RESEARCH ARTICLE

Land-use history determines stand structure and tree diversity in vanilla agroforests of northeastern Madagascar

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Abstract

Question: In human-modified tropical landscapes, agroforestry is considered a promising land use to reconcile biodiversity conservation with production goals. The role of agroforests regarding conservation may be strongly influenced by land-use history; however, few studies have explicitly investigated this. We therefore tested the importance of land-use history for habitat structure and tree diversity in vanilla agroforests situated in a human-modified tropical landscape.

Location: Smallholder mosaic landscape of northeastern Madagascar.

Methods: We studied tree stand structure, diversity and composition in vanilla agroforests of contrasting land-use history, old-growth forests, forest fragments and woody fallows after slash-and-burn agriculture, which all contribute to the smallholder mosaic landscape of northeastern Madagascar. The vanilla agroforests were either derived directly from forest or otherwise from woody fallows after slash-and-burn agriculture.

Results: Land-use history strongly influenced tree species diversity and composition in vanilla agroforests and also affected stand structure. Forest-derived agroforests maintained high levels of tree species diversity and differed in community composition from fallow-derived agroforests, which had relatively low levels of tree diversity. Additionally, forest-derived vanilla agroforests harboured a significantly higher percentage of endemic species than fallow-derived agroforests, and forest-derived agroforests also shared many species with old-growth forests and forest fragments. Fallow-derived vanilla agroforests harboured a lower percentage of endemic species than woody fallows.

Conclusion: Considering the land-use history of agroforests is important to unfold their full potential as elements in a multifunctional human-modified landscape. Forest-derived agroforests are an alternative to forest conversion through slash-and-burn agriculture and have the potential to sustain high levels of species diversity and important habitat structures. In contrast, fallow-derived agroforests regain stand

structure on degraded historically forested land and thereby have the potential to increase canopy cover and connectivity at the landscape scale.

1 | INTRODUCTION

Tropical biodiversity is threatened by past and ongoing forest loss, driven by a growing demand for land and resources (DeFries et al., 2004). Sustainable land-use options are therefore needed to maintain high levels of species diversity and habitat structure while ensuring food security (Foley et al., 2005; Godfray et al., 2010; Tscharntke et al., 2012). Particularly in tropical human-modified landscapes, agroforestry is considered a promising land-use option to meet production goals while maintaining forest stand structures, tree species diversity and associated life forms across biological kingdoms (Schroth et al., 2004; Bhagwat et al., 2008). However, agroforestry is multi-facetted: on the one hand, it may drive further forest conversion, thereby accelerating species loss and stand structure simplification (Rappole et al., 2003). On the other hand, agroforestry may restore tree cover and associated biodiversity, and ecosystem functions and services on historically forested and degraded lands (Martin et al., 2020a) and might therefore provide an attractive restoration practice (Brancalion et al., 2018; Giudice Badari et al., 2020).

Evaluating the conservation potential of tropical cash crop agroforestry systems such as coffee or cacao is often based on the comparison of structurally simple and structurally diverse agroforests (Moguel & Toledo, 1999; Rappole et al., 2003). However, agroforests have contrasting land-use histories and can be either forest- or open-land-derived (Martin et al., 2020a). In a conceptual study, Martin et al. (2020a) suggest that forest-derived agroforestry supports higher biodiversity than open-land derived agroforestry but essentially represents a degradation of forest, whereas open-land-derived agroforestry rehabilitates historically forested open land. Yet, 57% of the systematically reviewed studies did not describe the land-use history of focal agroforestry systems at all, and only very few made land-use history a central point of analysis (Martin et al., 2020a).

The important role of agroforestry in balancing conservation goals and economic development is very apparent in Madagascar (Jones et al., 2019). Madagascar is classified as a biodiversity hotspot (Myers et al., 2000; Ganzhorn et al., 2001; Buerki et al., 2013), and especially the eastern rainforests represent centres of endemism for plants and other taxa (Schatz, 2001; Goodman & Benstead, 2005; Willis, 2017). Yet, the eastern rainforests have been suffering from forest cover losses in recent years and evidence of natural forest regeneration is limited (Harper et al., 2007; Irwin et al., 2010). To date, northeastern Madagascar still holds the highest percentage of forest cover compared to the rest of the island, yet deforestation rates are constantly high (Vieilledent et al., 2018). This intensifies the call for land-use options that contribute to rural development, while maintaining as much

natural forest cover as possible (Jones et al., 2019). In this context, the cultivation of the orchid *Vanilla planifolia* in agroforests constitutes an important feature within the human-modified landscape of northeastern Madagascar (Osterhoudt & Dove, 2017). Vanilla is an important cash crop, considering both its share in the country's export earnings and its importance for livelihoods (Hänke et al., 2018). A rising global demand for vanilla in recent years therefore has led to a rapid expansion of vanilla agroforests in northeastern Madagascar (Llopis et al., 2019). Within vanilla agroforests, smallholders use small-statured trees as a support for the climbing orchid, while a variety of taller trees form the canopy above (Havkin-Frenkel & Belanger, 2018). Hence, vanilla agroforests comprise a wide range of tree densities and tree canopy cover (Hending et al., 2020). Furthermore, household surveys in northeastern Madagascar found that vanilla agroforests particularly differ in their land-use history: around 30% of agroforests are forest-derived, established by cleaning the understorey, thinning the forest, and planting vanilla under the canopy of the already established trees (Hänke et al., 2018). Roughly 70% of agroforests originate from fallow land that had formerly been burned within the slash-and-burn cycle for hill rice cultivation (locally known as *tavy*; Styger et al., 2007), before tree structures re-established and vanilla was planted (Hänke et al., 2018). Independent of their land-use history, all vanilla farming systems can be characterized as agroforests, since they permanently integrate trees and other large woody perennials into the crop cultivation system. This definition embraces a broad range of different management schemes with trees and large woody perennials that already existed prior to the agroforest establishment, but also encompasses spontaneous regrowth or actively planted trees or other tall woody plants (Schroth et al., 2004; Bhagwat et al., 2008). Recent studies show that vanilla agroforests can provide habitat for native wildlife (Hending et al., 2018; Hending et al., 2020; Martin et al., 2021), but it remains unclear to what extent the habitat structure and tree diversity are determined by land-use history. Furthermore, it is unclear how agroforest tree species communities are composed in these different agroforest types, and whether vanilla agroforests can provide suitable habitat for forest-dependent species, as many tropical species strongly depend on forest and do not occur in human-modified landscapes (Rembold et al., 2017).

In our study, we conducted inventories in forest- and fallow-derived vanilla agroforests, old-growth forests, forest fragments and woody fallow sites resulting from slash-and-burn agriculture, which represent the common tree-dominated land-use types of northeastern Madagascar. We used trees as a study group, given their importance as structure-providing elements (McElhinny et al., 2005) and their high diversity in northeastern Madagascar (Schatz, 2001; Callmander et al., 2011). We examined how land-use history affects

tree diversity and community composition within vanilla agroforests in this biodiversity hotspot in northeastern Madagascar. Specifically, we asked: (i) how do stand structure, tree diversity and community composition vary among vanilla agroforests of contrasting land-use history; (ii) how does land-use history influence total and endemic tree species diversity and species composition among vanilla agroforests; (iii) how do stand structure, tree diversity and community composition vary between vanilla agroforests of contrasting land-use history compared to other tree-dominated land-use types; and (iv) can vanilla agroforests of contrasting land-use history provide suitable habitat for forest-dependent tree species?

2 | METHODS

2.1 | Study area

We conducted fieldwork in the SAVA region of northeastern Madagascar (Figure 1a,b,c). The climate is tropical-humid with a mean annual temperature of 23.9°C and 2,258 mm of rainfall per year (means across 58 plots, based on CHELSA; Karger et al., 2017). Topographically, the region is characterized by coastal lowlands, merging into hills and mountains. The landscape was formerly covered with humid evergreen forest harbouring a high floristic diversity and high levels of endemism (Callmander et al., 2011). However, remnant areas of relatively undisturbed continuous old-growth forest only remain in protected areas (Schüßler et al., 2020). Outside of these, the landscape comprises a mosaic of land uses consisting of vanilla and paddy rice cultivation and different stages of slash-and-burn agriculture for hill rice and vegetable production interspersed with forest fragments. Slash-and-burn agriculture for hill rice production (Malagasy: *tavy*) is a major subsistence practice but also a driver of deforestation (Styger et al., 2007). Vanilla agroforests differ in land-use history and can either be derived from formerly burned fallow land with natural or planted woody regrowth, or from unburned thinned forest fragments (Figure 1d). Technically, vanilla agroforests could also be established directly in old-growth forest, but the legal establishment of forest-derived agroforests in the study region can nowadays exclusively take place in forest fragments, since old-growth forest in our study region is legally protected (Schüßler et al., 2020).
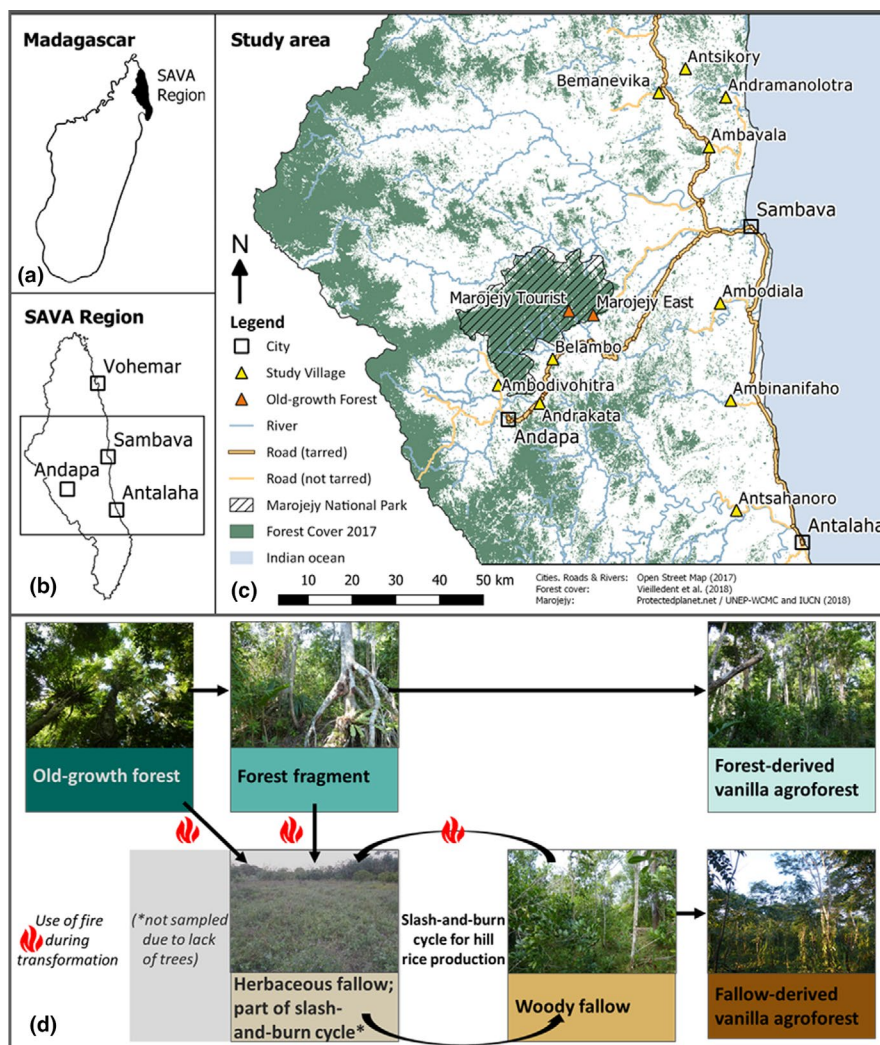
FIGURE 1 Study area map and study design overview: (a) the island of Madagascar with the SAVA region; (b) SAVA region with four main cities; (c) study area with 2017 forest cover (Vieilledent et al., 2018), 10 study villages, and the two sampling sites in Marojejy National Park; (d) a schematic concept of typical transformation pathways from old-growth forest into different land-use types highlighting the different land-use history pathways of vanilla agroforests. The fire icon symbolizes the use of fire during land-use transformation

2.2 | Study design and sampled land-use types

The five selected land-use types (forest- and fallow-derived vanilla agroforest, woody fallow, forest fragment and old-growth forest) represent the most common woody land cover types in the study region. Around each of the ten study villages (Figure 1c), we selected three vanilla agroforests, one forest fragment, and one naturally regenerating woody fallow part of the slash-and-burn cycle (Figure 1d). Vanilla agroforests were characterized by a variety of taller trees and small-statured support trees carrying the vanilla vines. Within the 30 chosen vanilla agroforests, 20 agroforests were derived from fallow land, and 10 agroforests were derived from forest fragments, as indicated by the landowners. On two fallow-derived agroforests, the landowners withdrew from the study, leaving us with 28 vanilla agroforests. The 10 naturally regenerating woody fallows (Malagasy: *savoka*) in our study had last burned 5–17 years prior to data collection and were characterized by a mix of herbaceous plants, shrubs, small trees and occasionally bamboos. The 10 chosen forest fragments were not impacted by fire, but showed signs of regular human disturbance for the extraction of timber, firewood and other products. In comparison to that, the old-growth forest plots were situated in the Marojejy National Park, where extraction of timber, firewood and other products is not allowed. The park has been protected since 1952 (Goodman, 2000; Goodman et al., 2018) and nowadays represents the largest remnant of relatively undisturbed low-altitude rainforest in the study region (see Figure 1b,c for a map of the study region). Within the Marojejy National Park, we chose 10 plots at two locations which showed least indication of recent human disturbance (five plots at each location) at elevations < 700 m a.s.l. (Appendix S1).

Overall, we worked on 58 plots (Appendix S2) and collected data between September 2018 and January 2019. The minimum distance to the nearest neighbouring plot spanned from 260 to 2,555 m (mean 827 m, *SD* 539 m). Plot elevation spanned from 20 to 819 m.a.s.l. (mean 208 m, *SD* 213 m); plot slopes spanned from 1.6° to 27.4° (mean 9.8°, *SD* 5.8°). We estimated slope and elevation values using the plugin "Raster Terrain Analysis" in QGIS (QGIS Development Team, 2016), based on the 30-m resolution digital surface model "ALOS World 3D" by the Japan Aerospace Exploration Agency (JAXA) and applied slope correction.

2.3 | Stand structure

We collected all data within circular plots (Paul et al., 2019) of 25-m radius. On each study plot we inventoried all plant species with free-standing stems of ≥ 8 cm diameter at breast height (DBH), hereafter "trees," also including arborescent palms, herbs and tree ferns but excluding lianas. Schatz (2001) suggested to use a DBH cut-off of 5 cm but this might include sterile saplings, without clear identification features. Additionally, a DBH cut-off of 5 cm would have increased our sample size and time investment per plot considerably. Thus, we chose a DBH cut-off of 8 cm to increase identification accuracy and economize time. For each plant, we measured the DBH at 1.3 m or immediately above the tallest buttress or stilt root, whenever this exceeded 1.3 m, following a standardized protocol (Condit, 2008). Based on the DBH measurements we calculated the basal area per tree, summed up basal area of all trees per plot and extrapolated it to m^2/ha.

Furthermore, we estimated the percentage of canopy closure per plot, derived from digital hemispherical photographs (Jonckheere et al., 2004). We used a Nikon D5100 camera (Nikon, Tokyo, Japan) equipped with a Sigma Circular Fisheye 4.5 mm 1:2.8 lens (Sigma, Kanagawa, Japan) with a field of view of 180°. To characterize the canopy above the vanilla support trees and understorey vegetation, we mounted the camera on a tripod at 2.4 m height. On each plot, we shot a series of photographs with different exposure values and manually selected the photographs showing the best contrast between sky and vegetation, following the protocol of Beckschäfer et al. (2013). We further processed the photographs to create a binary image representing sky and vegetation by using the software "ImageJ" (Rasband, 2014) and applied an automated thresholding technique following the protocol of Beckschäfer (2015). We derived gap fraction values and converted them to canopy closure values, to finally calculate the mean canopy closure percentage per plot (Appendix S3).

Additionally, we estimated the leaf area index (LAI) defined as the amount of leaf area in a canopy per unit ground area (Asner et al., 2003). We retrieved LAI values with a LI-COR LAI-2200C Plant Canopy Analyzer (LI-COR, Lincoln, USA). Using two sensors with 90° view caps, we collected below-canopy records on the plot and above-canopy records in nearby gaps, following the LI-COR Instruction Manual (LI-COR Biosciences, 2019). We mounted the sensors on a tripod at 2.4 m height to characterize the canopy above the vanilla support trees and understorey vegetation and recorded a total of 100 readings per plot. Finally, we processed the readings using the software "FV2200" (LI-COR Biosciences, 2019) and derived one mean LAI value with $m^2_{leaf\ area}/m^2_{ground}$ per plot (Appendix S3).

2.4 | Tree species diversity

We identified all living tree individuals with local and scientific names according to the Tropicos Madagascar Catalogue (http://www.tropicos.org/Project/Madagascar) with the help of one local expert and one taxonomic expert from Missouri Botanical Garden in Antananarivo. We collected samples for further comparison with herbarium specimens; voucher specimens are kept at the National Herbarium Tsimbazaza, Antananarivo and the herbarium of the University of Mahajanga. Information on origin and endemism for each species was derived from the Tropicos Madagascar Catalogue (accessed January 2020; Appendix S4).

The taxonomy of the highly diverse Malagasy tree flora is a dynamic field of research and species identification is a challenging task (Callmander et al., 2011). Tree identification is often based on reproductive features, so sterile tree individuals represent an additional challenge. However, we could minimize these cases by sampling

during the main flowering season. Nonetheless, we used a conservative identification approach and acknowledge that our tree species diversity assessment might underestimate the actual tree species diversity, especially for rare species, due to taxonomic uncertainties.

To assess and compare species diversities between land-use types, we used the Hill number framework, which transforms common diversity measures such as Shannon entropy or the Gini–Simpson index into effective numbers of species (Jost, 2006). This conversion unifies the different measures to the same unit (number of species), which allows for easier interpretation and comparison of the different diversity indices (Chao et al., 2014). We focussed on the three most common Hill number orders of species richness ($q = 0$), Shannon diversity ($q = 1$) and Simpson diversity ($q = 2$). Species richness ($q = 0$) is not sensitive to species frequency within the sample, so rare species are as important as common species. Shannon ($q = 1$) and Simpson diversity ($q = 2$) are frequency-based indices: Shannon diversity weights each species exactly by its frequency in the sample, favouring neither rare nor common species disproportionately (Jost, 2007). Simpson diversity emphasizes the more common species whereas uncommon species hardly contribute to the value (Jost, 2007). Jointly, theses three diversity measures provide insight into community diversity and evenness (Jost, 2007).

To compare the magnitude of species diversity differences across all plots and land-use types, we further integrated the Hill number framework into the sample-sized- and coverage-based rarefaction and extrapolation (R/E) approach (Chao et al., 2014). In this approach, all samples are standardized to an equal size, thus providing a fair comparison among incomplete samples (Chao et al., 2014).

2.5 | Data analysis

We compared the stand structure of all land-use types in terms of stem density (individuals/ha), basal area (m^2/ha), canopy closure (%) and LAI (m$^2_{leaf area}$/m$^2_{ground}$). Therefore, we tested if assumptions for normality and homogeneity of variances were met. If the residuals were homoscedastic, we tested for differences between the groups using analyses of variance (ANOVA) and Tukey's post hoc test. If the residuals were heteroscedastic, we used the non-parametric Kruskal–Wallis test, followed by Dunn's post hoc test (Ruxton & Beauchamp, 2008). For the diversity analysis, we calculated Hill number diversities for $q = 0$, 1 and 2 and computed sample-size and coverage-based R/E sampling curves based on abundance data using the R package *iNEXT* (Hsieh et al., 2016).

To display the numbers of shared and specialized tree species per land-use type, we used the R package *VennDiagram* (Chen, 2018). To assess differences in tree species composition between land-use types, we generated an abundance-based Bray–Curtis dissimilarity matrix with two dimensions, as Bray–Curtis dissimilarity focuses on compositional changes in species' identities (Anderson & Walsh, 2013). Based on this matrix, we applied a dispersion test using the betadisper function of the R package *vegan* (Oksanen et al., 2019), followed by a permutation test (999 permutations) to identify

differences in dispersion among groups, using the permutest function. To test for differences in tree species composition between land-use types, we used a pairwise permutational multivariate analysis of variance (PERMANOVA, 999 permutations; Anderson & Walsh, 2013) with a Bonferroni correction, using the pairwise.adonis function in the R package *pairwiseAdonis* (Martinez Arbizu, 2019). Finally, we performed non-metric multidimensional scaling (NMDS), using the metaMDS function of *vegan*. We performed all analyses in R 3.6.3 (R Core Team, 2019) and used the R package *ggplot2* (Wickham, 2011) for data visualization.

3 | RESULTS

3.1 | Stand structure

We recorded a total of 5,980 living stems belonging to 5,484 single or multi-stemmed trees. Stem density per hectare varied between the land-use types and reached from a median of 1,182 stems per hectare in old-growth forests to a median of 177 stems per hectare in woody fallows (Figure 2a). Forest fragments had a median stem density of 607 stems, forest-derived agroforests of 494 stems and fallow-derived agroforests of 331 stems per hectare (Figure 2a; Appendix S5). Basal area per hectare also varied between the land-use types and spanned from a median of 41 m^2/ha in old-growth forests to a median of 3 m^2/ha in woody fallows (Figure 2b). Forest-derived agroforests had a median basal area of 18 m^2/ha comparable to forest fragments (20 m^2/ha) and fallow-derived agroforests had a median basal area of 8 m^2/ha (Figure 2b; Appendix S6).

Canopy closure and LAI were significantly higher in old-growth forests than in both types of vanilla agroforests and woody fallows (Figure 2c,d; Appendices S7 and S8). Old-growth forests had a canopy closure median of 98% and a LAI median of 5.1, which was significantly higher than the LAI median in forest fragments (2.5). Within vanilla agroforests, forest-derived agroforests had a canopy closure median of 75% and a LAI median of 1.4, whereas fallow-derived agroforests had a canopy closure median of 54% and a LAI median of 1.5.

3.2 | Tree species diversity

Of the recorded 5,484 individuals, 90% were classified as trees (sensu stricto with woody stems; see Schatz, 2001), 2% as palms, 1% as tree ferns and 7% as arborescent herbs. Overall, we identified 455 species and morphospecies belonging to 195 genera and 71 families. The most species-rich families were Rubiaceae (34 species), Lauraceae (28 species), Fabaceae and Moraceae (both 25 species; Appendix S11).

Species richness per plot varied between land-use types and spanned from a median of 69 species in old-growth forests to a median of 10 species in woody fallows (Figure 2e). Forest-derived agroforests had a median of 27 species and fallow-derived
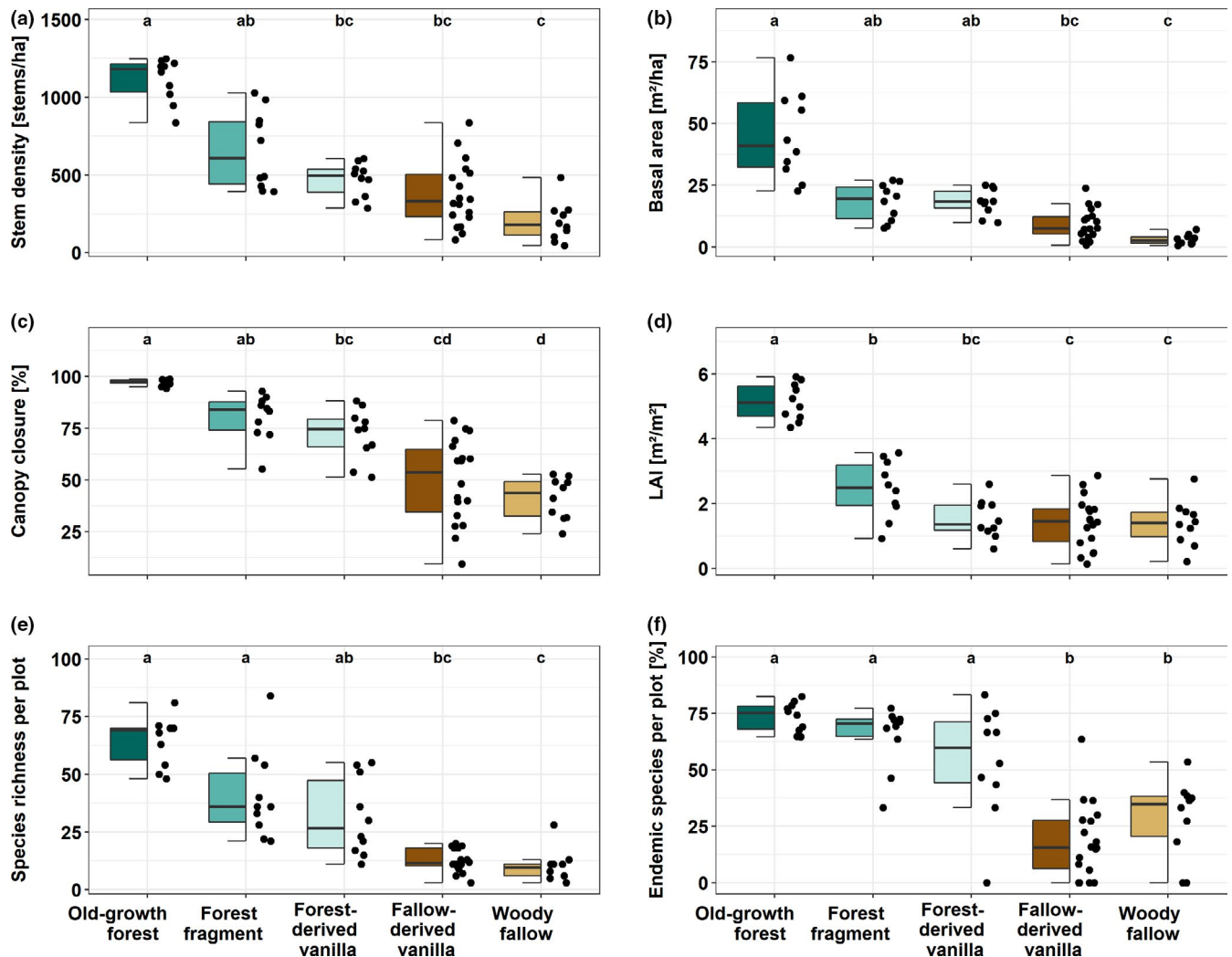
FIGURE 2 Stand structure and tree diversity of the five studied land-use types: (a) stem density [stems/ha]; (b) basal area [m²/ha]; (c) canopy closure [%]; (d) leaf area index [LAI ($m^2_{leaf\,area}/m^2_{ground}$)]; (e) tree species richness per plot; (f) percentage of endemic species per plot. The horizontal lines represent the median for each land-use type. The lower and upper limits of each box correspond to the first and third quartiles. The upper whiskers extend to the largest value whereas the lower whiskers extend to the smallest value, no further than 1.5 times the inter-quartile range from the limits of the box respectively. Letters indicate significant differences between land-use types. For panels (a), (b), (c) and (e), results are based on the Kruskal–Wallis rank sum test ($p < 0.05$) and Dunn's post hoc test. For panels (d) and (f), results are based on ANOVA and a Tukey's honestly significant difference (HSD) post hoc test (Appendix S5–S10)

agroforests of 12 species. Forest fragments had a median of 36 species (Figure 2e; Appendix S9).

Furthermore, forest-derived and fallow-derived agroforests differed significantly in both species richness ($q = 0$) and community evenness (Shannon diversity $q = 1$ and Simpson diversity $q = 2$), as indicated by the rarefaction and extrapolation curves with non-overlapping 95% confidence intervals (Figure 3). Comparing species richness ($q = 0$) and community evenness ($q = 1$ and $q = 2$) for all land-use types, rarefaction and extrapolation curves revealed a significant difference between the group of forest-derived agroforests, forest fragments and old-growth forests and the group of fallow-derived agroforests and woody fallows (Figure 3).

The group of forest-derived agroforests, forest fragments and old-growth forests showed overlapping 95% confidence intervals for

species richness, indicating species pools of similar sizes (Figure 3; Appendix S12). Confidence intervals of Shannon diversity curves for these three land-use types also overlapped. Confidence intervals of Simpson diversity curves only overlapped for forest-derived agroforests and forest fragments, whereas old-growth forests were higher and confidence intervals did not overlap with any other land-use type.

For the group of fallow-derived agroforests and woody fallows, rarefaction and extrapolation curves for species richness indicated similar-sized species pools, even though woody fallows showed a larger confidence interval than fallow-derived agroforests (Figure 3). Additionally, both Shannon and Simpson diversity curves for these two land-use types overlapped, indicating similar community evenness (Figure 3; Appendix S12).
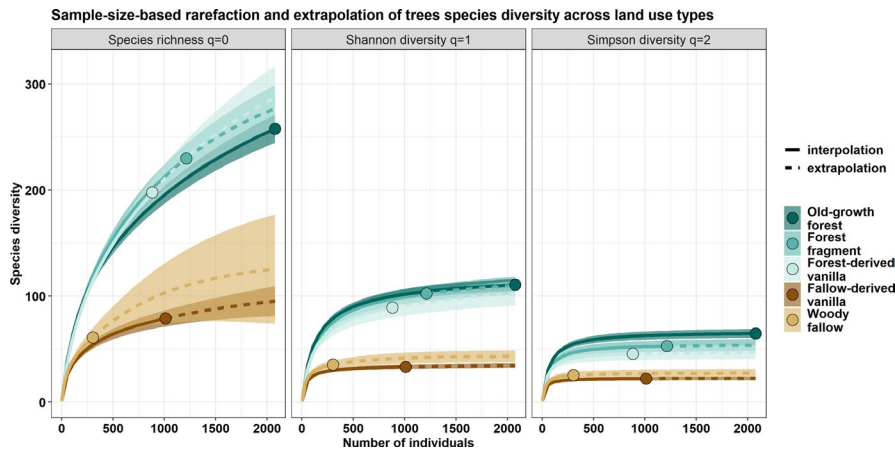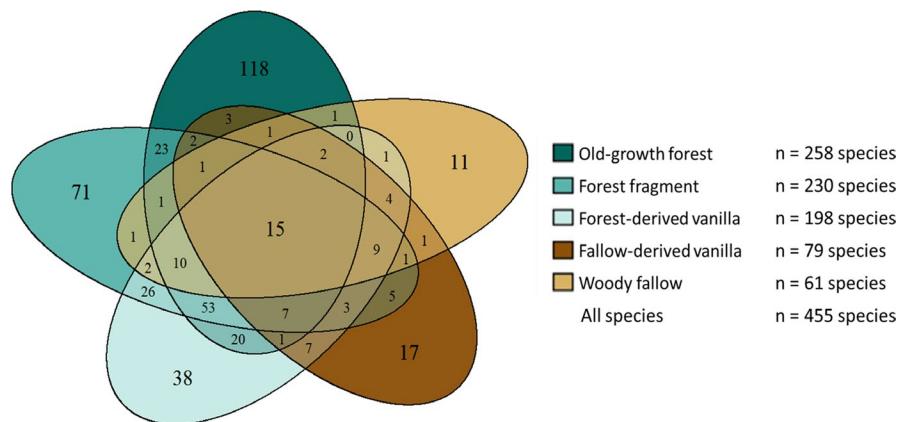
FIGURE 3 Sampling curves of sample size-based rarefaction (solid lines) and extrapolation (dashed curves), up to the base sample size of 2,078 individuals (the maximum reference sample size) of tree species diversity for Hill number orders $q = 0$, $q = 1$, and $q = 2$ across land-use types. The 95% confidence intervals (shaded regions) were obtained by a bootstrap method based on 200 replications (Appendix S12). Colours represent land-use types and reference samples are denoted by solid dots

FIGURE 4 Shared and exclusive tree species occurrence of 455 species in the five studied land-use types

Old-growth forest	n = 258 species
Forest fragment	n = 230 species
Forest-derived vanilla	n = 198 species
Fallow-derived vanilla	n = 79 species
Woody fallow	n = 61 species
All species	n = 455 species

3.3 | Tree species composition

Of all 455 inventoried tree species, 229 species (50%) occurred in the two vanilla agroforest types, among which 48 species occurred in both agroforest types and 150 only in forest-derived agroforests (Figure 4). Old-growth forests, forest fragments and forest-derived agroforests shared 53 species (14%) that did not occur in the fallow-derived agroforests or the woody fallows. The latter two shared 29 species (6%), that did not occur in any of the old-growth forest, forest fragment or forest-derived agroforest plots (Figure 4). Additionally, 221 species (47%) occurred only in old-growth forests or forest fragments, among these 118 species (26%) occurred exclusively in old-growth forest (Figure 4).

From the 455 species in this inventory, 279 (61%) were endemic, 114 (25%) native but not endemic, 34 (8%) introduced and 28 (6%) of unknown origin. Endemic species proportions per plot varied between the land-use types and spanned from a median of 75% in old-growth forests to 16% in fallow-derived agroforests (Figure 2f). In forest-derived agroforests, endemic species proportions had a median of

59%, which was significantly higher compared to fallow-derived agroforests (16%) and woody fallows (35%) (Figure 2f; Appendix S10).

Based on their proportional occurrence in each land-use type, the majority of the 279 endemic species were found in forest habitat: old-growth forests and forest fragments accounted for the largest share of endemic species and exclusively harboured 142 (51%) of the inventoried endemic species whereas we recorded only four (2%) endemic species exclusively in woody fallows or fallow-derived agroforests (Figure 5a). Forest-derived agroforests harboured 125 (45%), fallow-derived agroforests harboured 24 (9%), and woody fallows harboured 25 (9%) of the inventoried endemic species (Figure 5a).

The pattern was similar for the 114 native but not endemic species in our inventory. Old-growth forests and forest fragments accounted for the largest share of native species and exclusively harboured 57 (50%) of the inventoried native species, whereas we recorded only five (4%) native species exclusively on woody fallows or fallow-derived agroforests (Figure 5b). Forest-derived agroforests harboured 48 (42%), fallow-derived agroforests harboured 22 (19%),
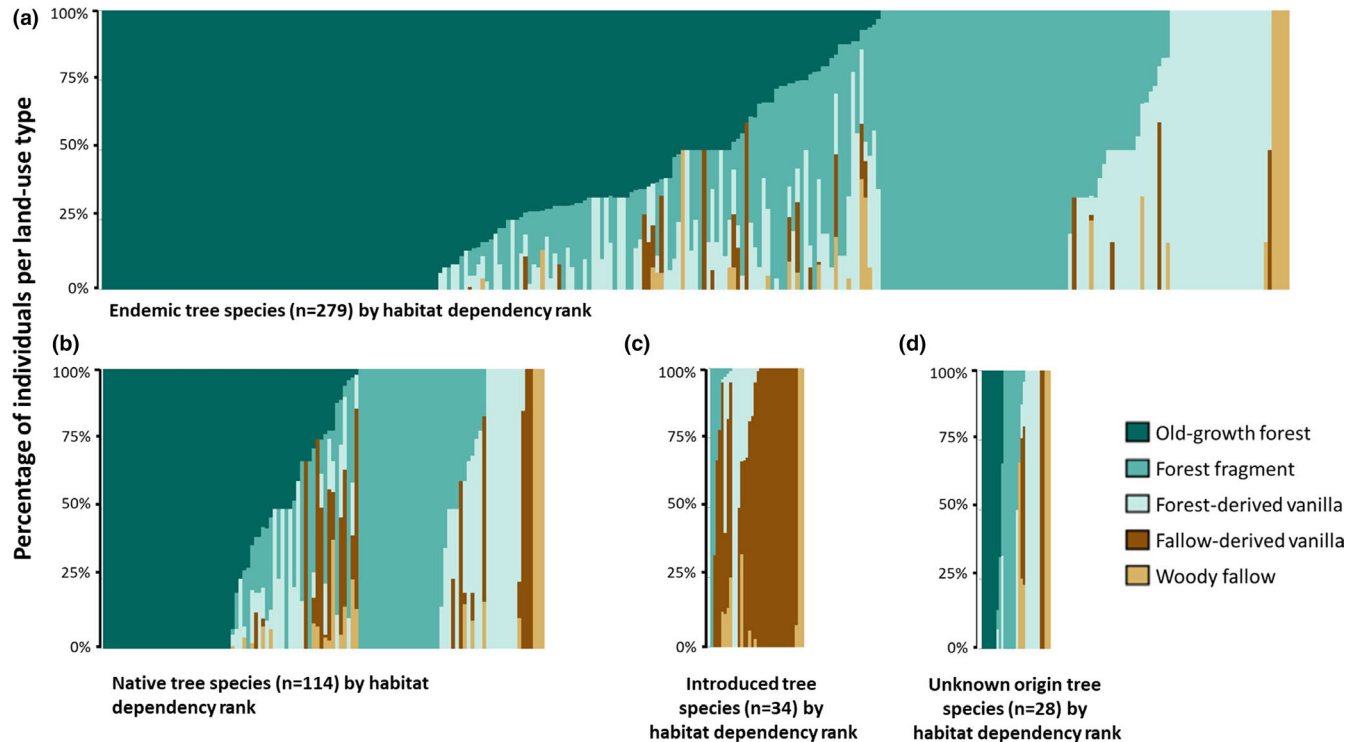
FIGURE 5 Forest dependency of 455 tree species and 5,484 tree individuals measured as the proportion of individuals of each species in each of the five land-use types: (a) proportion of 279 endemic species; (b) proportion of 114 native but not endemic species; (c) proportion of 34 introduced species; (d) proportion of 28 species of unknown origin in each of the five land-use types
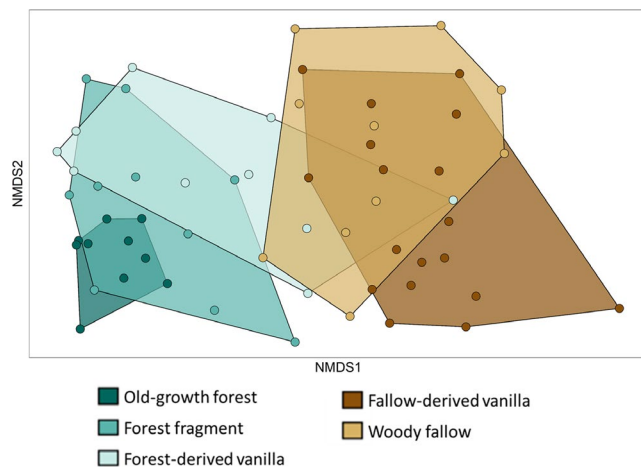

FIGURE 6 Species composition of the five land-use types as revealed by non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity ($k = 2$; stress level 0.19855). We tested for dispersion effects among groups (followed by a pairwise permutation test with 999 permutations) and identified dispersion differences between old-growth forest and all other land-use types (Appendix S13). Pairwise permutational multivariate analysis of variance (PERMANOVA, 999 permutations; with Bonferroni correction) between land-use types revealed significant differences between old-growth forest and all other land-use types. Forest-derived and fallow-derived vanilla agroforests also showed significant differences in species composition; all other pairs were not significantly different from each other (Appendix S14)

and woody fallows harboured 21 (18%) of the inventoried native species (Figure 5b).

Among the 34 introduced species, 29 (85%) species occurred in fallow-derived agroforests (Figure 5c) and 14 (41%) species were also found in forest-derived agroforests. Additionally, 10 (29%) species were recorded in woody fallows, eight (24%) species in forest fragments and no species in old-growth forests (Figure 5c). From the 28 species of unknown origin in our inventory, 75% were recorded only in forest-derived agroforests, old-growth forests and forest fragments (Figure 5d).

The land-use types differed in species composition, particularly between the group of forest-derived agroforests, forest fragments and old-growth forests and the group of fallow-derived agroforests and woody fallows, indicated by clear and tight clusters from the NMDS ordination (Figure 6). Significant differences in dispersion occurred between old-growth forests and all other land-use types but were not significant between vanilla agroforests (Appendix S13). Furthermore, species composition in forest- and fallow-derived agroforests was significantly different, as revealed by PERMANOVA results (Appendix S14). Species composition in forest-derived agroforests was more similar to that in forest fragments than in fallow-derived agroforests. Additionally, species composition in fallow-derived agroforests was more similar to that in woody fallows than in forest-derived agroforests, forest fragments or old-growth forests. Species composition in old-growth forests was significantly different compared to all other land-use types, as revealed by PERMANOVA results (Appendix S14).

4 | DISCUSSION

The mosaic landscape of northeastern Madagascar comprised a wide range of stand structure attributes and a high tree species diversity. We show that land-use history determined stand structure, tree diversity and community composition in vanilla agroforests. Forest-derived agroforest harboured a significantly higher tree diversity and a different community composition than fallow-derived agroforest with more endemic tree species in forest-derived agroforests compared to fallow-derived agroforests. Total and endemic tree species diversity in forest-derived agroforests was more similar to that in forest fragments and old-growth forests than that in fallow-derived agroforests; in the latter it was more similar to diversity in woody fallows than in forest-derived agroforests. We thus demonstrate that forest-derived agroforests can play an important role in providing habitat for forest-dependent tree species, but they result from forest degradation. In contrast, fallow-derived agroforests play a marginal role for tree species diversity but contribute to the recovery of stand structure on historically forested degraded land.

4.1 | Stand structure

Stem density, basal area, canopy closure and LAI were highest in old-growth forests. The median basal area in old-growth forests of 41 m²/ha was similar to the median value of 39 m²/ha for Malagasy lowland rainforests (Ibanez et al., 2019). Also the LAI median of 5.1 in old-growth forests in our study was similar to the mean LAI of 4.8 in tropical evergreen humid forests (Asner et al., 2003), indicating a continuous and little disturbed canopy. The significant decline of LAI from old-growth forests to forest fragments, vanilla agroforests and woody fallows indicates a structural simplification along with changing light regimes, that may affect the growth and mortality of tree seedlings and saplings and influence tree species diversity and composition (Montgomery & Chazdon, 2001; Rocha-Santos et al., 2016). The observed structural simplification is likely caused by different levels of human interference (Allnutt et al., 2013) or natural forces, e.g. cyclones (de Gouvenain & Silander, 2003).

Within vanilla forests, we observed variability in stand structure characteristics, where forest-derived vanilla agroforests were more similar to forest fragments, and fallow-derived agroforests were more similar to woody fallows. This further suggests that past land use is the main driver for stand structure dynamics and recovery opportunities in tropical tree-dominated habitats (Chazdon, 2003). Observations in other agroforestry systems also reported significant variations in stand structure characteristics within agroforests (e.g. Moguel & Toledo, 1999; Rappole et al., 2003; Hending et al., 2020) and even though these studies did not specifically address or report land-use history, the observed stand structure variation within these agroforests might also be influenced by land-use history differences. However, a case study from Cameroon reported that forest- and savannah-derived cacao agroforests exhibit an increasingly comparable stand structure within maturing agroforest (Nijmeijer

et al., 2019). Also, a chronosequence from vanilla agroforests in Madagascar showed that canopy structures initially differ but fallow-derived agroforests increase their canopy structures which become more similar to forest-derived agroforest canopy structures over time (Martin et al., 2020b). This indicates that forest-derived agroforests initially exhibit a higher canopy closure and basal area than fallow-derived agroforests but stand structure characteristics have the potential to become more similar over time.

Other species groups such as birds also respond to agroforest land-use history across the same plots: fallow-derived agroforests provide less valuable bird habitat but indirectly favour birds by contributing to recover stand structure on open, historically forested land (Martin et al., 2021). In contrast, forest-derived agroforests provide more valuable bird habitat and avoid total loss of natural tree cover even though they result from forest degradation which affects birds negatively (Martin et al., 2021). Yet, our results indicate that fallow-derived agroforests have the potential to recover stand structure characteristics and become structurally similar to forest-derived agroforests and this structural alignment becomes stronger over time (Martin et al., 2020b).

4.2 | Tree species diversity

Land-use history strongly determined tree species diversity in vanilla agroforests: vanilla agroforests harboured 229 species (50%) of all inventoried tree species and tree species diversity in forest-derived agroforests was more than twice as high as in fallow-derived agroforests. Overall, tree diversity in forest-derived agroforests was more similar to that in old-growth forests and forest fragments whereas tree diversity in fallow-derived agroforests was more similar to that in woody fallows. Therefore, we confirm that vanilla agroforests can play a substantial role in maintaining high levels of tree diversity within the human-modified landscape (Hending et al., 2020). In addition, we highlight that considering land-use history is pivotal to assess the conservation value of vanilla agroforests.

Additionally, tree species diversity in Madagascar is closely linked to the survival of other species groups such as lemurs (Ganzhorn et al., 1997). Given that many lemur species face extinction risk driven by habitat loss and human disturbance (Schwitzer et al., 2013; Schwitzer et al., 2014), they critically depend on the structural and phenological variability of trees offering a broad range of microhabitats and food resources for lemurs (Ganzhorn et al., 1997). Beside its ecological importance, tree diversity is also of benefit to human well-being by providing shade, fruits and a range of products, thereby reducing vulnerability to environmental, economic or social shocks (Reed et al., 2017). Especially in Madagascar, a high share of the country's population lives in rural areas with low infrastructure, and therefore their livelihoods highly depend on natural resources and tree products for domestic use and off-farm income (Zaehringer et al., 2017). Additionally, maintaining tree diversity may also increase resilience in light of climate change (Isbell et al., 2011).

4.3 | Tree species composition

Our results further show that land-use history strongly determines tree species composition in vanilla agroforests. In forest-derived agroforests, tree community composition partly overlapped with that in forest fragments, indicating that forest-derived agroforests provide the option to incorporate many forest trees into agricultural production systems, with only moderate compositional changes and species turnover compared to forest fragments. Especially if management practices allow for natural regeneration of native and endemic trees, these agroforests have the potential to contribute to long-term tree conservation in the agricultural landscape, as shown for other tropical agroforestry systems (Valencia et al., 2016).

Fallow-derived agroforests harboured proportionally fewer endemic tree species than woody fallows, but the community composition in both land-use types still overlapped, indicating that the transition from woody fallows to fallow-derived agroforests might not result in strong tree species turnover. Additionally, natural forest regrowth on woody fallows in Madagascar after slash-and-burn agriculture seems to be slow and often dominated by a few fast-growing pioneer species, eventually leading to a complete loss of woody species after several cropping cycles (Styger et al., 2007; Manjaribe et al., 2013; Zwartendijk et al., 2017).

Tree species communities in both agroforest types also included introduced species. These non-native species can act as invaders and alter habitat dynamics (Bos et al., 2008). However, non-native tree species also contribute to increase canopy cover and basal area and can also ameliorate degraded soils and promote understorey growth (Bollen & Donati, 2006). Furthermore, non-native trees can serve as important components in resilient smallholder farming landscapes and form fundamental pillars of the local economy and daily needs, such as for cash crop cultivation (e.g. clove) or fruit cultivation (Kull et al., 2014; Zaehringer et al., 2017).

Additionally, tree species community composition in old-growth forests was unique compared to all human-modified land-use types. Even though these differences might partly be driven by variances in group dispersion, as old-growth forests plots were spatially closer together than all other land-use type plots, the differences strongly indicate species turnover between old-growth forests and all other land-use types. Especially among endemics, 28% occurred exclusively in old-growth forests. Even though many endemics are rare and poorly studied, and there is limited understanding of individual species habitat requirements and dispersal syndromes (Buerki et al., 2013), more than 60% of the Malagasy endemic tree genera are known to be confined to humid forests for their survival (Schatz, 2001). Palms also exhibit a high diversity in Madagascar (Dransfield & Beentje, 1995) and were most abundant and diverse in old-growth forests. Given that more than 83% of Malagasy palm species are ranked as threatened due to habitat loss (Rakotoarinivo et al., 2014), this further underlines the irreplaceable value of old-growth forests for biodiversity in Madagascar (Schatz, 2001; Brown et al., 2015) and elsewhere (Gibson et al., 2011).

A loss of tree species in general and endemic and forest-dependent species in particular might also have cascading effects on functionally linked species groups, which depend on trees as habitat-providing elements and food resources (Ganzhorn et al., 1997; Irwin et al., 2010; Herrera, 2016). Furthermore, tree species composition might be influenced by seed dispersers such as frugivorous lemurs (Martinez & Razafindratsima, 2014). However, identifying and understanding the specific drivers of tree community change in agroforests, natural forest and fallow sites would strongly improve the development of management schemes to maintain tree species diversity in mosaic smallholder landscapes; however, this goes beyond the scope of this paper.

4.4 | Conservation implications

Vanilla agroforests rarely undergo drastic clearing after their initial establishment (Martin et al., 2020b) and if agroforest management interventions allow natural tree regeneration, the stand structure might recover at the plot level over time (Jagoret et al., 2018) and might even result in a canopy cover increase at the landscape scale (Martin et al., 2020c). Additionally, the establishment of agroforests on historically forested open land prevents further degradation on lands under slash-and-burn cultivation (Styger et al., 2007). Depending on management activities such as tree planting, cutting and pruning, both agroforest types might contribute to maintain or restore stand structure and functional processes and also contribute to increase canopy cover on the plot and landscape scale over time (Martin et al., 2020b). This becomes specifically important, as forest fragments in agricultural landscapes are likely to disappear over time (Schüßler et al., 2020). Indeed, predictions show that Malagasy lowland rainforest trees are vulnerable to both individual and combined effects of land use and climate change (Brown et al., 2015). Similar scenarios are unfolding in other tropical countries resulting in a worrying decline of the pantropical forest cover, despite protected areas (Hansen et al., 2020). Consequently, agroforests can enhance connectivity, dispersal and movement within a landscape matrix, as the matrix becomes structurally more similar to the remnant patches (Driscoll et al., 2013).

We conclude that forest-derived agroforests represent an alternative to forest conversion by slash-and-burn agriculture and have the potential to serve as habitat refugia and biodiversity reservoirs for forest-dependent species. If diverse and dense canopies are maintained, forest-derived agroforests can sustain high levels of tree species diversity and important habitat structures, corroborating results of Martin et al.(2020a). However, agroforests represent a degradation and a structural simplification in comparison to old-growth forests. If old-growth forests continue to decline, agroforests cannot replace these habitats. At the landscape scale, old-growth forest transformation may lead to habitat and species homogenization with negative and strong far-reaching impacts upon ecosystem stability and multifunctionality (Beenhouwer et al., 2013; van der Plas et al., 2016). Therefore,

we strongly argue against agroforest establishment in old-growth forests as it would decrease habitat complexity and impair native and endemic tree species and other forest-dependent species and is therefore not justifiable. Furthermore, if old-growth forest habitats are protected, the legal establishment of forest-derived agroforests can exclusively take place in forest fragments. However, forest fragments are important to maintain tree species diversity and habitat structures and should also be integrated into conservation schemes within multifunctional human-modified landscapes (Duriaux Chavarría et al., 2018).

Fallow-derived agroforests only have a limited contribution to maintaining tree diversity. However, fallow-derived agroforests permanently integrate trees into agricultural production. They also regain stand structure on degraded historically forested land and this structural alignment becomes stronger over time, thereby contributing to an increase in canopy cover and connectivity at the landscape scale (Martin et al., 2020b). This re-establishment of stand structure and vegetation on historically forested fallow land might also result in a quicker rehabilitation and build-up of soil nutrient stocks (Klanderud et al., 2010). Furthermore, fallow-derived agroforests can be integrated as a restoration approach into certification schemes to provide incentives to farmers to maintain or plant trees on historically forested open land (Giudice Badari et al., 2020). Especially since Madagascar is among the countries with highest mean restoration opportunity scores (Brancalion et al., 2019), fallow-derived vanilla agroforests could be integrated into the national restoration agenda.

Our findings show that agroforests should not be considered as a substitute but as an addition to forest conservation at the landscape level. Thus, agroforests can represent a means to retain or increase tree cover and connectivity in a multifunctional landscape, but it is key to consider their land-use history and management to unfold their full conservation potential and to mitigate further degradation and species loss.

AUTHOR CONTRIBUTIONS
KO, DAM, AW, MRS, HLTR and DH conceived the ideas and designed methodology; KO and MRS collected tree inventory data; KO and AM collected canopy closure and LAI data; KO processed and analyzed the data; KO led the writing of the manuscript. All authors contributed to the manuscript and gave final approval for publication.

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SUPPORTING INFORMATION

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

Appendix S1 Specification on the selection of old-growth forest sites

Appendix S2 Data on plot characteristics of 58 study plots with plot coordinates and environmental characteristics (available on OSF: https://doi.org/10.17605/OSF.IO/24Z6P)

Appendix S3 Data on tree derived variables such as stem density, basal area, mean canopy closure, mean LAI, species richness and percentage of endemic tree species of 58 study plots (available on OSF: https://doi.org/10.17605/OSF.IO/24Z6P)

Appendix S4 Specification of origin and endemism determination for each tree species

Appendix S5 Numeric test results comparing stem density (stems/ha) across land-use types as displayed with letters in Figure 2a of the main manuscript, based on a Kruskal–Wallis one-way analysis of variance and Dunn's post hoc test

Appendix S6. Numeric test results comparing basal area (m^2/ha) across land-use types as displayed with letters in Figure 2b of the main manuscript, based on a Kruskal–Wallis one-way analysis of variance and Dunn's post hoc test

Appendix S7 Numeric test results comparing mean canopy closure (%) across land-use types as displayed with letters in Figure 2c of the main manuscript, based on a Kruskal–Wallis one-way analysis of variance and Dunn's post hoc test

Appendix S8 Numeric test results comparing mean Leaf Area Index (m^2/m^2) across land-use types as displayed with letters in Figure 2d of the main manuscript, based on one-way ANOVA and Tukey's honestly significant difference (HSD) post hoc test

Appendix S9. Numeric test results comparing species richness per plot across land-use types as displayed with letters in Figure 2e of the main manuscript, based on a Kruskal–Wallis one-way analysis of variance and Dunn's post hoc test

Appendix S10 Numeric test results comparing percentage of endemic species per plot across land-use types as displayed with letters in Figure 2f of the main manuscript, based on one-way ANOVA and Tukey's honestly significant difference (HSD) post hoc test

Appendix S11 Data on 455 species and morphospecies, botanic families, geographic origin and occurrence per land-use type (available on OSF: https://doi.org/10.17605/OSF.IO/24Z6P)

Appendix S12. Hill numbers $q = 0$ (species richness); $q = 1$ (Shannon diversity) and $q = 2$ (Simpson diversity) and sample coverage per land use type

Appendix S13 Results of multivariate dispersion test (betadisp) based on a Bray–Curtis dissimilarity matrix and a pairwise permutation test (permutest, 999 permutations)

Appendix S14 Results of the pairwise permutational multivariate analysis of variance (PERMANOVA, 999 permutations) with a Bonferroni correction to test for differences in tree species composition between land-use types