rate of *C. swietenia* but did not significantly decrease the population growth rate of *G. gummifera* and *A. chundra* (Figure 6). This is due to the stem harvesting that occurs on *C. swietenia*, as the population growth rate in the "exclude stem harvesting" (includes not harvested and branch harvested individuals, excludes main stem harvested individuals) scenario was similar to that observed in the "no harvesting" scenario (Figure 6). As there was no recruitment of new individuals, none of these species had growing populations. The *A. chundra* population was significantly declining. The *C. swietenia* population was significantly declining in the presence of ambient levels of harvesting. In the no harvesting scenario, all individuals of this species survived and none transitioned to sprout, resulting in a small uncertainty (bootstrap CI) to the estimated population growth rate.

3.4 | Sensitivity analysis

Our sensitivity analysis indicated that the λ of *A. chundra* was most sensitive to changes in tree survival and *G. gummifera* was most sensitive the changes in the growth of trees (Figure 7). The λ of *C. swietenia* was most sensitive to changes in tree survival and in the proportion of trees that transition to sprout (Figure 7).

3.5 | Life table response experiment

The λ of *C. swietenia* was significantly different between the ambient harvesting (includes all individuals, including those with main stem harvesting) and no harvesting scenarios, and thus, an LTRE analysis was only performed for this species. Our LTRE indicated that for *C. swietenia* changes in the proportion of individuals that transitioned from tree to sprout drove the changes in λ observed between the ambient and no harvesting scenarios (Figure 8). The proportion of individuals that transitioned from tree to sprout decreased from 0.07 to 0 between ambient and no harvesting scenarios (Table 2), and λ was sensitive to changes in this vital rate (Figure 7).

4 | DISCUSSION

Harvesting of branches, fruits, and stems is a common activity occurring in forests, savannas, and woodlands throughout the world (Bawa et al., 2004). Many species that experience recurring harvesting of NTFPs face population decline over time (Gaoue et al., 2011; Gaoue et al., 2013; Peres et al., 2003). In our study, we found that harvesting significantly decreases the growth of two tree species, *G.gummifera* and *C.swietenia*. Only for *C. swietenia*, current harvesting levels (ambient scenario) resulted in a significantly lower population growth rate than would occur in the absence of harvesting. This species had higher overall incidences of harvesting on its individuals and was also the only species in our study that experienced harvesting of its main stem. We found a lack of recruitment across all species that is likely due to other threats, and as a result, these species are projected to decline. These results have important conservation implications for these three species and also contribute to a growing literature on the effect of harvesting on tree populations.

The proportion of individuals harvested and the type of harvesting differs across the three species. The higher harvesting rate of *C. swietenia* and *G. gummifera* compared to *A, chundra* is likely because the extracted fuelwood and collected fruits of these species are sold to local market (FES, 2003), whereas *A. chundra* is primarily used locally. The branches of *A. chundra* are primarily cut in the field as fodder for animals (especially for sheep and during the dry season), but not typically sold in local markets due to the difficulty in transporting the heavy branches (FES social survey 2018 unpublished).

TABLE 2 Coefficients for each vital rate regressions applied independently for each species (slope estimates, standard errors, and *p*-values for generalized linear models and multiple linear models, and additionally R^2 values for multiple linear models) testing whether tree size (log-transformed diameter) at time *t* and harvesting (presence or absence) significantly influenced tree vital rates: Probability of tree survival (logistic regression, generalized linear model), probability of surviving trees transitioning to the sprout state (logistic regression, generalized linear model), and tree size at $t+1$ (multiple linear regression, multiple linear model)

	Estimate	SE	*p*-value
Acacia chundra Survival			
Size	0.703	0.557	.207
Harvesting	17.811	8524	.998
Size*harvesting	−0.703	3711	1.000
Acacia chundra Transition to sprout			
Size	−1.289	0.623	**.0385***
Harvesting	−18.692	8524	.998
Size*harvesting	1.289	3711	1.000
Acacia chundra Growth (size at t + 1)			
Size	0.663	0.065	**<.001*****
Harvesting	−0.0543	0.360	.139
Size*harvesting	0.206	0.160	.204
	$R^2 = 0.739$		
Chloroxylon swietenia Survival			
Size	0.000	6933	1.000
Harvesting	−0.189	10,980	.999
Size*harvesting	−0.415	6933	1.000
Chloroxylon swietenia Transition to sprout			
Size	0.000	4205	1.000
Harvesting	21.04	6659	.997
Size*harvesting	−0.099	4205	1.000
Chloroxylon swietenia Growth (size at t + 1)			
Size	0.824	0.056	**<0.001*****
Harvesting	0.473	0.226	**.041***
Size*harvesting	−0.350	0.127	**.008****
	$R^2 = 0.806$		
Gardenia gummifera survival			
Size	2.089	0.773	**.007****
Harvesting	20.057	12,583	.999
Size*harvesting	−2.089	6197	1.000
Gardenia gummifera Transition to sprout			
Size	−2.570	1.160	**.027***
Harvesting	−19.790	12,584	.999
Size*harvesting	2.570	6197	1.000
Gardenia gummifera Growth (size at t + 1)			
Size	0.722	0.037	**<.001*****
Harvesting	−0.477	0.156	**.003****
Size*harvesting	0.158	0.077	**.044***
	$R^2 = 0.859$		

Bold values indicate statistically significant *p*-values.

While the proportion of *A. chundra* trees with harvesting damage during the time of our study was low, this could increase in the future if there are, for example, increases in the density of livestock animals. *C. swietenia* was the only species observed to have main stems harvested. The tall stem and pole of this species are useful for small timber and agricultural tools.

Harvesting only significantly affected the population growth rate of *C. swietenia*. We found that this decrease in the population growth rate was due to the presence of main stem harvesting for this species. Our LTRE analysis revealed that lower λ in ambient compared to no harvesting scenario was mostly due to trees transitioning into the sprout state. Transitioning to sprout was only seen for plants for which the main stem was harvested, and the population growth rate was sensitive to changes in this vital rate. Individuals in the sprout state had high survival but only 9.6% of them transitioned to the tree state during the study period. Both *A. chundra* and *G. gummifera* trees had individuals that transitioned to sprout, and this transition was more likely for smaller sized individuals. This is likely due to the effects of fire, which is more likely to top kill smaller individuals.

Our results show that branch harvesting significantly decreases growth of two species and population growth rate of a single species. Harvesting for local purposes can be sustainable and is often not the largest threat. For example, invasive species (Sinha & Brault, 2005; Ticktin et al., 2012) and fire (Sinha & Brault, 2005) have been shown to be larger threats than fruit harvesting to tree populations. Harvesting of stems and main branches has been shown to be more harmful to vital rates and population dynamics of trees than other forms of harvesting, such as fruit harvesting (Sinha and Bawa 2002), leaf harvesting (Binh, 2009; Schmidt et al., 2011; Zuidema et al., 2007), and bark harvesting (Stewart, 2009). In our study, people harvest both intermediate and large-sized trees, which is in contrast to other studies in which harvesters preferred large trees (Gaoue & Ticktin, 2007; Shackleton et al. 2015).

Not much was known about the demography of these species before our study, and our results show dramatic variation between them in their demographic rates and life histories. A trade-off between growth and survival is well established in plant demography, and shown consistently at local (Rüger et al., 2018; Wright et al., 2010) and global scales (Franco & Silvertown, 2004; Salguero-Gómez et al., 2016). *C. swietenia* has the highest survival and grows the slowest of the three species. This species and *A. chundra* have high wood density according to the global wood density database (Chave et al., 2009), and species with high wood density are known to have slower life histories and to have population growth rates with high elasticity to survival (Adler et al., 2014). While all three species can re-sprout basally, *C. swietenia* is also capable of making clonal sprouts that share the root system with the parent plant, and this could explain the high survival of sprouts of this species. *G. gummifera* has lower wood density than the other two species, and we observed the associated “fast” life history that is often associated with this trait. In particular, individuals of this species were observed to have more rapid growth, and the population growth rate was more sensitive to changes in growth than survival (Adler

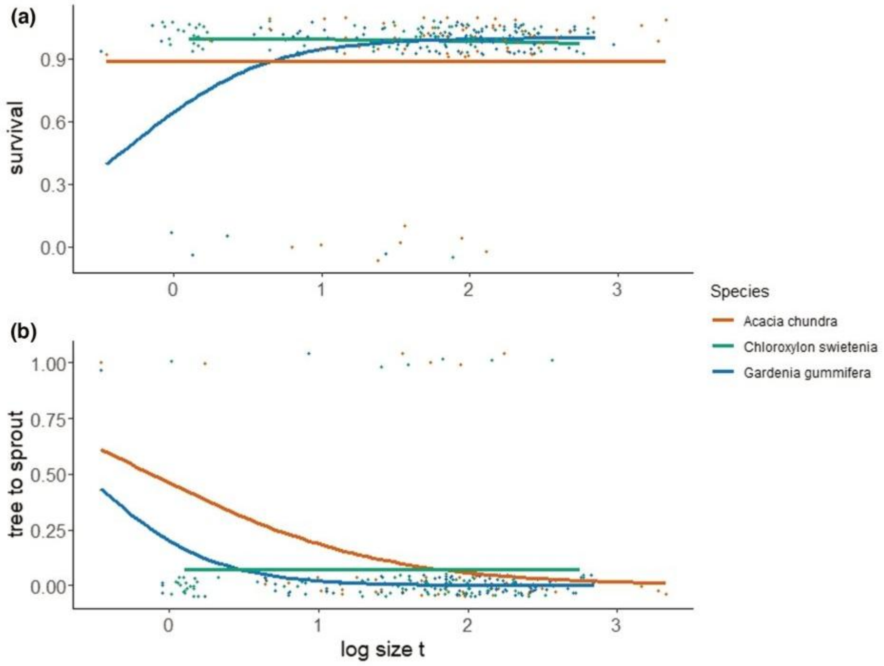


FIGURE 4 Vital rates of trees for three focal species as a function of their log size. a. Tree survival from one time step to the next. b. Trees transitioning to the discrete sprout state from one time step to the next

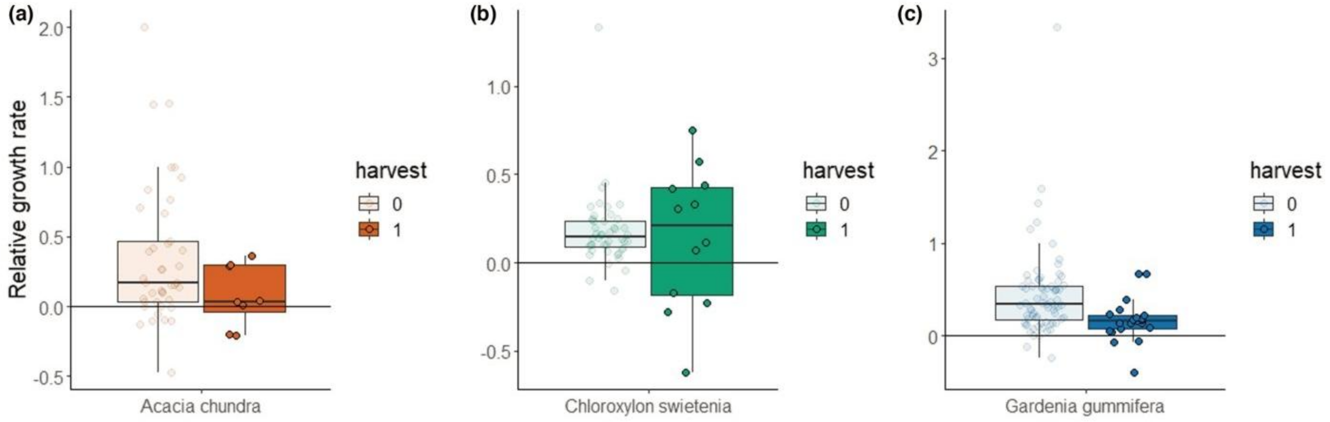


FIGURE 5 Relative growth rate of trees from one time step to the next (*[size t + 1 – Size t]/size t*) shown for each species and separated for individuals with harvesting damage and those without

et al., 2014). *A. chundra* had the highest wood density of our three species, but did not have the high survival that is often associated with this functional trait (Adler et al., 2014). This is likely because fire poses a significant threat to this species (Neeraja et al., 2021), especially if the bark of the tree is harvested prior to the fire.

If the lack of recruitment we observe continues in future, populations will decline. Persisting large trees will provide valuable resources (branches for harvesting) to the local community at least in the short term. We are limited in our ability to project how long these trees will persist into the future, because high sample sizes are necessary to estimate tree mortality, and small differences in tree mortality rates can cause large differences in population trajectories (McMahon et al., 2019). We have limited observations of mortality for our study species. Only one of 83 trees of *C. swietenia* was observed to die, and only 7 out of 63 trees of *A. chundra* and 4 out of 98 trees of *G. gummifera* were observed to die. All of the mortality for *A. chundra* occurred in a single plot that likely experiences frequent fire, and such aggregation in mortality makes it unclear if the mortality we observe for this species is representative of the larger region (McMahon et al., 2019).

We speculate that the lack of tree recruitment from seed in our study is linked to repeated fires, rainfall seasonality, and competition with native grasses and invasive species. We searched broadly for seedlings in both study years and found a very small number of individuals. Anthropogenic fires are common in this region (FES, 2003; Neeraja et al., 2021) and are set to promote a new flush of grasses for livestock grazing. Fire is known to directly kill seedlings and also harm seedling recruitment through secondary effects, such as soil erosion (Sinha and Bawa 2002, Sinha & Brault, 2005). Climate change might also harm seedling recruitment. Local people report that when there are dry years, particular two or more years in a row, they observe lower fruit production in *G. gummifera* (FES social

TABLE 3 Vital rate model parameters and population growth rate (λ) estimates and 95% bootstrapped confidence intervals for the three focal tree species in both the ambient and no harvesting scenarios. Results are shown for continuous state "tree" and discrete state "sprout"

		Ambient harvesting			No harvesting		
	State	**Estimate**	**Lower CI**	**Upper CI**	**Estimate**	**Lower CI**	**Upper CI**
Acacia chundra							
Survival	Tree	0.888	0.809	0.952	0.872	0.781	0.945
Transition to sprout_Intercept	Tree	−0.152	−3.516	1.657	−0.155	−3.924	1.537
Transition to sprout_Slope	Tree	−1.318	−3.416	0.356	−1.241	−3.121	0.678
Growth_Intercept	Tree	0.827	0.564	1.088	0.889	0.600	1.183
Growth_Slope	Tree	0.687	0.568	0.803	0.663	0.515	0.788
Growth_SD	Tree	0.255	0.191	0.315	0.260	0.182	0.321
Survival	Sprout	0	0	0	NA	NA	NA
Transition to tree	Sprout	NA	NA	NA	NA	NA	NA
Size distribution entering tree state_Mean	Sprout	NA	NA	NA	NA	NA	NA
Size distribution entering tree state_SD	Sprout	NA	NA	NA	NA	NA	NA
λ		0.863	0.755	0.934	0.843	0.719	0.925
Chloroxylon swietenia							
Survival	Tree	0.987	0.975	1	1	1	1
Transition to sprout	Tree	0.073	0.048	0.118	0	0	0
Growth_Intercept	Tree	0.552	0.412	0.685	0.472	0.280	0.841
Growth_Slope	Tree	0.765	0.674	0.852	0.823	0.628	0.919
Growth_SD	Tree	0.203	0.141	0.258	0.121	0.077	0.136
Survival	Sprout	0.945	0.899	0.991	NA	NA	NA
Transition to tree	Sprout	0.096	0.017	0.132	NA	NA	NA
Size distribution entering tree state_Mean	Sprout	0.541	0.510	0.616	NA	NA	NA
Size distribution entering tree state_SD	Sprout	0.116	0.034	0.124	NA	NA	NA
λ		0.915	0.890	0.950	1.000	0.999	1.000
Gardenia gummifera							
Survival_Intercept	Tree	0.583	−1.885	1.767	0.509	−0.757	2.016
Survival_Slope	Tree	2.223	1.272	6.371	2.088	1.129	3.003
Transition to sprout_Intercept	Tree	−1.370	−2.566	−0.124	−1.319	−2.566	−0.755
Transition to sprout_Slope	Tree	−2.467	−3.456	0	−2.310	−3.351	0
Growth_Intercept	Tree	0.748	0.650	0.905	0.844	0.650	1.037
Growth_Slope	Tree	0.752	0.679	0.801	0.722	0.616	0.818
Growth_SD	Tree	0.209	0.169	0.226	0.192	0.155	0.213
Survival	Sprout	0.587	0.527	0.666	NA	NA	NA
Transition to tree	Sprout	0.212	0.106	0.340	NA	NA	NA
Size distribution entering tree state_Mean	Sprout	1.431	1.3707	1.512	NA	NA	NA
Size distribution entering tree state_SD	Sprout	0.211	0.121	0.253	NA	NA	NA
λ		0.998	0.994	1.000	0.998	0.991	0.999

survey 2018 unpublished) and subsequently have no income generation from fruit collection. In the Eastern Ghats and Deccan Plateau, climate change is already increasing the length of the dry season (Ramachandran et al., 2018) and may be increasing the intensity of fires. In addition, we suggest that fire-tolerant C_4 grasses such as *Cymbopogon* species and invasive woody species such as *Lantana camara*, *Pterolobium indicum* may also limit recruitment of tree seedlings through direct competition for light and space (FES, 2003).

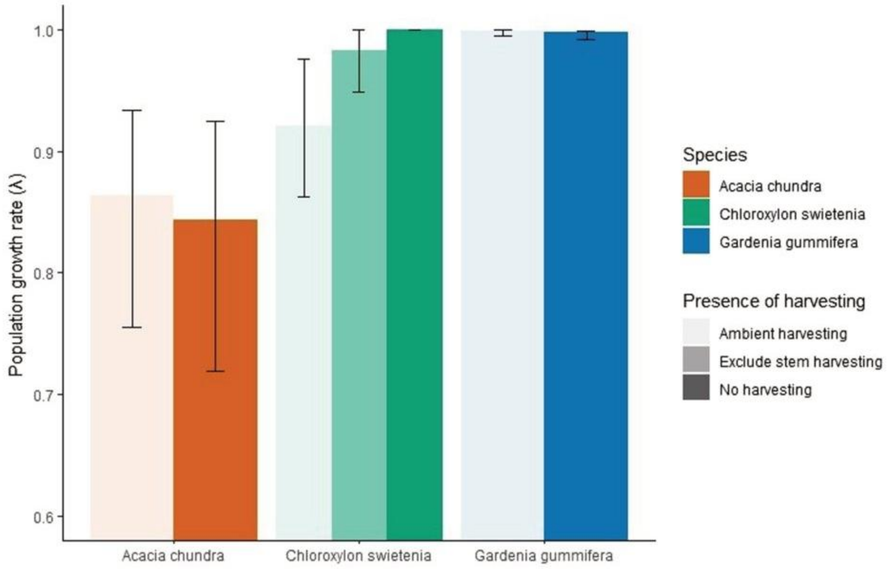


FIGURE 6 Population growth rate (λ) for each of the three study species under three scenarios of harvesting: Ambient harvesting (includes all individuals), exclude stem harvesting (includes not harvested and branch harvested individuals, excludes main stem harvested individuals) and no harvesting (includes only individuals with no observed harvesting damage). The exclude main stem harvesting scenario is only relevant for *C. swietenia*. Point estimate and 95% bootstrap CI

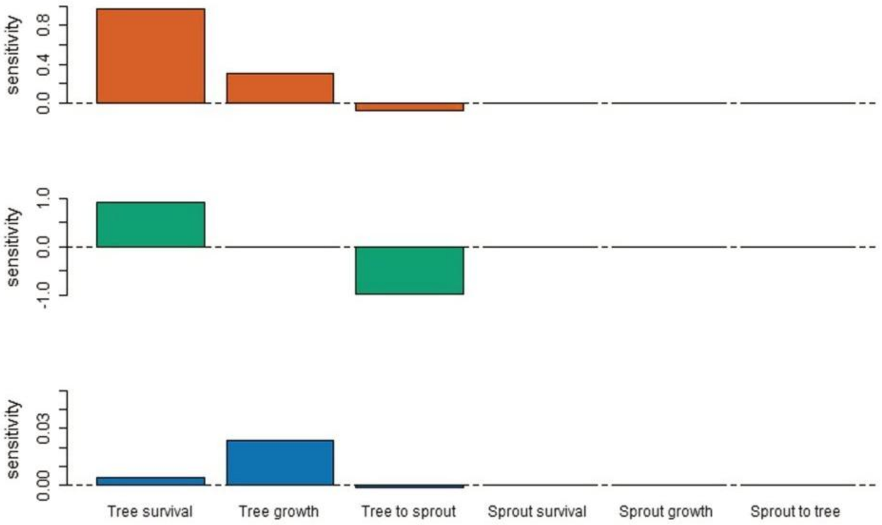


FIGURE 7 Sensitivity of population growth rate (λ) to changes in vital rates for three species using the vital rates in the ambient harvesting scenario: Top is *A. chundra*, middle is *C. swietenia*, bottom is *G. gummifera*

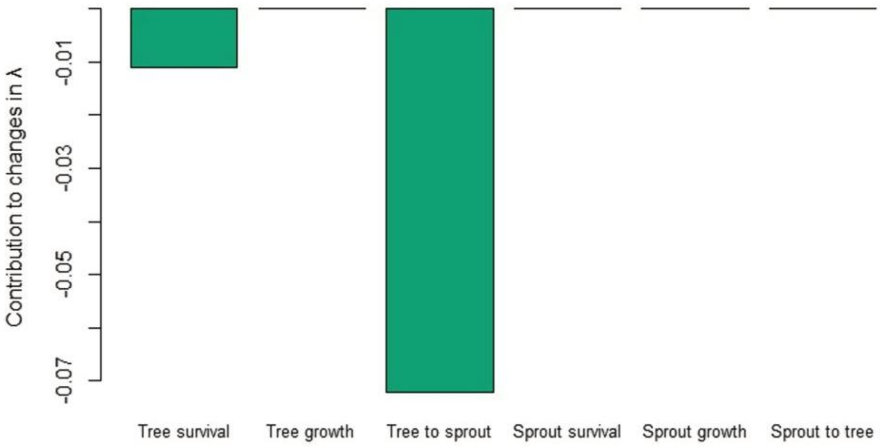


FIGURE 8 Life table response experiments (LTRE) of *C. swietenia* decomposing the contribution of vital rates to observed changes in λ between ambient (includes all individuals) and no harvesting (includes only individuals with no observed harvesting damage) scenarios. Negative values for contribution indicate the vital rate was higher in the no harvesting scenario compared to the ambient harvesting scenario

Conservation actions are already underway in this region to support people and nature. Before and during the study period, villages surrounding our study area had a high dependency on forests for fuelwood for income generation (Balachander & Dyda, 2006). The extracted fuelwood was sold to hotels and used for brick kilns along with household need (Chalise & Yadama, 2011). The construction timber need of the villagers has been greatly reduced due to state government-subsidized housing for rural people in the last decade, which has resulted in a large number of communities building houses out of brick and cement that are permanent (i.e., pucca houses). Household fuelwood needs have reduced due to the distribution of LPG by the state governments, and by improved cook stoves, and supplies of biogas units and pressure cookers from the Foundation for Ecological Security (FES) (FES, 2003; Peipert et al., 2008, FES social survey 2018 unpublished).

Although our demographic results focus on a single location, harvesting and other potential threats (e.g., climate change, habitat loss, and fire) are known to occur throughout the region. Our three focal species are all endemic to India (*A. chundra* is endemic to India, Sri Lanka, and Myanmar), and in particular, *C. swietenia* is only present in peninsular India. *C. swietenia* is currently IUCN red listed as vulnerable, *G. gummifera* as least concern (IUCN Red list 1998) and *A. chundra* is not yet assessed. The current listings may underestimate the threats of extinction for these tree species due to lack of detailed studies assessing threats, and studies like ours can contribute to changing the status of these species so that they can be more appropriately prioritized for conservation.

AUTHOR CONTRIBUTIONS

Neeraja U.V: Data curation (lead); Formal analysis (lead); Investigation (equal); Visualization (lead); Writing-original draft (lead); Writing-review & editing (equal). Saneesh C.S: Investigation (equal); Visualization (supporting), Writing-review & editing (equal). Hemalatha Reddy: Investigation (equal); Writing-review & editing (equal); Venkat Dyda: Supervision (supporting); Writing-review & editing (equal); Funding acquisition (supporting). Gautam N. Yadama: Funding acquisition (supporting), Conceptualization (supporting); Writing-review & editing (equal); Tiffany M. Knight: Conceptualization (lead); Data curation (supporting); Investigation (Lead); Formal analysis (supporting); Funding acquisition (lead); Project administration (lead); Resources (lead); Supervision (lead); Visualization (supporting); Writing-original draft (supporting); Writing-review & editing (equal).

ACKNOWLEDGMENTS

This work was funded by Washington University's I-CARES research award (GNY and TMK), by the Alexander von Humboldt Foundation under the framework of the Humboldt Professorship and by the Helmholtz Recruitment Initiative of the Helmholtz Association (both to TMK). NV and TMK gratefully acknowledge the support of iDiv funded by the German Research Foundation (FZT-118-202548816). We thank Mallikarjuna and Boyapalle village community, FES staff Justus Joshua, Dhanasekaran and Kaushalendra Rao for support in the field and enriching discussions. We thank Dr. Roxanne Leberger for help with R code for visualizations and Dr. Aldo Compagnoni for useful comments and suggestions that helped improve the manuscript. We thank S. Levin, S. Evers and M. Andrezjak for helpful discussions. We are grateful to two anonymous reviewers that provided useful comments. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.mcvdnck27 (Neeraja et al., 2022). The data and R code that produce the results of this study are available in. https://github.com/neerajavenkataraman/IPM_dry-tropical-trees.

ORCID

Uma Venkataraman Neeraja https://orcid.org/0000-0002-9749-3870
Cherapurath Soman Saneesh https://orcid.org/0000-0002-9461-2272
Gautam N. Yadama https://orcid.org/0000-0002-5907-1132
Tiffany M. Knight https://orcid.org/0000-0003-0318-1567

REFERENCES

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences, USA*, *111*, 740–745. https://doi.org/10.1073/pnas.1315179111

Asian Regional Workshop (Conservation & Sustainable Management of Trees, Viet Nam, August 1996) (1998). *Chloroxylon swietenia*. The IUCN Red List of Threatened Species 1998: e.T33260A9765049. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T33260A9765049.en

Balachander, T., & Dyda, V. (2006). Information for decision making: Challenges for village communities. Paper prepared for 11th Biennial Conference of International Association for the Study of Common Property, Bali, Indonesia, June 19–23, 2006.

Bawa, K. S., Raven, P. H., & Seidler, R. (2004). Reconciling conservation paradigms. *Conservation Biology*, *18*, 859–860.

Bhuyan, P., Khan, M. L., & Tripathi, R. S. (2003). Tree diversity and population structure in undisturbed and human-impacted stands of tropical wet evergreen forest in Arunachal Pradesh, eastern Himalayas, India. *Biodiversity Conservation*, *12*(8), 1753–1773.

Binh, B. M. (2009). *Rattans of Vietnam: Ecology, demography and harvesting*. Utrecht University. PhD thesis.

Brummitt, N. A., Bachman, S. P., Griffiths-Lee, J., Lutz, M., Moat, J. F., Farjon, A., Donaldson, J. S., Hilton-Taylor, C., Meagher, T. R., Albuquerque, S., Aletrari, E., Andrews, A. K., Atchison, G., Baloch, E., Barlozzini, B., Brunazzi, A., Carretero, J., Celesti, M., Chadburn, H., … Nic Lughadha, E. M. (2015). Green plants in the red: A baseline global assessment for the IUCN sampled red list index for plants. *PLoS One*, *10*, e0135152.

CAMP Workshops on Medicinal Plants, India (January 1997) (1998). *Gardenia gummifera*. The IUCN Red List of Threatened Species 1998: e. T34622A9879266. https://doi.org/10.2305/IUCN.UK.1998.RLTS.T34622A9879266.en

Convention on Biological Diversity (2021). First draft of the Post-2020 global biodiversity framework. https://www.cbd.int/doc/c/abb5/591f/2e46096d3f0330b08ce87a45/wg2020-03-03-en.pdf

Convention on Biological Diversity (2018). Aichi biodiversity targets. https://www.cbd.int/sp/targets/

Chalise, N., & Yadama, G. (2011). System dynamics modeling of livelihoods and Forest commons in dryland communities of Andhra Pradesh. In J. M. Lyneis & G. P. Richardson (Eds.), *Proceedings of the 29th international conference of the system DynamicsSociety, edited by* (pp. 607–628). Curran Associates.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, *12*, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Crouse, D. T., Crowder, L. B., & Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, *68*, 1412–1423.

Cunningham AB, Mbenkum FT. (1993). Sustainability of harvesting Prunus africana bark in Cameroon: A medicinal plant in international trade. People and Plants Working Paper 2. Division of Ecological Sciences, UNESCO.

Davidar, P., Sahoo, S., Mammen, P. C., Acharya, P., Puyravaud, J. P., Arjunan, M., Garrigues, J. P., & Roessingh, P. (2010). Assessing the extent and causes of forest degradation in India: Where do we stand? *Biological Conservation*, *143*, 2937–2944.

Easterling, M. R., Ellner, S. P., & Dixon, P. M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, *81*, 694–708. https://doi.org/10.1890/0012-9658(2000)081[0694:SSSAAN]2.0.CO;2

Ellner, S. P., Childs, D. Z., & Rees, M. (2016). *Data-driven modelling of structured populations: A practical guide to the integral projection model* (p. 329). Springer.

Endress, B. A., Gorchov, D. L., & Berry, E. J. (2006). Sustainability of a non-timber forest product: Effects of alternative leaf harvest practices over 6 years on yield and demography of the palm Chamaedorea radicalis. *Forest Ecology and Management*, *234*, 181–191.

Fire management global assessment. (2006). *FAO forestry paper* (p. 119). FAO.

Foundation for Ecological Security (2003). Biomass assessment in Sadhukonda reserve forest and adjoining areas, Madanapalle, Andhra Pradesh, India. Working Paper 9.

Franco, M., & Silvertown, J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology*, *85*, 531–538. https://doi.org/10.1890/02-0651

Grogan, J., Landis, R. M., Free, C. M., Schulze, M., Lentini, M., & Ashton, M. S. (2014). Bigleaf mahogany Swietenia macrophylla population dynamics and implications for sustainable management. *Journal of Applied Ecology*, *51*(3), 664–674. https://doi.org/10.1111/1365-2664.12210

Gaoue, O. G., & Ticktin, T. (2007). Patterns of harvesting foliage and bark from the multipurpose tree Khaya senegalensis in Benin: Variation across ecological regions and its impacts on population structure. *Biological Conservation*, *137*, 424–436.

Gaoue, O. G., Horvitz, C., & Ticktin, T. (2011). Non-timber forest product harvest in variable environments: Modeling the effect of harvesting as a stochastic sequence. *Ecological Applications*, *21*(5), 1604–1616. https://doi.org/10.1890/10-0422.1

Gaoue, O. G., Horvitz, C. C., Ticktin, T., Steiner, U. K., & Tuljapurkar, S. (2013). Defoliation and bark harvesting affect life-history traits of a tropical tree. *Journal of Ecology*, *101*, 1563–1571.

Gaoue, O. G. (2015). Transient dynamics reveal the importance of early life survival to the response of a tropical tree to harvest. *Journal of Applied Ecology*, *53*, 112–119. https://doi.org/10.1111/1365-2664.12553

Gaoue, O.G & Horvitz, C.C (2019). Climate, rather than human disturbance, is the main driver of age-specific mortality trajectories in a tropical tree. https://doi.org/10.1016/j.ecolmodel.2019.03.007

Isaza, C., Bernal, R., Galeano, G., & Martorell, C. (2017). Demography of Euterpe precatoria and Mauritia flexuosa in the Amazon: Application of integral projection models for their harvest. *Biotropica*, *49*(5), 653–664. https://doi.org/10.1111/btp.12424

Kaye, T. N., Pendergrass, K. L., Finley, K., & Kauffman, J. B. (2001). The effect of fire on the population viability of an endangered prairie plant. *Ecological Applications*, *11*, 1366–1380.

Khare, C. P. (Ed.). (2007). *Indian medicinal plants; an illustrated dictionary*. Springer.

Kothari, A., Suri, S., & Singh, N. (1995). Conservation in India: A new direction. *Economic and Political Weekly*, *30*, 2755–2766.

Levin, S., Childs, D., Compagnoni, A., Evers, S., Knight, T. M., & Salguero-Gómez, R. (2021). Ipmr: Flexibly implement integral projection models in R. *Methods in Ecology and Evolution.*, *12*, 1826–1834. https://doi.org/10.1111/2041-210X.13683

Mandle, L., & Ticktin, T. (2012). Interactions among fire, grazing, harvest and abiotic conditions shape palm demographic responses to disturbance. *Journal of Ecology*, *100*, 997–1008.

Martínez-Ballesté, A., & Martorell, C. (2015). Effects of harvest on the sustainability and leaf productivity of populations of two palm species in Maya Homegardens. *PLoS One*, *10*(3), e0120666. https://doi.org/10.1371/journal.pone.0120666

McMahon, S. M., Arellano, G., & Davies, S. J. (2019). The importance and challenges of detecting changes in forest mortality rates. *Ecosphere*, *10*, 1.

Neeraja, U.V., Saneesh, C.S., Dyda, V., Reddy, H., Yadama, G. N., & Knight, T. M. (2022). Data from: Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. Dryad Digital Repository. doi:https://doi.org/10.5061/dryad.mcvdnck27

Neeraja, U. V., Saneesh, C. S., Rajendrakumar, S., Dyda, V., & Knight, T. M. (2021). Fire alters diversity, composition, and structure of dry tropical forests in the eastern Ghats. *Ecology and Evolution*, *11*, 6593–6603. https://doi.org/10.1002/ece3.7514

Nic Lughadha, E., Bachman, S. P., Leão, T. C. C., Forest, F., Halley, J. M., Moat, J., Acedo, C., Bacon, K. L., et al. (2020). Extinction risk and threats to plants and fungi. *Plants*, *People*, *Planet*, *2*, 389–408. https://doi.org/10.1002/ppp3.10146

Peres, C. A., Baider, C., Zuidema, P. A., Wadt, Ĺ. H. O., Kainer, K. A., Gomes-Silva, D. A. P., Salomão, R. P., Simões, L. L., Franciosi, E. R. N., Cornejo Valverde, F., Gribel, Ŕ., Shepard, G. H., Jr., Kanashiro, M., Coventry, P., Yu, D. W., Watkinson, A. R., & Freckleton, R. P. (2003). Demographic threats to the sustainability of Brazil nut exploitation. *Science*, *302*, 2112–2114. https://doi.org/10.1126/science.1091698

Peipert, J., Severyn, T., Hovmand, P. S., & Yadama, G. N. (2008). *Modelling the dynamics of the energy, environment, and poverty nexus: a study of biogas unit diffusion in Andhra Pradesh, India* (p. 13). Washington University in St. Louis, USA.

Remya, K., Ramachandran, A., & Jayakumar, S. (2015). Predicting the current and future suitable habitat distribution of *Myristica dactyloides* Gaertn. using MaxEnt model in the Eastern Ghats India. *Ecological Engineering*, *82*, 184–188. https://doi.org/10.1016/j.ecoleng.2015.04.053

Ramachandran, R. M., Roy, P. S., Chakravarthi, V., Sanjay, J., & Joshi, P. K. (2018). Long-term land use and land cover changes (1920–2015) in eastern Ghats, India: Pattern of dynamics and challenges in plant species conservation. *Ecological Indicators*, *85*, 21–36. https://doi.org/10.1016/j.ecolind.2017.10.012

Robbins, P. (2012). *Political ecology: A critical introduction* (Second ed.). Wiley.

Rüger, N., Comita, L. S., Condit, R., Purves, D., Rosenbaum, B., Visser, M. D., Wright, S. J., & Wirth, C. (2018). Beyond the fast–slow continuum: Demographic dimensions structuring a tropical tree community. *Ecology Letters*, *21*(7), 1075–1084.

Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., Zuidema, P. A., de Kroon, H., & Buckley, Y. M. (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proc Natl Acad Sci U S A*, *113*, 230–235. https://doi.org/10.1073/pnas.1506215112

Sankara Rao, K., Swamy, R. K., Kumar, D., Arun Singh, R., & Gopalakrishna Bhat, K. (2019). Flora of Peninsular India. http://peninsula.ces.iisc.ac.in/plants.php?name=Acaciachundra

Schmerbeck, J., & Fiener, P. (2015). Wildfires, ecosystem services, and biodiversity in tropical dry Forest in India. *Environmental Management*, *56*, 355–372. https://doi.org/10.1007/s00267-015-0502-4

Schmidt, I., Mandle, L., Ticktin, T., & Gaoue, O. (2011). What do matrix population models reveal about the sustainability of non-timber forest product harvest? *Journal of Applied Ecology*, *48*, 815–826.

Shackleton, C. M., Ticktin, T., & Pandey, A. K. (2015). *Ecological sustainability for non-timber forest products* (pp. 3–11). Routledge Press.

Shahabuddin, G., & Prasad, S. (2004). Assessing ecological sustainability of non-timber forest produce extraction: The Indian scenario. *Conservation and Society*, *2*(2), 2.

Sinha, A., & Brault, S. (2005). Assessing sustainability of nontimber Forest product extractions: How fire affects sustainability. *Biodiversity and Conservation*, *14*, 3537–3563. https://doi.org/10.1007/s10531-004-0827-4

Sharma, S., & Mujumdar, P. (2017). Increasing frequency and spatial extent of concurrent meteorological droughts and heatwaves in India. *Scientific Reports*, *7*, 15582. https://doi.org/10.1038/s41598-017-15896-3

Stewart, K. (2009). Effects of bark harvest and other human activity on populations of the African cherry (*Prunus africana*) on Mount Oku, Cameroon. *Forest Ecology and Management*, *258*, 1121–1128.

Survase, S. A., & Raut, S. D. (2011). Ethnobotanical Study of some Tree Medicinal Plants in Marathwada. Maharashtra. *Journal of Ecobiotechnology*, *3*(2), 17–21.

Ticktin, T. (2004). The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology*, *41*, 11–21.

Ticktin, T. (2005). Applying a metapopulation framework to the management and conservation of a non-timber forest species. *Forest Ecology and Management*, *206*, 249–261.

Ticktin, T., Ganesan, R., Paramesha, M., & Setty, S. (2012). Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees. *Journal of Applied Ecology*, *49*, 774–784.

Tuljapurkar, S., & Caswell, H. (1997). *Structured population models in marine, terrestrial and freshwater systems*. Chapman & Hall.

Vaz Monteiro, M., Doick, K. J., & Handley, P. (2016). Allometric relationships for urban trees in Great Britain. *Urban Forestry and Urban Greening*, *19*, 223–236. https://doi.org/10.1016/j.ufug.2016.07.009

Venter, S. M., & Witkowski, E. T. F. (2013). Using a deterministic population model to evaluate population stability and the effects of fruit harvesting and livestock on baobab (*Adansonia digitata* L.) populations in five land-use types. *Forest Ecology and Management*, *303*, 113–120. https://doi.org/10.1016/j.foreco.2013.04.013

Yadama, G. N., Hovmand, S. P., Foundation for Ecological Security (FES), & Chalise, N. (2010). Community Driven Modeling of Social-Ecological Systems: Lessons from Andhra Pradesh, India. Proceedeings of the 28th International Conference of the System Dynamic Society. Seoul, South Korea.

Wright, S. J., Kitajima, K., Kraft, N. J. B., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J., Díaz, S., Engelbrecht, B. M. J., Harms, K. E., Hubbell, S. P., Marks, C. O., Ruiz-Jaen, M. C., Salvador, C. M., & Zanne, A. E. (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, *91*, 3664–3674. https://doi.org/10.1890/09-2335.1

Zuidema, P. A., & Boot, R. G. A. (2002). Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: Impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology*, *18*, 1–31.

Zuidema, P., de Kroon, H., & Werger, M. (2007). Testing sustainability by prospective and retrospective demographic analyses: Evaluation for palm leaf harvest. *Ecological Applications*, *17*, 118–128.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Neeraja, U. V., Saneesh, C. S., Dyda, V., Reddy, H., Yadama, G. N., & Knight, T. M. (2022). Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. *Biotropica*, *00*, 1–14. https://doi.org/10.1111/btp.13135

Chapter 4

Tree composition and structure in wooded and more open savannas in a semi-arid landscape in India

This chapter has been submitted to PeerJ

Neeraja, U.V., Dyda, V., Saneesh, C.S and Knight, T.M

Tree composition and structure in wooded and more open savannas in a semi-arid landscape in India.

U.V. Neeraja[1,2*]

Venkat Dyda[4]

C.S. Saneesh[3,2]

Tiffany M. Knight[1,3,2]

1. Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany.
2. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany.
3. Department of Community Ecology, Helmholtz Centre for Environmental Research- UFZ, Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany.
4. Foundation for Ecological Security, Seshappa Thota, Madanapalle, Andhra Pradesh 517325, India.

*Author for correspondence:

neeraja.venkataraman@idiv.de

Keywords: Species composition, Nestedness, Turnover, Size structure, Eastern Ghats

Abstract

Vegetation surveys of forest ecosystems and information about the size distribution of trees provides valuable information about how tree community composition changes across habitat types and about the status of the regeneration processes. Here, we sample the species identity and size of 666 individual trees across two broad habitat types, wooded savanna and open savanna, in the Eastern Ghats. We found that tree community composition differed significantly between open savanna and wooded savanna, and that this was primarily due to species turnover between the habitat types. This turnover is likely due to edaphic differences as well as differences in past and current land use between the habitat types. The importance value indices, which identify the species that are most significance to community structure, show that different tree species are important to structure across the habitat types. The size structure of trees shows a similar right-skewed pattern in both habitat types, but this is likely due to different types and intensities of anthropogenic disturbances. Fires are more common in the wooded savanna habitat whereas grazing and harvesting are more common in the open savannas. Our study has important implications for future management, in particular for open savanna habitats, which harbor unique species and ecosystem services but tend to be undervalued and under-protected.

Introduction

Trees and other woody plants generate critical ecosystem services for humanity, including a wide variety of regulating (e.g., carbon sequestration), supporting (e.g., providing habitat for most of the world's biodiversity), provisioning (fuelwood, construction wood, and non-timber forest products) and cultural services (Shackleton et al. 2011, Reed et al. 2017, Gibson et al. 2017, Diaz et al. 2018, Enquist et al. 2020). There are an estimated 73000 tree species on Earth (Cazzolla Gatti et al. 2022), and vegetative surveys and inventory are critical to understanding the distributions and habitat associations of these species. Tree species occur in a variety of habitats, including reserve forests, as well as rural landscapes that are managed by local people, termed as common lands (Chazdon 2009). Vegetative surveys that encompass many habitat types combined with analysis tools examining tree composition changes can assess whether the tree species that are present in non-forest habitat types are a nested subset of the species in forests or if instead there is species turnover between forests and other habitat types (Baselga 2010). It is useful to understand composition changes across land use and habitat gradients, as this informs whether restoration activities aimed at afforestation could actually result in homogenization and be harmful for biodiversity (Veldman et al. 2019).

Data on the size structure of tree populations can inform about the status of regeneration processes in different habitat types (Goff and West 1975, Zenner 2005, Maua et al. 2020) and on the value of the population (biological and economical; Bailey and Dell 1973). In natural habitats with limited human disturbances, continuous regeneration should take place. This regeneration, combined with mortality rates that are either much higher for smaller individuals or U-shaped (i.e., higher mortality at both ends of the diameter distribution) should lead to stem size distributions that have either a negative exponential (reverse J-shape) or sigmoid shape (Rubin et al., 2006, Lines et al., 2010, Alessandrini et al. 2011). Human disturbances that reduce recruitment rates or alter mortality should lead to more even stem size distributions (Baker et al., 2005, Coomes and Allen, 2007).

The country of India is home to 2603 tree species, 650 of which are endemic (BGCI 2021). India has a wide diversity of habitats that support its unique floristic diversity. Semi-arid zones in India occupy 34% of its land area (Ramarao et al. 2018) and contain a mosaic of dry forests, grasslands and agricultural lands with different intensities of use and edaphic characteristics. Common lands that are open grassy systems are often considered to be wastelands and are undervalued and unrecognized (Kumar et al. 2020, Ratnam et al. 2016, Ratnam et al. 2019). Despite their importance to rural households, these lands are not granted legal status, and are therefore vulnerable to habitat conversion (e.g., plantations, Parr et al. 2011, Murphy et al. 2016). One of the most important interventions of the government towards strengthening rural livelihoods was the NREGA 2005 program (NREGA 2010), which initiated tree planting to restore wastelands to diversify income streams and improve access to fuelwood, fodder and non-timber forest products. Species such as *Pongamia pinnata* (fuelwood and seeds) and *Azadirachta indica* (seeds, fodder) were widely planted.

Colonial forestry legacy in India has traditionally classified the Eastern Ghats and Deccan Plateau as either Tropical Dry deciduous forests or wastelands (Wasteland Atlas of India 2018, 2019). However, recent research disputes the notion of wastelands and classifies the entire area as a tropical grassy biome (Nerlekar et al. 2022, Madhusudan and Vanak 2019, Kumar et al. 2020, Ratnam et al. 2016, Ratnam et al. 2019). Studies on the composition of woody plants across more open (open savanna) vs. more closed (wooded savanna) habitats within the tropical grassy biome of the Eastern Ghats provide insights into the possible processes (edaphic vs. land use) that might shape tree distributions and the policies that might be necessary to conserve tree biodiversity in this region.

Here, we examine the composition and size distribution of trees across two broad habitat types, wooded savanna and open savanna, in the semi-arid region of the Eastern Ghats. We specifically ask the following questions: (1) Does tree community composition differ between open savanna and wooded savanna, and if so, how much of this is due to nestedness (open savanna having a nested subset of the species in wooded savanna) vs. turnover (open savanna and wooded savanna harboring differ tree species)? (2) What is the distribution of size classes for tree species located in each habitat type?

Methods

Study area

Our study area, lies in the intersection of Eastern Ghats and Deccan Plateau within the Anantapur District, Andhra Pradesh (Figure 1). The Anantapur district is the second driest region in India (Rao et al. 2013), and our study area lies between 13°56’20” and 14°7’20” North and 78°19’30” and 78°27’20” East. The climate is tropical arid, with a mean annual temperature of 33.7°C and a mean annual rainfall of 553 mm (FES 2011). It falls under the dry rain shadow area of the southern Deccan plateau. The rainfall is unevenly distributed in time, with long periods of drought being common.

We study two habitat types within our study area: open savanna (Figure 2A) and wooded savanna (Figure 2B). These habitats are a mixed tree-C_4 grass system with varying densities of woody cover. The wooded savanna habitat is located within Eswaramala Reserve Forest (ERF). In both habitat types, there are different soil types (rock outcrop, shallow depth and moderate depth) and soil textures (rocklands, fine loamy and loamy skeletal) present (Pasupuleti et al. 2019). The classification of the ERF as a forest reserve in the 1900s was likely because there were edaphic differences between this area and the surrounding landscape that allowed the ERF to have higher tree cover. Lands categorized as reserve forests in colonial India were those that were viewed valuable for timber, (e.g., areas with high tree cover).

In addition, due to the different levels of protection, the ERF and the surrounding landscape have experienced different types and intensities of human use for more than 100 years. The ERF is actively used by local people for timber and non-timber forest products and grazing by sheep and goats (FES 2011; Rajendrakumar 2014; FES social survey 2018), and is burned often to promote new flush of grasses for grazing livestock during the dry season (Neeraja et al. 2021). Open savanna in our study surround the ERF and are used as common lands for grazing and harvesting. These consist of small hillocks with grasses and scattered trees. There are regulations for cutting and grazing in the ERF. Therefore, grazing and harvesting are more common and higher in the open savanna habitats, whereas fires are more common in wooded savanna. Developmental activities such as water and soil conservation measures such as pits, bunds and contour trenches can be carried out in the open savanna without regulations whereas these activities are restricted in reserve forests (wooded savanna). Activities such as quarrying, logging and mining are prohibited in reserve forests.

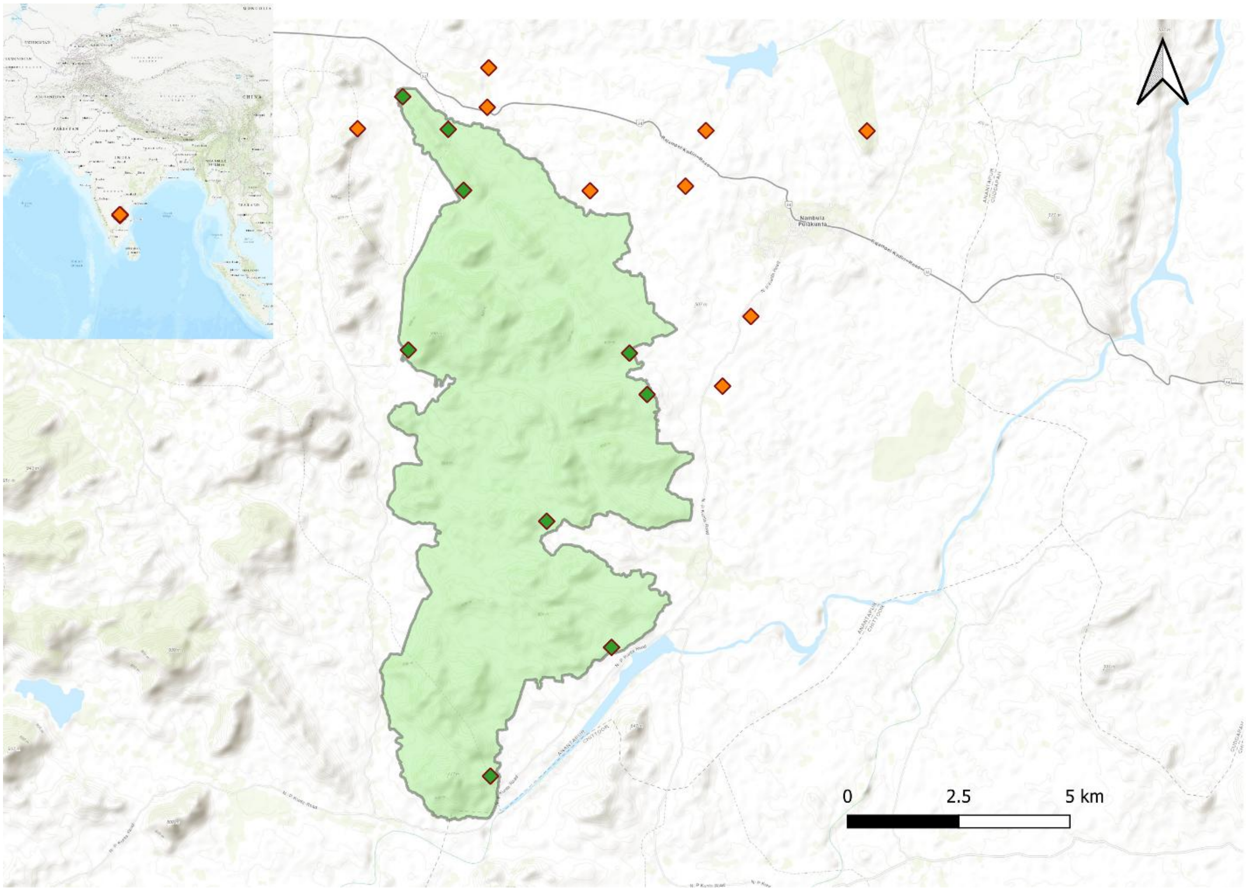


Figure 1: Map showing the study location. Inset map shows this study area within the context of the country (India). Our sampling sites (points) are within and outside the Eswaramala Reserve Forest (boundary). Sampling sites are color-coded based on the habitat. Orange points represent sampling sites in open savanna and green point represents sampling sites in wooded savanna (within Eswaramala reserve forest).

Figure 2A: Photos of sampling sites in the open savanna habitat.

Figure 2B: Photos of sampling sites in the wooded savanna habitat (within the Eswaramala reserve forest)

Data collection

Eighteen sampling sites were chosen, nine within the ERF (wooded savanna) and nine that are part of the revenue department and gram panchayat (village council) and hence are partially protected by the local community and by the state forest department (open savanna). We randomly chose the locations for our sampling sites in these areas based on the criterion that sites must be separated from each other by a minimum distance of 1000m. This led to the possibility of 30 sampling locations. Our final selection of the 18 sites from these randomly chosen locations involved practical considerations for field sampling (e.g., we preferentially chose sites near locations that were being sampled by NGOs at the same time for logistical ease and field safety). Within each sampling site, we sampled three circular plots with a 10 m radius that were separated from each other by a distance of 100m. Plots within site were pooled for analysis.

Our study focused on sampling tree species, which are defined as woody plant species that are capable of a height of at least two meters (for single stemmed woody plants) or capable of having at least one of the stems with a girth of more than five centimeters (for multi-stemmed woody plants) (Beech et al. 2017). In 2018, all individual trees in each plot were identified and counted, including young stage classes, such as saplings and small re-sprouting individuals. All the individuals were identified using the guide to the regional flora viz. Flora of Andhra Pradesh vol I, II and III (Pullaiah and Chennaiah 1997; Pullaiah and Ali Mouali 1997; Pullaiah 1997). We measured girth GBH (or collar girth when GBH was not possible) of all stems in both habitat types.

Data analysis

1. Composition of trees across habitat types

We compute Importance value indices (IVI) for all tree species for each habitat to determine their ecological significance in the community structure (Curtis and McIntosh 1950) using the function *importance value* from *biodiversity R* package in R (Kindt et al. 2007). IVI is calculated as the sum of relative density (abundance), relative dominance (basal area) and relative frequency (number of plots they occur in). IVI values range between 0 and 300. To test for differences in species composition across habitat types we used two approaches. First, we used Permutational Multivariate Analysis of Variance (PERMANOVA) Using Distance Matrices to test whether habitat types differed in their community composition (Bray Curtis), using the function *adonis* from *vegan* package in R (Oksanen et al. 2015). We used Non-metric Multidimensional Scaling (NMDS) to visualize dissimilarity (Bray Curtis) in plant composition across sites in the two using the *metaMDS* function in *vegan* (Oksanen et al. 2015) and the *ggplot2* package for graphical representation. Next, we used the *beta.pair.abund* function of the package *betapart* to partition beta diversity into components of turnover and nestedness (Baselga and Orme, 2012) within and among habitats. In this approach, the Bray-Curtis total dissimilarity between samples (βBC) is partitioned into a component of a) Balanced variation (βBal) which quantifies when species composition changes across habitat types through species replacement (i.e., turnover) and b) Abundance gradient (βGra) which quantifies when individuals are lost from one habitat type to the other but without species loss or when species disappear from one habitat type (i.e., nestedness). We used PERMANOVA to test for differences in turnover and nestedness between habitats using R function *adonis* from vegan package.

2. Size distribution of trees across habitat types

We model the size distribution of the tree species in both habitat types. We modeled size distribution using Weibull's distribution. The parameters of Weibull distributions were determined using maximum likelihood estimation using the function *fitdist* from *fitdistrplus* package in R. The shape parameter of the Weibull parameter is used to interpret the distribution of tree sizes. A shape parameter or gamma <1 indicates a negative exponential reverse j shaped distribution, gamma of >1 and < 3.6 indicates right skewed distribution and gamma of <= 3.6 indicates left skewed distribution. (Delignette-muller & Dutang 2015).

All statistical analyses and visualizations were conducted in R programming version 3.6.2 (R Core Team 2019).

Results

A total of 25 tree species were recorded in the wooded savanna and 15 tree species in the open savanna. Among species found in our study area, *Dolichandrone atrovirens*, *Butea monosperma*, *Gardenia gummifera*, *Ziziphus mauritiana*, *Aegle marmelos* are endemic to peninsular India. The total number of individuals counted and measured were 371 and 295 in wooded savanna and open savanna respectively. Importance value index shows that *Azadirachta indica*, *Pongamia pinnata* and *Acacia chundra* are the most structurally significant species in the open savanna, whereas, *Dolichandrone atrovirens*, *Chloroxylon* *sweitenia* and *Hardwickia binata* are the most significant species in the wooded savanna (Table 1).

Open savanna		Wooded savanna	
Species	IVI	Species	IVI
Azadirachta indica	96.5633	*Dolichandrone atrovirens*	52.058
Pongamia pinnata	58.7731	*Chloroxylon sweitenia*	26.1311
Acacia chundra	26.551	*Hardwickia binata*	25.2549
Annona squamosa	19.486	*Dalbergia paniculata*	25.2461
Holoptelia integrifolia	19.0289	*Acacia chundra*	20.9663

Table 1. Importance value indices (IVI) shown for the five most structurally significant tree species in open savanna and in wooded savanna habitats.

Tree species composition significantly varied between open and wooded savanna (ANOSIM p=0.003, Figure 3).

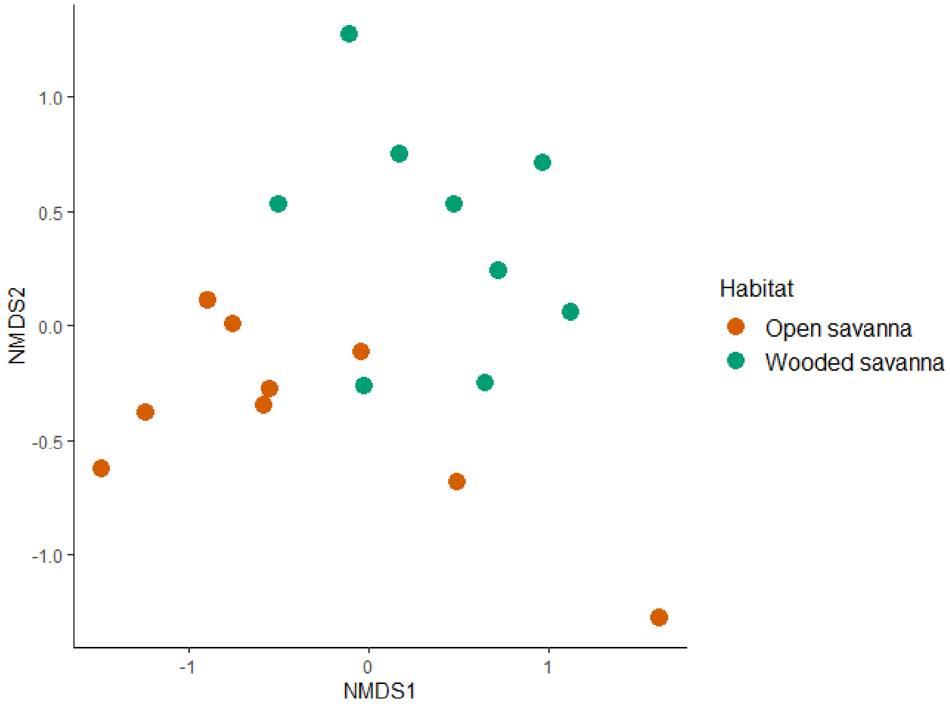
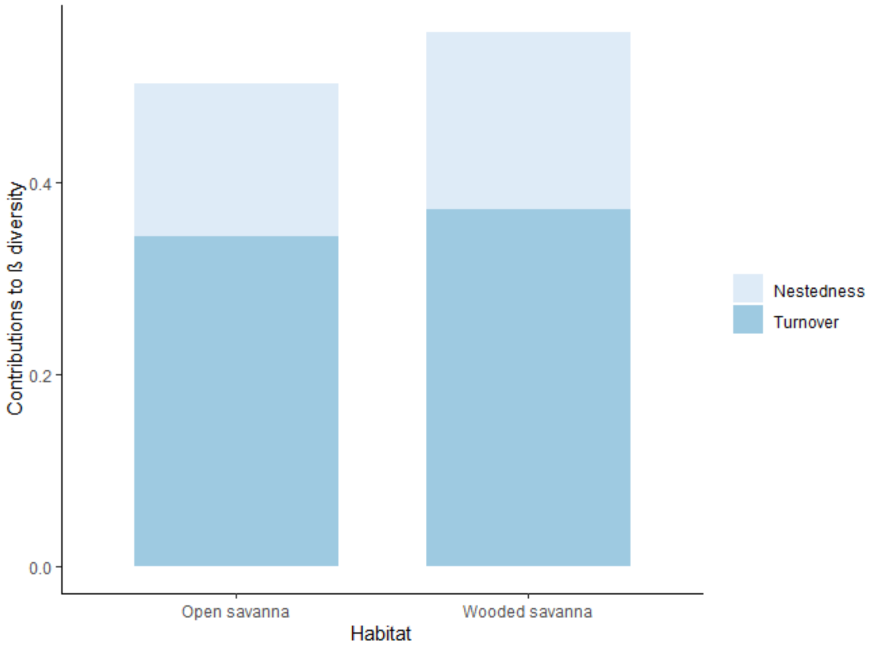


Figure 3. NMDS visualization of tree species composition (Bray-Curtis) in open savanna and wooded savanna habitat types. Points represent a sampling site.

We found a significant turnover in beta-diversity across habitat types ($R^2 = 0.204$; $P = 0.002$), but not significant nestedness ($R^2 = 0.18$; $P = 0.28$). Hence differences in species composition between the two habitats is due to abundance-based species turnover (Figure 4). Within each habitat type, turnover across sampling sites also contributes more to beta diversity than nestedness (Figure 4).



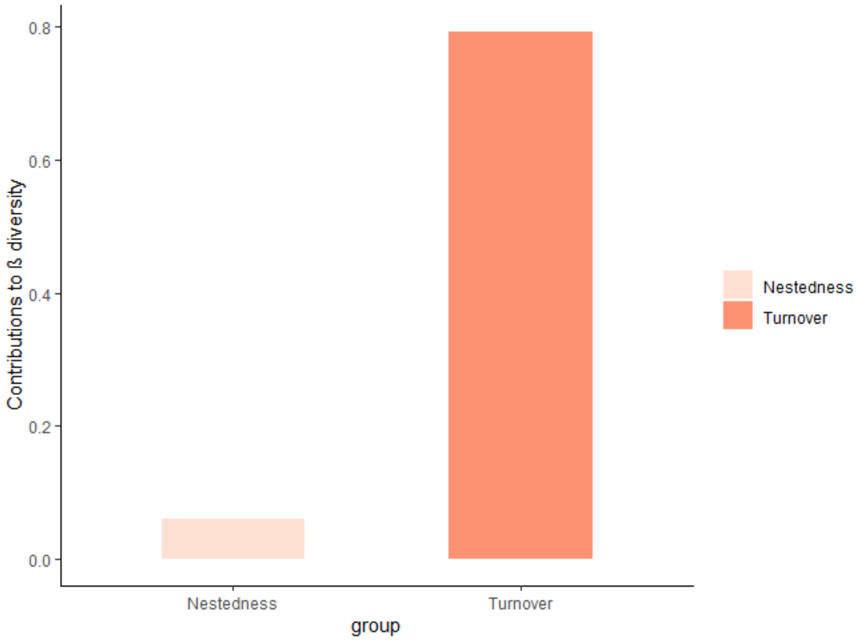


Figure 4. Bar graph showing nestedness and turnover components of total beta diversity across sampling sites within a habitat type (top) and across habitat types (bottom). Y- axis represents the contributions to the total beta diversity.

Trees in the open savanna have a higher proportion of individuals in the smaller size classes whereas wooded savanna have a higher proportion in the intermediate size classes (Figure 5). The Weibull distribution shape parameter estimate was lower than 3.6 in both habitats indicating that size distribution of trees is right skewed in both habitats.

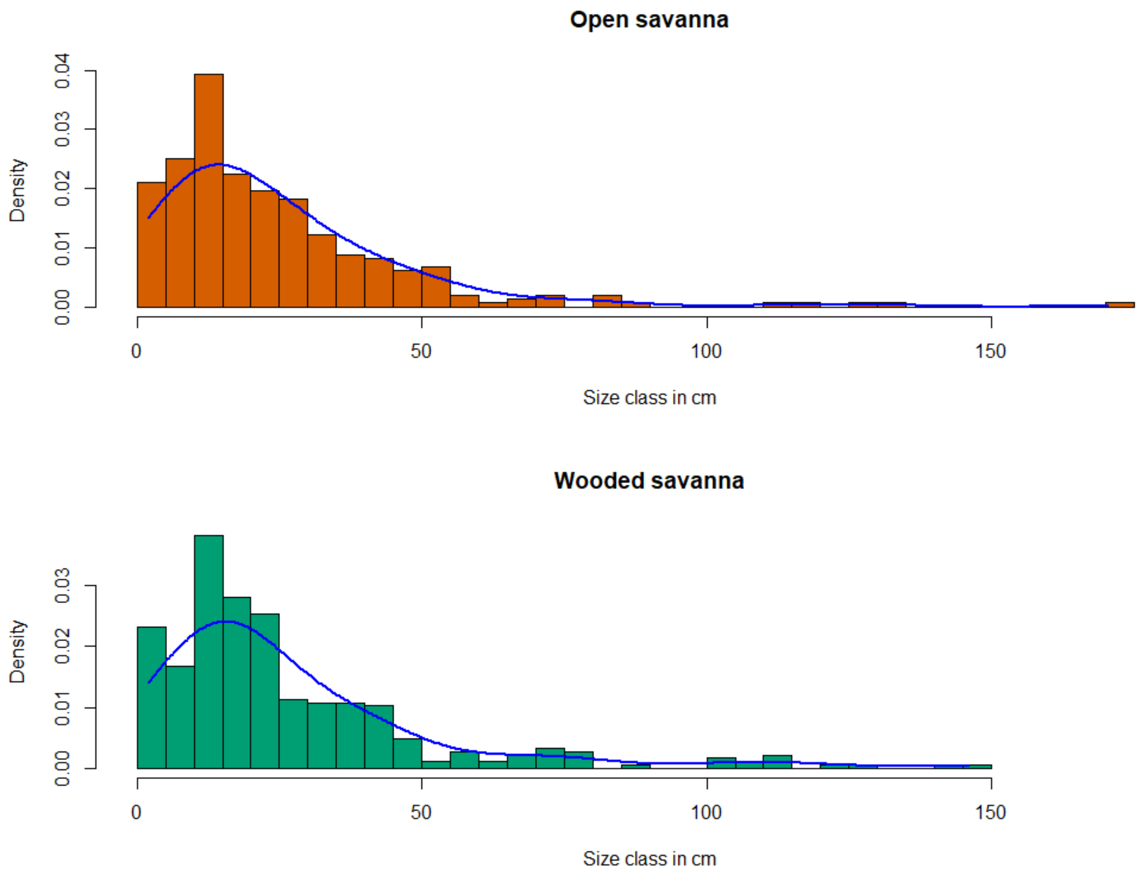


Figure 5: Size distribution of trees in open savanna and wooded savanna overlaid by Weibull density function. Sizes represent girth measured in centimeters.

Discussion

Our results show that tree species composition differs between wooded savanna and open savanna habitats, and this is mainly due to species turnover. This turnover of species is likely due to edaphic differences (such as soil depth and thickness) and past and current land use emerging out of encroachment and subsequent regularization by government. Species that preferentially grow on clay soils with moderate depth were found predominately in the wooded savanna and species that can grow on rocky soils area (subject to frequent erosion resulting in soil erosion/wash-down) were found in the open savanna. Notably, there is little overlap in the names of the five most important structurally important species from the importance value indicator analysis. In the open savannas, *Azadirachta indica* and *Pongamia pinnata* were the most structurally important tree species. These two species were widely planted in the open savannas after the establishment of the joint forest management programme in post-colonial India, which aimed to meet fuelwood and other biomass needs of the local people and reduce their dependency on reserve forests. *Azadirachta indica* is a useful fodder species (including its use as Green Leaf Manure (GLM) that has the ability to grow on dry, shallow, poor soils and also has high dispersal and establishment. It is a naturalized species originating in dry forests of Myanmar and parts of Siwaliks. *Pongamia pinnata* was planted for biodiesel purposes and cultivated as an avenue plants, and is used locally as a fodder species, its leaves are used for mulching and seeds and barks for medicinal uses.

In the wooded savannas, the most structurally important tree species was *Dolichandrone atrovirens*, which grows well on clay loamy soil and is able to resprout profusely following fire (Neeraja et al. 2021). *Acacia chundra* was the only species that was of high importance in both habitat types. This species has traits that allow it to persist in the face of disparate anthropogenic pressures, such as thick bark that protects individuals from fire in the wooded savannas (Neeraja et al. 2021), and heavy wood that makes individuals less preferred for harvesting in the open savannas (Neeraja et al. 2022).

There were several tree species that were rarely encountered in our study but are vital for livelihoods. These include *Wrightia tinctoria* and *Holoptelia integrifolia* in the open savannas, which are cultivated for fuelwood and medicinal uses, and *Albizia amara* in the wooded savannas, which is a valuable timber species. Local people report that *A. amara* was harvested in large scale decades ago resulting in their rarity in our current study.

Open savannas have long been considered as degraded wastelands (Wasteland atlas of India 2019). However, these open savannas have significant value to people, to the rural economy, and to biodiversity. Grazing on these open savannas is crucial to the viability of most of the small and marginal landholders and most rural livelihoods are directly and indirectly linked to livestock. Pastoralism does not involve intensive year-round use of open habitats and hence creates space for biodiversity to persist alongside. Community protection by pastoralists of common grazing grounds and the biodiversity that resides in them exists in many areas in peninsular India (Vanak 2013).

Because the value of open savannas is unrecognized, there are multiple conflicts between the forest department, the revenue department and local people. These unprotected lands are often targeted for land conversion to solar plants and afforestation projects (Vanak 2013, Madhusudan and Vanak 2022). At our study site, two of our open savanna sites were lost after our sampling due to the establishment of a large solar park set up in NP Kunta in 2017 that continues to expand leading to the loss of only “spaces of the poor”. Such conversions threaten important life support systems for the rural economy that affect agriculture and livestock, and threaten fauna such as arthropods and amphibians unique to these habitats (Madhusudan and Vanak 2022). The Foundation for Ecological Security, a local conservation NGO, works to actively discourage these types of activities. In particular, they have been discouraging additional tree planting and working to manage the open savannas in a way that encourages the natural regeneration of existing root stock including the naturally occurring seedlings and saplings that graduate into Poles and Crowns.

Size structure of tree individuals is similar in both habitat types, and the right skewed pattern is characteristic for locations with anthropogenic disturbances that limit regeneration and recruitment (Sapkota et al. 2019). While the size structure of the trees in the two habitat types is similar, the underlying causes are likely different across habitats and species. The wooded savanna is dominated by young resprouting individuals, especially those belonging to *Dolichandrone atrovirens* and *Chloroxylon swietenia*. Fires are more frequent in this habitat and clonal sprouting gives rise to intermediate sized stems that dominate the wooded savanna. Although fire is an integral part of the system (Sankaran 2005), with increase in frequency and extent of fires, only certain species with fire tolerant traits will be able to persist in the future (Neeraja et al. 2021). In the open savanna, disturbances from harvesting are more common (e.g., cutting for brickmaking). Individual trees, particularly *Pongamia pinnata*, that were cut at base have resprouted and now make up the small-sized individuals that dominate in the open savannas.

While size structure can suggest mechanisms that may limit the survival, growth or recruitment of populations, it cannot conclusively assess threats to and future trends of plant populations (Virillo et al 2011). It is necessary to follow individuals through time in both habitat types in order to quantify demography, and the effects of threats on demographic rates over time. Demographic studies require a good sample size of individuals in various size classes. Our study is designed to allow for long-term demographic sampling. All individual trees in this study were tagged and detailed information about their locations were recorded. For ten tree species that occur across both habitat types, we tagged individuals in additional plots to enable sufficient sample size for future demographic study.

In conclusion, the wooded savanna and open savanna habitats harbor different species that are valuable to local communities. Hence, it is important to study and conserve both habitat types because of the unique ecosystem services that they provide. Open savannas are currently protected by the local communities that use them, but are in immediate need of conservation attention and legal protection. Size structures indicate that anthropogenic disturbances might threaten the recruitment of trees in both habitat types. Future research that monitors the demography of species will provide valuable information that would allow for the sustainable management of these ecosystems.

Acknowledgements

This work was funded by the Alexander von Humboldt Foundation under the framework of the Humboldt Professorship, by the Helmholtz Recruitment Initiative of the Helmholtz Association (both to TMK). NV and TMK gratefully acknowledge the support of iDiv funded by the German Research Foundation (FZT 118 – 202548816). We thank the staff of the Foundation for Ecological Security for support in the field and valuable discussions.

References

Alessandrini, A., Biondi, F., Di Filippo, A., Ziaco, E. and Piovesan, G., 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. Forest Ecology and Management, 262(11), pp.1950-1962.

Bailey, R.L. and Dell, T.R., 1973. Quantifying diameter distributions with the Weibull function. Forest Science, 19(2), pp.97-104.

Baker, P.J., Bunyavejchewin, S., Oliver, C.D. and Ashton, P.S., 2005. Disturbance history and historical stand dynamics of a seasonal tropical forest in western Thailand. Ecological Monographs, 75(3), pp.317-343.

Baselga, A. and Orme, C.D.L., 2012. betapart: an R package for the study of beta diversity. Methods in ecology and evolution, 3(5), pp.808-812.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global ecology and biogeography, 19(1), pp.134-143.

BGCI., 2021. State of the World's trees. BGCI.

Cazzolla Gatti, R., Reich, P.B., Gamarra, J.G., Crowther, T., Hui, C., Morera, A., Bastin, J.F., De-Miguel, S., Nabuurs, G.J., Svenning, J.C. and Serra-Diaz, J.M., 2022. The number of tree species on Earth. Proceedings of the National Academy of Sciences, 119(6), p.e2115329119.

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E. and Miller, S.E., 2009. The potential for species conservation in tropical secondary forests. Conservation biology, 23(6), pp.1406-1417.

Coomes, D.A. and Allen, R.B., 2007. Mortality and tree-size distributions in natural mixed-age forests. Journal of Ecology, 95(1), pp.27-40.

Delignette-Muller, M.L. and Dutang, C., 2015. fitdistrplus: An R package for fitting distributions. Journal of statistical software, 64, pp.1-34.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M., Baste, I.A., Brauman, K.A. and Polasky, S., 2018. Assessing nature's contributions to people. Science, 359(6373), pp.270-272.

Foundation for Ecological Security (FES), 2011. Ecological Baseline Assessment of Kadiri watershed Anantapur District in Andhra Pradesh. http://fes.org.in/studies/ecological-baseline-assessment-of-kadiri-watershed.pdf.

Goff, F.G. and West, D., 1975. Canopy-understory interaction effects on forest population structure. Forest Science, 21(2), pp.98-108.

Kumar, D., Pfeiffer, M., Gaillard, C., Langan, L., Martens, C. and Scheiter, S., 2020. Misinterpretation of Asian savannas as degraded forest can mislead management and conservation policy under climate change. Biological Conservation, 241, p.108293.

Madhusudan, M.D. and Vanak, A.T., 2022. Mapping the distribution and extent of India's semi-arid open natural ecosystems. Journal of Biogeography.

Maua, J.O., MugatsiaTsingalia, H., Cheboiwo, J. and Odee, D., 2020. Population structure and regeneration status of woody species in a remnant tropical forest: A case study of South Nandi forest, Kenya. Global Ecology and Conservation, 21, e00820.

Murphy, B.P., Andersen, A.N. and Parr, C.L., 2016. The underestimated biodiversity of tropical grassy biomes. Philosophical Transactions of the Royal Society B: Biological Sciences, 371(1703), p.20150319.

Neeraja, U.V., Rajendrakumar, S., Saneesh, C.S., Dyda, V. and Knight, T.M., 2021. Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats. Ecology and Evolution, 11(11), pp.6593-6603.

Neeraja, U.V., Saneesh, C.S., Dyda, V., Reddy, H., Yadama, G.N. and Knight, T.M., 2022. Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. Biotropica, 54(6), pp.1376-1389.

Nerlekar, A.N., Chorghe, A.R., Dalavi, J.V., Kusom, R.K., Karuppusamy, S., Kamath, V., Pokar, R., Rengaian, G., Sardesai, M.M. and Kambale, S.S., 2022. Exponential rise in the discovery of endemic plants underscores the need to conserve the Indian savannas. Biotropica, 54(2), pp.405-417.

Oksanen, J., 2015. Vegan: an introduction to ordination.

Pullaiah, T. 1997. Flora of Andhra Pradesh (India) Vol III. Scientific Publishers Jodhpur, India, 922-1349.

Pullaiah, T. and Ali Mouali, D. 1997. Flora of Andhra Pradesh (India) Vol II. Scientific Publishers Jodhpur, India, 464-921.

Pullaiah, T. and Chennaiah, E. 1997. Flora of Andhra Pradesh (India) Vol I. Scientific Publishers Jodhpur, India, 1-463.

Rajendrakumar, S. 2014. Floristic Richness in catchment areas of Papgani River-A tributary of river Pennar, Andhra Pradesh, India. International Journal of Environment, 3(1): 177-204.

Ramarao, M.V.S., Sanjay, J., Krishnan, R., Mujumdar, M., Bazaz, A. and Revi, A., 2019. On observed aridity changes over the semiarid regions of India in a warming climate. Theoretical and applied climatology, 136, pp.693-702.

Ratnam, J., Sheth, C. and Sankaran, M., 2019. African and Asian savannas: Comparisons of vegetation composition and drivers of vegetation structure and function. Savanna woody plants and large herbivores, pp.25-49.

Ratnam, J., Tomlinson, K.W., Rasquinha, D.N. and Sankaran, M., 2016. Savannahs of Asia: antiquity, biogeography, and an uncertain future. Philosophical Transactions of the Royal Society B: Biological Sciences, 371(1703), p.20150305.

Reed, J., van Vianen, J., Foli, S., Clendenning, J., Yang, K., MacDonald, M., Petrokofsky, G., Padoch, C. and Sunderland, T., 2017. Trees for life: The ecosystem service contribution of trees to food production and livelihoods in the tropics. Forest Policy and Economics, 84, pp.62-71.

Rubin, B.D., Manion, P.D. and Faber-Langendoen, D., 2006. Diameter distributions and structural sustainability in forests. Forest Ecology and Management, 222(1-3), pp.427-438.

Sankaran, M., 2005. Fire, grazing and the dynamics of tall-grass savannas in the Kalakad-Mundanthurai Tiger Reserve, South India. Conservation and Society, pp.4-25.

Sapkota, R.P., Stahl, P.D. and Norton, U., 2019. Anthropogenic disturbances shift diameter distribution of woody plant species in Shorea robusta Gaertn.(Sal) mixed forests of Nepal. Journal of Asia-Pacific Biodiversity, 12(1), pp.115-128.

Vanak, A. 2013. Conservation and sustainable use of dry grassland ecosystem in peninsular India: A quantitative framework for conservation landscape planning. Report to Ministry of Environment and Forests. 40 pages.

Veldman, J.W., Aleman, J.C., Alvarado, S.T., Anderson, T.M., Archibald, S., Bond, W.J., Boutton, T.W., Buchmann, N., Buisson, E., Canadell, J.G. and Dechoum, M.D.S., 2019. Comment on "The global tree restoration potential". Science, 366(6463), eaay7976.

Virillo, C.B., Martins, F.R., Tamashiro, J.Y. and Santos, F.A.M.D., 2011. Is size structure a good measure of future trends of plant populations? An empirical approach using five woody species from the Cerrado (Brazilian savanna). Acta Botanica Brasilica, 25, pp.593-600.

Zenner, E.K., 2005. Development of tree size distributions in Douglas-fir forests under differing disturbance regimes. Ecological applications, 15(2), pp.701-714.

Chapter 5

General discussion

Dry tropics are important ecosystems that are threatened by land use change and climate change. There are knowledge gaps in understanding the effects of these changes to the long-term persistence and biodiversity of plants in these ecosystems (reviewed by Powers et al. 2018). In this thesis, I tackled questions related to human practices of fire and harvesting on tree population and community responses. Specifically, I investigated the effect of recent fires on diversity, composition and structure of trees in a forest-savanna habitat. I asked how current levels of harvesting influence demographic vital rates and population growth of tree species. A motivation of my thesis was to focus on the Eastern Ghats, which tends to get less research attention compared to other regions in India such as the Western Ghats and Himalayans (Panda et al. 2019). The trees communities that are the focus of this research are important to livelihoods of local communities in this region, and my aim is to provide information that helps us to better understand these ecosystems and promote their sustainable management and conservation while also serving the needs of these local communities. In this chapter, I summarize the key findings across the different chapters of my thesis, discuss the relevance and potential applications of my results for conservation, and give ideas for future research.

5.1 Key findings

In chapter II, I examined how recent fires influence the diversity, composition and structure of woody communities in dry forests (Neeraja et al. 2021). First, I found that fires are increasing in frequency in the region of Andhra Pradesh. Just three months after my manuscript was published, another paper examined fire frequencies using more coarse grain data for the entire country and found that 55% of forests in India (3.73 million ha) experience intermittent fires each year (Sewak et al. 2021). Further, since my publication, there have been calls to the G20 for multi-national collaborations with respect to forest fires in order to jointly set management priorities and to develop international agreements to help conserve forests and savannas and the ecosystem services they provide (Kala 2023).

Also, in chapter II, I discovered that even though stem density increases in plots that are recently burned, fires lower species richness. This is because fire provides a strong environmental filter for the few species with fire tolerant traits such as clonal resprouting and thick bark (Neeraja et al. 2021). Such environmental filtering has long been studied in forests in other regions of the world, such as North America (e.g., Heinselman 1973, Anoszko et al. 2022). However, for each region, it is important to have studies that focus on the tree species and traits that are filtered by fire. This enables future work aimed at modeling scenarios for forest conservation. Thus, my research makes an important contribution for the Eastern Ghats.

Also, in chapter II, I found that in the presence of fire, the size structure of the tree community consisted of smaller-sized resprouting individuals, shifting the structural and functional composition of the dry forests. It is well known that smaller trees offer fewer resources, such as fruits, leaves and bark, to local communities (e.g., Sambo et al. 2020), and thus I expect that the structural changes I observed to this forest-savanna ecosystem have consequences for the local communities in the Eastern Ghats.

In chapter III, I quantified the influence of ambient levels of harvesting on the demographic vital rates and population growth of three dry forest tree species. I hypothesized that harvesting would decrease demographic vital rates and population growth rates of the species, mainly due to stem harvesting. I found that harvesting significantly decreased the growth of two of the three tree species, and significantly reduces the population growth rate of one tree species (Neeraja et al. 2022). The negative influence of the population growth rate on this species was mainly due to stem harvesting forcing individuals to resprout from base. Further, I found no evidence of successful seedling recruitment for any of the three focal species (Neeraja et al. 2022).

Chapter III was published in a special feature in *Biotropica* honoring Professor Kamal Bawa, a scientist that has made important contributions to our understanding of the viability of tree populations in forest-dependent human communities (e.g., Menon et al. 2000). My manuscript in the feature was set up in contrast to the results discovered by Kumar and colleagues (2022) in Central India, in which strong recruitment was found following fuelwood harvesting. I suggest the different between our studies might be due to the high fire frequency in the Eastern Ghats, which kills recruiting seedlings.

In chapter IV, I investigated the composition and size structure of woody species in two habitats: wooded savanna and open savanna ecosystems. I find that there is compositional dissimilarity between the two habitats and that this mainly due to species turnover rather than due to one habitat having a nested subset of the species found in the other. The size structure of woody plants in both habitats are similar indicating the presences of anthropogenic disturbances in both. This chapter provides an interesting baseline for future demographic research on the tree species in these ecosystems, and it is my strong desire to continue this line of research.

5.2 Relevance and potential application for conservation

My results provide knowledge on the influence of fires on woody species richness in the Eastern Ghats (Neeraja et al. 2021) which host many endemic species (Panda et al. 2013). This provides the baseline information needed for many conservation practices, such as (1) identifying species that are less fire resistant and might need conservation attention in order to persist, (2) planning strategies for fire management, which can include creating fire breaks to prevent the spread of fire, and early detection and suppression of fires, and (3) community engagement with local stakeholders to promote the protection of their forest resources as part of the fire management strategy.

My results provide knowledge on the demography and the effects of harvesting on endemic tree species of the Eastern Ghats, a region for which few demographic studies are available (Salguero-Gómez et al. 2015). Such demographic data provides a view of the long-term trajectory of populations if the current management remains. Optimistically, I found that branch harvesting at its current rate is sustainable. However, my results projected population decline for all species, likely due fire, which causes a lack of recruitment.

My results have already been used by a local NGO to discuss the future of forest-savanna management with local communities. Specifically, the Foundation for Ecological Security works closely with local communities to promote ecological conservation and sustainable development. They foster a participatory decision-making process, by encouraging local communities to actively contribute to the development of fire management plans. Through consultations and meetings, community members, along with the forest department, discuss and identify strategies that align with both ecological conservation goals and the needs and aspirations of the local communities.

My results can contribute to quantitative threat assessment for IUCN red listing (Hernández-Yáñez et al. 2022). Demographic data is instrumental in determining if a population is expected to decline, and if so at what rate. In particular, the lack of recruitment observed indicates that concerns about the long-term persistence of my focal species, and such quantitative information is critical to an assessment of the species' overall risk of extinction. Life history traits, such as generation time, longevity, and age of maturity can be calculated for these species using my demographic data, and these are important features in IUCN assessments. My research has identified fire as the primary threat to these species, and such threat assessments help to prioritize conservation actions.

My thesis highlights the importance of conserving both reserve forests and open savanna. Currently, open savannas do not have a legal protection status in India. However, these ecosystems harbor unique tree species that are not found in reserve forests and are important areas for local endemic fauna (Vanak 2019, Rastogi et al. 2022). In my study area for chapter IV, I have recently witnessed the loss of substantial habitat to make room for a large-scale solar park. While solar power can contribute positively to mitigating climate change, there are many competing needs for sustainable forest livelihoods and biodiversity conservation that were not considered due to the lack of protection of these areas.

5.3 Future Directions

My research was observational, and experimental research in the future would make it possible to disentangle the effects of fire, drought and harvesting on plant population and community responses, as well as understand if the combination of these factors is additive or non-additive. C_4 grasses, such as those in the genus *Cymbopogon*, are now common in the understory of these forest-savanna ecosystems. It is possible that both exclusion of fire and removal of these grasses is necessary to restore the diversity of woody plants and offer the full spectrum of ecosystem services to local communities. This is because the dominance of C_4 grasses provides biomass that fuels fires, possibly increasing fire intensity and extent. It will be an important component of future research to disentangle the effects that grasses and fire have on woody plant biodiversity and composition.

It is also important to understand the historical fire regime of the area and the fire regime that would be sustainable for biodiversity and ecosystem services in the future. We know that savanna ecosystems have existed in India for over a million years, as indicated by fossil and molecular evidence and from the diverse and endemic C_4 grasses, such as *Cymbopogon* spp. (Ratnam et al. 2016). While savanna plant communities in the Eastern Ghats were historically shaped by the monsoonal climate, fire and wild herbivores, more recently human activities have likely changed the fire regime. For example, while domesticated animals have been present in the Eastern Ghats for thousands of years (Allchin 1963, Paddayya 1973, Singh et al. 2013), the number of these animals has increased in recent years with rising human populations. We know that the fire regime has changed in recent years (Neeraja 2021) due to anthropogenic fires that promote new growth grasses that are palatable to livestock combined with more arid conditions created by climate change (Senande-Rivera et al. 2022).

While it is clear that fires have been an integral part of the system for a long time, and have shaped the evolution of the modern plant communities that occur in the Eastern Ghats today, it would be useful to have even more detailed information on how the fire frequency, intensity and extent has changed through time. This would help us better understand these systems and plan a fire management strategy to support nature and people. Fire management will almost certainly have to consider the regional context, the climate and current land use.

In order to create scenarios for how management aimed at reducing the frequency of fire will influence recruitment of seedlings for the focal species in this dissertation, future research is needed to quantify the recruitment of trees in the absence of fire. It is unclear how long fire needs to be absent to allow some of the fire sensitive tree species to recruit to a large enough size class that they can survive fire. The demographic research in this dissertation was only able to focus on existing individuals and resprouting individuals, but lacks information about seedling recruitment and growth. Further, it is also unknown how many fires resprouting individuals can withstand before they run out of stored resources and die. Future research following these individuals after each fire could provide this information.

The information on demography and population dynamics in chapter III focuses on a particular habitat type (wooded savannas) and three focal species. It would be important to expand this research in the future to more species and habitat types. Chapter IV sets up the possibility for this future research, as several of the species were present in sufficient sample sizes for demographic analyses. I tagged these individuals with the plan to monitor their fates in the future. It has now been five years since, and the time is ripe for a demographic resurvey.

Finally, the research in this dissertation could be expanded to better understanding how functional traits explain plant responses to fire, harvesting, habitat affiliations. Chapter II begins this line of thinking, as bark thickness and sprouting ability can explain community patterns in response to fire. Research by others in this region has demonstrated that functional traits can explain the distinction between dry forests and moist forests (Ratnam et al. 2019).

5.4 Conclusions

This thesis contributes to a growing literature on the effects of natural and anthropogenic factors on the community composition and demography of woody plants. Little of our current knowledge comes from the Eastern Ghats. As climate change continues to advance and human populations put more pressure on these natural ecosystems, knowledge of species responses becomes more critical to managing ecosystems in future. I hope that my thesis will inspire future research in this important ecosystem.

References

Aditya, V. and Ganesh, T., 2019. Deciphering forest change: linking satellite-based forest cover change and community perceptions in a threatened landscape in India. Ambio, 48(7), pp.790-800.

Adolph, B., Butterworth, J., Conroy, C. and Morris, M., 2001. Common pool resources in Semi-arid India problems and potentials. Natural Resources Institute (NRI), Chatham, UK. Synthesis Report CRIDA/CWS/AKRSP (I) WRM Ltd./MSU/NRI Common Pool Resources Research Project Report, (4).

Agarwala, M., DeFries, R.S., Qureshi, Q. and Jhala, Y.V., 2016. Changes in the dry tropical forests in Central India with human use. Regional Environmental Change, 16, pp.5-15.

Allchin F.R. 1963. Neolithic Cattle Keepers of South India: A Study of Deccan Ash Mounds. Cambridge University Press, New York, USA. 189 pp.

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C., Salgado-Negret, B., Smith, C.M., Trierweiler, A., Van Bloem, S.J. and Waring, B.G., 2017. Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? Environmental Research Letters, 12(2), p.023001.

Anoszko, E., Frelich, L.E., Rich, R.L. and Reich, P.B., 2022. Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. Ecosphere, 13(3), p.e3952.

Baeten, L., Vangansbeke, P., Hermy, M., Peterken, G., Vanhuyse, K. and Verheyen, K., 2012. Distinguishing between turnover and nestedness in the quantification of biotic homogenization. Biodiversity and Conservation, 21, pp.1399-1409.

Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Nally, R. M., Thomson, J. R., Frosini, S., Ferraz, D. B., Louzada, J., Hugo, V., Oliveira, F., Parry, L., Ribeiro, R., Solar, D. C., Vieira, I. C. G., Aragão, L. E. O. C., Begotti, R. A., & Braga, R. F. 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature, 535, 144– 147.

Bertuzzo, E., Suweis, S., Mari, L., Maritan, A., Rodríguez-Iturbe, I. and Rinaldo, A., 2011. Spatial effects on species persistence and implications for biodiversity. Proceedings of the National Academy of Sciences, 108(11), pp.4346-4351.

Blonder, B., Both, S., Coomes, D.A., Elias, D., Jucker, T., Kvasnica, J., Majalap, N., Malhi, Y.S., Milodowski, D., Riutta, T. and Svátek, M., 2018. Extreme and highly heterogeneous microclimates in selectively logged tropical forests. Frontiers in Forests and Global Change, 1, p.5.

Bond, W. J., & Midgley, J. J. 2003., The evolutionary ecology of sprouting in woody plants. International Journal of Plant Sciences, 164(S3), S103-S114.

Carvalho, J.C., Cardoso, P. and Gomes, P., 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. Global Ecology and Biogeography, 21(7), pp.760-771.

Caswell, H. and Cohen, J.E., 1991. Disturbance, interspecific interaction and diversity in metapopulations. Biological Journal of the Linnean Society, 42(1-2), pp.193-218.

Crawley, M. J. (1990). The population dynamics of plants. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 330(1257), 125-140.

da Silva, P.G., Lobo, J.M., Hensen, M.C., Vaz-de-Mello, F.Z. and Hernández, M.I., 2018. Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. Diversity and Distributions, 24(9), pp.1277-1290.

Davies, S. J., Abiem, I., Salim, K. A., Aguilar, S., Allen, D., Alonso, A., ... & Yap, S. L. 2021., ForestGEO: Understanding forest diversity and dynamics through a global observatory network. Biological Conservation, 253, 108907.

DeFries, R., Agarwala, M., Baquie, S., Choksi, P., Khanwilkar, S., Mondal, P., Nagendra, H. and Uperlainen, J., 2022. Improved household living standards can restore dry tropical forests. Biotropica, 54(6), pp.1480-1490.

Easterling, M.R., Ellner, S.P. and Dixon, P.M., 2000. Size-specific sensitivity: applying a new structured population model. Ecology, 81(3), pp.694-708.

Elangovan, M., Perumalla K.B., Tonapi, V., Subbarao V., Sivaraj L. (2012). Cultivated Grasses and their Wild Relatives in Andhra Pradesh and their Conservation Concerns. Plant Genetic Resources. 25. 166-173.

FAO. (2020). Global Forest Resources Assessment 2020: Main report. Food and Agriculture Organisation of the United Nations.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K. and Helkowski, J.H., 2005. Global consequences of land use. science, 309(5734), pp.570-574.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K. and Helkowski, J.H., 2005. Global consequences of land use. Science, 309(5734), pp.570-574.

Foundation for Ecological Security (FES). 2011. Ecological Baseline Assessment of Kadiri watershed Anantapur District in Andhra Pradesh. Retrieved from http://fes.org.in/studies/ecological-baseline-assessment-of-kadiri-watershed.pdf

Foundation for Ecological Security. 2003. Biomass assessment in Sudhukonda Reserve Forest and adjoining areas, Madanapalle, Andhra Pradesh, India (Working Paper No. 9)

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M. and Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. science, 327(5967), pp.812-818.

Grogan, J., Landis, R.M., Free, C.M., Schulze, M.D., Lentini, M. and Ashton, M.S., 2014. Big-leaf mahogany S wietenia macrophylla population dynamics and implications for sustainable management. Journal of Applied Ecology, 51(3), pp.664-674.

Heinselman, M.L., 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary research, 3(3), pp.329-382.

Hennekens, S.M., Jandt, U., Jansen, F. and Jiménez-Alfaro, B., 2021. sPlotOpen–An environmentally balanced, open-access, global dataset of vegetation plots. Global Ecology and Biogeography, 30(9), pp.1740-1764.

Hernández-Barrios, J.C., Anten, N.P. and Martínez-Ramos, M., 2015. Sustainable harvesting of non-timber forest products based on ecological and economic criteria. Journal of Applied Ecology, 52(2), pp.389-401.

Hernández-Yáñez, H., Kim, S.Y. and Che-Castaldo, J.P., 2022. Demographic and life history traits explain patterns in species vulnerability to extinction. PloS one, 17(2), p.e0263504.

Hilde, C.H., Gamelon, M., Sæther, B.E., Gaillard, J.M., Yoccoz, N.G. and Pélabon, C., 2020. The demographic buffering hypothesis: evidence and challenges. Trends in Ecology & Evolution, 35(6), pp.523-538.

Hoffmann, W.A., 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology, 80(4), pp.1354-1369.

Kala, C.P., 2023. Environmental and socioeconomic impacts of forest fires: A call for multilateral cooperation and management interventions. Natural Hazards Research.

Kale, M. P., Ramachandran, R. M., Pardeshi, S. N., Chavan, M., Joshi, P. K., Pai, D. S., Bhavani, P., Ashok, K., & Roy, P. S. 2017. Are climate extremities changing forest fire regimes in India? An analysis using MODIS fire locations during 2003–2013 and gridded climate data of India meteorological department. Proceedings of the National Academy of Sciences, India Section A: Physical Sciences, 87, 827– 843.

Kodandapani, N., Cochrane, M. A., & Sukumar, R. 2004. Conservation threat of increasing fire frequencies in the Western Ghats, India. Conservation Biology, 18(6), 1553– 1561.

Kumar, A., Kumar, G., Saikia, P., Khare, P.K. and Khan, M.L., 2022. Spatial pattern of tree diversity and impacts of ecological disturbances on forest structure in tropical deciduous forests of Central India. Biotropica, 54(6), pp.1363-1375.

Kumi, S., Addo-Fordjour, P., Fei-Baffoe, B., Belford, E.J. and Ameyaw, Y., 2021. Land use land cover dynamics and fragmentation-induced changes in woody plant community structure in a mining landscape, Ghana. Trees, Forests and People, 4, p.100070.

Lambin, E.F. and Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. Proceedings of the national academy of sciences, 108(9), pp.3465-3472.

Laurance, W. F. (2004). Forest-climate interactions in fragmented tropical landscapes. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359(1443), 345-352.

Mandle, L. and Ticktin, T., 2012. Interactions among fire, grazing, harvest and abiotic conditions shape palm demographic responses to disturbance. Journal of Ecology, 100(4), pp.997-1008.

Mani, M.S., 1974. The vegetation and phytogeography of the Eastern Ghats. Ecology and biogeography in India, pp.197-203.

Martin, D.A., Osen, K., Grass, I., Hölscher, D., Tscharntke, T., Wurz, A. and Kreft, H., 2020. Land-use history determines ecosystem services and conservation value in tropical agroforestry. Conservation Letters, 13(5), p.e12740.

Menon, S., Pontius, R.G., Rose, J., Khan, M.L., and Bawa, K.S. 2000. Identifying conservation priority areas in the tropics: A land-use change modeling approach. Conservation Biology, 15, 501–512.

Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V. and Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. Journal of biogeography, 33(3), pp.491-505.

Murphy, P.G. and Lugo, A.E., 1986. Ecology of tropical dry forest. Annual review of ecology and systematics, 17(1), pp.67-88.

Needham, J., Merow, C., Chang-Yang, C.H., Caswell, H. and McMahon, S.M., 2018. Inferring forest fate from demographic data: from vital rates to population dynamic models. Proceedings of the Royal Society B: Biological Sciences, 285(1874), p.20172050.

Neeraja, U.V., Rajendrakumar, S., Saneesh, C.S., Dyda, V. and Knight, T.M., 2021. Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats. Ecology and Evolution, 11(11), pp.6593-6603

Neeraja, U.V., Saneesh, C.S., Dyda, V., Reddy, H., Yadama, G.N. and Knight, T.M., 2022. Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. Biotropica, 54(6), pp.1376-1389.

Paddayya K. 1973. Investigations into the Neolithic Culture of the Shorapur Doab, South India. EJ Brill, Leiden, the Netherlands. 137 pp.

Panda, P.C., Mahapatra, A.K., Acharya, P.K. and Debata, A.K., 2013. Plant diversity in tropical deciduous forests of Eastern Ghats, India: A landscape level assessment. Int J Biodivers Conserv, 5(10), pp.625-639.

Panda, R.M., Behera, M.D., Roy, P.S. and Ramachandran, R.M., 2019. On the relationships between plant species richness and the environment: a case study in Eastern Ghats, India. Environmental monitoring and assessment, 191, pp.1-10.

Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K. and Butterworth, C.A., 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359(1443), pp.515-538.

Pennington, R.T., Lehmann, C.E. and Rowland, L.M., 2018. Tropical savannas and dry forests. Current Biology, 28(9), pp. R541-R545.

Ponton, C., Giosan, L., Eglinton, T.I., Fuller, D.Q., Johnson, J.E., Kumar, P. and Collett, T.S., 2012. Holocene aridification of India. Geophysical Research Letters, 39(3).

Powers, J.S., Feng, X., Sanchez-Azofeifa, A. and Medvigy, D., 2018. Focus on tropical dry forest ecosystems and ecosystem services in the face of global change. Environmental Research Letters, 13(9), p.090201.

Ramachandran, R.M., Roy, P.S., Chakravarthi, V., Joshi, P.K. and Sanjay, J., 2020. Land use and climate change impacts on distribution of plant species of conservation value in Eastern Ghats, India: a simulation study. Environmental monitoring and assessment, 192, pp.1-21.

Ramesh, S. and Kaplana, K., 2015. Ecological integrity and environmental protection for Vijayawada region–Scattered Eastern Ghats. International Journal of Sustainable Built Environment, 4(1), pp.109-116.

Rao, D.S., Ramamirtham, C.P., Murty, A.V.S., Muthusamy, S., Kunhikrishnan, N.P. and Khambadkar, L.R., 1992. Oceanography of the Arabian Sea with particular reference to the southwest monsoon. CMFRI Bulletin, 45, pp.4-8.

Rastogi, S., Chanchani, P., Sankaran, M. and Warrier, R., 2022. Grasslands half-full: investigating drivers of spatial heterogeneity in ungulate occurrence in Indian Terai. Journal of Zoology, 316(2), pp.139-153.

Ratnam, J., Chengappa, S.K., Machado, S.J., Nataraj, N., Osuri, A.M. and Sankaran, M., 2019. Functional traits of trees from dry deciduous "forests" of southern India suggest seasonal drought and fire are important drivers. Frontiers in Ecology and Evolution, 7, p.8.

Ratnam, J., Tomlinson, K.W., Rasquinha, D.N. and Sankaran, M., 2016. Savannahs of Asia: antiquity, biogeography, and an uncertain future. Philosophical Transactions of the Royal Society B: Biological Sciences, 371(1703), p.20150305.

Rawat, G.S., 1997. Conservation status of forests and wildlife in the Eastern Ghats, India. Environmental Conservation, 24(4), pp.307-315.

Reddy, C.S., Reddy, K.N., Prasad, P.R.C. and Raju, V.S., 2003. Threatened endemic plants from eastern Ghats, India. EPTRI-ENVIS Newsletter, 9(2), pp.3-7.

Reddy, C.S., Varma, Y., Brahmam, M. and Raju, V., 2008. Prioritisation of endemic plants of Eastern Ghats for Biological conservation. In Proceedings of the National Seminar on Conservation of Eastern Ghats. EPTRI, Hyderabad (pp. 3-13).

Reddy, M.C., Murthy, K.S.R., Rani, S.S. and Pullaiah, T., 2016. Ethnobotany of Useful Plants in Eastern Ghats and Adjacent Deccan Region. In Ethnobotany of India, Volume 1 (pp. 381-414). Apple Academic Press.

Reddy, V.R., Reddy, M.G., Saravanan, V., Bandhii, M. and Springate-Baginski, O., 2004. Participatory forest management in Andhra Pradesh: A review. Development Economics Working Papers, (22158).

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Buckley, Y.M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D.A., Brinks, E. and de Buhr, H., 2015. The compadre Plant Matrix Database: an open online repository for plant demography. Journal of Ecology, 103(1), pp.202-218.

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Buckley, Y.M., Che-Castaldo, J., Caswell, H., Hodgson, D., Scheuerlein, A., Conde, D.A., Brinks, E. and de Buhr, H., 2015. The compadre Plant Matrix Database: an open online repository for plant demography. Journal of Ecology, 103(1), pp.202-218.

Sambo, O., Oumarou, O., Adjima, T. and Issaka Joseph, B., 2020. Fruit production in Balanites aegyptiaca is highly variable across tropical arid zones of West Africa: implications for sustainability. The Journal of Horticultural Science and Biotechnology, 95(2), pp.211-221.

Schmerbeck, J., 2011. Linking dynamics and locally important ecosystem services of South Indian dry forests: an approach. Journal of Resources, Energy and Development, 8(2), pp.149-172.

Senande-Rivera, M., Insua-Costa, D. and Miguez-Macho, G., 2022. Spatial and temporal expansion of global wildland fire activity in response to climate change. Nature Communications, 13(1), p.1208.

Setty, R.S., Bawa, K., Ticktin, T. and Gowda, C.M., 2008. Evaluation of a participatory resource monitoring system for nontimber forest products: the case of amla (Phyllanthus spp.) fruit harvest by Soligas in South India. Ecology and Society, 13(2).

Sewak, R., Vashisth, M. and Gupta, L., 2021. Forest Fires in India: A Review. J. Univ. Shanghai Sci. Technol., 23(7), pp.247-259.

Silveira, F.A., Arruda, A.J., Bond, W., Durigan, G., Fidelis, A., Kirkman, K., Oliveira, R.S., Overbeck, G.E., Sansevero, J.B.B., Siebert, F. and Siebert, S.J., 2020. Myth-busting tropical grassy biome restoration. Restoration Ecology, 28(5), pp.1067-1073.

Simon, G.L. and Peterson, C., 2019. Disingenuous forests: A historical political ecology of fuelwood collection in South India. Journal of Historical Geography, 63, pp.34-47.

Singh, A.K., 2013. Probable Agricultural Biodiversity Heritage Sites in India: XVII. The South-Central Region of Eastern Ghats. Asian Agri-History, 17(3), pp.199-220.

Singh, S., Kumar Jr, S., Kolte, A.P. and Kumar, S., 2013. Extensive variation and sub-structuring in lineage A mtDNA in Indian sheep: genetic evidence for domestication of sheep in India. PLoS One, 8(11), p.e77858.

Siyum, Z.G., 2020. Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. Ecological processes, 9(1), p.25.

Sunderland, T., Apgaua, D., Baldauf, C., Blackie, R., Colfer, C., Cunningham, A.B., Dexter, K., Djoudi, H., Gautier, D., Gumbo, D. and Ickowitz, A., 2015. Global dry forests: a prologue. International Forestry Review, 17(2), pp.1-9.

Thekaekara, T., Vanak, A. T., Hiremath, A. J., Rai, N. D., Ratnam, J., & Sukumar, R. 2017. Notes from the other side of a forest fire. Economic & Political Weekly, 52(25), 22-25.

Ticktin, T., 2005. Applying a metapopulation framework to the management and conservation of a non-timber forest species. Forest Ecology and Management, 206(1-3), pp.249-261.

Tubbesing, C.L., York, R.A., Stephens, S.L. and Battles, J.J., 2020. Rethinking fire-adapted species in an altered fire regime. Ecosphere, 11(3), p.e 03091.

Vanak, A.T., 2019. Wastelands of the mind: the identity crisis of India's savanna grasslands.

Vitousek, P. M. (1994). Beyond global warming: ecology and global change. Ecology, 75(7), 1861-1876.

Winkler, K., Fuchs, R., Rounsevell, M., & Herold, M. 2021. Global land use changes are four times greater than previously estimated. Nature communications, 12(1), 2501.

Wright, D.H. and Reeves, J.H., 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia, 92, pp.416-428.

Yadama, G.N., Hovmand, P.S. and Chalise, N., 2010. Community driven modeling of social-ecological systems: lessons from Andhra Pradesh, India. In Proceedings of the 28th international conference of the System Dynamic Society. Seoul, South Korea.

Acknowledgments

I would like to express my special appreciation and gratitude to my supervisor, Tiffany Knight. Thank you, Tiffany for your guidance and encouragement at every step of my journey. I will cherish your mentorship forever, I have learnt so much from you that I will carry forward in my future journey. I would like to thank my PhD Advisory Committee (PAC) Ingolf Kuehn, Aldo Compagnoni and Venkat Dyda for their valuable inputs and discussions at various stages of this journey.

I would like to thank the members of Spatial Interaction Ecology (SIE) for being the most amazing colleagues. I have learnt from and been inspired by all of you. Leana, Sam, Amibeth, Martin, Sanne, Michael, Valentin, Anne, Sarah, Nina and Elena, and my yDiv peers Andrea, Eduardo and Thore, thank you all for being an encouraging, caring and a jolly bunch throughout this journey.

I would like to acknowledge Foundation for Ecological Security (FES) for sharing their time and knowledge and for motivating my research questions. I would like to thank Himani, Rahul, Anil and Jagadeesh Rao at FES Anand and Hemalatha, Raksha and Shreeranga at FES Madanapalle for the enriching discussions on commons. Thank you, Saneesh for your help during fieldwork and life in Madanapalle. I would like to thank the local community members, Malli anna, Gangireddy anna and Ramanji for their support in the field and for sharing their knowledge with me.

Everything that I am, my mother helped me to be. No words of gratitude are enough to acknowledge her unconditional support throughout my journey. Amma, you are my forever. I know you are proud of me and cheering me on, I miss you. Nana and Vijay, thank you very much for being my strength, and for your care and support. To my husband and best friend Karthik, thank you for being my rock and constant companion through all the highs and lows and for being my loudest cheerleader. I am grateful for my friend Sumana for motivating me at every step and for her ability to cheer me up always. Finally, I would like to thank my flatmates for a home away from home. I am grateful for Jens for always being there for me, for comfort and humour, Emily for all the laughs and good times and my KG9 sister Amelie for being with me through it all, for the warmth, unwavering support and a forever friendship.

Appendices

Supplementary material for Chapter 2

Neeraja, U.V., Rajendrakumar, S., Saneesh, C.S., Dyda, V. and Knight, T.M., 2021. Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats. *Ecology and Evolution*, 11(11), pp.6593-6603. https://doi.org/10.1111/btp.13135

Appendix A. Community dissimilarity and geographic distance of sampling plots.

We used Mantel Tests with the *mantel* function from the package *vegan* in R to test the relationship between geographic distance and pairwise dissimilarity (Bray Curtis index) in 2008 and 2018. We used the *vegdist* function to compute dissimilarity indices for community composition data from package *vegan* in R. Geographic distance between sites was calculated as Haversine distance from the package *geosphere* (Hijmans, 2016) in R. All statistical analyses were conducted in R programming version 3.6.2 (R Core Team 2017).

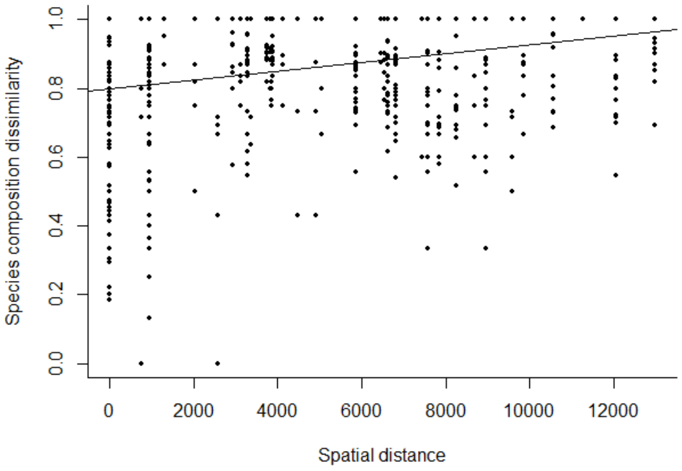


Fig. A.1. Relationship between community dissimilarity and geographic distance for 2008 plots. Pairwise dissimilarities are plotted as a function of the distance between the sampling plots. Mantel statistic r: 0.2363, p<0.0

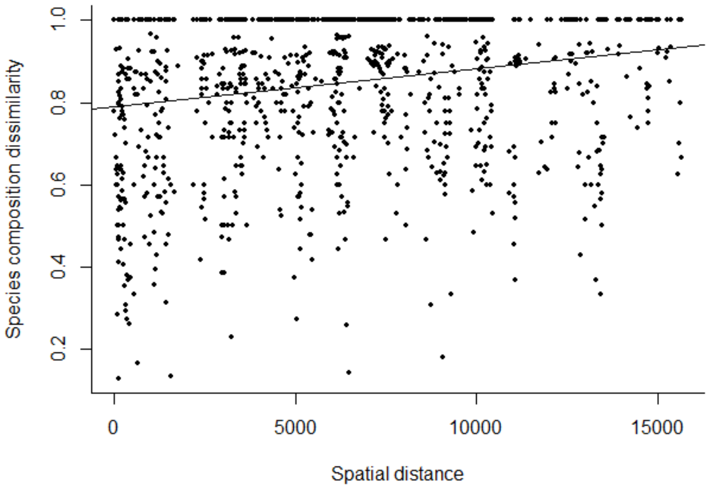


Fig. A.2. Relationship between community dissimilarity and geographic distance for 2018 plots. Pairwise dissimilarities are plotted as a function of the distance between the sampling plots. Mantel statistic r: 0.1999, p<0.001

Appendix B. Tree species composition across four categories representing sampling years and the presence and absence of fire. This visualization includes eight plots that had only one tree species. Because two of these plots are clear outliers, these eight plots were removed from the statistical analysis and visualization in the main paper.

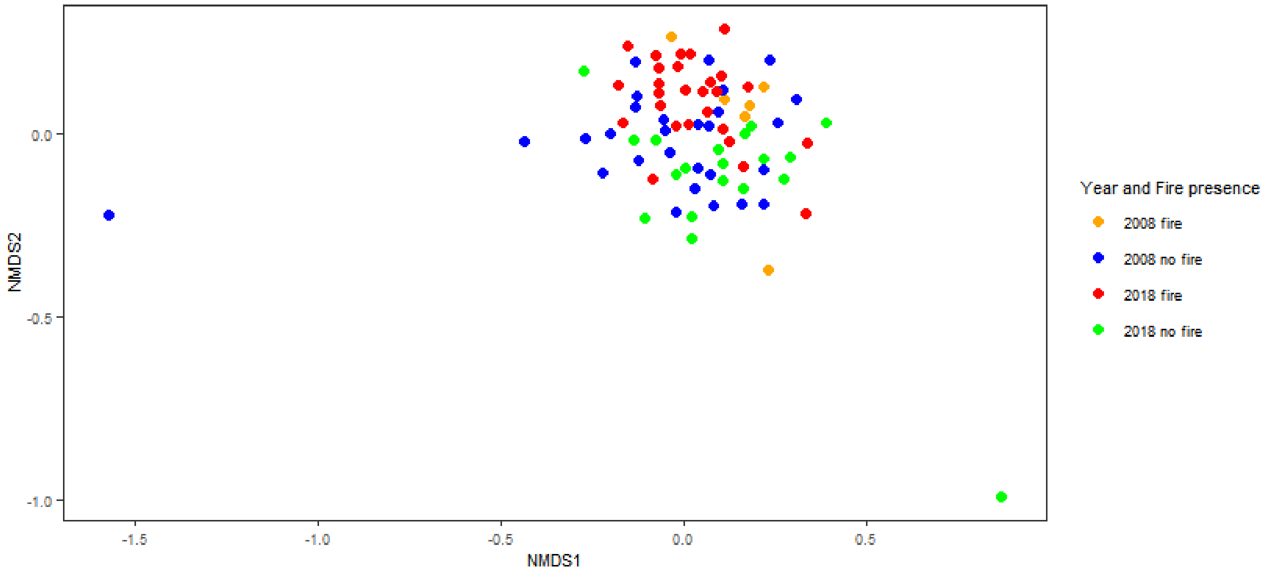


Fig. B.1 NMDS ordination of tree species composition (stress=0.158) showing all the vegetation plots in four categories representing sampling years and the presence and absence of fire.

Appendix C. Categories of bark thickness and resprouting ability for 10 focal tree species.

Family	**Species**	**Mean GBH**	**Mean bark thickness**	**Relative bark thickness**	**Category**
Fabaceae	*Albizia amara*	60.26	0.26	1.35	Thin (Anil and Parthasarthy 2016)
Erythroxylaceae	*Erythroxylum monogynum*				Thin (Sasidharan 2006)
Fabaceae	*Dalbergia paniculata*	52.40	0.610	3.65	Thin
Hernandiaceae	*Gyrocarpus americanus*	43.5	1	7.22	Thin
Fabaceae	*Acacia chundra*	40.69	0.98	7.57	Thin
Lamiaceae	*Premna tomentosa*	21	0.53	7.97	Thin
Bignoniaceae	*Dolichandrone atrovirens*	36.12	1.03	8.99	Thick
Fabaceae	*Cassia fistula*	26.25	0.80	9.62	Thick
Rutaceae	*Chloroxylon swietenia*	37.6	1.18	9.85	Thick
Apocynaceae	*Wrightia tinctoria*	28.51	0.92	10.16	Thick

Table C.1. Categories of bark thickness for 10 focal tree species. To quantify bark thickness, co-author Saneesh CS measured girth at breast height (GBH) and bark thickness measurements of trees. Relative bark thickness was calculated as (Mean Bark thickness/ Mean diameter)*100 following Hoffman et al. 2012, Lawes et al. 2013. Tree species were grouped into thin and thick bark based on quantile grouping using *cut2* function from *Hmisc* package in R to make the continuous numerical variable into categorical. Additional citations supporting the categories of thin or thick for each focal tree species are also given in the Category column

Family	**Species**	**Resprouting type**
Fabaceae	*Albizia amara*	Basal (own observation)
Erythroxylaceae	*Erythroxylum monogynum*	Basal (own observation)
Fabaceae	*Dalbergia paniculata*	Basal (Saha and Howe 2003)
Hernandiaceae	*Gyrocarpus americanus*	Non sprouting (Otterstrom 2006)
Fabaceae	*Acacia chundra*	Basal (own observation)
Lamiaceae	*Premna tomentosa*	Basal (own observation)

Bignoniaceae	*Dolichandrone atrovirens*	Clonal (own observation)
Fabaceae	*Cassia fistula*	Clonal (own observation)
Rutaceae	*Chloroxylon swietenia*	Clonal (own observation)
Apocynaceae	*Wrightia tinctoria*	Basal (own observation)

Table C.2. Categories of resprouting type for 10 focal tree species. Information on resprouting is based on field observations of the authors and/or the literature cited. Basal sprouters are capable of resprouting from their root collar. Clonal sprouters are capable of producing root sprouts and root collar sprouts.

Appendix D: Stems density (stems per plot) in plots with no fire presence and fire presence.

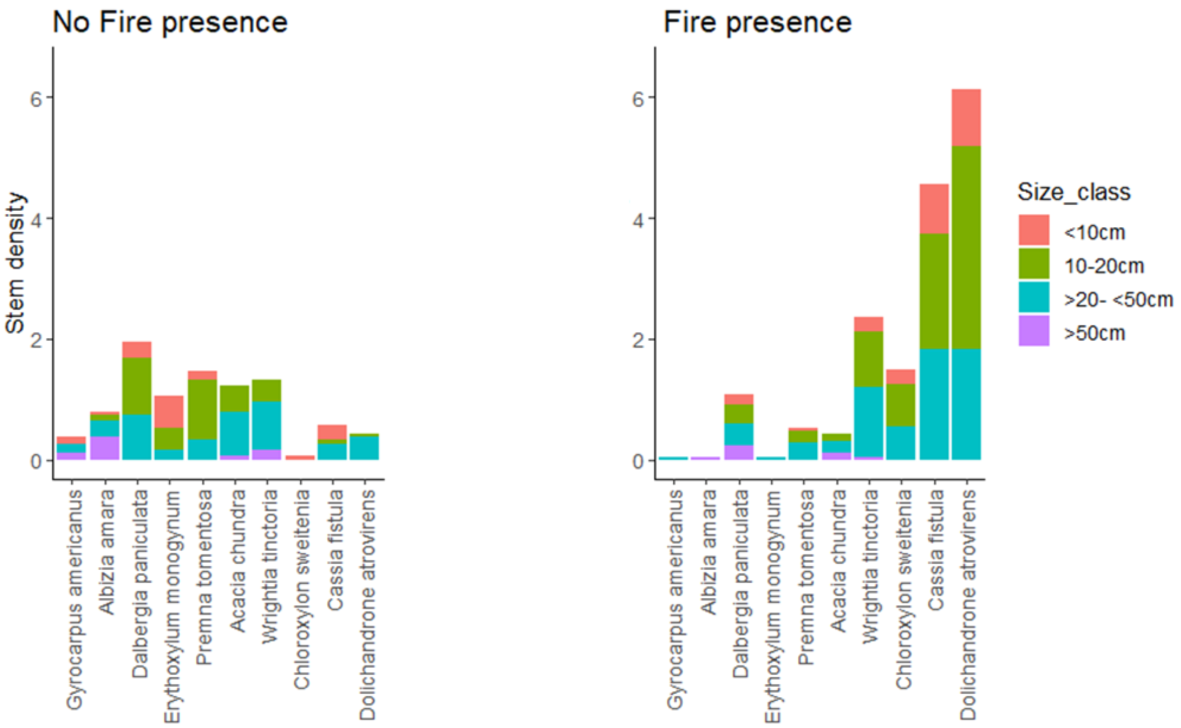


Fig. D. 1 Stems per plot of 10 focal tree species in plots with no fire presence (left) and plots with fire presence (right) in 2018.

References.

Hijmans, Robert J., 2016. Geosphere: Spherical Trigonometry. https://CRAN. R-project. org/package= geosphere

Hedge V, Chandran MDS & Gadgil M., 1998. Variation in Bark Thickness in a Tropical Forest Community of Western Ghats in India; Functional Ecology 12: 313-318. https://doi.org/10.1046/j.1365-2435.1998.00191.x

Saha, S., Howe, H.F., 2003. Species composition and fire in a dry deciduous forest. Ecology 84 (12), 3118–3123. https://doi.org/10.1890/02-3051

Otterstrom, S. M., Schwartz, M. W., Velazquez-Rocha, I., 2006. Responses to Fire in selected tropical dry forest trees. Biotropica 38: 592–598. https:/doi.org/ 10.1111/j.1744-7429.2006.00188.x.

Anil, K., Parthasarathy, N., 2016. Bark traits of woody species and bark resource use by faunal community in tropical dry evergreen forest of India. Int. J. Curr. Res. Biosci. Plant Biol. 3(2), 77-90. http://dx.doi.org/10.20546/ijcrbp.2016.302.010

Sashidharan N, 2006. Illustrated Manual on Tree Flora of Kerala supplemented with computer aided identification. Kerala Forest Research Institute Research report 282.

Hoffmann, W.A., E.L. Geiger, S.G. Gotsch, D.R. Rossatto, L.C.R. Silva, O.L. Lau, M. Haridasan, and A.C. Franco. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes.Ecology Letters 15: 759–768. doi: 10.1111/j.1461-0248.2012.01789.x

Lawes MJ, Midgley JJ, Clarke PJ. 2013. Costs and benefits of relative bark thickness in relation to fire damage: A savanna/forest contrast. Journal of Ecology. 101. doi: 10.1111/1365-2745.12035.

Supplementary material for Chapter 3

Neeraja, U.V., Saneesh, C.S., Dyda, V., Reddy, H., Yadama, G.N. and Knight, T.M., 2022. Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. *Biotropica*, 54(6), pp.1376-1389. https://doi.org/10.1002/ece3.7514

Harvesting has variable effects on demographic rates and population growth across three dry forest tree species

U.V. Neeraja[1,2*], C.S. Saneesh[3,2], Venkat Dyda[4], Hemalatha Reddy[4], Gautam N. Yadama[6], Tiffany M. Knight[1,3,2]

1. Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany.

2. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstrasse 4, 04103 Leipzig, Germany.

3. Department of Community Ecology, Helmholtz Centre for Environmental Research- UFZ, Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany.

4. Foundation for Ecological Security, Seshappa Thota, Madanapalle, Andhra Pradesh 517325, India.

5. Boston College School of Social Work, 140 Commonwealth Ave, McGuinn Hall, Chestnut Hill, MA 02467, USA.

*Author for correspondence: neeraja.venkataraman@idiv.de

Figure S1. Photos of main stem harvesting on *Chloroxylon swietenia*.

Figure S2. Photos of branch harvesting on *Acacia chundra*.

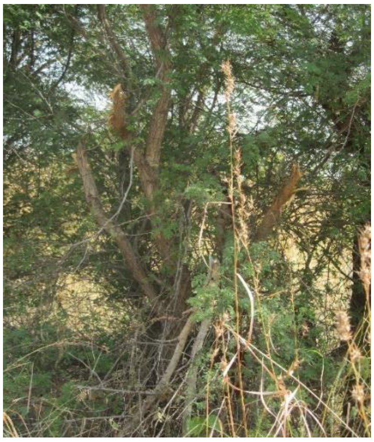


Figure S3. A single individual of *Gardenia gummifera* in the sprout state.

List of publications and authors' contributions

Chapter 2

Neeraja, U. V., S. Rajendrakumar, C. S. Saneesh, Venkat Dyda, and Tiffany M. Knight. Fire alters diversity, composition, and structure of dry tropical forests in the Eastern Ghats. *Ecology and Evolution* 11, no. 11 (2021): 6593-6603.

NUV, VD and TMK conceived the ideas; NUV and TMK designed the methodology; NUV, SR and CSS collected the data; NUV and SR curated the data; NUV analyzed the data with the help from TMK; NUV led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Overall contribution of NUV was 70%.

Chapter 3

Neeraja, U. V., C. S. Saneesh, Venkat Dyda, Hemalatha Reddy, Gautam N. Yadama, and Tiffany M. Knight. Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. *Biotropica* 54, no. 6 (2022): 1376-1389.

TMK and GNY conceived the ideas; TMK designed the methodology; NUV, TMK, HR and CSS collected the data; NUV curated the data; NUV and TMK analyzed the data; NUV led the writing of the manuscript; TMK and VD provided supervision. All authors contributed critically to the drafts and gave final approval for publication. Overall contribution of NUV was 70%.

Chapter 4

Neeraja, U. V., Venkat Dyda, C. S. Saneesh and Tiffany M. Knight. Tree composition and structure in wooded and more open savannas in a semi-arid landscape in India. (submitted)

NUV, VD and TMK conceived the ideas; NUV and TMK designed the methodology; NUV and CSS collected the data; NUV curated the data; NUV and TMK analyzed the data; NUV led the writing of the manuscript. All authors contributed critically to writing and reviewing of the manuscript. Overall contribution of NUV was 80%.

Curriculum vitae

Personal Information

Name: Neeraja Venkataraman

Education

2018 – present	Ph.D. Ecology Martin Luther University of Halle-Wittenberg (MLU)/ German Centre for Integrative Biodiversity Research (iDiv), Germany Thesis title: Influence of anthropogenic factors on woody species composition, structure and demography in Eastern Ghats, India Supervisor: Prof. Dr. Tiffany Knight
2012– 2015	M.Sc. Master in Global Change Ecology University of Bayreuth, Germany Dissertation: Adaptation of aquatic macroinvertebrates to pesticides
2007 – 2011	B.E. Bachelor of Engineering in Biotechnology Visveshwaraya Technological University, India

Work experience

Aug 2022- present	Research Officer (Monitoring and Evaluation) Forest Stewardship Council
Jan 2018 – Dec 2022	Doctoral researcher at Martin Luther Universitaet Halle-Wittenberg (MLU)/ German Centre for Integrative Biodiversity (iDiv), Germany
Apr 2017 - Dec 2017	Research assistant at iDiv, Leipzig, Germany Demographic monitoring of woody species
Apr 2016 - Mar 2017	Research assistant at UFZ Helmholtz Centre for Environmental Research, Leipzig, Germany Satellite imagery analysis of long-term vegetation plots, Literature review and analysis of tools to analyze vegetation imagery.
Dec 2015 - Mar 2016	Research assistant at UFZ Literature review and analysis on forest restoration and connectivity in the context of Mexico

Aug 2014 - Sept 2015	Research assistant and Master Dissertation at UFZ Master dissertation: “Adaptation of aquatic macroinvertebrates to pesticides”
Feb 2013 - Feb 2014	Research assistant at Bayreuth Centre of Ecology and Environmental Research, Universität Bayreuth, Germany Kilimanjaro ecosystem under global change: Analysis of soil samples

Publications

Neeraja, U. V., Saneesh, C. S., Dyda, V., Reddy, H., Yadama, G. N., & Knight, T. M. 2022. Harvesting has variable effects on demographic rates and population growth across three dry forest tree species. Biotropica, 00, 1–14. https://doi.org/10.1111/btp.13135

Neeraja, U.V., Rajendrakumar, S., Saneesh, C.S., Dyda, V., Knight, T.M., 2021. Fire alters diversity, composition and structure of dry tropical forests in the Eastern Ghats. Ecology and Evolution. https://dx.doi.org/10.1002/ece3.7514

Rakosy D, Motivans E, Ştefan V, Nowak A, Świerszcz S, Feldmann R, et al. 2022. Intensive grazing alters the diversity, composition and structure of plant-pollinator interaction networks in Central European grasslands. PLoS ONE 17(3): e0263576. https://doi.org/10.1371/journal.pone.0263576

Conference participation

- British Ecological Society 2019, Belfast, UK (Talk)
- ISEB1: Celebrating Ecology and Evolution in India, Indian Society of Evolutionary Biologists 2019, Bangalore, India (Poster)
- 14th National Silviculture Conference on "Forest & Sustainability: Securing a Common Future" 2018, Indian Institute of Science, India

Courses and workshops

- yDiv Graduate School courses (for eg. Measurement of Biodiversity, Fire Ecology, Ecological Networks and Coexistence etc.)
- Stage-based demographic models in ecology, evolution and conservation biology, NERC, University of Oxford.
- Forest geospatial data, National Remote sensing Centre, India

Computing skills

- Proficient in Microsoft Office (MS Excel, MS Word, MS Access, MS Powerpoint)
- Proficient in R programming language
- Working knowledge of QGIS and ArcGIS application
- Working knowledge of data visualization software Tableau
- Basic 2D and 3D animation

Languages

- English: Advance, German- B1
- Other languages- Telugu, Tamil, Kannada and Hindi

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Influence of anthropogenic factors on woody species composition, structure and demography in Eastern Ghats, India“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Neeraja Venkataraman, Halle (Saale), 22.05.2023