Check for updates

Received: 11 August 2023 | Accepted: 12 October 2023

DOI: 10.1111/1365-2745.14221

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Tillage agriculture and afforestation threaten tropical savanna plant communities across a broad rainfall gradient in India

Ashish N. Nerlekar[1] | **Avishkar Munje**[2] | **Pranav Mhaisalkar**[3] | **Ankila J. Hiremath**[4] | **Joseph W. Veldman**[1]

[1]Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, USA

[2]Fergusson College, Pune, Maharashtra, India

[3]Brandenburg Technical University, Cottbus, Germany

[4]Ashoka Trust for Research in Ecology and the Environment, Bengaluru, Karnataka, India

Correspondence
Ashish N. Nerlekar
Email: ashishnerlekar@tamu.edu

Funding information
National Institute of Food and Agriculture, Grant/Award Number: 1016880; National Science Foundation, Grant/Award Number: DEB-1931232; Texas A&M University ECCB High Impact Research Grant; Texas A&M OGAPS Dissertation Fellowship; Texas A&M Tom Slick Graduate Fellowship

Handling Editor: Giselda Durigan

Abstract

1. The consequences of land-use change for savanna biodiversity remain undocumented in most regions of tropical Asia. One such region is western Maharashtra, India, where old-growth savannas occupy a broad rainfall gradient and are increasingly rare due to agricultural conversion and afforestation.
2. To understand the consequences of land-use change, we sampled herbaceous plant communities of old-growth savannas and three alternative land-use types: tree plantations, tillage agriculture and agricultural fallows ($n=15$ sites per type). Study sites spanned 457 to 1954 mm of mean annual precipitation—corresponding to the typical rainfall range of mesic savannas globally.
3. Across the rainfall gradient, we found consistent declines in old-growth savanna plant communities due to land-use change. Local-scale native species richness dropped from a mean of 12 species/m^2 in old-growth savannas to 8, 6 and 3 species/m^2 in tree plantations, fallows and tillage agriculture, respectively. Cover of native plants declined from a mean of 49% in old-growth savannas to 27% in both tree plantations and fallows, and 4% in tillage agriculture. Reduced native cover coincided with increased cover of invasive species in tree plantations (18%), fallows (18%) and tillage agriculture (3%).
4. In analyses of community composition, tillage agriculture was most dissimilar to old-growth savannas, while tree plantations and fallows showed intermediate dissimilarity. These compositional changes were driven partly by the loss of characteristic savanna species: 65 species recorded in old-growth savannas were absent in other land uses. Indicator analysis revealed 21 old-growth species, comprised mostly of native savanna specialists. Indicators of tree plantations (nine species) and fallows (13 species) were both invasive and native species, while the two indicators of tillage agriculture were invasive. As reflective of declines in savanna communities, mean native perennial graminoid cover of 27% in old-growth savannas dropped to 9%, 7%, and 0.1% in tree plantations, fallows and tillage agriculture, respectively.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.
© 2023 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

5. *Synthesis*. Agricultural conversion and afforestation of old-growth savannas in India destroys and degrades herbaceous plant communities that do not spontaneously recover on fallowed land. Efforts to conserve India's native biodiversity should encompass the country's widespread savanna biome and seek to limit conversion of irreplaceable old-growth savannas.

KEYWORDS
biodiversity, fire, grassland, herbivores, India, land-use change, plant species richness

1 | INTRODUCTION

While a multitude of drivers of global change are transforming Earth's grassy biomes, land-use change has emerged as an acute and widespread cause of biodiversity loss in tropical savannas (Lapuz et al., 2021; Newbold et al., 2016; Parr et al., 2014). Much of our understanding on the ecological consequences of land-use change for tropical savanna plant communities comes from studies in South America (e.g., Almeida et al., 2011; Cava et al., 2018; Laste et al., 2019) or has been inferred from studies of subtropical savannas in North America (Kirkman et al., 2004), southern Africa (Zaloumis & Bond, 2016) and Australia (Fensham et al., 2016). As recognition grows that Asia supports savannas that are ancient and extensive, so too has grown the number of calls by ecologists to improve their representation in studies of tropical conservation (e.g., Ratnam et al., 2016).

Plant communities of tropical savannas are highly susceptible to changes in land use that disrupt historical disturbance regimes of frequent fire and herbivory or that introduce novel stresses that deplete belowground bud banks (Buisson et al., 2019; Veldman et al., 2015). Two land uses that are both pervasive and incompatible with savanna biodiversity are tillage agriculture and plantation forestry (Bremer & Farley, 2010; Searchinger et al., 2015). In the Brazilian *Cerrado*, a biodiversity hotspot, 46% of savannas have been converted for agriculture (Rausch et al., 2019; Strassburg et al., 2017), and in Africa, humid savannas are being targeted as a new agricultural frontier (Searchinger et al., 2015). Tillage destroys savanna communities by killing underground organs of long-lived perennial plants that are extremely slow to recolonize after agricultural is abandoned (Fensham et al., 2016; Koch et al., 2016). In addition to tillage agriculture, tree planting—whether motivated by wood production, forest restoration, or carbon sequestration—is a growing threat to savannas (Vetter, 2020 and references therein). In plantations, dense trees, coupled with fire exclusion, outcompete light-demanding, fire-dependant, savanna plant communities, whose diversity does not rapidly recover even after trees are harvested (Zaloumis & Bond, 2016).

Across the tropics, savannas occupy a broad range of mean annual precipitation (MAP) that contributes to their patterns of plant diversity and their vulnerability to land-use change. While the limits of the tropical savanna biome span approximately 100 to 2500 mm MAP and vary by continent, most savannas occur in the range of 500 to 2000 mm MAP (Lehmann et al., 2011). Because these mesic savannas of intermediate rainfall rely on fire and herbivory to prevent forest formation (Hoffmann et al., 2012; Murphy & Bowman, 2012), they are often misperceived as degraded forests and undervalued in conservation initiatives (Parr et al., 2014; Veldman, 2016). Furthermore, the precipitation range of mesic savannas is highly suitable for growing crops and trees, making them attractive targets for agricultural expansion (Strassburg et al., 2017) and afforestation (Veldman et al., 2019). To understand the biodiversity consequences of land-use change in tropical savannas demands an approach that considers rainfall gradients. Studies in many of the world's grasslands and savannas find that herbaceous plant diversity is often positively related to rainfall (Adler & Levine, 2007; Cleland et al., 2013; Dingaan et al., 2017; Ma et al., 2010; Smith et al., 2022). Whether such MAP-diversity patterns interact with land-use type to shape herbaceous plant biodiversity of tropical savannas of Asia remains unclear.

Savannas of western Maharashtra, India, span a broad rainfall gradient (~440 to 2000 mm MAP) that is just ~100-km wide at its narrowest point (Burns & Kulkarni, 1927; Oke, 1972; Figure 1; Figure S1). These savannas are increasingly converted for other land uses (Roy et al., 2015), making them ideal for studying consequences of land-use change across a rainfall gradient. The rainfall gradient in western Maharashtra is negatively correlated with mean annual temperature (MAT) of 23.0–26.6°C, such that one end of the gradient is cooler and wetter and the other is drier and warmer (Oke, 1972; Figure S2). Few tropical savannas offer a rainfall gradient this wide in such a narrow geographical region. The well-studied south to north savanna precipitation gradient in Kruger National Park of South Africa spans 350–750 mm MAP over about 350 km (e.g., Govender et al., 2006). The North Australian Tropical Transect spans a 1250 mm gradient (400–1650 mm MAP) over 1000 km (Hutley et al., 2011). Western Maharashtra's precipitation gradient enables the study of savanna plant communities that are plausibly part of a single regional species pool that includes many endemics (Dabadghao & Shankarnarayan, 1973; Datar, 2016; Nerlekar et al., 2022).

With the goal of improving our knowledge of tropical savannas of Asia, in this study, we sought to understand the ecological consequences of land-use change for herbaceous plant diversity and community composition across the rainfall gradient in western Maharashtra, India. We sampled 60 sites, with $n = 15$ belonging to each of four land-use types: old-growth savannas, tree plantations,

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

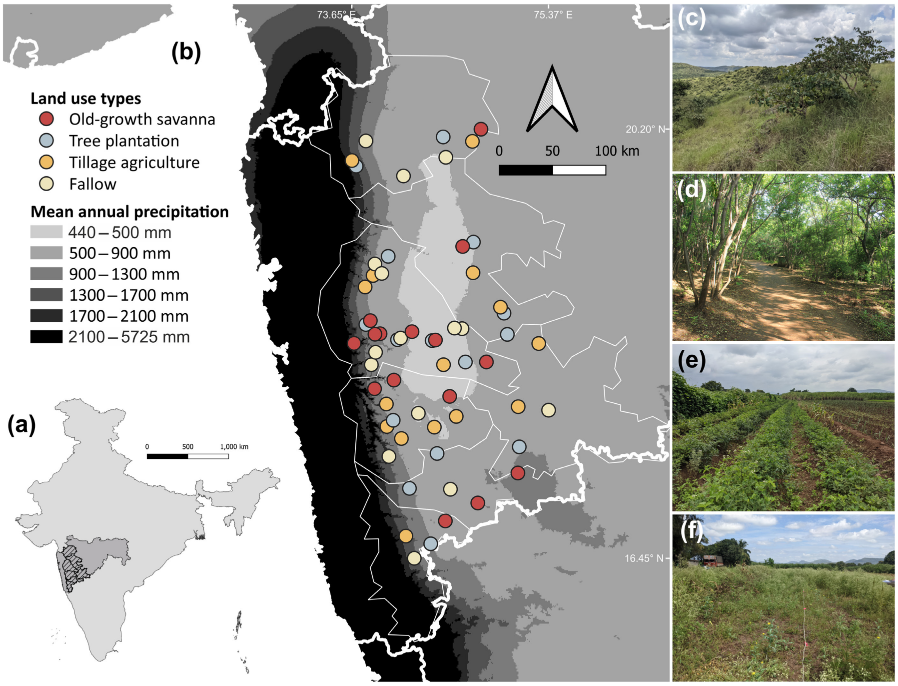

FIGURE 1 Map of the study region and representative images of study sites. (a) The state of Maharashtra (dark grey) in India along with the location of seven western districts as black-hatched shading. (b) Study sites (colour-coded by land-use type) distributed across ~1500 mm of the broader precipitation gradient; thick white lines represent borders of the state of Maharashtra and thin white lines are the seven districts. Examples of land-use types: (c) old-growth savanna, (d) tree plantation, (e) tillage agriculture and (f) fallow.

tillage agriculture and agricultural fallows. Specifically, we focussed on the consequences of conversion of old-growth savannas for the following response variables: (1) local-scale native plant richness, (2) native plant cover, (3) community composition, including old-growth savanna indicator species, (4) perennial graminoid cover, and (5) invasive species cover. We expect that the results of this study will contribute to data-driven policies to conserve the biodiversity of India's imperilled savanna biome.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in 45,000 km^2 of western Maharashtra, India, at sites ranging in MAP from 457 to 1954 mm (Figure 1). The precipitation gradient is correlated with other bioclimatic gradients, for example, MAT (23–26.6°C; Figure S2). The precipitation gradient is created by the rain shadow of the Western Ghats Mountains, a global biodiversity hotspot (Myers et al., 2000). Like most tropical savannas (Lehmann et al., 2011), precipitation is highly seasonal, with the majority of rainfall during the monsoon months of July to September.

Annual rainfall in tropical India is associated with the distribution of two savanna types, characterized by broad-leaf and fine-leaf trees, both of which were represented in our sampling (Ratnam et al., 2016; Figure S1). Broad-leaf savannas are found in mesic regions, with at least 700 mm and up to 2100 mm MAP, and support relatively high tree densities. Common trees of broad-leaf savanna include *Terminalia tomentosa* (Combretaceae), *Anogeissus latifolia* (Combretaceae) and *Lannea coromandelica* (Anacardiaceae); common grasses include members of the fire-adapted Andropogoneae (Poaceae), such as *Heteropogon contortus*, *Cymbopogon martini* and *Themeda* spp. (Ratnam et al., 2016). Fine-leaf savannas typically occupy more xeric zones (MAP as little as 400 mm) and support sparse tree cover (Ratnam et al., 2016); distribution of the two types of savannas overlap in regions with 700–1000 mm MAP. Common trees of fine-leaf savannas are *Acacia leocophloea* (Fabaceae), *Acacia catechu* (Fabaceae) and *Boswellia serrata* (Burseraceae). While the same common grasses of Andropogoneae are dominant in both broad- and fine-leaf savannas, several Chloridoideae (Poaceae) taxa have greater representation in the fine-leaf savannas (Dabadghao & Shankarnarayan, 1973; Ratnam et al., 2016). Savannas of tropical India contain at least 206 endemic plants, many of which are globally threatened (Nerlekar et al., 2022). Maharashtra's savannas support the livelihoods of thousands of *Dhangar* pastoralists by provisioning forage for sheep, goats and cattle (Malhotra & Gadgil, 1981). The *Dhangar* can be credited for maintaining the disturbance regimes of old-growth savannas through traditional management of frequent fire and herbivory.

2.2 | Land use types

To represent the historical herbaceous plant communities that existed prior to widespread land-use change in western Maharashtra,

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

we used old-growth savannas as the reference ecosystem state (Veldman et al., 2015). To select old-growth savannas, we first generated a list of potential sites based on regional floristic literature and consultation with regional botanical experts (see Acknowledgments). We then further evaluated sites to ensure they were free from exogenous anthropogenic disturbances (i.e., tillage agriculture, mining, settlements; Buisson et al., 2019), as verified from historical Google Earth imagery (available from 2006 to 2021), a recently published map of 'open natural ecosystems' (Madhusudan & Vanak, 2021), and consultation with botanists familiar with local land-use history. We also ensured that sites supported intact disturbance regimes of frequent grazing, burning, or both (i.e., endogenous disturbances, Buisson et al., 2019; Table S1). Frequent grass-fueled surface fires ignited by either lightning or humans are recognized as the historical regime for mesic Indian savannas (Pyne, 1994; Riedel et al., 2021; Thekaekara et al., 2017). Therefore, while annual human-ignited fires might be more frequent than occurred historically, we consider this as a modest departure from the historical fire regime when compared to long-term fire exclusion that results in an ecosystem state transition from old-growth savanna to forest. In addition to the historical role of frequent fires, Indian savannas have been frequently grazed and browsed for millions of years (Jukar et al., 2021; Ratnam et al., 2016). In many Indian savannas, domestic livestock has supplemented or replaced native herbivores since the Holocene (Riedel et al., 2021). Because low-to-moderate intensity of herbivory by domestic livestock in tropical savannas can serve as a surrogate for native herbivores, which have been extirpated (Durigan et al., 2022; Veblen et al., 2016), we considered old-growth savannas managed with livestock to have an intact historical grazing regime (Buisson et al., 2019). Our broad definition of old-growth savannas for this socio-ecological landscape thus encompasses modest departures from the historical disturbance regimes, in addition to modest departures from historical plant composition and edaphic factors.

To select tree plantations, we identified sites that were afforested during the post-colonial era (since 1947; Table S2). Most plantations are of exotic species, typically *Gliricidia sepium* (Fabaceae), *Eucalyptus globulus* (Myrtaceae) and *Cassia siamea* (Fabaceae). There are some native tree plantations as well, which are commonly planted with *Azadirachta indica* (Meliaceae), *Acacia catechu* (Fabaceae) and *Dalbergia sissoo* (Fabaceae). All sites were grazed by domestic livestock, wild herbivores or both (Table S2).

For tillage agriculture, we included sites that were actively used to grow cash and food crops including millets, pigeon pea, corn, soybean, sugarcane and cotton that require tilling of the soil (Table S3). Inclusion of sites also depended on their accessibility and on permission from farmers to sample their fields.

Lastly, for fallows, we selected parcels of land with evidence of previous cultivation, including bunds (raised earth) around the parcel, and presence of tillage agriculture adjacent to the parcel (Table S4). To further confirm land-use history, where possible, we consulted landowners and visually inspected historical Google Earth satellite imagery (available from 2006 to 2021). All fallow sites were grazed by domestic livestock and some were also subjected to periodic burns (Table S3).

2.3 | Field sampling

During September and October 2021, the peak growing season for herbaceous plants, we sampled a total of 60 sites, $n = 15$ in each of the four land use types (Figure 1). Prior to the field sampling, we randomly selected sites with the goal of stratifying across the rainfall gradient. For the stratification, we created a regional map based on the long-term MAP from a 30-year period (1970–2000; 1 km^2 resolution; Fick & Hijmans, 2017). While our goal was to sample sites stratified by MAP, we ultimately sampled fewer sites than expected in the 1500- to 2000-mm interval. This was because the wettest portion of the MAP gradient occupied a small area and contained only a few sites that met our selection criteria.

At each of the 60 sites for which we had permissions to sample from the landowners, we established three 200-m^2 sampling plots (20 m × 10 m) oriented in a random compass direction. In western Maharashtra, old-growth savannas and tree plantations typically occur as large patches: Our old-growth sites ranged from 6 to 6160 ha with a median of 40 ha; tree plantations ranged from 8 to 403 ha with a median of 66 ha. Given their large area, we were able to randomly locate plots within old-growth and plantation sites without concern they would overlap or extend beyond the site. By contrast, the size of tillage agriculture and fallow sites was small (0.1–0.4 ha). To capture variation in the tillage agriculture and fallow land-use types, we sampled three separate fields, each with one plot that we oriented to fit within the field. For all the four land use types, we ensured that the three plots at each site were located within a circular area of diameter <3 km. At some sites, availability of suitable tillage agriculture and fallowed fields, as well as challenges to acquire permission from landowners, resulted in our sampling of fields that were adjacent to one another. In these cases, we ensured that there were at least 20 m between plots.

We measured herbaceous plant communities in seven 1-m^2 sub-plots, positioned along the centre line of the 200-m^2 plot, and calculated the mean of the seven sub-plots for subsequent data analyses. We visually estimated per cent cover by species (excluding crops in tillage agriculture) and used these data to determine local-scale species richness (i.e., species per 1 m^2) and community composition. To measure and identify woody species within each 200-m^2 plot, we used a variety of sampling techniques suitable for individuals of different size classes (Foster et al., 1998). For trees with a diameter at breast height (DBH, 1.3 m) ≥10 cm (i.e., large trees), we measured DBH of all individuals in the 200-m^2 plot. For trees of DBH ≥1 cm and <10 cm (i.e., small trees), we sampled a 2 × 20-m subplot (40 m^2) positioned along the centre line of the plot. To estimate per cent cover of shrubs (multi-stemmed woody plants), we used a 20-m line-intercept (Canfield, 1941). Lastly, we quantified woody regeneration by counting the number

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of seedlings, small tree saplings and woody resprouts <1.3 m tall or <1 cm DBH in the seven 1 m^2 plots. For identification, nomenclature and classification of plant functional groups and native/invasive status, we referred to several floras for the region (Supplementary methods).

To characterize soils, we collected two 10-cm diameter samples of the top 10-cm of mineral soil (excluding leaf litter and duff) from the ends of the 20-m centre line of the plot, which we pooled for each site. The samples were analysed by the Soil Science Laboratory of the College of Agriculture, Pune, India, for pH, electrical conductivity, organic carbon, available nitrogen, phosphorus, potassium, cation exchange capacity and soil texture.

2.4 | Data analyses

To test the effects of land use on herbaceous plant richness and cover while accounting for the gradient in MAP, we performed analysis of co-variance (ANCOVA), which models a continuous predictor (MAP) and a categorical treatment (land-use type). Since the response variables (species richness and cover) did not meet the equal variance assumption, we applied a $\log_{10}(1+x)$ transformation. We then fit the ANCOVA model using the *lme* function from the *nlme* package in *R. v. 4.1.0* (Pinheiro et al., 2021; R Core Team, 2021). We ran the model with 180 data points (representing each of three plots per site for $n=60$ sites), with 'site' as a random effect. To see whether the model met assumptions of normality, we plotted the quantile–quantile plots and residuals of the ANCOVA model. In cases where we detected significant main effects of land use, we conducted a post hoc pairwise Tukey test in the package *multcomp* (Hothorn et al., 2008). Finally, we visualized the results using the *ggplot2* package (Wickham, 2016; Figure 2). While the model retains the three plots per site, we plotted the means of $n=15$ sites per land-use type, which are the units of replication. Using the same approach, we repeated the ANCOVA for native perennial graminoid cover (i. e., grasses and sedges) and invasive species cover. As supplementary analyses, we also performed a similar ANCOVA for total (native + invasive) herbaceous richness and cover, cover by plant functional types (i.e., annual and perennial forbs and graminoids), tree basal area, shrub cover and woody regeneration. For models that severely violated the assumptions of normality for the ANCOVA, we performed a Kruskal–Wallis test followed by a pairwise Wilcox test (Figures S3–S5).

To understand the response of herbaceous species composition to land use, we performed non-metric multidimensional scaling (NMDS), using the *metaMDS* function in the *vegan* package (Oksanen et al., 2020). For compositional analyses, we worked with a site × species matrix in which we used the mean per cent cover of each of 283 species in three plots to represent each of the $N=60$ sites. Prior to ordination, we converted the raw per cent cover values to proportional abundances using the function *decostand* in *vegan* and created a Bray–Curtis (abundance based) dissimilarity matrix. For the NMDS, we use $k=3$ dimensions to evaluate the extent of original dissimilarity retained in the ordination (stress). To test for pairwise differences between composition of groups (i. e., land-use types), we used the *pairwiseAdonis* package (Martinez Arbizu, 2017). To further understand compositional differences, we identified significant ($p<0.05$) indicator species for each land-use type using the package *indicspecies* (Cáceres & Legendre, 2009). To statistically test and quantify the variation in community composition explained by land use, MAP, and the interaction term, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) in the *vegan* package. To visualize how MAP and land use interact to shape composition, we plotted sites by land-use type using the first two NDMS dimensions and scaling them by MAP (Figure 3A). As supplementary analyses, we also visualized nonlinear relationships between land-use types and MAP using the function *ordisurf* in *vegan* (Figure S6).

Finally, in supplemental analyses, we sought to understand how three additional factors (woody plants, multivariate climatic data and soil variables) might mediate, or provide alternative explanations, for patterns of plant richness, cover, MAP and land use (Supplementary Analyses; Figures S5, S7–S13). To understand how climate and soil variables shape plant composition, we used the principal components of the multivariate climate and soil data as predictor variables alongside land use and MAP in a PERMANOVA model.

3 | RESULTS

3.1 | Herbaceous plant richness and cover

During our sampling, we found 283 herbaceous plant taxa, with 262 identifiable to species, 11 to genus, seven to family and three that remained unidentified. Out of the 283 herbaceous taxa, 196 were forbs, 85 were graminoids and two were pteridophytes (Table S5). Out of the 273 species that were identifiable to at least genus, 47 (17%) were invasive (Table S5). Old-growth savannas contained 175 species (163 native and 12 invasive) in total, out of which 65 (all native) were absent in other land use types; tree plantations contained 156 species in total (127 native and 29 invasive), out of which 20 (16 native and four invasive) were not found in any other land use; fallows had 171 species in total (132 native and 39 invasive), out of which 20 (17 native and three invasive) were not found in any other land use; tillage agriculture had 96 species in total (62 native and 34 invasive), only seven (three native four invasive) of which were not found in other land uses (Figure 3B; Table S5).

In our model of local-scale native species richness (Figure 2A), we found that land-use type (ANCOVA, $F_{3,52}=29.8$; $p<0.0001$), but not MAP or the interaction of land use and MAP, was a significant predictor. Mean native species richness was greatest in the old-growth savannas (12 species/m^2, range = 7–18) and lowest in tillage agriculture (3 species/m^2, range = 1–5); tree plantations (8 species/m^2,

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

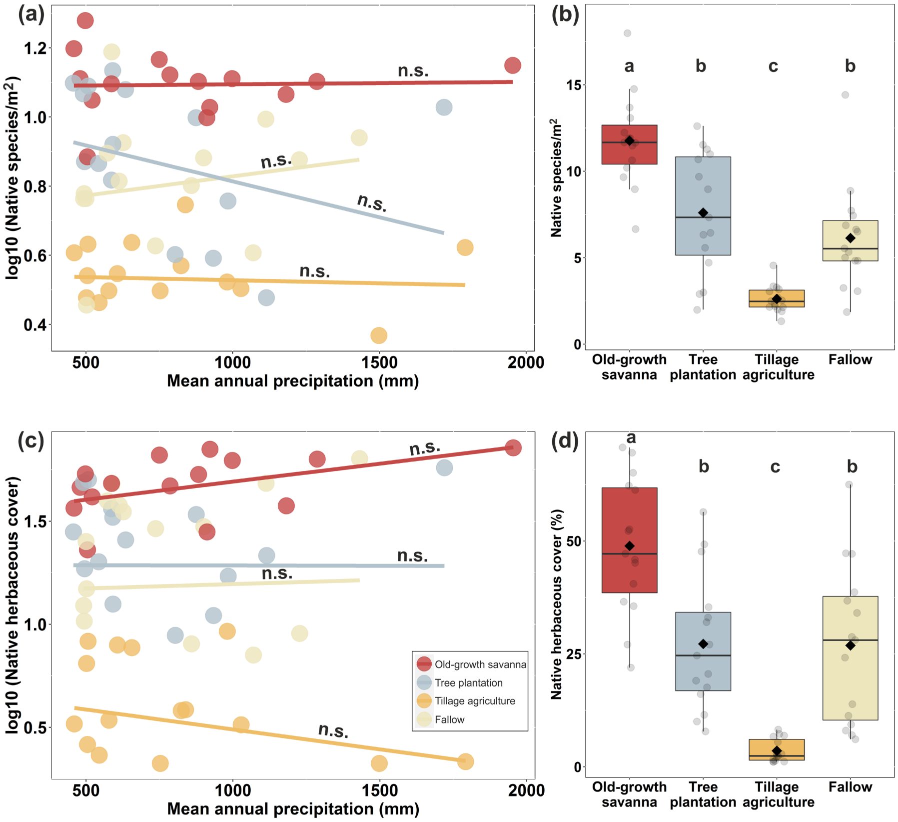

FIGURE 2 Species richness and cover of native herbaceous plants in four land-use types ($n=15$ sites per type) across a precipitation gradient in western Maharashtra, India. (A) Mixed effect model of local-scale richness (native species/m^2) indicated a significant effect of land use ($p<0.0001$) but not mean annual precipitation (MAP) or an interaction (ANCOVA, conditional $R^2=0.74$). (B) Native species richness in each land-use type (not accounting for MAP). (C) Mixed effect model of native herbaceous plant cover indicated a significant effect of land use ($p<0.0001$) but not MAP or an interaction (ANCOVA, conditional $R^2=0.61$). (D) Native species cover in each land-use type (not accounting for MAP). For (B) and (D), upper and lower limits of the boxes indicate 1st and 3rd quartiles respectively; the horizontal line represents the median; whiskers extend up to 1.5 times the inter-quartile range; diamonds indicate means; letters differ at $p<0.05$ (pairwise Tukey test).

range = 2–13) and fallows (6 species/m^2, range = 2–14) had similar richness (Figure 2B).

In our model of native herbaceous plant cover (Figure 2C), we found that land-use type (ANCOVA, $F_{3,52}=45.3$; $p<0.0001$), but not MAP or the interaction of land use and MAP, was the only significant predictor. Among land use types, mean native cover in old-growth savannas (49%, range = 22–71) was greater than tree plantations (27%, range = 8–56), fallows (27%, range = 6–62) and tillage agriculture (4%, range = 1–8; Figure 2D). When invasive and native plant cover were modelled together, mean cover in old-growth savannas (49%, range = 22–71), tree plantations (45%, range = 21–93) and fallows (45%, range = 9–85) were comparable, while tillage agriculture (7%, range = 3–17) was significantly lower (Figure S3). Old-growth savannas supported greater native perennial graminoid cover (27%, range = 6–58) than tree plantations (9%, range = 0–21), tillage agriculture (0.1%, range = 0–0.5) and fallows (7%, range = 0–22; Figure 3C). Mean cover of invasive species was highest in tree plantations (18%, range = 0.2–59) and fallows (18%, range = 1–63), lower in tillage agriculture (3%, range = 0.3–12) and negligible in old-growth savannas (0.063%, range = 0.005–0.4; Figure 3D).

3.2 | Plant species composition

Analysis of herbaceous plant communities via ordination bi-plots of NMDS axes 1 and 2 indicated statistically significant separation of the four land use types (Figure 3A). Composition of old-growth savannas was most dissimilar to tillage agriculture ($R^2=0.28$; adjusted $p=0.006$), followed by fallows ($R^2=0.22$; adjusted $p=0.006$) and tree plantations ($R^2=0.14$; adjusted $p=0.006$). Among the land-use types, only tree plantations showed a marginal overlap with the composition of old-growth savannas (Figure 3A). PERMANOVA revealed that compositional variation among study sites was primarily driven by land-use type ($R^2=0.22$, $p=0.001$), while MAP ($R^2=0.038$, $p=0.001$) and the interaction of land use and MAP ($R^2=0.064$, $p=0.004$) each explained a minor proportion of community composition.

Old-growth savannas contained the greatest number of indicator species (21), including the long-lived native C_4 grasses (Poaceae) *Cymbopogon martini*, *Chrysopogon fulvus*, *Sehima nervosum*, *Heteropogon contortus*; the annual native grasses (Poaceae) *Melanocenchris jacquemontii* and *Oropetium thomaeum*; and certain native forbs, such as *Cyanotis fasciculata*, *C. tuberosa*

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

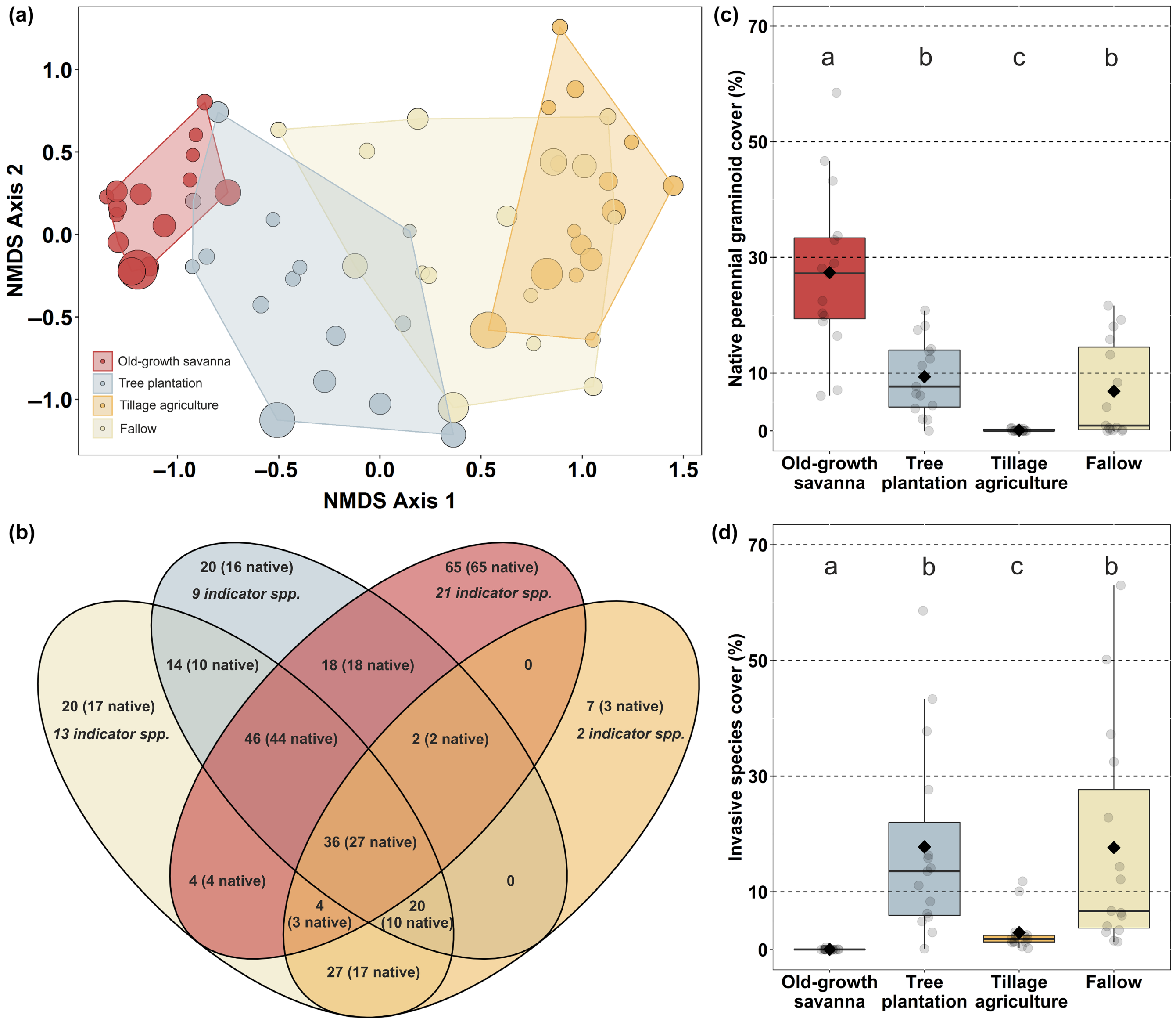

FIGURE 3 Savanna plant community composition in four land-use types ($n = 15$ sites per type) across a precipitation gradient in western Maharashtra, India. (A) Herbaceous plant composition visualized using NMDS ($k = 3$ dimensions, stress $= 0.141$); circles represent sites and are scaled in proportion to MAP; shaded polygons are convex hulls encompassing all sites for each land use. Composition of all land use types are statistically distinct (PERMANOVA, $p < 0.05$). (B) Venn diagram of shared and unique species in the four land-use types. Total number of species (native + invasive) are followed by number of native species in parentheses; numbers of indicator species are in italics. (C) Native perennial graminoid cover and (D) invasive plant cover; upper and lower limits of the boxes indicate 1st and 3rd quartiles respectively; the horizontal line represents the median; whiskers extend up to 1.5 times the inter-quartile range; diamonds indicate means; letters differ at $p < 0.05$ (Kruskal–Wallis followed by pair-wise Wilcox test).

(Commelinaceae), and *Vigna indica* (Fabaceae; Figure 3B; Table S5). Tree plantations contained nine indicator species, which included invasives, such as *Hyptis suaveolens* (Lamiaceae), *Bidens pilosa* (Asteraceae), and *Achyranthes aspera* (Amaranthaceae), some native forbs including *Sida* sp. (Malvaceae), *Lepidagathis cristata* (Acanthaceae), and the native grasses (Poaceae) *Tetrapogon tenellus* and *Tripogon jacquemontii*. Fallows contained 13 indicator species, including native grasses (Poaceae) in the genus *Eragrostis* as well as *Cynodon dactylon*, the invasives *Parthenium hysterophorus* (Asteraceae) and *Corchorus olitorius* (Malvaceae), and forbs including *Merremia emarginata* (Convolvulaceae) and *Oldenlandia aspera* (Rubiaceae). The only two indicator species of tillage agriculture were the invasive ruderal forbs *Convolvulus arvensis* (Convolvulaceae) and *Solanum nigrum* (Solanaceae; Figure 3B; Table S5).

3.3 | Contributions of woody plant, bioclimatic and soil variables

For tree basal area, woody regeneration and shrub cover, the ANCOVA models strongly violated the equal variance assumption (see Section 2), which limited our ability to assess land use and

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

MAP interactions. Basal area for both large and small trees was greatest in the tree plantations, followed by old-growth savannas, and negligible in the other two land uses (Figure S5). Further analysis revealed that tree basal area in plantations was negatively correlated with compositional similarity to old-growth savannas ($R^2=0.26$, $p=0.031$; Figure S11c). Shrub cover and woody regeneration were greater in tree plantations compared to all other land use types (Figure S5).

Neither bioclimatic nor soil variables provided additional insight into overall patterns of native plant diversity, except in tree plantations, where MAT and soil texture were related to species richness. For bioclimatic variables, the first principal component (PC1) explained 48% of variation and represented the climatic gradient from dry-warm sites to wet-cool sites (Figure S7). PC1 was highly correlated with MAP ($R^2=0.67$, $p<0.0001$; Figure S8) and MAT ($R^2=0.29$, $p<0.0001$). In the ANCOVA, both the bioclimatic PC1 and MAT were only predictive of native species richness in tree plantations—where cooler, wetter tree plantations tended to have lower native plant diversity compared to warmer, drier sites (Figures S9 and S10). MAT was also negatively correlated with tree basal area in plantations ($R^2=0.31$, $p=0.0178$; Figure S11a). For soil variables, PC1 explained 22% of variation corresponding to a gradient of soil texture (from silty to sandy soils; Figure S12). In the ANCOVA, the soil PC1 was only a significant predictor of native plant diversity in tree plantations (Figure S13). In the PERMANOVA, the PC1 of bioclimatic variables ($R^2=0.019$, $p=0.077$), PC1 of soil variables ($R^2=0.013$, $p=0.47$) and their interaction ($R^2=0.01$, $p=0.74$) explained negligible additional variation in plant community composition than that explained by the interaction of land use and MAP.

4 | DISCUSSION

In this study, conducted across a 1500-mm precipitation gradient in tropical India, we found that conversion of old-growth savannas to tillage agriculture destroys distinctive herbaceous plant communities that do not spontaneously recover on fallowed land (Figures 2 and 3). Similarly, afforestation alters savanna plant community composition and reduces native plant diversity but with effects that are less dramatic than conversion to tillage agriculture (Figures 2 and 3). Among key evidence of the conservation values of Maharashtra's old-growth savannas, we found that they had high native perennial graminoid cover, were characterized by 21 indicator species and supported 65 species that were absent in alternative land-use types (i. e., tillage agriculture, tree plantations and fallows; Figure 3). These findings confirm that old-growth savannas in India face similar consequences of land-use change as tropical and sub-tropical savannas in South America (Ferraro et al., 2021; Haddad et al., 2021; Koch et al., 2016), Australia (Fensham et al., 2016) and Africa (Zaloumis & Bond, 2016). In doing so, this study offers evidence for why conservation efforts in India, as well as other parts of Asia, where savannas have been historically overlooked and undervalued, should seek to limit agricultural conversion and afforestation of old-growth savannas (Joshi et al., 2018; Lapuz et al., 2021; Ratnam et al., 2016).

Given that our sites spanned such a wide range in MAP, we were surprised to find no effect of precipitation on the local-scale richness or herbaceous cover of Maharashtra's old-growth savannas (Figures 2A and 3A). Thus, our results are inconsistent with studies finding a positive relationship between diversity and MAP for grasslands globally (Adler & Levine, 2007; Cleland et al., 2013; Smith et al., 2022). These results suggest that tropical savanna plant diversity cannot be assumed to decline along humid to semi-arid gradients and point to the ecological importance of fires and grazers in savanna plant community assembly (Table S1). We suspect that in Maharashtra, at the drier end of the precipitation gradient, frequent grazing and infrequent burning elevates savanna plant diversity by reducing the dominance of palatable grasses (Anderson et al., 2007; Archibald et al., 2019; Hempson et al., 2015; Table S1). Conversely, we suspect that at the wetter end of the gradient, frequent burning and infrequent grazing reduces savanna plant diversity by promoting unpalatable perennial fire-adapted grasses that competitively exclude forbs (Archibald et al., 2019; Grman et al., 2021; Sankaran, 2009). While the lack of MAP effect on old-growth savanna richness and cover was surprising, the dramatic effect of tillage agriculture was as expected.

Our findings of reduced native plant diversity due to conversion for tillage agriculture (Figure 2B,D) underscores the existential threat to tropical savanna biodiversity posed by land-use conversion that involves severe soil disturbance (Nerlekar & Veldman, 2020; Figure 2B,D). Tillage impacts native savanna plant communities by destroying belowground bud banks of savanna forbs and grasses (e.g., Koch et al., 2016), disrupting fire and grazing regimes, and limiting recruitment of savanna specialists by, for example, periodic weeding and tilling. The application of fertilizers in tillage agriculture favours crop species, weedy ruderal species and invasive species over old-growth savannas specialists (O'Connor, 2005; Tilman, 1987). Indeed, based on our soil analyses, it appears that fertilizers and other soil amendments applied by farmers explains the association between higher available phosphorus and higher pH in tillage agriculture compared with old-growth savannas (Figure S12; Table S6).

Unfortunately, we found few of the savanna species that are eliminated by agricultural conversion to reestablish on fallowed land (Figures 2 and 3). The low native plant diversity and high cover of invasives (Figure 2) in fallows of Maharashtra are similar to patterns from young secondary grasslands globally (Nerlekar & Veldman, 2020), as well as the sub-tropical *Terai* grasslands of north India (Shukla, 2009). Despite hopes that agricultural abandonment can offer opportunities for restoration, fallows can only provide significant benefits for savanna biodiversity if they remain untilled for a long period of time (Crawford et al., 2022). Globally, fallows are re-cultivated on average every 14 years (Crawford et al., 2022) and in India the area under fallows declined from 8.1% in 1995 to 6.8% in 2005 (Roy et al., 2015). In sum, we interpret our results to suggest that fallows are unlikely to play a role in conserving India's savanna

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

flora, much like the limited role of fallows in supporting grassland birds (Kher & Dutta, 2021).

In addition to the consequences of agricultural conversion, our results demonstrated that tree planting erodes old-growth savanna communities by reducing native species richness and cover, while promoting invasive species (Figures 2 and 3). Tree plantations in Maharashtra supported on average four fewer native species/m^2, with species losses that included the threatened endemic plants *Drimia razii* (Asparagaceae) and *Jatropha nana* (Euphorbiaceae; Table S5; Figure 2B). While overall, tree plantations diminished native plant diversity and altered composition in our sites, there was large variation in the magnitude of these negative effects, with richness and composition of some tree plantations being very similar to old-growth savannas, but quite dissimilar in others (Figures 2A and 3A). Supplementary analyses suggest that this large variation is partly explained by tree basal area and MAT (Figures S9–S11). We found that in plantations tree basal area declines with temperature and that both basal area and MAT are negatively correlated with native herbaceous species richness (Figures S9–S11a,b). Likewise, the compositional similarity of herbaceous communities in plantations to old-growth savannas was negatively correlated with tree basal area (Figure S11c), suggesting that tree density helps explain why some plantations at the warmer-drier end of the gradient clustered closer to old-growth savannas than others in the NMDS (Figure 3A; Figure S6). This explanation would be consistent with other studies showing that savanna plant diversity declines as a function of tree density (e.g., Harrington et al., 2003).

5 | CONCLUSION

This study of herbaceous plant communities in western Maharashtra, India, demonstrates that agricultural conversion and afforestation destroy and degrade undervalued old-growth savannas. Specifically, we show that across a broad precipitation gradient tillage agriculture eliminates savanna plant species, including keystone perennial grasses, which do not rapidly recolonize fallows. We therefore suggest that agricultural fallows are unlikely to play a role in passive savanna restoration in tropical India and that in the absence of active restoration, tillage agriculture results in a permanent loss of savanna plant diversity. We also found that tree planting in old-growth savannas reduces native herbaceous species richness and promotes the spread of invasive species, albeit to a lesser degree than agricultural conversion. We are concerned that as a signatory to the Bonn challenge, India's commitment to restore millions of hectares wrongly targets old-growth savannas for afforestation. We hope that conservation scientists and environmental policymakers will use our results as evidence of the negative consequence of tree planting in old-growth savannas and implement safeguards against afforestation. Finally, amid the emphasis on climate change in ecology and conservation (Caro et al., 2022), our results from savannas of India remind us not to lose sight of the immediate threat of land-use change to tropical biodiversity.

AUTHOR CONTRIBUTIONS

Ashish N. Nerlekar conceived the study idea; Ashish N. Nerlekar, Avishkar Munje, Ankila J. Hiremath, Joseph W. Veldman designed the study methods; Ashish N. Nerlekar, Avishkar Munje, Pranav Mhaisalkar collected the data; Ashish N. Nerlekar analysed the data with input from Joseph W. Veldman and Ankila J. Hiremath; Ashish N. Nerlekar led the manuscript writing, with guidance from Joseph W. Veldman and input from Avishkar Munje and Ankila J. Hiremath; all authors contributed to manuscript drafts and approved of the final submission.

ACKNOWLEDGEMENTS

ANN thanks the botanical experts who helped identify old-growth savanna sites and species: Sharad Kambale, Milind Sardesai, Jagdish Dalavi, Mayur Bhagwat, Alok Chorghe and Arun Chandore. We are grateful to all the landowners who allowed us to sample their farms, and particularly the families of Noopur Borawake and Sameer Ranruii. Vishal Sonawane provided invaluable logistical support during field sampling. AM thanks Swapnil Thatte and Sandeep Bapat for information on native grazers at old-growth savannas around Pune. ANN was supported by the Texas A&M OGAPS Dissertation Fellowship, Texas A&M Tom Slick Graduate Fellowship, and a High-Impact Research Grant from the Texas A&M Department of Ecology and Conservation Biology. JWV is supported by USDA-NIFA Sustainable Agricultural Systems Grant 2019-68012-29819, USDA-NIFA McIntire-Stennis Project 1016880, and the National Science Foundation under award DEB-1931232. We dedicate this study to Maharashtra's pastoralists, whose traditional burning and livestock practices help maintain the biodiversity of old-growth savannas.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14221.

DATA AVAILABILITY STATEMENT

Data underlying the analyses are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.cjsxksncn (Nerlekar et al., 2023).

ORCID

Ashish N. Nerlekar https://orcid.org/0000-0002-3737-882X
Avishkar Munje https://orcid.org/0009-0005-2377-8928
Pranav Mhaisalkar https://orcid.org/0000-0003-1077-1856
Ankila J. Hiremath https://orcid.org/0000-0002-9708-2959
Joseph W. Veldman https://orcid.org/0000-0001-6231-8223

REFERENCES

Adler, P. B., & Levine, J. M. (2007). Contrasting relationships between precipitation and species richness in space and time. *Oikos*, *116*(2), 221–232.

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Almeida, S., Louzada, J., Sperber, C., & Barlow, J. (2011). Subtle land-use change and tropical biodiversity: Dung beetle communities in Cerrado grasslands and exotic pastures. *Biotropica*, *43*(6), 704–710.

Anderson, T. M., Ritchie, M. E., & McNaughton, S. J. (2007). Rainfall and soils modify plant community response to grazing in Serengeti National Park. *Ecology*, *88*(5), 1191–1201.

Archibald, S., Hempson, G. P., & Lehmann, C. (2019). A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytologist*, *224*(4), 1490–1503.

Bremer, L. L., & Farley, K. A. (2010). Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation*, *19*(14), 3893–3915.

Buisson, E., Le Stradic, S., Silveira, F. A., Durigan, G., Overbeck, G. E., Fidelis, A., Fernandes, G. W., Bond, W. J., Hermann, J., Mahy, G., Alvarado, S. T., Zaloumis, N. P., & Veldman, J. W. (2019). Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews*, *94*(2), 590–609.

Burns, W., & Kulkarni, L. B. (1927). A line survey of grassland with reference mainly to rainfall. *The Journal of the Indian Botanical Society*, *6*(3&4), 103–108.

Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, *90*(12), 3566–3574.

Canfield, R. H. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry*, *39*(4), 388–394.

Caro, T., Rowe, Z., Berger, J., Wholey, P., & Dobson, A. (2022). An inconvenient misconception: Climate change is not the principal driver of biodiversity loss. *Conservation Letters*, *15*, e12868.

Cava, M. G., Pilon, N. A., Ribeiro, M. C., & Durigan, G. (2018). Abandoned pastures cannot spontaneously recover the attributes of old-growth savannas. *Journal of Applied Ecology*, *55*(3), 1164–1172.

Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., Gross, K. L., Gherardi, L. A., Hallett, L. M., Hobbs, R. J., Hsu, J. S., Turnbull, L., & Suding, K. N. (2013). Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology*, *94*(8), 1687–1696.

Crawford, C. L., Yin, H., Radeloff, V. C., & Wilcove, D. S. (2022). Rural land abandonment is too ephemeral to provide major benefits for biodiversity and climate. *Science Advances*, *8*(21), eabm8999.

Dabadghao, P. M., & Shankarnarayan, K. A. (1973). *The grass cover of India*. Indian Council of Agriculture Research.

Datar, M. N. (2016). Floristic diversity and effect of anthropogenic activities on human-dominated grasslands in subtropical regions of peninsular India. *Tropical Grasslands-Forrajes Tropicales*, *4*(1), 8–18.

Dingaan, M. N., Tsubo, M., Walker, S., & Newby, T. (2017). Soil chemical properties and plant species diversity along a rainfall gradient in semi-arid grassland of South Africa. *Plant Ecology and Evolution*, *150*(1), 35–44.

Durigan, G., Pilon, N. A., Souza, F. M., Melo, A. C., Re, D. S., & Souza, S. C. (2022). Low-intensity cattle grazing is better than cattle exclusion to drive secondary savannas toward the features of native Cerrado vegetation. *Biotropica*, *54*(3), 789–800.

Fensham, R. J., Butler, D. W., Fairfax, R. J., Quintin, A. R., & Dwyer, J. M. (2016). Passive restoration of subtropical grassland after abandonment of cultivation. *Journal of Applied Ecology*, *53*(1), 274–283.

Ferraro, A., Fidelis, A., Silva, G. S. D., Martins, A. R., Piedade, S. M. D. S., & Appezzato-da-Glória, B. (2021). Long-term Pinus plantations reduce the bud bank in Cerrado areas. *Applied Vegetation Science*, *24*(1), e12537.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315.

Foster, R. B., Hernandez, N. C., Kakudidi, E. K., & Burnham, R. J. (1998). *Rapid assessment of tropical plant communities using variable transects: An informal and practical guide*. Field Museum of Chicago.

Govender, N., Trollope, W. S., & Van Wilgen, B. W. (2006). The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology*, *43*(4), 748–758.

Grman, E., Zirbel, C. R., Bauer, J. T., Groves, A. M., Bassett, T., & Brudvig, L. A. (2021). Super-abundant C4 grasses are a mixed blessing in restored prairies. *Restoration Ecology*, *29*, e13281.

Haddad, T. M., Pilon, N. A. L., Durigan, G., & Viani, R. A. G. (2021). Restoration of the Brazilian savanna after pine silviculture: Pine clearcutting is effective but not enough. *Forest Ecology and Management*, *491*, 119158.

Harrington, T. B., Dagley, C. M., & Edwards, M. B. (2003). Above-and belowground competition from longleaf pine plantations limits performance of reintroduced herbaceous species. *Forest Science*, *49*(5), 681–695.

Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., Moxley, C., Owen-Smith, N., Peel, M. J. S., Smith, I. P. J., & Vickers, K. J. (2015). Ecology of grazing lawns in Africa. *Biological Reviews*, *90*(3), 979–994.

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*(7), 759–768.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*(3), 346–363.

Hutley, L. B., Beringer, J., Isaac, P. R., Hacker, J. M., & Cernusak, L. A. (2011). A sub-continental scale living laboratory: Spatial patterns of savanna vegetation over a rainfall gradient in northern Australia. *Agricultural and Forest Meteorology*, *151*(11), 1417–1428.

Joshi, A. A., Sankaran, M., & Ratnam, J. (2018). 'Foresting' the grassland: Historical management legacies in forest-grassland mosaics in southern India, and lessons for the conservation of tropical grassy biomes. *Biological Conservation*, *224*, 144–152.

Jukar, A. M., Lyons, S. K., Wagner, P. J., & Uhen, M. D. (2021). Late quaternary extinctions in the Indian subcontinent. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *562*, 110137.

Kher, V., & Dutta, S. (2021). Rangelands and crop fallows can supplement but not replace protected grasslands in sustaining Thar Desert's avifauna during the dry season. *Journal of Arid Environments*, *195*, 104623.

Kirkman, L. K., Coffey, K. L., Mitchell, R. J., & Moser, E. B. (2004). Ground cover recovery patterns and life-history traits: Implications for restoration obstacles and opportunities in a species-rich savanna. *Journal of Ecology*, *92*(3), 409–421.

Koch, C., Conradi, T., Gossner, M. M., Hermann, J. M., Leidinger, J., Meyer, S. T., Overbeck, G. E., Weisser, W. W., & Kollmann, J. (2016). Management intensity and temporary conversion to other land-use types affect plant diversity and species composition of subtropical grasslands in southern Brazil. *Applied Vegetation Science*, *19*(4), 589–599.

Lapuz, R. S., Jaojoco, A. K. M., Reyes, S. R. C., De Alban, J. D. T., & Tomlinson, K. W. (2021). Greater loss and fragmentation of savannas than forests over the last three decades in Yunnan Province, China. *Environmental Research Letters*, *17*(1), 014003.

Laste, D. K. C., Durigan, G., & Andersen, A. N. (2019). Biodiversity responses to land-use and restoration in a global biodiversity hotspot: Ant communities in Brazilian Cerrado. *Austral Ecology*, *44*(2), 313–326.

Lehmann, C. E., Archibald, S. A., Hoffmann, W. A., & Bond, W. J. (2011). Deciphering the distribution of the savanna biome. *New Phytologist*, *191*(1), 197–209.

Ma, W., He, J. S., Yang, Y., Wang, X., Liang, C., Anwar, M., Zeng, H., Fang, J., & Schmid, B. (2010). Environmental factors covary with plant diversity–productivity relationships among Chinese grassland sites. *Global Ecology and Biogeography*, *19*(2), 233–243.

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Madhusudan, M. D., & Vanak, A. (2021). Mapping the distribution and extent of India's semi-arid open natural ecosystems. *ESS Open Archive*, 24 July 2021.

Malhotra, K., & Gadgil, M. (1981). The ecological basis of the geographical distribution of the Dhangars: A pastoral caste-cluster of Maharashtra. *South Asian Anthropologist*, *2*(2), 49–59.

Martinez Arbizu, P. (2017). *PairwiseAdonis: Pairwise multilevel comparison using Adonis*. R package version 0.4.1.

Murphy, B. P., & Bowman, D. M. (2012). What controls the distribution of tropical forest and savanna? *Ecology Letters*, *15*(7), 748–758.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858.

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

Nerlekar, A. N., & Veldman, J. W. (2020). High plant diversity and slow assembly of old-growth grasslands. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(31), 18550–18556.

Nerlekar, A. N., Munje, A., Mhaisalkar, P., Hiremath, A. J., & Veldman, J. W. (2023). Data from: Tillage agriculture and afforestation threaten tropical savanna plant communities across a broad rainfall gradient in India [data set]. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.cjsxksncn

Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., De Palma, A., Ferrier, S., Hill, S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C. W. T., Emerson, S., Di Gao, G. P.-H., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B. I., Whitmee, S., … Purvis, A. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*, *353*(6296), 288–291.

O'Connor, T. G. (2005). Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the southern Drakensberg, South Africa. *Journal of Applied Ecology*, *42*(5), 975–988.

Oke, J. G. (1972). Studies in grassland ecology of the Maharashtra state I. Ecological classification of grassland patterns found in different ecological habitats and their botanical characterization. *Indian Forester*, *98*(2), 86–108.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *Vegan: Community ecology package*. R package version 2.5-7.

Parr, C. L., Lehmann, C. E., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*, *29*(4), 205–213.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2021). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-153.

Pyne, S. J. (1994). Nataraja: India's cycle of fire. *Environmental History Review*, *18*(3), 1–20.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

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

Rausch, L. L., Gibbs, H. K., Schelly, I., Brandão, A., Jr., Morton, D. C., Filho, A. C., Strassburg, B., Walker, N., Noojipady, P., Barreto, P., & Meyer, D. (2019). Soy expansion in Brazil's Cerrado. *Conservation Letters*, *12*(6), e12671.

Riedel, N., Fuller, D. Q., Marwan, N., Poretschkin, C., Basavaiah, N., Menzel, P., Ratnam, J., Prasad, S., Sachse, D., Sankaran, M., Sarkar, S., & Stebich, M. (2021). Monsoon forced evolution of savanna and the spread of agro-pastoralism in peninsular India. *Scientific Reports*, *11*(1), 1–13.

Roy, P. S., Roy, A., Joshi, P. K., Kale, M. P., Srivastava, V. K., Srivastava, S. K., Dwevidi, R. S., Joshi, C., Behera, M. D., Meiyappan, P., Sharma, Y., Jain, A. K., Singh, J. S., Palchowdhuri, Y., Ramachandran, R. M., Pinjarla, B., Chakravarthi, V., Babu, N., Gowsalya, M. S., … Kushwaha, D. (2015). Development of decadal (1985–1995–2005) land use and land cover database for India. *Remote Sensing*, *7*(3), 2401–2430.

Sankaran, M. (2009). Diversity patterns in savanna grassland communities: Implications for conservation strategies in a biodiversity hotspot. *Biodiversity and Conservation*, *18*(4), 1099–1115.

Searchinger, T. D., Estes, L., Thornton, P. K., Beringer, T., Notenbaert, A., Rubenstein, D., Heimlich, R., Licker, R., & Herrero, M. (2015). High carbon and biodiversity costs from converting Africa's wet savannahs to cropland. *Nature Climate Change*, *5*(5), 481–486.

Shukla, R. P. (2009). Patterns of plant species diversity across Terai landscape in north-eastern Uttar Pradesh, India. *Tropical Ecology*, *50*(1), 111.

Smith, M. D., Koerner, S. E., Avolio, M. L., Komatsu, K. J., Eby, S., Forrestel, E. J., Collins, S. L., Wilcox, K. R., Ahumada, R., Morgan, J. W., Oliva, G., Oñatibia, G. R., Overbeck, G. E., Peter, G., Quiroga, E., Sankaran, M., Wu, J., Yahdjian, L., & Yu, Q. (2022). Richness, not evenness, varies across water availability gradients in grassy biomes on five continents. *Oecologia*, *199*(3), 649–659.

Strassburg, B. B., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A. E., Filho, F. J. B. O., Scaramuzza, C. A. D. M., Scarano, F. R., Soares-Filho, B., & Balmford, A. (2017). Moment of truth for the Cerrado hotspot. *Nature Ecology & Evolution*, *1*(4), 1–3.

Thekaekara, T., Vanak, A. T., Hiremath, A. J., Rai, N. D., Ratnam, J., & Raman, S. (2017). Notes from the other side of a forest fire. *Economic & Political Weekly*, *52*(25–26), 22–25.

Tilman, D. (1987). Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, *57*(3), 189–214.

Veblen, K. E., Porensky, L. M., Riginos, C., & Young, T. P. (2016). Are cattle surrogate wildlife? Savanna plant community composition explained by total herbivory more than herbivore type. *Ecological Applications*, *26*(6), 1610–1623.

Veldman, J. W. (2016). Clarifying the confusion: Old-growth savannahs and tropical ecosystem degradation. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *371*(1703), 20150306.

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., de Sá Dechoum, M., Diaz-Toribio, M. H., Durigan, G., Ewel, J. J., Fernandes, G. W., Fidelis, A., Fleischman, F., Good, S. P., Griffith, D. M., … Zaloumis, N. P. (2019). Comment on 'the global tree restoration potential'. *Science*, *366*(6463), eaay7976.

Veldman, J. W., Buisson, E., Durigan, G., Fernandes, G. W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G. E., Veldman, R. G., Zaloumis, N. P., Putz, F. E., & Bond, W. J. (2015). Toward an old-growth concept for grasslands, savannas, and woodlands. *Frontiers in Ecology and the Environment*, *13*(3), 154–162.

Vetter, S. (2020). With power comes responsibility—A rangelands perspective on forest landscape restoration. *Frontiers in Sustainable Food Systems*, *4*, 549483.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Zaloumis, N. P., & Bond, W. J. (2016). Reforestation or conservation? The attributes of old growth grasslands in South Africa. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *371*(1703), 20150310.

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

SUPPORTING INFORMATION

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

Table S1: Descriptions for $n = 15$ old-growth savanna sites.

Table S2: Descriptions for $n = 15$ tree plantation sites.

Table S3: Descriptions for $n = 15$ tillage agriculture sites.

Table S4: Descriptions for $n = 15$ fallow sites.

Table S5: Herbaceous plants sampled in four land-use types across a precipitation gradient in western Maharashtra, India.

Table S6: ANCOVA results for 10 soil variables modelled individually with land use, MAP and their interaction.

Figure S1: Old-growth savannas sampled across the 1500 mm MAP gradient (459 mm – 1954 mm MAP) in western Maharashtra, India.

Figure S2: Relationship between mean annual precipitation (MAP) and mean annual temperature (MAT).

Figure S3: Total species richness and cover of all herbaceous plants (invasive and native combined) in four land-use types ($n = 15$ sites per type) across a precipitation gradient in western Maharashtra, India.

Figure S4: Total herbaceous plant cover (invasive + native species) in each land-use type classified into functional types; (a) perennial graminoids (b), annual graminoids (c), perennial forbs (d) annual forbs.

Figure S5: Attributes of woody plant density across land use types; (a) basal area for large trees, with a diameter at breast height (DBH) ≥10 cm (b) basal area for small trees—i.e., trees with DBH from 1 cm to 10 cm (c) shrub cover percentage (d) woody regeneration—i.e., stems <1.3 m tall and/or <1 cm DBH.

Figure S6: Savanna plant community composition in four land-use types ($n = 15$ sites per type) across a nonlinear representation of the precipitation gradient in western Maharashtra, India.

Figure S7: Principal Component Analysis to identify the most important bioclimatic variables.

Figure S8: Relationship between mean annual precipitation (MAP) and the first Principal Component (PC1) of the bioclimatic variables.

Figure S9: Relationship between herbaceous native plant richness and the first two Principal Components of the bioclimatic factors PCA.

Figure S10: Relationships between herbaceous native plant richness, herbaceous cover, and mean annual temperature.

Figure S11: Relationships between mean annual temperature and basal area of large trees in tree plantations (a); native herbaceous species richness and basal area of large trees in tree plantations (b); compositional similarity of herbaceous plants to old-growth savannas and basal area of large trees in tree plantations (c).

Figure S12: Principal Component Analysis of soil chemical and physical variables.

Figure S13: Relationship between herbaceous plant richness and soil variables, as summarized by the first (a) and the second (b) principal components of the soil variables.

How to cite this article: Nerlekar, A. N., Munje, A., Mhaisalkar, P., Hiremath, A. J., & Veldman, J. W. (2024). Tillage agriculture and afforestation threaten tropical savanna plant communities across a broad rainfall gradient in India. *Journal of Ecology*, *112*, 98–109. https://doi.org/10.1111/1365-2745.14221

13652745, 2024, 1, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14221 by Texas A&M University Libraries, Wiley Online Library on [28/01/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License