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RESEARCH ARTICLE

Stability in tapia woodlands amid non-native expansion: Integrating traditional ecological knowledge and remote sensing to track 73 years of tree cover in Madagascar

Elliot D. Convery-Fisher[1,2] | **Adam J. M. Devenish**[3] | **Sam Staddon**[1] | **Christian A. Kull**[4] | **F. Laura Rafanomezantsoa**[5] | **Tianjanahary Randriamboavonjy**[6] | **Caroline E. R. Lehmann**[1,2]

[1]School of GeoSciences, University of Edinburgh, Edinburgh, UK; [2]Taxonomy and Macroecology, Royal Botanic Garden Edinburgh, Edinburgh, UK; [3]Trait Diversity and Function, Royal Botanic Gardens, Kew, London, UK; [4]Institut de géographie et durabilité, Université de Lausanne, Lausanne, Switzerland; [5]Ecole Supérieure des Sciences Agronomiques, Université d'Antananarivo, Antananarivo, Madagascar and [6]Kew Madagascar Conservation Centre, Royal Botanic Gardens, Kew, Antananarivo, Madagascar

Correspondence
Elliot D. Convery-Fisher
Email: elliot.fisher2@gmail.com

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Abstract

1. Afromontane ecosystems, characterised by mosaics of fire-adapted grassy ecosystems and fire-sensitive forests, are biodiversity hotspots facing escalating pressures from non-native species, climate and land-use change. Madagascar's Central Highlands is one such hotspot, hosting woodlands dominated by endemic *Uapaca bojeri* (tapia) which are important to local livelihoods and biodiversity conservation. Despite their social–ecological importance, multi-decadal dynamics of tree cover remain poorly understood, particularly differential responses from native versus non-native tree species to socio-ecological drivers.
2. We investigated tree cover trajectories across the Central Highlands by integrating ground-based vegetation surveys (40 plots), historical remote sensing analysis (80 sites) spanning 73 years (1949–2022), and traditional ecological knowledge (TEK) documented through 32 focus groups with 114 members of community forest management associations. We examined whether native tapia woodlands declined as has been widely assumed, how non-native forestry species (*Pinus* spp. and *Eucalyptus* spp.) spread and the factors driving these dynamics.
3. Tapia woodlands showed multi-decadal (1949–2022) structural stability confirmed by both remote sensing (−0.52% change, $p = 0.0810$) and TEK shared during 81% of focus groups. TEK revealed compositional change within superficially stable tapia stands, with losses of companion species.
4. Non-native forestry species cover increased substantially (+17.4%, $p < 0.001$) over the same period, with expansion accelerating after 1991. Expansion was greatest near roads, with model predictions indicating +26% total increase at roadside

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sites compared to sites far from roads over 73 years (Year × Distance to Road: $\beta = -0.152$, $p = 0.002$).

5. *Synthesis*. Tapia woodlands demonstrate structural resilience, challenging widespread narratives of human-driven deforestation in the Central Highlands of Madagascar, although compositional losses of companion species reveal that not all biodiversity within stable canopies is equally conserved. Meanwhile, rapid non-native encroachment poses increasing threats to ecosystem services that rural communities depend on. Integrating TEK with remote sensing facilitated detection of compositional losses and offers a transferable framework for monitoring heterogeneous landscapes that have been challenging to monitor using conventional methods.

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KEYWORDS
Afromontane, conservation, environmental monitoring, invasive species, Madagascar, tapia woodlands, traditional ecological knowledge

1 | INTRODUCTION

Afromontane regions are biodiversity hotspots characterised by ecosystem mosaics of fire-prone grassy ecosystems and fire-sensitive forests that have persisted for millennia (Castilla-Beltrán et al., 2023; Meadows & Linder, 1993). Typically situated at elevations between 1300 and 4100 m, but can be as low as 400 m (Gehrke & Linder, 2014), across Sub-Saharan Africa (Carbutt & Edwards, 2015; White, 1978), these mosaics support critical ecological functions and livelihoods (Clark et al., 2021). Their diverse yet understudied flora and fauna are frequently range-restricted, endangered and endemic (Gehrke & Linder, 2014). However, mounting pressures from climate change, land-use change, non-native species and altered fire regimes threaten both biodiversity and nature-dependent communities (Archibald, 2016; Chapman et al., 2004; Engelbrecht et al., 2015; Moritz et al., 2012). As pressures on land intensify, there is a pressing need to monitor ecosystem change and inform contextually appropriate management supporting both biodiversity and local livelihoods (Silander et al., 2024).

Tree cover dynamics in Afromontane ecosystems reflect interactions among climate, topography, fire and human activities. Climate, topography and fire maintain woodlands by limiting woody vegetation growth and supporting fire-adapted species (Meadows & Linder, 1993; Scholes & Archer, 1997). Humans have long influenced Afromontane ecosystems both reducing tree cover through fire use and selective wood harvesting (Laris, 2002; Mitchard & Flintrop, 2013) and increasing tree cover through fire suppression and tree planting (Archer et al., 2017). Today, human activities operate on unprecedented scales, accelerating rates of ecosystem change across Sub-Saharan Africa (Castilla-Beltrán et al., 2023; Powell et al., 2023). However, specific trends in ecosystem change in Afromontane mosaics remain poorly documented, making it difficult to assess their resilience (Powell et al., 2023).

Of particular concern is the apparent spread of non-native forestry species such as *Acacia* spp., *Eucalyptus* spp. and *Pinus* spp., which can rapidly transform ecosystems by disrupting ecosystem function and displacing native flora (Carbutt, 2012; Martin et al., 2025). Introduced by colonial foresters to develop plantations and woodlots in the 19th century, these species remain widely promoted in contemporary reforestation and aid projects, often with little regard for local biodiversity (Moura et al., 2019; Veldman et al., 2015). Climate change compounds these biotic pressures through shifting precipitation patterns and rising temperatures affecting ecosystem dynamics such as tree growth and fire regimes (Stevens et al., 2022). Therefore, comprehensive monitoring of non-native spread is urgently needed to provide a scientific basis for targeted management interventions.

Madagascar's Central Highlands exemplify challenges facing Afromontane ecosystems. Endemic *Uapaca bojeri* (tapia) woodlands support rural livelihoods through edible fruits, wild silk from endemic moths (*Borocera madagascariensis*) and timber (Gade, 1985; Kull & Birkinshaw, 2022). The variable structure, ranging from mixed-tree canopies of *Sarcolaena oblongifolia* and *Pentachlaena latifolia* to monodominant *U. bojeri* stands above diverse grassy understoreys, reflects their co-evolution with traditional fire management practices over the last 1000 years (Kull, 2002; Solofondranohatra et al., 2018). However, since the 1920s colonial and post-colonial forestry institutions have characterised tapia woodlands as degraded forest remnants because of an assumption that closed forests are the natural climax community (Klein, 2002), leading to reforestation with non-native forestry species like *Pinus* spp. and *Eucalyptus* spp. Perceptions of recent widespread loss of tapia woodlands contributed to an IUCN red list of ecosystems 'endangered' classification (Keith et al., 2013), despite palaeoecological evidence suggesting that woodland-grassland mosaics have persisted for millennia in the region (Burney, 1987;

Razafimanantsoa et al., 2024). Therefore, understanding tree cover change over the last century can inform ecosystem management and challenge discourses that have shaped both policy and perceptions of these landscapes.

Over recent decades, studies of tapia dynamics present conflicting results. Remote sensing over 1994–2014 shows overall tree cover increases in Madagascar's highlands (McConnell et al., 2015), while tapia-specific research shows spatially and temporally heterogeneous patterns: stability in some regions (Kull, 2002) and decline in others (de Haulleville et al., 2018; Rajoelison, 2009). However, these studies share methodological limitations with difficulty differentiating tree cover types (McConnell et al., 2015), insufficient sampling to draw quantitative conclusions (Kull, 2013) or restricted temporal extent (de Haulleville et al., 2018). Such challenges are exacerbated when detecting change in open-canopied vegetation using satellite data alone, as open canopy structures can be spectrally confused with grass and soil backgrounds, making them difficult to classify with automated methods (Mitchard & Flintrop, 2013).

Integrating traditional ecological knowledge (TEK) alongside scientific knowledge has emerged as a promising approach to monitor and interpret vegetation change (Brown et al., 2018). Defined as 'a cumulative body of knowledge and beliefs, handed down through generations about the relationship of living beings with one another and their environment' (Berkes & Folke, 2000), TEK can provide enhanced insights into landscape change through lived experiences shaped by repeated observations across generations (Joa et al., 2018). In the Ethiopia. Agreement across scientific and traditional knowledge systems enhanced understanding of threats to montane forests by highlighting insecure land tenure as a key driver (Steger et al., 2020). Engaging with TEK can amplify marginalised voices, introduce alternative explanations and encourage conservation approaches reflecting diverse perspectives (Molnár & Babai, 2021; Ruiz-Mallén & Corbera, 2013). Fairhead and Leach (1996) demonstrated in West Africa how management, informed by TEK, actively cultivated forest patches, increasing tree cover contrary to previous assumptions. Similarly in coastal southwest Madagascar, centuries of traditional land-use practices are positively correlated with ecosystem function (Davis et al., 2025). In South Africa, non-native tree cover is often valued by communities for its livelihood benefits, showing the importance of socio-cultural perspectives in ecological monitoring (Ngorima & Shackleton, 2019). However, Madagascar's Central Highlands lacks integrated assessments that combine TEK with quantitative scientific methods to provide a holistic view of tree cover change dynamics (Lehmann, Archibald, et al., 2022; Lehmann, Morton, et al., 2022).

Here we employ a multi-method approach triangulating evidence from complementary sources to examine multi-decadal tree cover change in Afromontane ecosystems. We combine historical remote imagery analysis (1949–2022) with TEK documented through focus groups to quantify and interpret changes in tree cover across the study area. Additionally, we use vegetation plots to assess current stand structure, species composition and recruitment patterns. We seek to overcome individual methodological limitations and provide a detailed, locally informed perspective on changes in two critical woody vegetation types: tapia woodlands and non-native forestry species. Our research addresses three key questions: (1) What are the historical (1949–2022) trends in tree cover for tapia woodlands and non-native forestry species in Madagascar's Central Highlands? (2) How have ecological and socio-economic factors influenced these changes, and how are these perceived by local communities? (3) What are the current recruitment patterns for tapia and non-native forestry species across the landscape?

2 | MATERIALS AND METHODS

2.1 | Study site

The Central Highlands of Madagascar feature a mosaic of grasslands, tapia woodlands, gallery forests, agricultural fields, urban areas and plantations of non-native forestry species such as *Pinus* spp. and *Eucalyptus* spp. (Moat & Smith, 2007) (Figure 1). Elevations range from 800 to 2600 m, with a subhumid climate (1200–1700 mm annual rainfall) and a dry season lasting 5–7 months (Nanjarisoa et al., 2018).

Tapia woodlands have a disjunct distribution covering approximately 1319 km^2 across the western ramparts (800–1600 m elevation) of the Central Highlands (Figure 1) (Moat & Smith, 2007). The five major zones are (1) Arivonimamo near Antananarivo, (2) Ambohimanjaka, including sub-site Ibity, between Antsirabe and Ambositra, (3) Ambatofinandrahana, including sub-site Anjoma, west of Ambositra, (4) Itremo west of Ambatofinandrahana and (5) Isalo National Park in the south (excluded from this study due to incomplete coverage of aerial photographs) (Figure 1) (Kull & Birkinshaw, 2022). Ibity is treated as a distinct sub-site given its quartzitic substrate and higher elevation range (1400–2200 m), which support tapia woodland distinct from the broader Ambohimanjaka zone. Similarly, Anjoma represents a geographically distinct eastern portion of the Ambatofinandrahana tapia woodland landscape and is analysed separately.

Community management areas (Arivonimamo, Ambohimanjaka and Ambatofinandrahana) operate under community forest management associations, *Vondron' Olona Ifotony* (VOIs). Community forest management agreements transferred natural resource management responsibilities to community forest associations in the late 1990s in a bid to reduce deforestation and benefit local communities (Jones et al., 2022). Prior to the Gestion Locale Sécurisée (GELOSE) law (Loi no. 96-025; Gouvernement de Madagascar, 1996), which established VOIs, tapia woodlands were technically state-owned 'open access' lands under the jurisdiction of the national Forest Service. In practice, they were managed through Dina (customary local laws) (Kull, 2004). Within Itremo is the Itremo Massif, designated an IUCN Category V Protected Landscape in 2015 and managed by Kew Madagascar Conservation Centre in partnership with local VOIs. Ibity was designated an IUCN Category V Protected Landscape in 2015, co-managed by Missouri Botanical Garden and local VOIs.

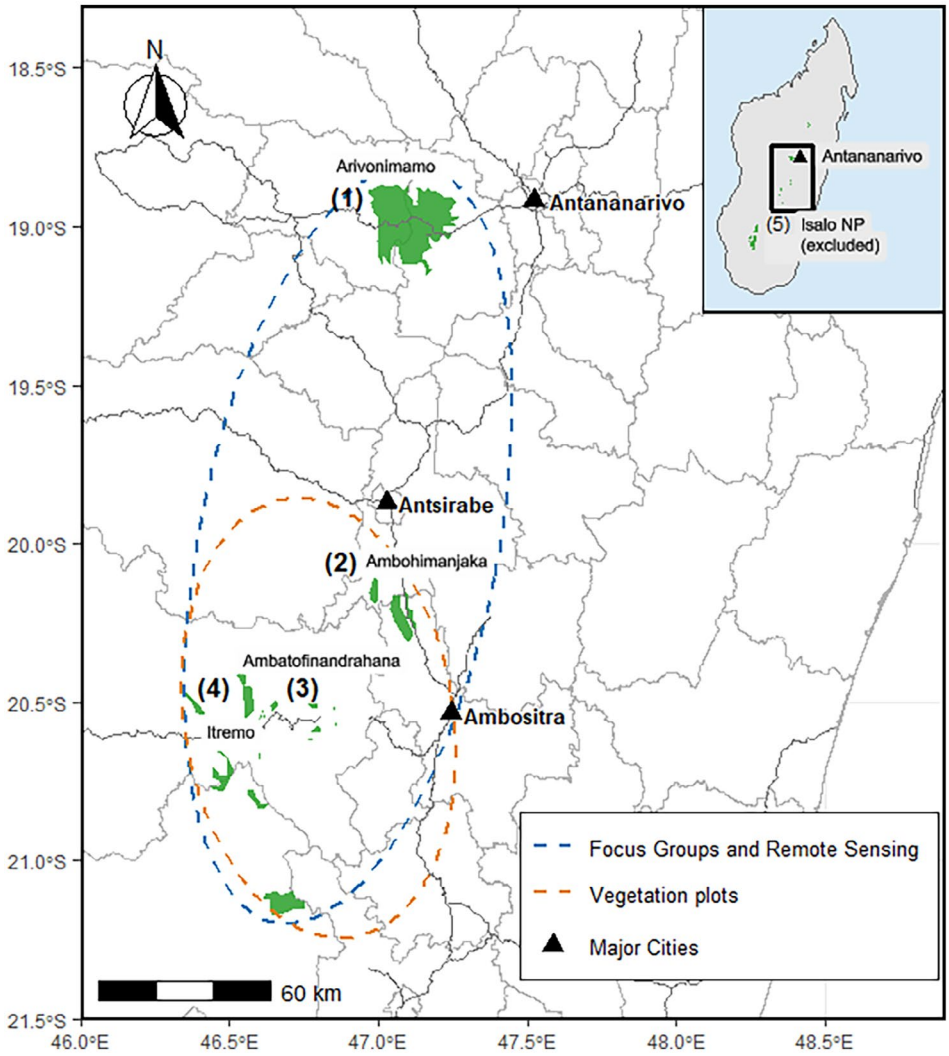


FIGURE 1 Distribution of tapia woodlands across Madagascar's Central Highlands showing locations of study sites and spatial resolution of the datasets. (A) Overview map showing tapia woodland distribution (green shaded areas), spatial coverage of remote sensing and focus groups (blue ellipse) and vegetation plots (orange ellipse). Four major zones are shown: (1) Arivonimamo, (2) Ambohimanjaka, (3) Ambatofinandrahana and (4) Itremo. Two sub-sites are distinguished within their parent zones: Ibity (within Ambohimanjaka) and Anjoma (within Ambatofinandrahana), a geographically distinct eastern portion of the tapia woodland landscape. A fifth zone, Isalo National Park, was excluded due to incomplete aerial photograph coverage. For detailed maps of each region showing spatial distribution of data collection sites see Appendix S1.

Prior to designation of both Protected Landscapes, they were managed through community and customary arrangements.

2.2 | Overall methodological approach

To assess changes in tapia woodlands and non-native species dynamics, we integrated: (1) field-based vegetation plots to validate remotely sensed estimates of tree cover, capture current stand structure and recruitment patterns; (2) multi-decadal remote sensing analysis to quantify historical tree cover changes; and (3) focus groups to document TEK regarding tree cover change and its drivers. To integrate datasets, we employed complementary triangulation (Nightingale, 2003).

2.3 | Data collection

Data collection followed a chronological sequence, with vegetation plots established first to inform site selection for remote sensing analysis; the analysis and results sections are organised thematically by research question.

2.3.1 | Stand structure and permanent vegetation plots

We established 40 permanent vegetation plots (each 50 m × 50 m; 0.25 ha) in tapia woodlands in 2021 (Figure 1). Plot locations were identified prior to the remote sensing analysis and selected along

a gradient of distance to the nearest road and positioned at least 1 km apart.

In each plot, all tree stems taller than 1 m were tagged with *x*-*y* coordinates, stem diameter at 0.3 m height and species recorded. In these ecosystems, 1 m height represents a bottleneck for establishment, as seedlings must pass through a fire-vulnerable height threshold before reaching fire-tolerant size (N'Dri et al., 2022). In each plot, seedling recruitment was assessed using 21 circular subplots (1 m diameter each), counting seedlings per circular subplot by species (Lehmann, Archibald, et al., 2022; Lehmann, Morton, et al., 2022). Seedlings were defined as juvenile plants less than 1 m in height. At each subplot, canopy cover was measured using a spherical densitometer.

2.3.2 | Remote sensing of tree cover change

To quantify long-term change in tree cover we analysed georeferenced historical remote images, that is aerial photography (1949–1950, 1991–1992) and high-resolution satellite (2022) images. We used images spanning three time intervals for 1949–1950, 1991–1992 and 2022 for 80 sites, evenly split between tapia woodland ($n = 40$) and non-native forestry species areas ($n = 40$) (Figure 1). Remote sensing sites ($n = 80$) were distributed across four regions: Arivonimamo ($n = 14$), Ambohimanjaka ($n = 28$), Ambatofinandrahana ($n = 20$), Itremo ($n = 18$). The 80 sites were selected to represent homogeneous stands to minimise classification errors and enable clear tracking of changes within each vegetation type over time. Sites were selected based upon complete temporal coverage across the three time periods (1949/50, 1991/92, 2022), preliminary field observations and visual interpretation of recent imagery. Each site was classified as 'tapia woodland' or 'non-native forestry' based on canopy dominance (>80% of canopy cover).

Aerial photographs from 1949/50 and 1991/2 were sourced from Madagascar's national cartographic agency in 2001 and 2021. Aerial photographs (1:40,000) were scanned at a 1200 dpi resolution providing approximately 5 m resolution. High spatial resolution historical remote images allowed differentiation of tapia canopy from non-native forestry species based on distinct canopy characteristics but not between non-native species. Images were geo-rectified using ground control points and topographic maps (Morgan et al., 2010). For 2022, we utilised high-resolution satellite imagery from the PlanetScope (Dove) constellation (PlanetLabs), consisting of four spectral bands (blue, green, red and near infrared) at approximately 3–5 m native spatial resolution. These images were corrected for radiometric and geometric errors, mosaiced and resampled to 4.77 m spatial resolution using nearest neighbour resampling in QGIS v3.24 to match the historical data. All images were processed, geo-rectified and analysed using QGIS v3.24 (QGIS Development Team, 2022), preserving discrete pixel values for classification.

Following Lehmann et al. (2008), a georeferenced 200 × 300 m grid with 651 sample points at 10 m intervals was constructed at each site. Tree cover was calculated as a percent of the ground area based on tree presence/absence at each sample point. While image quality varied between analogue aerial photographs (1949, 1991) and digital satellite imagery (2022), the distinct canopy structure of tapia woodlands versus non-native plantations remained clearly distinguishable across all image types at our 10 m sampling interval (Kull, 2013).

We validated our remote sensing approach using contemporary 2022 data to ensure temporal consistency. First, we compared remotely sensed canopy cover estimates from 2022 PlanetScope imagery with ground-based densitometer measurements at 12 of our 40 permanent vegetation plots where historical aerial photograph coverage overlapped. Second, we conducted visual field assessments at 35 additional sites (for a total of 47 validation sites across all regions) by recording GPS coordinates and comparing observed vegetation types with 2022 satellite imagery classifications both in-field and during post-processing.

Ground-based and remotely sensed canopy cover estimates were significantly correlated ($R = 0.761$, $p = 0.013$, $n = 12$) with $R^2 = 0.580$ (see Appendix S7), values within the range reported for historical aerial photograph analysis in open woodland systems (Mitchard & Flintrop, 2013), though the sample is limited by logistical constraints of matching historical photograph coverage with accessible field sites. Remote sensing overestimated cover by an average of +15.0% (RMSE = 17.1%, relative RMSE = 60.9%). These field assessments confirmed accurate classification of dominant tree cover type (tapia vs. non-native) in 33 of 35 sites (94.2% accuracy). This validation confirmed the reliability of our classification approach for the 2022 time point; earlier time points (1949, 1991) relied on identical classification protocols but could not be ground-validated due to temporal separation.

2.3.3 | Engagement with TEK

We conducted 32 focus groups with 114 participants from 16 VOIs over 4 months in 2021 (July–August) and 2022 (April–May; Table 1; Figure 1). We employed purposive sampling to select VOI members as participants, based on their regular interaction with and knowledge of tapia woodlands, emphasising older individuals (≥40 years) for historical insights (Joa et al., 2018). Participant demographic was predominantly male (reflecting the gender composition of the VOI membership; Table 1). At each site, one focus group included general members, and another included more active VOI members like presidents and patrollers. Groups of 3–5 participants engaged in 30–45-min discussions conducted in Malagasy, run by Elliot Convery-Fisher and facilitated by Laura Rafanomezantsoa. Participants discussed whether they had witnessed changes in: tapia woodlands and non-native species extent, condition and abundance over their lifetimes; ecosystem uses and management practices; and explanations of observed, or lack of, change (see Appendix S2).

TABLE 1 Distribution of focus group participants across study periods and community forest management associations (*Vondron'Olona Ifotony*, VOIs). Data show number of VOIs engaged, focus groups conducted, total participants and gender distribution for each study period. Participants were selected based on their regular interaction with and knowledge of tapia woodlands. See Appendix S3 for participant demographics by region.

Year	Month	Number of VOIs	Number of focus groups	Number of participants	Gender
2021	July–August	6	12	42	Male = 28, Female = 14
2022	April–May	10	20	72	Male = 61, Female = 11

2.4 | Ethics

The research was reviewed and approved by the University of Edinburgh's School of Geosciences' Research Ethics and Integrity Committee (#GEOS2022-585). It was conducted with free, prior and informed consent from all participants.

2.5 | Data analysis

2.5.1 | Knowledge integration approach

Nightingale (2020) identifies three forms of triangulation for integrating knowledge systems: *convergent triangulation*, which seeks identical results from different methods to validate findings; *complementary triangulation*, which combines different methods to produce a fuller picture of the research problem; and *divergent triangulation*, which uses contradictions between methods to expand understanding of complex phenomena. We employed complementary triangulation because it was most appropriate for our research aims of understanding and interpreting observable ecological phenomena by extending understanding beyond what traditional methods alone can provide (Fielding, 2012). We examined two primary relationship types between our datasets: convergence (where datasets showed similar patterns) and complementarity (where one dataset provided explanatory context for patterns observed in the other). Specifically, we categorised local observations of change based on focus group consensus for specific areas, compared these with corresponding remote sensing and field measurements across regions, and examined explanatory factors provided through TEK to interpret observed patterns. We focused on convergence and complementarity as our research questions centred on understanding change patterns rather than resolving contradictions between knowledge types (Nightingale, 2003) (see Appendix S4 for further details).

2.5.2 | Quantifying multi-decadal tree cover trends and their drivers (research questions 1 and 2)

To quantify changes in tree cover over time and their drivers through quantitative spatial analysis, we used linear mixed-effects models (LMEMs) developed in the package *lme4* (Bates et al., 2015) R version 4.2.2. LMEMs were suitable for the data given their hierarchical structure, with tree cover measurements nested within multiple sites across different regions (Pinheiro & Bates, 2010).

The response variable was tree cover (% ground area) measured at three time points (1949, 1991, 2022) (Table 2). Fixed effects included *year*, *elevation*, *slope*, *distance to the nearest town* and *distance to the nearest road* to capture the role of initial tree density, environmental factors, temporal trends and intensity of human use (Table 3). Year was scaled with 1949 = 0, 1991 = 42 and 2022 = 73, maintaining the actual temporal spacing of observations. All continuous predictors were *z*-standardised (mean = 0, standard deviation = 1) to facilitate comparison of effect sizes. We assessed potential multicollinearity among predictor variables by examining the correlation matrix from our model output (Thompson et al., 2017).

The random effects structure included nested effects of (1|*location*|*plot*) where *location* represents administrative regions ($n = 6$) and *plot* represents individual sampling sites ($n = 40$). This structure accounts for spatial clustering as variation in starting conditions is captured by site-level random intercepts. Separate models were developed for tapia woodlands and non-native forestry species.

Model selection followed an information-theoretic approach using the dredge function from the *MuMIn* package (Bartoń, 2023). We compared all possible combinations of fixed effects and selected models within ΔAICc <2 of the top-ranked model. For models within this threshold, we used model averaging to obtain parameter estimates weighted by AICc support. Model diagnostics included examination of residual plots, Q-Q plots for normality and variance inflation factors (VIF <2 for all retained predictors).

2.5.3 | Locally observed change and its attributed drivers (research questions 1 and 2)

To understand tree cover change and its drivers from the perspective of lived experience, we analysed participants' responses using thematic content analysis and descriptive statistics. We developed a coding framework to identify recurring themes related to perceived changes in tapia woodland and non-native forestry species extent and composition, explanations for observed changes, management practices and impacts. The frequency and distribution of themes were quantified across focus groups, with each focus group providing a single consensus response for observed changes in ecosystem extent and composition, including the categorisation of local observations

TABLE 2 Explanatory and response variables in statistical analysis of tree cover change.

Variable	Explanation	Unit	Rationale
Response variables			
Tree cover	Proportion of ground area covered by tree canopy	% Ground area	Measured from georeferenced historical images at three time points
Explanatory variables			
Year	Time since initial observation	Years (scaled: 0, 42, 73)	Captures temporal trends in tree cover; scaled to preserve uneven sampling intervals
Distance to the nearest town	The distance from the site to the closest town	km	Proxy for human activity impact on tree cover
Distance to the nearest road	The distance from the site to the closest road	km	Indicates accessibility, with closer proximity potentially leading to more human disturbance or facilitation of invasive species spread in a landscape where individuals travel long distances on foot
Elevation	Height above sea level at the site	m	Influences climate, vegetation types and disturbance likelihood
Slope	Steepness of the terrain at the observation site	Degrees	Influences soil stability, vegetation growth pattern and disturbance likelihood
Random effects			
Location	Administrative region	Categorical ($n=6$)	Accounts for unmeasured site-specific factors and spatial autocorrelation
Plot (nested in Location)	Individual sampling site	Categorical ($n=40$)	Captures site-specific variation, including initial cover conditions

TABLE 3 Global model specifications for linear mixed-effects analyses of annual tree cover change. Models examine (a) tapia woodland cover and (b) non-native forestry species cover in relation to temporal trends, topographic factors and anthropogenic influences. Interactions between year and other predictors test whether rates of change vary with environmental or accessibility gradients. Random effects account for spatial clustering by region and site.

Analysis	Global model
(a) Tapia woodland cover (% ground area at 1949, 1991 and 2022) in relation to time and environmental/accessibility factors. Assessed at 40 sites from historical remote images	Cover ~ Year + Year × Elevation + Year × Slope + Year × Distance to Town + Year × Distance to Road + (1|Location/Plot)
(b) Non-native forestry species cover (% ground area at 1949, 1991 and 2022) in relation to time and environmental/accessibility factors. Assessed at 40 sites from historical remote images	Cover ~ Year + Year × Elevation + Year × Slope + Year × Distance to Town + Year × Distance to Road + (1|Location/Plot)

of change of both tapia woodlands and non-native forestry species (increase, decrease or no change) for specific areas.

2.5.4 | Characterising current stand structure and recruitment (research question 3)

To characterise current stand structure, species composition and recruitment patterns, we used the following height thresholds: juveniles (1–2 m), small trees (2–4 m), medium trees (4–7 m) and large trees (>7 m), reflecting size-related fire tolerance and competitive ability (Fisher et al., 2014). To compare demography among *U. bojeri*, *Pinus* spp. and *Eucalyptus* spp. descriptive statistics were undertaken with the *dplyr* package (version 0.7.6; Wickham, 2016), R version 4.2.2.

3 | RESULTS

3.1 | Tapia woodland stability (1949–2022)

Over the 73-year study period (1949–2022), tapia woodlands demonstrated structural stability, with mean cover remaining essentially unchanged at approximately 45% (1949: 41.3% ± 2.96 SE; 1991: 42.8% ± 3.02 SE; 2022: 40.5% ± 2.83 SE; Figure 2a). Regional patterns showed heterogeneity in baseline cover and temporal trajectories (Figure 2a), with some regions exhibiting modest increases (e.g. Arivonimamo: 39%–51%) while others showed declines (e.g. Anjoma: 89%–73%; Itremo: 36%–28%). However, these regional patterns did not constitute a systematic landscape-wide temporal trend. Models including *year* or its interactions received no support (all ΔAICc >3.5).

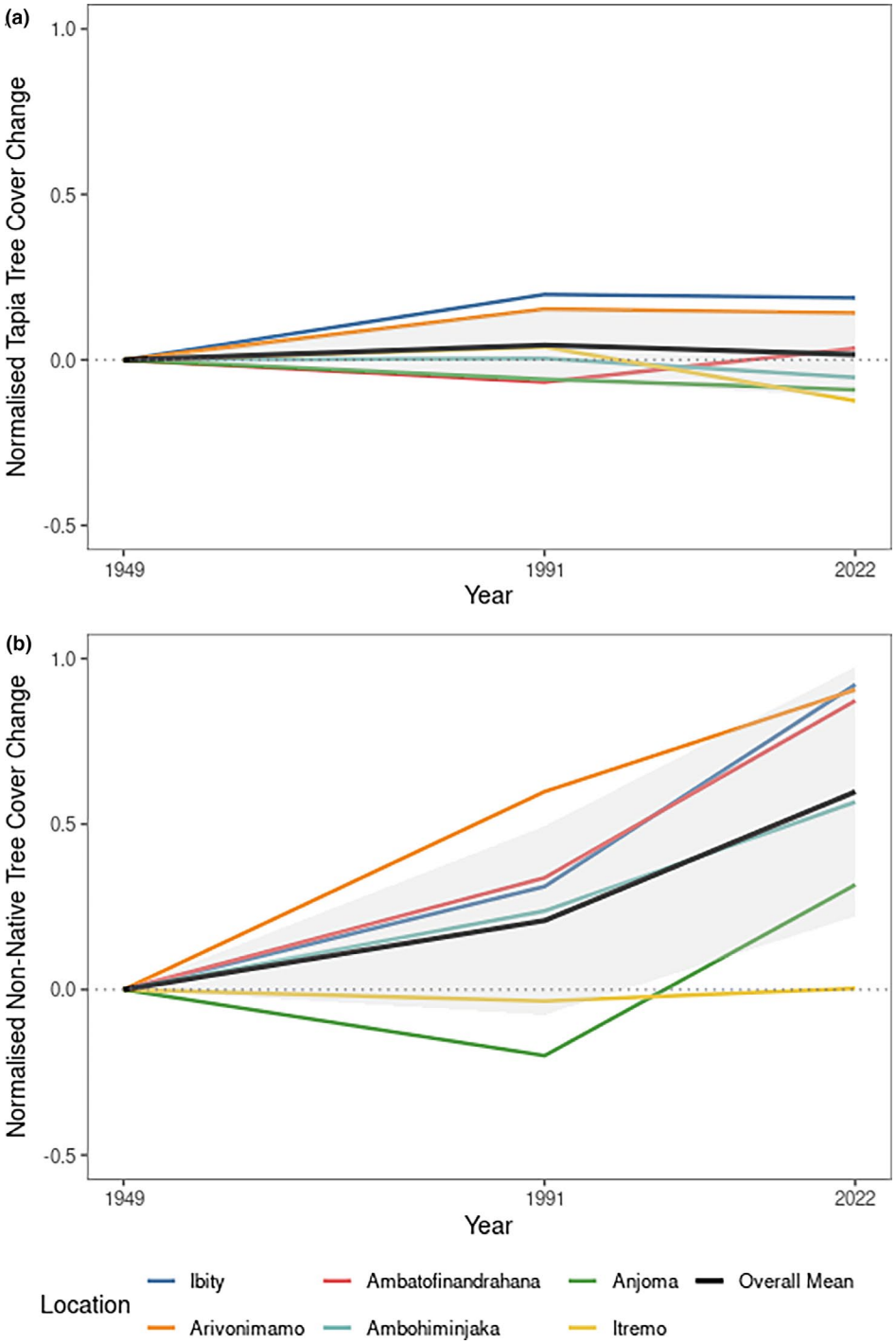


FIGURE 2 Trajectories of remotely assessed tree cover change across the central highlands between 1949 and 2022 for (a) tapia and (b) non-native woody species. For visualisation purposes, we present normalised change values ranging from −1 to 1 that were calculated, with positive values indicating an increase in tree cover relative to the 1949 baseline. Lines represent the mean normalised change for different zones, including sub-sites.

Statistical models identified elevation, distance to town and slope as potential predictors of tapia woodland cover, though multiple models received nearly equivalent support (ΔAICc <0.15; Table 4a). The most parsimonious model included only elevation (R^2_marginal = 0.038), while a model including distance to town and slope provided better fit (R^2_marginal = 0.23) at the cost of additional parameters. Model-averaged coefficients (Table 5a) indicated that elevation was the most consistently supported predictor across competitive models (conditional average: $\beta = -9.85$, SE = 5.03, $p = 0.050$, 95% CI: −19.71, −0.01).

Fixed effects across all competitive models (ΔAICc <2) explained modest amounts of variance (R^2_marginal = 0.04–0.23), whereas random effects accounted for approximately 70% of total variance (R^2_conditional = 0.68–0.76). Random effects accounted for substantial

variance in the data, with *location* (administrative region) explaining variance = 216.0 (SD = 14.7) and nested *plot* effects explaining variance = 105.5 (SD = 10.3), reflecting spatial heterogeneity in baseline tapia cover but consistent lack of temporal trends across sites. Other variables tested, including distance to nearest town, distance to nearest road, and slope, did not contribute significantly to model performance and were not retained in top-ranked models (all ΔAICc >2).

TEK converged with the remotely sensed findings. In 81% of focus groups (see Appendix S8), participants indicated that tapia cover remained the same during their lifetime (≥40 years). As one VOI patroller described *'The landscape has changed but not really the tapia'*. (FG-AM1-21) and another *'the area covered by tapia trees is about the same'* (FG-IT5-22). A VOI president confirmed, *'the area of tapia is similar to when I was a child'*, (FG-IT1-22) while another VOI president agreed, *'the tapia here is about the same'* (FG-AB3-21).

In 19% of focus groups, participants indicated that tapia cover had declined, primarily because of clearing for agriculture, wood harvesting for charcoal and a drying disease that was killing the tapia. However, this latter factor was only mentioned around Itremo.

Participants attributed tapia woodland stability to the transfer of management [within the last 20 years] to VOIs. One VOI president outlined *'before the VOI there was a reduction in tapia, but since the time [2002] we began to protect the forest, we have noticed that there has been an increase in tapia and other species'*. (FG-AB5-22). A VOI forest patroller corroborated *'the health of tapia is now better than before because of the VOI and now that there is no fire. The tapia grows better too now because of the VOI'* (FG-AB4-22). Another VOI forest patroller who felt the tapia woodland had increased in size during their lifetime argued *'before the VOI, there was a loss of tapia but now we have increased the amount of forest by planting trees. The forest area is bigger and denser now because of the VOI'* (FG-IB2-22).

TABLE 4 Model rankings, AICc weights and variance explained for models predicting annual change in tree cover for (a) tapia and (b) non-native woody species. Each model includes key predictors: Elevation (E), distance to nearest road (DR), distance to nearest town (DT), slope (S) and year (Y). A total of 32 models were considered in the full subset regression. We present only the top models (ΔAICc <2) ranked by ΔAICc, alongside their relative likelihood (AICc weight) and percentage of deviance explained. *k* shows the number of parameters in each model, ΔAICc the difference between the model AICc and the minimum AICc in the set of models, AICc weights (w_i) are the relative likelihood of model *i*.

Model	*k*	ΔAICc	w_i	R^2_m	R^2_c
(a) Tapia woodland cover					
E	5	0.00	0.118	0.038	0.757
DT + S	6	0.01	0.117	0.228	0.679
DT + E + S	7	0.09	0.112	0.176	0.685
E + S	6	0.14	0.110	0.094	0.710
Null model	4	1.43	0.057	0.000	0.747
Y	5	3.52	0.017	<0.001	0.747
(b) Non-native forestry species cover					
Y + DR + Y × DR	7	0.00	1.000	0.264	0.484
Y	5	10.3	0.006	0.155	0.420
Null model	4	34.9	<0.001	0.000	0.188

3.2 | Non-native species expansion and its drivers

Non-native forestry species exhibited expansion over the 73 year study period (1949–2022), with mean cover increasing from 9.0% ± 2.14 SE in 1949 to 26.3% ± 3.08 SE in 2022 (1991: 9.4% ± 1.87 SE; Figure 2b), representing a total increase of 17.4% (p <0.001). This expansion accelerated markedly after 1991, with the most rapid cover gain occurring in the most recent 31-year period. Regional

TABLE 5 Model-averaged coefficients for predictors of tree cover. For tapia, estimates are based on models within ΔAICc <2, weighted by AICc support. For non-native species, a single model received support. The intercept represents mean cover when all predictors are at their mean values (*z*-standardised predictors = 0).

Predictor	Estimate	Std. error	Adjusted SE	*Z*-score	*p*-value	95% CI
(a) Tapia woodland cover						
Intercept	44.03	5.05	5.1	8.64	<0.001***	[34.03, 54.03]
Elevation	−9.85	4.98	5.03	1.96	0.050*	[−19.71, −0.01]
Distance to Town	−4.54	2.86	2.89	1.57	0.116	[−10.20, 1.12]
Slope	−5.35	2.78	2.81	1.91	0.057	[−10.86, 0.16]
Distance to Road	−2.82	2.25	2.28	1.24	0.216	[−7.29, 1.65]
(b) Non-native forestry species cover						
Intercept	6.2	2.33	—	2.66	<0.001***	[1.63, 10.77]
Year	0.209	0.038	—	5.51	<0.001***	[0.13, 0.28]
Distance to Road	0.190	2.9	—	0.07	0.948	[−5.49, 5.87]
Year × Distance to Road	−0.152	0.048	—	−3.15	0.002**	[−0.25, −0.06]

Note: *p <0.001; **p <0.01; ***p <0.05.

patterns showed heterogeneity in expansion rates (Figure 2b), with increases in Arivonimamo (2%–39%) and Anjoma (4%–52%), while Itremo remained essentially stable (9.5%–9.5%).

Statistical models identified year and distance to roads as the dominant predictors of non-native species expansion, with a significant interaction indicating that expansion rates varied with accessibility (Table 4b). A single model received unequivocal support (best model AICc = 991.0 vs. year-only AICc = 1001.3; ΔAICc = 10.3), including year, distance to roads and their interaction as fixed effects (R^2_marginal = 0.26, R^2_conditional = 0.48). The positive year effect ($\beta = 0.209$, 95% CI: 0.13, 0.28; SE = 0.038, $t = 5.51$, $p < 0.001$; Table 5b) indicates a mean annual increase of 0.21% in cover at average road distance (20 m). The significant negative interaction term (Year × DistToRoad: $\beta = -0.152$, 95% CI: −0.25, −0.06; SE = 0.048, $t = -3.15$, $p = 0.002$) suggests that expansion rates were substantially higher at sites closest to roads, with model predictions indicating +26% total increase at roadside sites compared to +4% at sites 40 km from roads over the 73 year period.

Fixed effects for non-native species explained substantially more variance (R^2_marginal = 0.26 vs. 0.04 for tapia), reflecting strong directional temporal trends rather than static spatial patterns. Random effects showed Plot-level variance (variance = 62.4, SD = 7.90) substantially exceeding Location variance (variance = 2.25, SD = 1.50), indicating that site-specific factors rather than regional climate or management patterns primarily drove spatial variation in non-native cover. Other variables tested, including elevation, slope and distance to nearest town, did not contribute significantly to model performance and were not retained in the best model.

TEK converged with the remotely sensed findings. Most focus groups (83%) confirmed increases in non-native trees in and around tapia woodlands. As one VOI member asserted, *'there are many, many more pines than before, say 50 years ago'* (FG-AR4-22), and another member said, '*there are pines in the tapia forest, so we cut them to keep numbers low'* (FG-AB8-22). A VOI forest patroller said, *'the pines here are many, very many. They grow everywhere in the grasslands and in the tapia forest'* (FG-AR4-22). Within 90% of focus groups, respondents confirmed that non-native forestry species were growing *inside* the tapia woodland in some areas; a VOI president suggested, *'pines grow really fast and spread very easily even in the [tapia] forest'* (FG-AR5-22). *'Yes, there are many pines in the tapia forest'* commented one VOI member (FG-IB4-22).

Focus groups (42%) highlighted concern about the impacts of the pines on tapia. A VOI forest patroller and local guide argued, *'pines are harmful to the tapia. They do not allow other trees to grow around them, killing other trees and making them grow slowly by growing above the tapia'* (FG-AR4-22). Another VOI forest patroller was concerned, *'the pines lead to the tapia drying out…removing the pine helps the tapia'* (FG-IT1-21). 36% of focus groups were unaware of any impact of pine on tapia. While 22% of focus groups indicated the positive impact of pine in reducing the reliance on tapia as a source of fuel and timber, as one VOI member explained, *'we now cut [pines] to keep numbers low. We cut them into planks and carry them out of the forest. We get all our wood from the pine and eucalyptus now'* (FG-AM2-22). Another VOI leader suggested, *'now with the pines the people do not need to go into the tapia for wood'* (FG-AM2-22).

Participants indicated that non-native forestry species were planted and allowed to spread due to their utility and rapid growth. A VOI member discussed '*they [pines] are very good for building the house and when cooking the food*' (FG-AR4-22). Another member said similarly that '*eucalyptus is very useful for making charcoal, so we let them grow*' (FG-AM2-22). Focus groups also reported that pines and eucalyptus were often chosen for reforestation activities. One VOI president explained *'in the past, we were given [pine] seeds by the authorities to plant and now there are many pines close to the village'* (FG-AM4-22).

3.3 | Compositional change beneath structural stability

Vegetation plot data and TEK together reveal compositional changes within apparently stable tapia stands. Across 40 vegetation plots, we recorded 47 woody species, with a mean richness of 6.0 ± 2.9 species per plot. *Pinus* occurred in 85% ($n = 34$) and *Eucalyptus* in 17.5% ($n = 7$) of all plots. *Uapaca bojeri* (tapia) comprised 95.8% of all recorded stems and contributed a mean basal area of 3.15 ± 1.24 m^2 per plot (maximum: 6.44 m^2). In contrast, *Pinus* and *Eucalyptus* contributed 0.095 ± 0.16 and 0.15 ± 0.22 m^2, respectively. Tapia trees had significantly larger stem diameters than non-native species (11.4 ± 9.4 vs. 7.8 ± 7.9 cm; $t = -9.16$, $p < 0.001$), but similar height (3.28 ± 2.13 vs. 3.39 ± 2.53 m; $t = 0.86$, $p = 0.39$) (Figure 3).

Stand structure varied between sites. In Ambatofinandrahana, tapia trees were generally larger, with a mean stem diameter of 16.3 ± 11.6 cm and a height of 4.5 ± 2.3 m. In contrast, trees in Ambohimanjaka were smaller (9.8 ± 7.8 cm diameter; 2.9 ± 1.9 m height), reflecting a higher density of younger or smaller stems. This trend extended to non-native species; both *Pinus* spp. (0.165 ± 0.199 m^2) and *Eucalyptus* spp. (0.209 ± 0.282 m^2) had greater basal area in Ambatofinandrahana than in Ambohimanjaka (*Pinus*: 0.016 ± 0.015 m^2; *Eucalyptus*: 0.060 ± 0.064 m^2).

Tapia seedlings were recorded in 31 plots, with an average of 3.1 ± 2.7 seedlings per plot (see Appendix S6). Pine seedlings were found in 6 plots (mean: 0.33 ± 0.82). Seedling counts showed active recruitment for all three species (including *Eucalyptus* spp.), with tapia having the highest seedling counts (see Appendix S6).

TEK highlighted species compositional losses. In 59% of focus groups, participants described historical losses of companion species within tapia woodlands, particularly *S. oblongifolia* and *P. latifolia* due to selective harvesting. One VOI member detailed *'before, there used to be more different types of trees in the tapia forest, such as large v [S. oblongifolia], which have been removed'*. (FG-AB2-21) and another agreed *'previously, people cut all the hezana [P. latifolia] and voandrozana [S. oblongifolia] for charcoal and wood so there are not very many left'* (FG-IT4-21). Similarly, a VOI patroller suggested '*the types of trees are different than before, we have lost many of the other trees that are not*

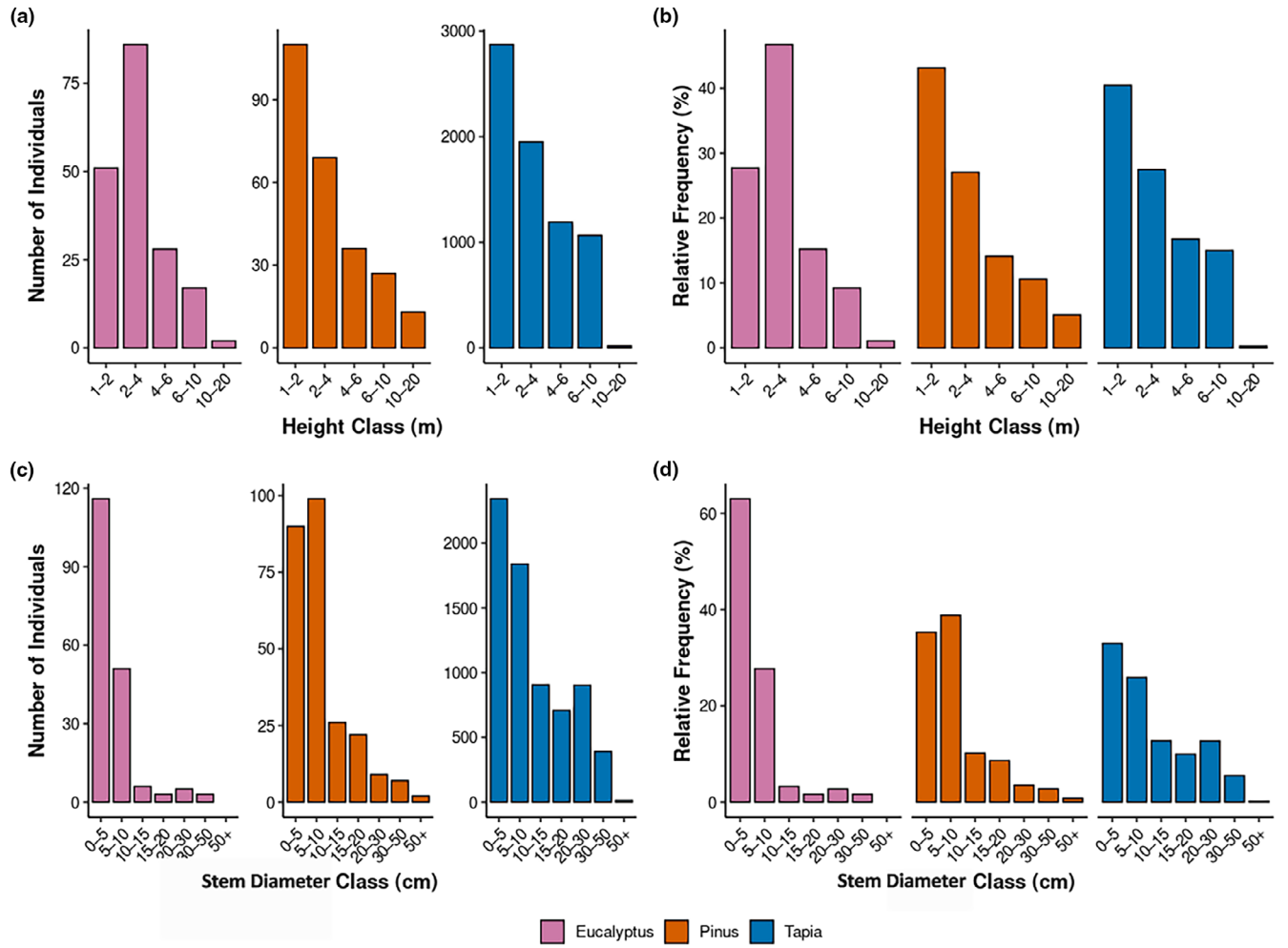


FIGURE 3 Size-class distributions of native (*Uapaca bojeri*) and non-native forestry species (*Eucalyptus robusta* and *Pinus kesiya*) measured across 40 plots in the Ambatofinandrahana and Ambohimanjaka regions. Panels show (a) absolute height distributions, (b) relative height frequency, (c) absolute stem diameter distributions and (d) relative stem diameter frequency for three dominant species. Relative frequency is expressed as the proportion of individuals in each class per species.

tapia' (FG-AM1-21). However, not all participants agreed. A VOI president explained *'the types of trees are like what I remember but some of them are much larger now. The VOI have tried to increase the amount of forest by planting [native] trees'* (FG-IB2-22).

4 | DISCUSSION

Our integration of remote sensing analysis, TEK and vegetation surveys yields three key insights into Madagascar's Afromontane ecosystems. First, tapia woodland demonstrates remarkable structural stability over 73 years (−0.52%, $p = 0.0810$), challenging widespread deforestation narratives. Second, non-native forestry species have expanded substantially over the last 73 years (+17.4%, $p < 0.001$), with road networks facilitating spread likely due to ease of access initially for planting. Now, they are actively recruiting and spreading independently. Third, remote sensing of structural stability of tapia masks compositional change detectable only through integration of TEK.

4.1 | Structural stability masks compositional change in tapia woodlands

Our findings of multi-decadal stability in tapia canopy cover, even near human infrastructure, contribute to a growing body of evidence from Madagascar suggesting that long-term traditional land-use practices can be positively associated with ecosystem function and resilience rather than inevitable degradation (Davis et al., 2025; Phelps et al., 2022). This observed stability stands in contrast to recent IUCN assessments and previous regional studies that have suggested a downward trend in tapia woodland extent (Alvarado et al., 2014). Instead, our results align with earlier observations by Kull (2013, 2002) and support Solofondranohatra et al.'s (2020) assertion that these open woodlands represent a stable, fire-adapted state within a landscape mosaic. The two zones with formal protected area status, Itremo and Ibity, were only designated in 2015, meaning the stability observed across our 73 year study period is not simply due to formal protection. Tapia woodland's structural persistence likely emerges from a synergy of ecological and cultural factors, where traditional fire

regimes and customary management practices, motivated by the production of wild silk and fruit, act as a stabilising force for the *U. bojeri* canopy (Kull & Birkinshaw, 2022).

While the *U. bojeri* canopy remains resilient, our field and TEK data reveal a 'decoupling' between structural stability and compositional integrity. We found an increased presence of non-native forestry species in several sites, alongside the selective loss of understory species such as *S. oblongifolia* and *P. latifolia*. Participants attributed these losses to historic selective harvesting for specific purposes such as making planks, constructing carts and building homes given the hardy nature of the timber of these species (Rakotondrasoa et al., 2013), suggesting not all species within tapia woodlands are equally conserved, underpinned by differing cultural and economic importance attributed to species. As structural stability can coexist with compositional change, it suggests that supplementary support is needed to preserve the full spectrum of woodland biodiversity.

4.2 | Non-native forestry species are expanding rapidly

Non-native forestry species have expanded dramatically across Madagascar's Central Highlands, with expansion accelerating since 1991. The rapid spread of non-native forestry species likely represents the modern manifestation of historical and contemporary tree-planting policies (Kull & Birkinshaw, 2022). Similar to other Afromontane ecosystems, colonial forestry introduced *Pinus* spp. and *Eucalyptus* spp. to the Central Highlands to restore ecosystems perceived as 'degraded' and establish timber plantations for development (Moura et al., 2019). Road proximity facilitated expansion (Year × Distance to Road: $\beta = -0.152$, 95% CI: −0.25, −0.06; $p = 0.002$), supporting seed dispersal likely through increased propagule pressure from tree planting in easily accessible sites, disturbance and human-mediated dispersal (Head, 2017; Hulme, 2009; Rajaonarivelo et al., 2022).

Field data confirmed this ongoing spread, with non-native forestry species (primarily *Eucalyptus robusta* and *Pinus kesiya*) present in 85% of vegetation plots and reported as growing directly within tapia woodlands by 90% of focus groups. Size-class distributions are dominated by smaller individuals, indicating active recruitment of non-native species alongside native *U. bojeri*, demonstrating potential for continued expansion and invasion. With ongoing settlement expansion in Madagascar's Central Highlands (IOM, 2020), this trend is likely to accelerate, serving as a cautionary example for other Afromontane regions facing similar pressures from non-native species stemming from colonial legacies coupled with infrastructure development.

Participants highlighted potential for non-native species to invade, as well as alleviate pressure on native ecosystems. Participants expressed concerns about negative impacts from non-native species competition, aligning with research showing that fast-growing non-natives monopolise light and nutrients (Kacheche & Mzuza, 2021) and alter fire regimes (Brooks et al., 2004) and catchment hydrology (Martin et al., 2025). In Madagascar specifically, dense stands of *Pinus* spp. may compromise shade-intolerant *U. bojeri*, endangering wild silk production and other ecosystem services critical to local communities (Kull & Birkinshaw, 2022). However, in 22% of focus groups, participants highlighted benefits of non-native species in providing alternative timber and fuel resources, potentially contributing to tapia stability. As in other systems, non-native species introduce both opportunities and vulnerabilities for local livelihoods and biodiversity by offsetting pressure on local native ecosystems (Shackleton et al., 2019).

The ecological impacts of non-native species are likely to intensify over time, as non-native species effects generally worsen from young to mid-aged stands through processes such as allelopathic suppression of understory vegetation and increased fire risk (Kacheche & Mzuza, 2021; Martin et al., 2025). Given that our size-class data revealed dominance of smaller individuals in both *E. robusta* and *P. kesiya* populations, indicating that most non-native stands in the study area are still in early establishment phases, the ecological costs relative to current livelihood benefits may shift substantially as these young populations mature into mid-aged stands. Future research is needed to quantify how the relative socio-economic benefits and ecological costs of non-native species change over stand age to inform conservation management strategies cognisant of livelihood needs.

4.3 | Remote sensing and TEK in monitoring Afromontane ecosystems

Both remote sensing and TEK converged to indicate stability in tapia cover and substantial increases in non-native species. Other studies integrating remote sensing and TEK have demonstrated that convergence between scientific data and local observations strengthened confidence in ecological assessments in South Africa (Chalmers & Fabricius, 2007) and Ethiopia (Steger et al., 2020). Convergence leverages the quantitative generality of remote sensing and the observational richness of TEK, which are valuable given previous contradictory reports regarding ecosystem dynamics (de Haulleville et al., 2018; Kull, 2013).

TEK revealed change undetectable via remote sensing. While remote sensing provided quantitative measurements of tree cover change, TEK revealed compositional changes within these ecosystems. The value of TEK to reveal changes 'below the canopy' has been documented across diverse ecosystems such as in the Peruvian Amazon where there was agreement between remotely sensed measures of forest and local reports of dynamics (Paneque-Gálvez et al., 2018). In the Ethiopian Highlands, Steger et al. (2020) demonstrated how combining satellite-derived indices with TEK clarified the ecological dynamics of shrub encroachment. In both cases, TEK provided species-level and compositional insights that were otherwise obscured by spectral generalisations.

Without TEK, we would have missed the loss of companion species within otherwise stable tapia stands. By going 'below the canopy', we provide one of the first integrated analyses of Afromontane ecosystems that captures long-term compositional

changes detectable only through sustained, place-based ecological knowledge.

4.4 | Limitations

We interpret our findings within the context of measurement uncertainty inherent in historical aerial photograph analysis. We acknowledge that a systematic overestimation bias (+15%) and measurement error (60.9% relative RMSE) mean that small changes (<15%) approach the limits of detection for our method. We emphasise that for the purposes of longitudinal change detection, systematic error is less problematic as the bias is consistent across the time-series; it does not invalidate the observed trajectories. The +17.4% expansion of non-native species represents a clear 'signal' that exceeds our error thresholds, whereas the negligible change in tapia cover indicates landscape-scale stability within the limits of our detection. In addition, we note the lack of historical ground-truth data, a common constraint in long-term studies, yet we found consistency across independent lines of evidence to provide confidence in our findings.

While our triangulated approach offers valuable insights, focus groups may have obscured divergent perspectives. We used focus groups to gather views across the large spatial extent we examined for tree cover change, but we recognise this decision may have dampened potential avenues of divergence between and within knowledge systems.

Participants were recruited through VOI networks and may have emphasised positive conservation outcomes to maintain favourable relationships with potential funders or avoid criticism of local management approaches. However, our triangulated approach helps to mitigate this by providing independent validation of findings. Participants readily reported negative changes (such as companion species losses and pine encroachment) alongside positive ones, suggesting they were not uniformly providing socially desirable responses. We note also that women's ecological knowledge likely differs from that of men (Nightingale, 2003), suggesting a need for future intentional recruitment of women in future work.

In the field, we selected plots that were dominated by either tapia or non-native species, leaving out mixed stands due to classification concerns of the remote sensing. While this decision allowed us to achieve a high classification accuracy, our approach may not fully capture the complexity of transitional or mixed areas where both vegetation types are present in significant proportions (increasingly frequently) likely resulting in an underestimation of the spread of non-native species particularly *within* tapia woodlands: a novel vegetation type increasing in prevalence across the region.

5 | CONCLUSION

Our study challenges narratives of pervasive forest loss in Madagascar's Central Highlands caused by rural communities by demonstrating long-term structural stability of tapia woodlands, despite growing anthropogenic pressures and regional land-cover change. We highlight that local management can effectively preserve tapia woodland structure. Historic and contemporary processes have facilitated non-native species invasion in Afromontane grassland-forest mosaics, serving as pervasive drivers of environmental change. While these non-native species provide livelihood benefits that alleviate pressure on native ecosystems, the rationale for tolerating their spread diminishes once local fuel and timber needs are met.

The loss of companion species within stable tapia stands likely reduces ecosystem resilience, potentially jeopardising livelihoods dependent on ecosystem services such as silk harvesting. Without intervention, current trends suggest tapia woodlands may become pine-dominated stands that shade out native species and dampen regenerative capacity, with impacts intensifying as young non-native populations mature. Consequently, the targeted management of source populations, removal of non-native forestry species from high-conservation areas, alongside targeted efforts to restore companion species within affected tapia stands remains urgent priorities.

Our findings advocate for reassessing tapia's IUCN 'endangered' classification, distinguishing between structural stability and compositional change. Conservation assessments of ecosystems with contested histories, such as those conducted by the IUCN, would perhaps benefit from incorporating the lived experiences and observations of local communities who depend on these landscapes into those assessments. This would centre the perspectives of those whose livelihoods are interwoven with these systems, to provide an assessment that incorporates both ecological and social priorities, which may avoid future landscapes being 'written off' because of labels that are applied to them.

AUTHOR CONTRIBUTIONS

Elliot D. Convery-Fisher, Caroline E. R. Lehmann and Sam Staddon conceived of the ideas. Elliot D. Convery-Fisher, Caroline E. R. Lehmann, Christian A. Kull, Sam Staddon and Adam J. M. Devenish designed the methodology. Elliot D. Convery-Fisher and F. Laura Rafanomezantsoa collected the data. Tiana Randriamboavonjy provided in-country logistical and pastoral support. Elliot D. Convery-Fisher analysed with input from F. Laura Rafanomezantsoa, Caroline E. R. Lehmann, Sam Staddon and Adam J. M. Devenish. Elliot D. Convery-Fisher led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Digital Dryad Repository: https://doi.org/10.5061/dryad.2fqz61344.

ORCID

Elliot D. Convery-Fisher https://orcid.org/0009-0007-8089-1243
Adam J. M. Devenish https://orcid.org/0000-0001-5240-622X
Sam Staddon https://orcid.org/0000-0002-9449-8764
Christian A. Kull https://orcid.org/0000-0002-7516-7898
Tianjanahary Randriamboavonjy https://orcid.org/0000-0001-5767-3992
Caroline E. R. Lehmann https://orcid.org/0000-0002-6825-124X

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SUPPORTING INFORMATION

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

Figure S1. (A) Map of the study area showing the distribution of tapia woodlands and spatial resolution of the data sets. (B) Detailed maps of the regions show locations of traditional ecological knowledge collection points within VOIs (red circles), demographic survey plots (orange dots; $n = 40$) and historical aerial image (HAI) sites (blue dots; $n = 80$).

Figure S2. Temporal scale of the data collected.

Table S1. Distribution of participants across VOIs in the study site.

Figure S3. Conceptual framework for knowledge integration through complementary triangulation.

Table S2. Study site characteristics and research methods by zone.

Figure S4. Seedling counts by species.

Table S3. Comparison between remotely sensed cover and ground-based cover estimates.

Table S4. Perceptions of tree cover and condition change in key vegetation types: tapia woodlands and non-native forestry species.

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