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Land-use intensification increases richness of native and exotic herbaceous plants, but not endemics, in Malagasy vanilla landscapes

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Abstract

Aim: North-eastern Madagascar is a hotspot of plant diversity, but vanilla and rice farming are driving land-use change, including slash-and-burn management. It still remains unknown how land-use change and land-use history affect richness and composition of endemic, native and exotic herbaceous plant species.

Location: North-eastern Madagascar.

Methods: We assessed herbaceous plants along a land-use intensification gradient ranging from unburned land-use types (i.e. old-growth forest, forest fragment and forest-derived vanilla agroforest) to burned land-use types (i.e. fallow-derived vanilla agroforest, woody fallow and herbaceous fallow) and rice paddy. We compared land-use types and analysed the effects of land-use history, canopy closure and landscape forest cover on species richness. Additionally, we analysed species compositional changes across land-use types.

Results: Across 80 plots, we found 355 plant species (180 native non-endemics, 57 exotics, 60 endemics and 58 species of unknown origin). Native and exotic species richness increased with increasing land-use intensity, whereas endemics decreased. Unburned land-use types had higher endemic species richness (4.28 ± 0.37 [mean ± *SE*]) than burned ones (2.4 ± 0.21). Exotic and native species richness, but not endemics, decreased with increasing canopy closure. Increasing landscape forest cover reduced exotic, but not native or endemic richness. Species composition of old-growth forests was unique compared to all other land uses and forest-derived, not fallow-derived vanilla agroforests, had a similar endemic species composition to forest fragments.

Main conclusions: Our results indicate that old-growth forests and forest fragments are indispensable for maintaining endemic herbaceous plants. We further show that

the land-use history of agroforests should be considered in conservation policy. In forest-derived vanilla agroforests, management incentives are needed to halt loss of canopy closure, thereby maintaining or even enhancing endemics. In conclusion, considering species origin (endemic, native and exotic) and composition is essential for the identification of suitable management practices to avoid irreversible species loss.

KEYWORDS

Herbaceous plants, land-use history, Madagascar, slash-and-burn, species origin, vanilla agroforest

1 | INTRODUCTION

Madagascar is one of the principal centres of vascular plant diversity in the world (Kreft & Jetz, 2007; Mutke et al., 2011) with more than 80% endemic species (Callmander et al., 2011). Most of the Malagasy endemic flora has only been found in old-growth forests (Ganzhorn et al., 2014; Irwin et al., 2010), making their conservation a priority (Gibson et al., 2011; Mittermeier et al., 1998). However, during the last six decades, nearly half of the Malagasy forest cover has been lost due to land-use change and now only about 15% of the country is forested (Harper et al., 2007; Vieilledent et al., 2018a). The remaining protected natural forests are still subjected to pressures (e.g. selective logging, hunting) that reduce the effectiveness of the protected areas to preserve their biodiversity (Geldmann et al., 2019; Laurance et al., 2012). Hence, concerns arose on the ability of protected natural forests in Madagascar, like in many other tropical countries, to preserve their biodiversity in the future.

Conservationists and researchers have suggested agroforestry systems as another way to sustain biodiversity while producing food (Bhagwat et al., 2008). Agroforestry systems can harbour high biodiversity (Finegan & Nasi, 2004; Phalan et al., 2011; Steffan-Dewenter et al., 2007) and have values for ecosystem services (Tscharntke et al., 2011). Structurally complex agroforestry systems maintain more biodiversity compared to intensified plantations (De Beenhouwer et al., 2013). In addition, complex agricultural landscapes that include agroforestry systems can help to prevent local extinction of species and maintain ecosystem services for crops with natural forest cover in the matrix (Grass et al., 2019). To increase the effectiveness of protected areas in maintaining biodiversity, agricultural matrices should thus be considered since agriculture has become dominant in tropical regions (Perfecto & Vandermeer, 2008).

Tropical agricultural landscapes can take many different forms. For instance, in north-eastern Madagascar, the agricultural landscape is mainly dominated by small-scale agriculture converted from rainforest (Llopis et al., 2019). In the region, vanilla, a vine and hemi-epiphytic orchid that requires a support tree and shade, is farmed in small-scale agroforestry systems (Hänke et al., 2018; Havkin-Frenkel & Belanger, 2010). This crop can be planted directly inside a forest, without using fire, or on open-land, that has been derived from slash-and-burn agriculture (i.e. *tavy*, a slash-and-burn agricultural technique used in Madagascar; Martin, Osen, et al., 2020). However, little is known about how forest conversion into cropland affects plant

biodiversity taking into account land-use history of agroforests in the tropics (exception see Martin, Osen, et al., 2020; Shumi et al., 2019).

North-eastern Madagascar is the largest producer of vanilla in the world (FAO, 2020; The World Bank, 2019). The region retains a higher forest cover compared to other regions of Madagascar (Vieilledent et al., 2018a) and is thus considered as a conservation priority area (Rogers et al., 2010). However, slash-and-burn agriculture associated with staple crops such as rice remains the main driver of deforestation in the region (Zaehringer et al., 2016). Moreover, in the last decade, there has been a considerable increase in the price of vanilla, resulting in the conversion of remaining forests to vanilla agroforests (Llopis et al., 2019). Analysing the value of vanilla production landscapes for sustaining plant biodiversity is therefore necessary to develop conservation strategies for human-modified land-use types. Although preserving endemic species is a key objective of biological conservation globally (Tucker et al., 2012), there has been only one study assessing how endemic, native and exotic plant species richness respond to on-plot vegetation structure in vanilla agroforest (see Hending et al., 2019). To date, few studies assessed how herbaceous plant communities are affected by land-use history in agricultural landscapes in Madagascar.

In this paper, we assessed the effect of land-use change on herbaceous plants in the Malagasy vanilla production landscapes using species richness and community composition as measures. Our four research objectives were to: (1) investigate species richness and endemism of herbaceous plants along a land-use intensification gradient; (2) identify land-use practices that sustain the greatest amount of endemic and native, but least exotic plants; (3) assess the effects of land-use history, shade and surrounding landscape forest cover on species diversity; and (4) evaluate dissimilarities between land-use types in terms of species compositions and growth forms. We hypothesized that the response of herbaceous plant species richness to land-use intensification and environmental parameters would differ based on the species' origin. Additionally, we expected a response of species composition to land-use intensification.

2 | MATERIALS AND METHODS

2.1 | Study area and study design

We carried out fieldwork in 2018 in the SAVA (Sambava, Antalaha, Vohemar, Andapa) region in north-eastern Madagascar. The climate

in the region is tropical humid (annual rainfall of 2,223 mm) with a mean annual temperature of 24°C (mean across 80 plots, data extracted from Karger et al. (2017)). The original vegetation is tropical rainforest classified as lowland humid evergreen forest (Moat & Smith, 2007).

Across the study region, we selected 12 sites: two sites inside Marojejy National Park and 10 villages (Figure 1a; for more details on villages selection see Appendix section 1a). In each site of Marojejy NP, we selected five plots of old-growth forest and in each village, we selected seven plots: one forest fragment, one woody fallow, one herbaceous fallow, one rice paddy and three vanilla agroforests. Overall, we selected 80 plots (70 plots in villages and 10 plots in old-growth forest sites). The size of each plot was 25 m radius. The average distance from one plot to the closest neighbouring plot was 719 m (±438 m) with a minimum of 260 m. The average elevation was 192 m.a.s.l. (±207 m.a.s.l.) with minimum of 7 m.a.s.l. and maximum of 819 m.a.s.l. For our study, we categorized vanilla agroforests based on their land-use history: forest-derived vanilla agroforest and fallow-derived vanilla agroforest. Thus, we had seven land-use types: Old-growth forest, Forest fragment, Forest-derived vanilla agroforest, Fallow-derived vanilla agroforest, Woody fallow, Herbaceous fallow and Rice paddy (Figure 1b).

Old-growth forest (N = 10) was exclusively located in Marojejy NP. In our study region, only Marojejy NP had largely intact forest at an elevation below 800 m.a.s.l (see Appendix section 1b for

more details). *Forest fragment* (N = 10, one plot per village) represented remaining natural forest outside of protected areas which was small and heavily used for timber extraction. *Forest-derived vanilla agroforest* (N = 10 up to three plots per village) referred to vanilla agroforests planted directly inside a forest by removing small trees and clearing the shrubby understory vegetation without fire. *Fallow-derived vanilla agroforest* (N = 20, up to three plots per village) represented a vanilla agroforest that was established on fallow land. Fallow land is a stage within the slash-and-burn cultivation cycle (*Malagasy: tavy*), where fallow land is abandoned for periods of varying duration before it is used for another cultivation cycle. To establish a vanilla plantation on fallow land, farmers used existing tree structures and/or plant additional trees to provide both shade and climbing structures for the vanilla orchids (Martin, Osen, et al., 2020). Forest- and fallow-derived vanilla were not always present in all villages which has created an uneven distribution of our land-use types (Figure 1b; see Appendix section 1c for further details). *Woody fallow* (N = 10, one plot per village) represented land that was used for slash-and-burn agriculture 5–17 years prior to the study and where shrubs and small trees have regrown and formed secondary vegetation. Woody fallow is occasionally used by villagers for zebu grazing and for extracting wood for construction, fire-wood and charcoal production. *Herbaceous fallow* (N = 10, one plot per village) referred to land that was used for hill rice production as part of
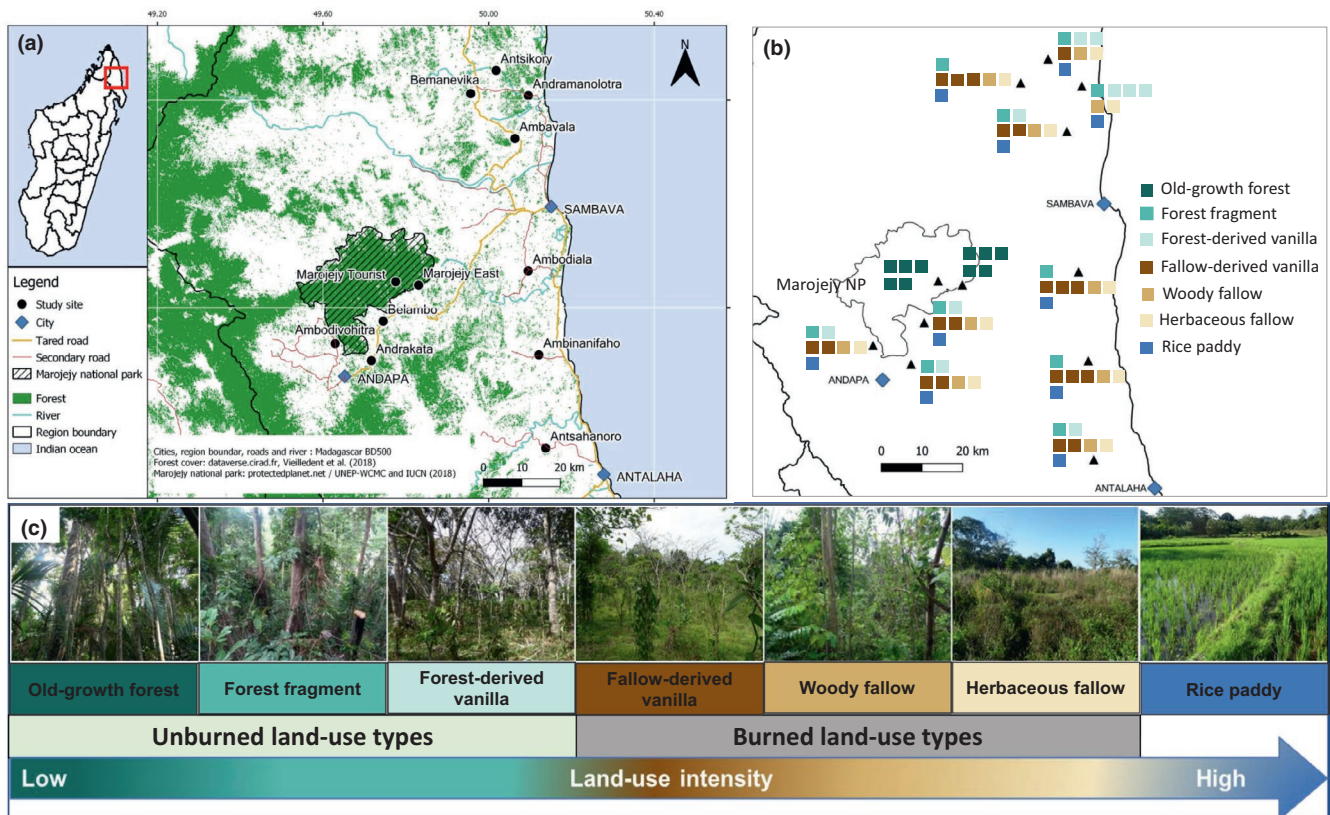

FIGURE 1 Study design overview. Map of study sites with the forest cover of the study region in 2017 from Vieilledent et al. (2018b) (a), representation of land-use types in each site (b), and photographs of land-use types along the land-use intensity gradient (c) in north-eastern Madagascar

slash-and-burn agriculture two years before the data collection. The land was dominated by herbaceous plants, but few shrubs had regenerated naturally. *Rice paddy* (*N* = 10, one plot per village) was an irrigated rice field and represented the most intensive land use in the region (Figure 1c). In our study region, rice paddies are small units of flooded fields and divided or structured by banks.

Based on these descriptions, land-use types differed largely based on their land-use history and we therefore categorized them into lands that had never been burned before, hereafter called *unburned land-use types* (old-growth forest, forest fragment and forest-derived vanilla agroforest) and land formerly used for or part of slash-and-burn agriculture cycle hereafter called *burned land-use types* (fallow-derived vanilla agroforest, woody fallow and herbaceous fallow). We did not assign rice paddy to neither burned or unburned land-use history, but kept it as an individual category called rice paddy, as it represents agricultural land in the floodplain which is not commonly converted from or to other land-use types described in this study.

We defined the order of land-use types along the land-use intensity gradient based on their land-use history, tree stem density and usage (e.g. grazing and extraction of wood). We considered that lands with low tree stem density had higher land-use intensity compared to lands with higher tree stem density. Therefore, our land-use intensity gradient was, from low to high land-use intensity, as follows: old-growth forest, forest fragment, forest-derived vanilla agroforest, fallow-derived vanilla agroforest, woody fallow, herbaceous fallow and rice paddy (Figure 1c).

2.2 | Herbaceous plants assessment and species origin categorisation

In each plot, we evenly distributed eight subplots of 2 m × 2 m at fixed positions (see Figure S1). For rice paddy, we used the rice field banks to assess the herbaceous plants to avoid bias from temporal changes within rice fields (before and after harvest) as the rice field banks are less affected by rice cultivation or harvest. In each rice paddy plot, we established our subplots on the banks covering the standardized 4 m^2 area but with varying length and width depending on the size of the bank and we kept an even distance between each subplot. In each subplot, we assessed herbaceous vascular plants by selecting only plants that did not possess a woody stem above ground at maturity and counted their abundance (individual plant number). When a species was very dominant in one subplot, we estimated their abundance by extrapolating the number of individual plant from a small area (10 cm x 10 cm) in which we could count the individual plant (Carpenter et al., 1999). We also attributed each species to one of the following categories based on its growth form: fern, vine (climbing plants excluding fern), graminoids (Poaceae and Cyperaceae) and other herb (non-climbing flowering herbs). We collected herbarium samples when the identification of a species was impossible in the field. We deposited all herbarium specimens (1,879 specimens in total) at the herbarium

of the Plant Biology and Ecology Department at the University of Antananarivo in Madagascar.

For each species assessed and identified, we searched whether it is endemic (i.e. it exists only in Madagascar), native non-endemic (hereafter called *native*, exists naturally in Madagascar but also elsewhere) or introduced (hereafter called *exotic*, does not exist in Madagascar naturally) using the following online plant databases: Catalogue of the Plants of Madagascar (Madagascar Catalogue, 2019), African Plant database (CJB-SANBI, 2019), GBIF (GBIF.org, 2019) and Plants of the World online (The Royal Botanic Gardens Kew, 2019; see detailed description in Appendix Section 1).

2.3 | Canopy closure and landscape forest cover assessment

We derived mean canopy closure values from five hemispherical images per plot using a Nikon D5100 camera equipped with a Sigma Circular Fisheye 4.5 mm 1:2.8 lens (see detailed description in Appendix Section 2). On rice paddy and herbaceous fallow plots, we did not measure canopy closure but assumed 0% canopy closure as these two land-use types did not contain any trees.

To determine the landscape forest cover surrounding each of our plots, we used forest cover data from Vieilledent et al. (2018b) based on 2017 binary (Forest / non-forest) forest cover data with 30 m resolution. We performed the calculation in R version 3.6.1 (R Core Team, 2019) using the R-package "raster" (Hijmans, 2019) within a 500 m radius buffer around plot centres. The 500 m radius buffer was chosen to minimize overlap between buffers as well as allow a meaningful characterisation of the surrounding landscape (Roschewitz et al., 2005).

2.4 | Data analysis

We performed all data analysis and visualization using R version 3.6.1 (R Core Team, 2019). For our analysis, we aggregated the data from all subplots to the plot level by summing up the species abundance and combining all species assessed. To measure the completeness of our samples and estimate species accumulation per land-use type, we computed coverage-based rarefaction and extrapolation curves and individual-based species accumulation curves with abundance data using the R-package *iNEXT* (Hsieh et al., 2016).

To depict the variation of species richness across the land-use intensification gradient, we fitted overall, native, exotic and endemic species richness separately in generalized linear mixed models (GLMMs) with the R-package "glmmTMB" (Brooks et al., 2017) using land-use types as a fixed effect and villages (including the two old-growth forest sites) as a random effect. We applied generalized Poisson family (Consul & Famoye, 1992) for overall and native species richness due to significant over/under-dispersion indicated by the R-package "DHARMa" (Hartig, 2020), and Poisson family for endemic and exotic species

richness. Then, we evaluated the differences between land-use types using one-way ANOVA and Tukey post hoc test with function *glht* in the R-package "multcomp" (Hothorn et al., 2008) at the $p < .05$ level.

To analyse the effects of environmental parameters on overall, endemic, native and exotic species and to understand the drivers of species richness across land-use intensification, we refitted their species richness separately using GLMMs with the R-package "glmmTMB." We used village and land-use type as random effects and we applied generalized Poisson family for overall, native and endemic richness and Poisson family for exotic species richness. For overall and each species origin, we used land-use history, canopy closure and landscape forest cover as fixed explanatory variable in the full model. Then, we performed model ranking based on Akaike's information criterion (AICc; Burnham & Anderson, 2004), using the *dredge* function of the R-package "MuMIn" (Barton, 2019) and we selected the models with the lowest AICc as final models. When land-use history was included in a final model, we performed a Tukey post hoc test to compare unburned land-use types, burned land-use types and rice paddy to one another using the function *glht* of the R-package "multcomp." For all variables and the multi-comparisons, we considered $p < .05$ as a significant effect or difference. To visualize both, the variation of species richness across land-use types and the effect of environmental variables on species richness, we used the R-package *ggplot2* (Wickham, 2016).

To study species compositional changes across land-use types, we calculated Jaccard dissimilarity index of overall species as well as native, exotic and endemic species separately using the function *vegdist* of the R-package "Vegan" (Oksanen et al., 2019). We used non-metric-multidimensional-scaling (NMDS) to visualise the overall species compositional differences with the function *metaMDS* of the R-package "Vegan." To show which land-use types are associated to which growth forms, we correlated each growth form's proportion (= species number of each growth form out of overall number of species) across plots on top of the NMDS using the function *envfit* of the R-package "Vegan." We tested for significant differences in species composition between land-use types for all species and the three origin categories by performing permutational multivariate analysis of variance (PERMANOVA) with 999 permutations using the function *adonis* in the R-Package "Vegan." Then, we did pairwise comparisons of land-use types in terms of species composition using the function *pairwise.adonis* in the R-package "pairwiseAdonis" (Arbizu, 2017) with 999 permutations. Additionally, we visualised the co-occurrence of native, exotic and endemic species across the seven land-use types using the R-package "UpSetR" (Conway et al., 2017).

3 | RESULTS

In total, we recorded 44,248 herbaceous plants across 80 plots. Overall, we found 355 plant species of which we identified 294 at species level and 61 as morphospecies (Table S1). We considered three morphospecies as endemic because they belonged to endemic genera of Madagascar and considered the remaining 58 morphospecies as of unknown origin. Among all 297 species attributed to an origin category, 60 were endemic to Madagascar, 180 were native and 57 were exotic.

Based on the coverage-based rarefaction and extrapolation curve, all land-use types presented an adequate sampling effort with sample coverage of more than 98% (Figure S2a). The individual-based species accumulation curves showed that burned land-use types (except woody fallow) had higher species richness compared to unburned ones (Figure S2b). Rice paddy and fallow-derived vanilla agroforest had the highest accumulated species richness compared to other land-use types (Figure S2c). None of the land-use types showed clear asymptotic curves (Figure S2b–c).

3.1 | Species richness across land-use intensification gradient

Overall species richness, including 59 morphospecies, increased with increasing land-use intensity (Figure 2a). Forest fragments ([mean ± SD]: 14.1 ± 6.6) had the lowest species richness, whereas rice paddies (49.4 ± 7.6) had the highest species richness compared to other land-use types (Figure 2a; Table S2 and S3). We found no significant difference in overall species richness between forest-derived vanilla agroforests and fallow-derived vanilla agroforests, nor between forest fragments and old-growth forests (Figure 2a, Table S2).

Native and exotic species richness increased with increasing land-use intensity (Figure 2b-c). For both origins, old-growth forests (5.1 ± 3.3 for native, 0.9 ± 0.9 for exotic) and forest fragments (6.3 ± 4.5 for native, 1.5 ± 1 for exotic) had the lowest herbaceous plant species richness and rice paddies the highest (31.9 ± 4.2 for native, 14.6 ± 3.6 for exotic; Table S3). Fallow-derived vanilla agroforests had a higher exotic plant species richness compared to forest-derived vanilla agroforests, but we found no difference in native herbaceous plant species richness between the two types of agroforests (Figure 2b-c, Table S2 and S3).

In contrast to native and exotic species, endemic species richness decreased with increasing land-use intensity (Figure 2b). Old-growth forests (5.5 ± 2.5), forest fragments (4.4 ± 2.7) and forest-derived vanilla agroforests (3.9 ± 1.4) did not differ significantly from one another and had a higher endemic species richness compared to all other land-use types (Table S2 and S3). We found a significantly higher endemic species richness in forest-derived vanilla agroforests compared to fallow-derived vanilla agroforests (Figure 2b, Table S2 and S3). Forest-derived vanilla agroforests, woody fallows and herbaceous fallows did not differ in endemic species richness from each other (Figure 2b). Overall, rice paddies had the lowest number of endemic species (1.7 ± 0.7; Figure 2b, Table S3).

3.2 | Effect of environmental parameters on species richness

Based on our model selection, the best model for overall species richness and for native species richness included canopy
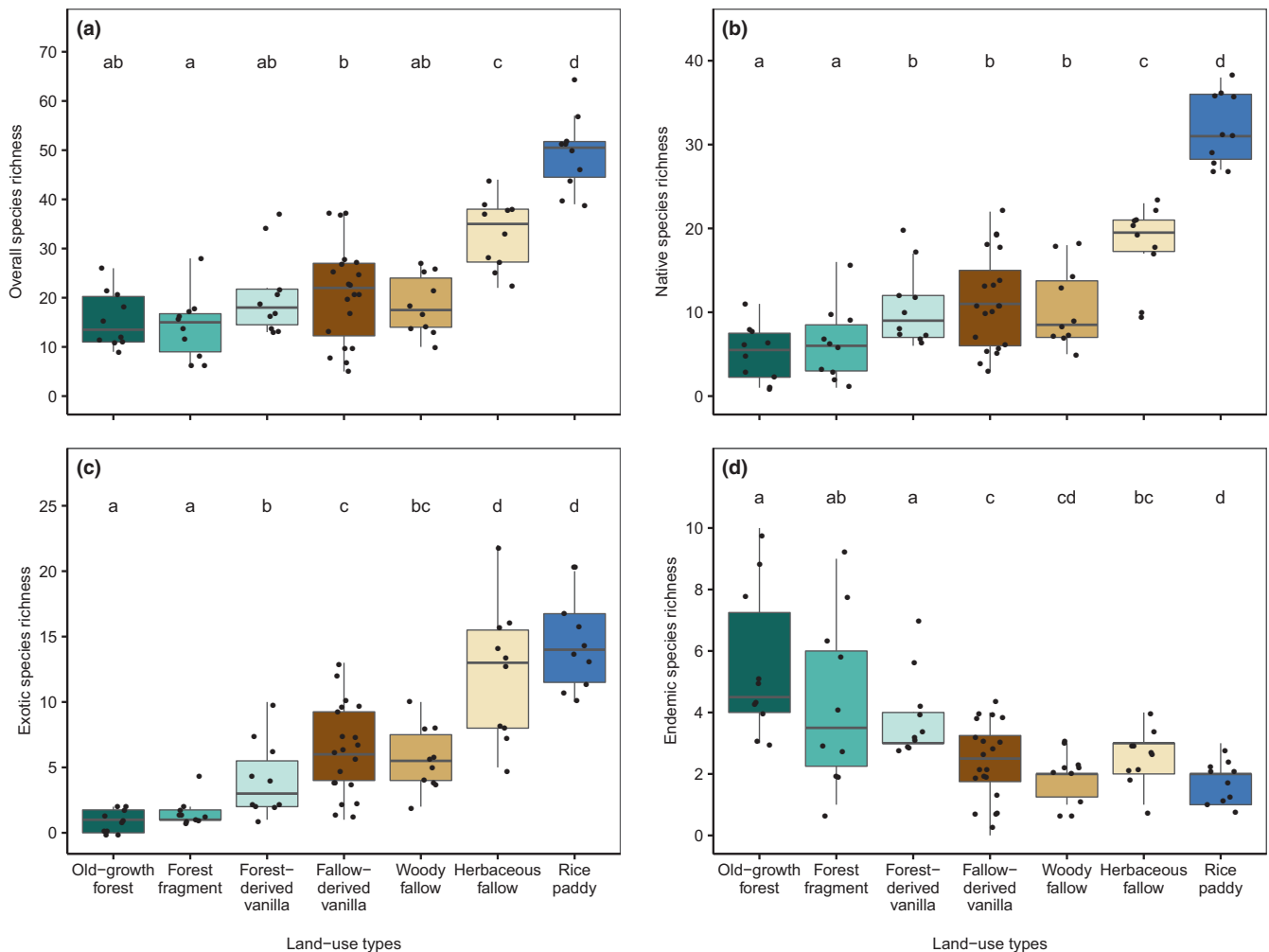
FIGURE 2 Richness of overall (a), native (b), exotic (c) and endemic (d) herbaceous plants species across a land-use intensity gradient in north-eastern Madagascar. Letters indicate significant differences between land-use types after ANOVA/Tukey post hoc test with $p < .05$ for significant differences. Lower and upper boundaries of the box display 25th and 75th percentiles of the observational values respectively, the line inside of the box is the median, the lower vertical line is the 10th percentile, the upper vertical line is 90th percentiles. Dots are the species richness per plot.

closure and land-use history as explanatory variables ($R^2_{overall} = 0.54$, $R^2_{native} = 0.59$, Table 1, Table S4). For exotic species richness, the best model included canopy closure and landscape forest cover ($R^2_{exotic} = 0.68$, Table 1, Table S4) while the best model for endemic species richness included land-use history and landscape forest cover ($R^2_{endemic} = 0.45$, Table 1, Table S4).

When examining the effect of environmental parameters, we found that increasing canopy closure was negatively associated to overall, native and exotic species richness ($p < .001$, Table 1, Figure 3b, e and h). For land-use history, we did not find a significant difference in overall and native species richness between unburned and burned land-use types (Table 1, Figure 3a and d). However, land-use history was decisive for the number of endemic species (Table 1) with lower richness in burned land-use types compared to unburned land-use types and rice paddy ($p < .001$, Figure 3j). Landscape forest cover did not significantly influence species richness, except for the number of exotic species, which were negatively related to an increase in landscape forest cover ($p = .01$, Table 1, Figure 3i). We

detected a marginally significant increase of endemic species richness with increasing landscape forest cover ($p = .07$, Figure 3l).

3.3 | Species compositional changes

The analysis of species compositional changes revealed that overall species changed significantly across the land-use types, as shown in the NMDS ordination (Figure 4) and PERMANOVA results ($R^2 = 0.26$, $p < .001$, Table S5). Pairwise comparison of land-use types in terms of overall species composition indicated that all land-use types were significantly different from one another ($p < .05$). In terms of species growth form, we found that fallow-derived vanilla agroforest and woody fallow were associated with high proportion of graminoid species and low proportion of ferns while old-growth forests and forest fragments were related to a high proportion of fern species (Figure 4). Rice paddy and herbaceous fallow were mostly associated to other herbs and a very low proportion of vines.

TABLE 1 Generalized linear mixed-effect models (GLMs) explaining the overall, native, exotic and endemic species richness of herbaceous plants in north-eastern Madagascar

Responses	Predictors	Estimate	Standard error	Z-value	p-value	AICc	Marginal R^2
Overall species richness	(Intercept)	**3.514**	**0.187**	**18.790**	**<.001**	573.6	0.54
	Canopy closure	**−0.008**	**0.002**	**−4.029**	**<.001**		
	Land-use history (Burned land-use types)	−0.098	0.142	−0.689	.491		
	Land-use history (Rice paddy)	**0.402**	**0.200**	**2.007**	**.045**		
Native species richness	(Intercept)	**2.728**	**0.230**	**11.853**	**<.001**	495.0	0.59
	Canopy closure	**−0.009**	**0.003**	**−3.635**	**<.001**		
	Land-use history – Burned land-use types	0.104	0.179	0.582	.561		
	Land-use history – Rice paddy	**0.745**	**0.243**	**3.071**	**.002**		
Exotic species richness	(Intercept)	**2.526**	**0.168**	**15.016**	**<.001**	396.6	0.68
	Canopy closure	**−0.017**	**0.003**	**−5.788**	**<.001**		
	Landscape forest cover	**−0.007**	**0.003**	**−2.449**	**.0143**		
Endemic species richness	(Intercept)	**1.454**	**0.089**	**16.422**	**<.001**	291.2	0.45
	Land-use history (Burned land-use types)	**−0.576**	**0.136**	**−4.247**	**<.001**		
	Land-use history (Rice paddy)	**−0.914**	**0.239**	**−3.818**	**<.001**		
	Landscape forest cover	0.106	0.058	1.828	.068		

Bold values indicate significant effects.

For native species composition across land-use types, we found significant differences based on PERMANOVA tests indicating changes of species composition across land-use types ($R^2 = 0.27$, $p = .001$, Table S5). Based on pairwise comparisons, we did not find a significant difference between old-growth forests and forest fragments ($R^2 = 0.07$, $p = .134$) and between forest-derived vanilla agroforests and fallow-derived vanilla agroforests in terms of native species composition ($R^2 = 0.05$, $p = .055$). Old-growth forest and forest fragments had 11 native species in common (Figure 5a) which include several fern species such as *Bolbitis auriculata* and *Asplenium cf. normale* (Table S6). Forest- and fallow-derived vanilla agroforests had more than 20 native species (Figure 5a) from different families in common (e.g. Cyperaceae, Poaceae, Fabaceae, Asteraceae; Table S6).

In terms of exotic species composition, we detected a significant change of species composition across land-use types ($R^2 = 0.35$, $p = .001$). We found similarities only between old-growth forests and forest fragments ($R^2 = 0.12$, $p = .153$) as the only two exotic species (*Olyra latifolia* and *Clidemia hirta*) recorded from old-growth forest were also found in forest fragments (Figure 5b, Table S6).

Endemic species compositional change was significant across all land-use types ($R^2 = 0.23$, $p = .001$). However, forest fragments and forest-derived vanilla agroforests were not significantly different in terms of endemic species composition ($R^2 = 0.07$, $p = .222$). In total, nine endemic species were recorded in both forest-derived vanilla agroforests and forest fragments (Figure 5c). Additionally, we found that old-growth forests and forest fragments had the highest number of species recorded exclusively in each of them (14 for old-growth forest and 13 for forest fragment; Figure 5). Also, we found that fallow-derived vanilla agroforests, woody fallows and herbaceous fallows had a similar endemic species composition (Table S5). Fallow-derived vanilla agroforests, woody fallows and herbaceous fallows had more endemic species in common (minimum four species) than endemic species unique to each land-use type (maximum two species; Figure 5c). *Emilia citrina*, *Emilia humifusa* and *Scleria madagascariensis* are the species that we most commonly found in fallow-derived vanilla agroforests, woody fallows and herbaceous fallows (Table S6).

For all categories of species (overall, native exotic and endemic species), unburned land-use types were significantly different compared to burned land-use types in terms of species composition ($R^2_{native} = 0.07$, $R^2_{exotic} = 0.16$, $R^2_{endemic} = 0.09$, $p = .001$). We found 68 native species recorded only on burned land-use types (Figure 5a) with many species of Poaceae, Cyperaceae and Asteraceae (Table S6). In terms of exotics, we recorded 28 species (more than half of all exotic species assessed (57)) exclusively in burned land-use types (Figure 5b). Regarding endemic species, unburned land-use types had more than 40 species that did not occur in burned land-use types (Figure 5). These species are mainly ferns (e.g. *Dryopteris subcrenulata*), Melastomataceae (e.g. *Gravesia guttata*) Acathanceae (*Hypoestes longituba*) and Orchidaceae (*Bulbophyllum baronii*). Burned land-use types had only seven endemic species that were not found in unburned land-use types (e.g. *Selaginella pervillei* and *Exomiocarpon madagascariense*; Table S6).
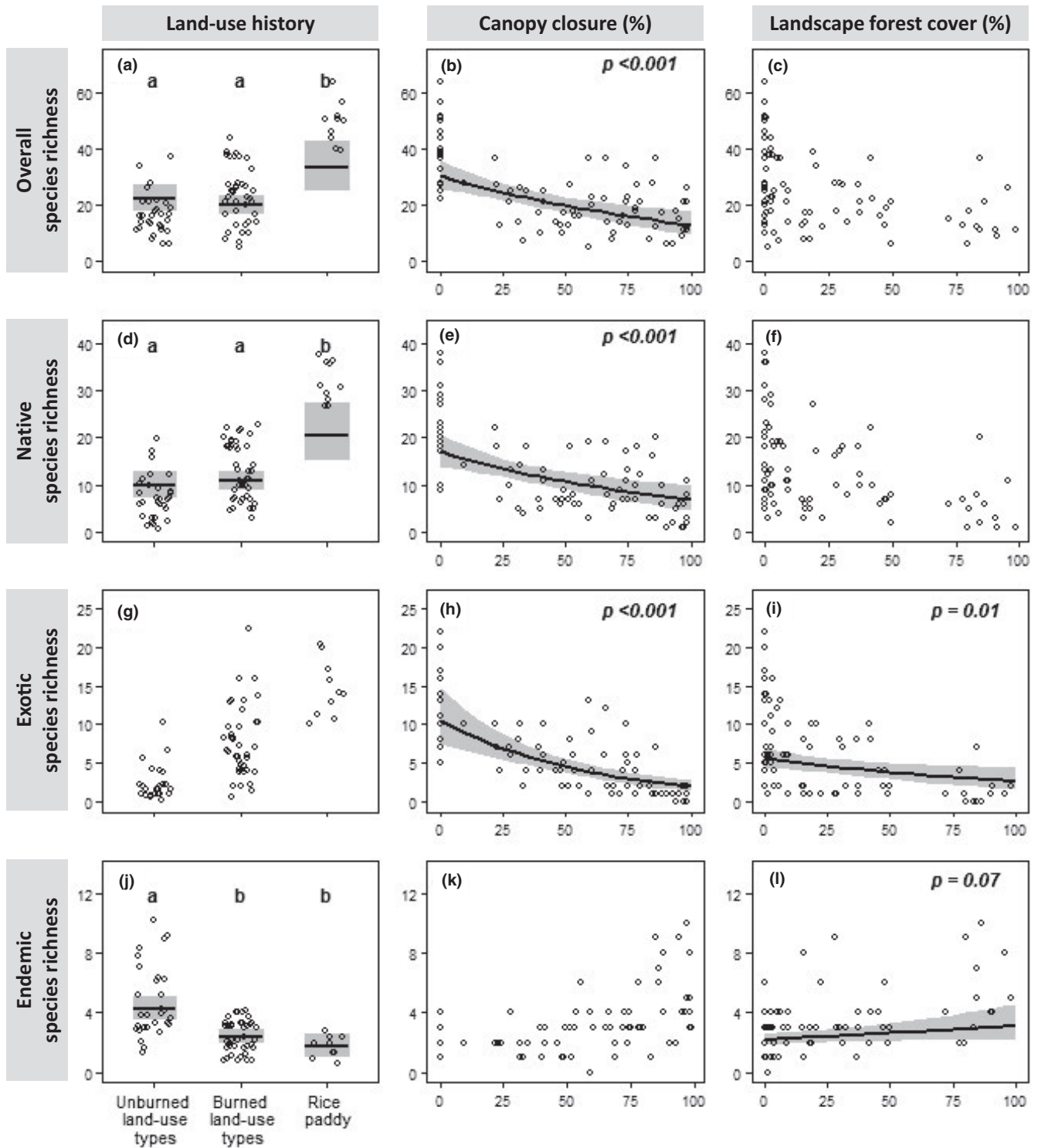
FIGURE 3 Effects of land-use history, canopy closure and landscape forest cover on overall (a–c), native (d–f), exotic (g–i) and endemic species richness (j–l) of herbaceous plant in north-eastern Madagascar based on multivariate GLMMs. Black lines indicate model predictions and ribbons indicate 95% confidence intervals. The absence of black lines and ribbons indicates that the parameter was not included in the final model of the corresponding species richness. Dots represent species richness per plot. Letters show differences between unburned land-use types, burned land-use types and rice paddy based on ANOVA/Tukey post hoc test with $p < .05$ for significant differences

4 | DISCUSSION

Our study shows that endemic species richness of herbaceous plants is decreasing under land-use intensification, while natives and

exotics are increasing. In terms of land-use history, endemic species richness was lower in burned land-use types than in unburned ones. Canopy closure decreased native and exotic species richness and higher landscape forest cover was related to lower exotic species

FIGURE 4 Non-metric-multidimensional-scaling (stress = 0.1657, non-metric fit, R^2 = 0.973 and linear fit R^2 = 0.885) of plots showing dissimilarities between land-use types in terms of overall species composition of herbaceous plants in north-eastern Madagascar based on Jaccard dissimilarity index. Dots represent plots, ellipsoids indicate standard error of the weighted average of scores for each land-use type, and arrows represent the association with the proportion of growth forms
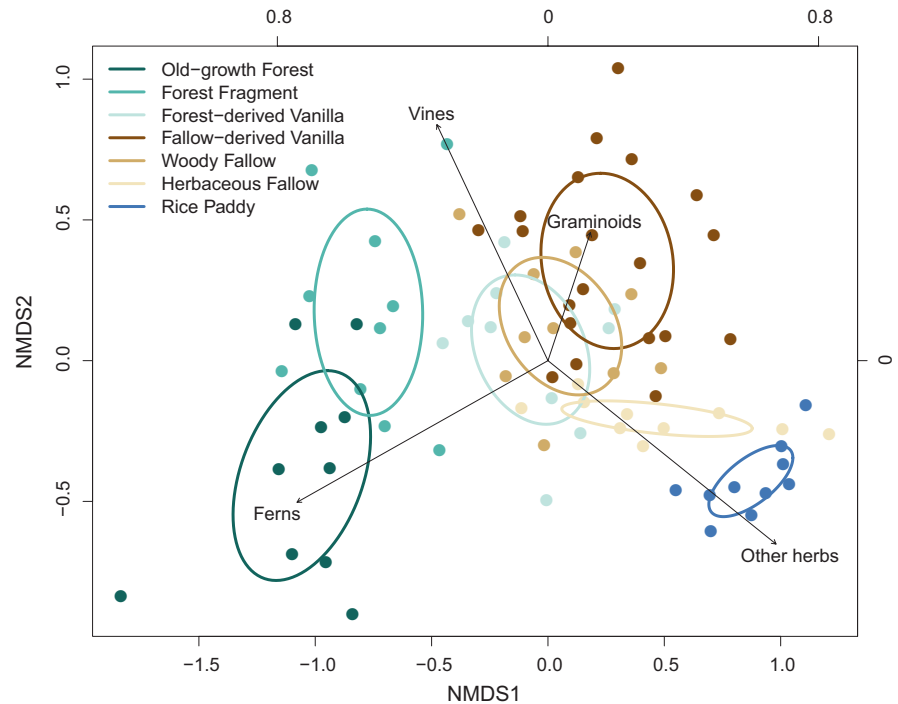
richness. These different patterns confirm our hypothesis of differential responses of species to land-use intensification and environmental parameters based on their origin. Land-use types showed significant differences in terms of endemic species composition as well as for native and exotic species. These findings further validate our hypothesis which predicted the change of species composition through land use. With these results, this study sheds new light on the effects of land-use intensification, land-use history, canopy closure and landscape forest cover on herbaceous plant diversity in Madagascar.

4.1 | Effect of land-use intensification and land-use history on herbaceous plant species richness and composition

Land-use history influenced endemic species richness, with lower species richness on burned land-use types compared to unburned ones. Moreover, endemic species composition differed significantly between unburned and burned land-use types with more species only found in unburned land-use types compared to burned ones. This indicates a negative effect of slash-and-burn agriculture on endemic species as already reported by Irwin et al. (2010). Moreover, endemic species richness decreased along the land-use intensity gradient with significant compositional change. This suggests that land-use intensification or transformation of old-growth forests into agricultural lands causes loss of endemic species (Brooks et al., 2002; De Beenhouwer et al., 2013). Additionally, endemic species of herbaceous plants were decreasing although the overall species richness was increasing with land-use intensity. However, for birds in the same landscape as this study, both, endemic and total species

richness declined along the land-use intensity gradient (Martin, Andriafanomezantsoa, et al., 2020). This highlights the importance of studying multiple species groups for conservation evaluation (e.g. Barlow et al., 2007) and suggests a specific response of herbaceous plant diversity (Gilliam, 2007).

Despite the similar species richness, old-growth forest differed from forest fragments and forest-derived vanilla in terms of endemic species composition and had the highest number of unique endemic species. This indicates that endemic species from old-growth forests are being replaced with species that are tolerant to disturbance (Hart & Chen, 2006) since forest fragments in north-eastern Madagascar are disturbed due to wood extraction. Thus, these results are in line with the well-known importance of old-growth forest for maintaining species that are intolerant to disturbance (Barlow et al., 2007; Gibson et al., 2011). Forest fragments and forest-derived vanilla agroforests did not differ in terms of endemic species composition and richness. These results highlight the importance of forest fragments, combined with wildlife-friendly farming systems such as forest-derived vanilla agroforestry, for providing habitat to endemic species in human-dominated landscapes (Bhagwat et al., 2008). This shows the need for considering different land-use types for endemic species conservation (Tscharntke et al., 2005) and for combining agricultural systems and forest habitats in the landscape matrix to preserve biodiversity (Grass et al., 2019; Perfecto & Vandermeer, 2008).

Non-endemic species richness increased with increasing land-use intensification. Looking at overall species composition, burned land-use types were associated with a high proportion of graminoids. Furthermore, native and exotic species composition was significantly different between burned and unburned
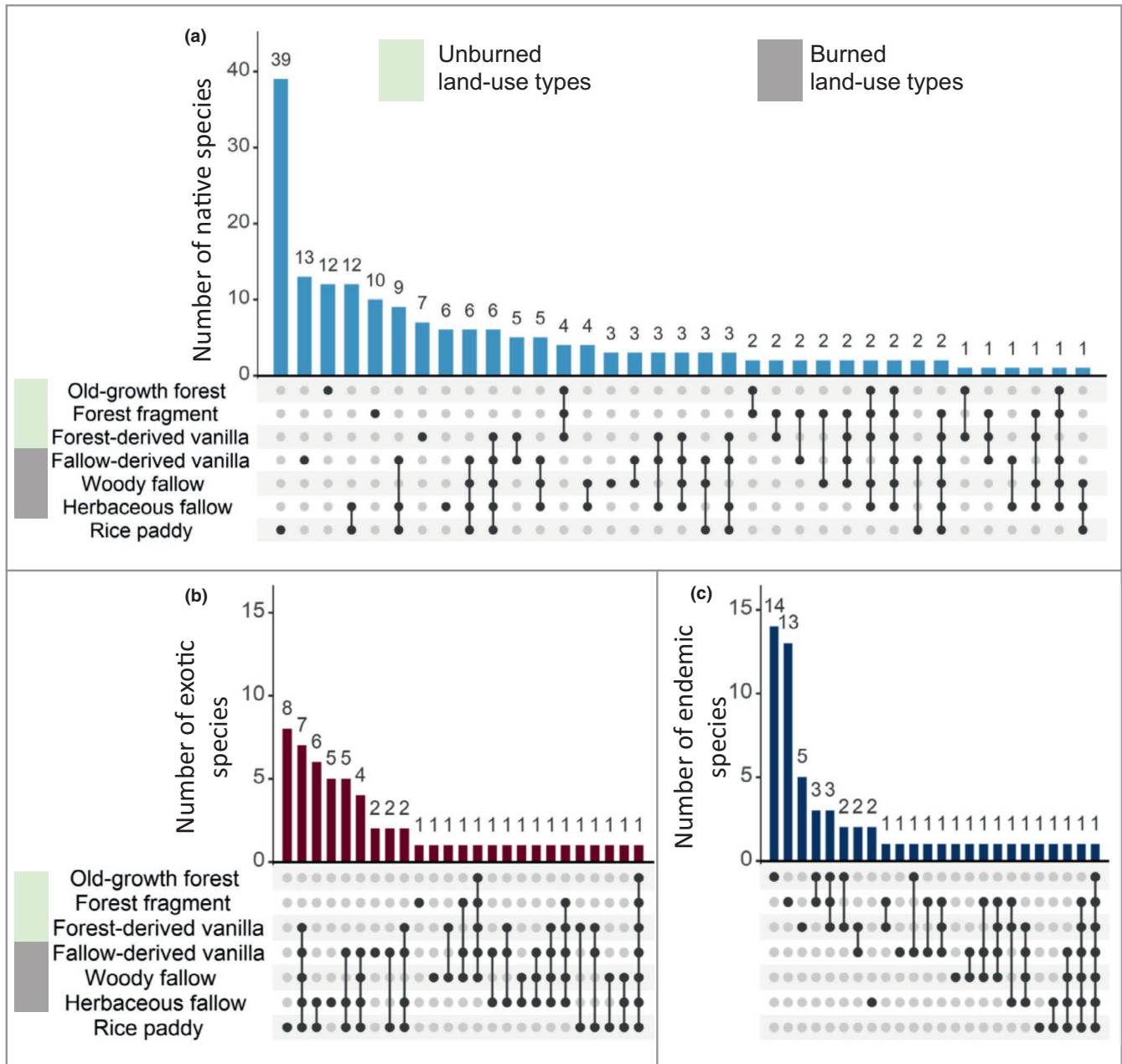
FIGURE 5 Distribution of native (a), exotic (b) and endemic (c) herbaceous plant species across seven land-use types in north-eastern Madagascar. Vertical bars show the number of species occurring in each of the unique combinations of land-use types represented by the single point for a set of species unique to a land-use type and the connected points for a set of species co-occurring in multiple land-use types (e.g. (c) three endemic species occurred in old-growth forest, forest fragment and forest-derived vanilla agroforest but in no other land-use type)

land-use types. These results indicate that burned rather than unburned land-use types were colonized by non-endemic species, for example fire-loving grasses that are not growing on unburned land-use types (Styger et al., 2007). Moreover, rice paddies had the highest richness of native species and different species composition compared to any other land-use types. This suggests that, despite the commonly intensive management of rice paddies, rice paddy banks can constitute an important reservoir of different native herbaceous plants, possibly due to its water regime (Kosaka et al., 2006).

4.2 | Effect of canopy closure and landscape forest cover on species richness

Species richness of native and exotic herbaceous plants decreased with increasing canopy closure. These results indicate that non-endemic herbaceous plants species show negative response towards dense canopies and thrive in open habitats. The increasing richness in open habitat suggests a colonisation of shade-intolerant species, especially graminoids (Hart & Chen, 2006; Plue et al., 2013). Tree removal is hence facilitating the regeneration of native herbaceous

plants as well as exotic species. Furthermore, exotic plant species richness decreased with an increasing forest cover in the landscape. These results confirm that exotic herbaceous plant species thrive in open habitats with low forest cover (e.g. Sánchez-Jardón et al., 2014) and in intensive agricultural systems, which can lead to taxonomic homogenization as graminoid species are becoming dominant on more intensively used land-use types (Marconi & Armengot, 2020). Additionally, many parts of our study region have only recently been deforested (Vieilledent et al., 2018a), suggesting that the exotic species richness might increase in the future due to a delayed ecological response termed colonisation credit (Lira et al., 2019). Therefore, this may explain why we found fewer exotic species on plots surrounded by more landscape forest cover which may have lost surrounding forest more recently.

4.3 | Study limitations

We identified 1,716 plants as 58 morphospecies with unknown origin (see Table S1) due to the absence of reproductive parts (flowers or spores). We found most of these morphospecies with unknown origin in old-growth forest and forest fragment (Table S6). There is a high probability that these species are endemic given that most of the families have high species endemicity rate (more than 70%) except for Cyperaceae, ferns, and Poaceae (39%–45% species endemicity rate; Callmander et al., 2011; Vorontsova et al., 2016). Besides this, we found some discrepancies in literature and databases on the origin of certain non-endemic species (Kull et al., 2012), thus, choices had to be made by prioritizing one information over another. Therefore, further research is needed on non-endemic plants in Madagascar to elucidate the controversy on their origins and reduce the uncertainty of future research.

We found that forest fragments and forest-derived vanilla agroforests had similar endemic herbaceous plant species richness and composition. However, conversion of forest fragments into forest-derived vanilla agroforests involves understory vegetation clearance and tree thinning (Martin, Osen, et al., 2020). This disturbance, combined with landscape degradation, could result in a loss of endemic herbaceous plant species in forest-derived vanilla agroforests if extinction debts are paid out in the future (Kuussaari et al., 2009). Such extinction debts can be caused by local and landscape habitat deterioration, depending on the plant reproduction strategy and other functional traits (Hylander & Ehrlén, 2013). This may potentially confound our results, but unfortunately our study is too short term to document extinction debts.

4.4 | Conservation implications

Preserving unique biological features and ecosystem functions is the central aim of biodiversity conservation. Herbaceous plants have value not only for their aesthetics but also for ecosystem functioning (Gilliam, 2007; Ouin & Burel, 2002). Hence, plant conservation value

evaluation should not only focus on trees but also encompass herbaceous plants since they are also very sensitive to habitat change (Gilliam, 2007). Understanding drivers of various aspects of herbaceous plant diversity is therefore crucial.

Our analysis of the herbaceous plant community has shown that species richness is increasing with land-use intensification, along with a decrease of canopy closure. This is in line with results from cacao plantations in Indonesia (Clough et al., 2011). However, the endemic species diversity analysis has shown that land-use history affects their richness and composition. Therefore, species richness alone is not a meaningful unit of analysis for herbaceous plant conservation, but the differentiation of the species according to origin (endemics, natives or exotics; e.g. Steffan-Dewenter et al., 2007) and their compositions (e.g. Rembold et al., 2017) is crucial to value different land-use types.

In north-eastern Madagascar, where vanilla farming and rice cultivation constitute the main drivers of land-use change (Zaehringer et al., 2016), forest fragments remain the most effective land-use type to preserve herbaceous plant diversity within human-dominated landscapes and should thus be preserved to conserve endemic species. As species groups respond differently to land-use change, maintaining forest fragments within agricultural landscapes increases the effectiveness of landscapes to maintain biodiversity (Grass et al., 2019), hence corroborating the importance to consider all land-use systems in the landscape (Lindenmayer et al., 2006). In case of converting forest into agricultural land, land conversion methods using land clearing without fire, for example, the establishment of forest-derived agroforests, minimize the loss of endemic species since unburned land-use types have a higher species richness and different species composition compared to burned land-use types.

In a landscape where most of the forest has been cleared for slash-and-burn agriculture and which is now consequently dominated by fallows and fallow-derived land uses, species that tolerate habitat disturbance are commonly found. Within the slash-and-burn system, a successive intensification with shorter fallow times is not recommended as it may lead to land degradation (Styger et al., 2007). Within the burned land-use types, fallow-derived vanilla agroforests can rehabilitate tree cover in the landscape and support ecosystem functioning (Martin, Osen, et al., 2020) while also being economically attractive for farmers (Hänke et al., 2018).

5 | CONCLUSIONS

The present study demonstrates that herbaceous plant richness, except endemics, increases with land-use intensification in north-eastern Madagascar. Land-use history influences endemic species richness of herbaceous plants, while dense canopies decrease native and exotic species richness but not endemic species richness. The conversion of forest fragments into forest-derived vanilla agroforests does not alter species richness nor composition of endemic herbs. The differentiation into categories of origin (endemic, native and exotic) allowed us to generate meaningful management advice that would benefit the preservation of endemic species. Hence,

species richness alone is not sufficient to evaluate the conservation value of ecosystems.

We conclude that vanilla agroforestry systems, particularly if forest-derived, can harbour many endemic herbaceous plants, which contrasts with other important tropical agroforestry systems (e.g. cacao) that typically have low conservation value for endemic herbaceous forests species. Forest-derived agroforests with dense canopies may be maintained with management incentives but the establishment of new forest-derived agroforests should be avoided to conserve endemic herbaceous plants in forest fragments as well as old-growth forests. Fallow-derived agroforests, on the other hand, may offer an opportunity to avoid degradation of fallow land that forms part of the slash-and-burn cultivation cycle.

We also identify land-use history as a key determinant of herbaceous plant species composition and richness. To maintain the current diversity of endemic plant species, the conservation of a diverse landscape with unburned old-growth forests, forest fragments and forest-derived vanilla agroforests is necessary.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest related to this paper.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13226.

DATA AVAILABILITY STATEMENT

All data used for this study are available on Dryad Digital Repository: https://doi.org/10.5061/dryad.pzgmsbcjp

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