

Topographical gradient of the structure and diversity of a woody plant community in a seasonally dry tropical forest in northwestern Madagascar

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Abstract

Few studies have evaluated the structure and dynamics of forests in Madagascar with high levels of endemism. Ankarafantsika National Park holds the largest of the remaining primary dry forests in northwestern Madagascar, where most of the forests have been lost or degraded by fire and other human activities. In this primary forest, we established a 15-ha forest dynamics monitoring plot and mapped and identified all woody stems with a diameter at breast height (DBH) ≥ 5 cm. The forest stand was characterized by small-sized individuals (75% of stems with DBH < 10 cm, with 99% of trees with height < 15 m), encompassing 35,758 tree and 513 liana individuals belonging to 160 species in 53 families (including 20 species of lianas accounting for 1.4% of the stems). Most species-rich families were Rubiaceae, Fabaceae, Lamiaceae, and Malvaceae, which together encompassed 43 tree species and 23% of all tree individuals. The plot was located on a hill consisting of white sand at elevations from 150 to 200 m, with a gentle slope down from southwest to northeast. Over this elevation gradient, stem density and species diversity increased with elevation, while tree height and diameter decreased. The most abundant two species, *Drypetes perrieri* (Putranjivaceae) and *Noronhia alleizettei* (Oleaceae) are evergreen, suggesting the importance of a nutrient conservation strategy. These results provide the foundational knowledge necessary for the conservation and restoration of natural semi-deciduous dry forests that used to cover large areas in northwestern Madagascar until recently.

KEYWORDS

forest dynamics monitoring plot, lianas, spatial variation, trees, white sand ecosystem

1 | INTRODUCTION

Plant species differ in preferred conditions to survive and grow (Lasky et al., 2013), and many studies have examined species–habitat associations as a key aspect of tree species diversity in tropical forests (e.g., Condit et al., 2013; Engelbrecht et al., 2007; John et al., 2007). Topography as a key determinant of soil, water, and other environmental conditions (e.g., Fan et al., 2020; Kupers et al., 2019) has been examined in relation to tree species distribution (e.g., Harms et al., 2001; Webb & Peart, 2000; Zuleta et al., 2020). In the 50-ha plot of Barro Colorado Island, Panama, for example, Harms et al. (2001) found that the composition of tree and shrub species differed between the plateau and slopes. Similarly, Webb and Peart (2000) found that nearly half of the abundant species showed associations with plateaus, upper slopes, or gullies in a Bornean rainforest.

Due to the environmental filtering of plant species, the structure and diversity of a tree community also exhibit trends along environmental gradients. However, how they change with topography differs among study sites. In an Ecuadorian wet forest, the number of tree stems and basal area (BA) decreased from the ridges plus upper slopes, lower slopes, to valleys, while species diversity was higher at lower elevations (Valencia et al., 2004). Similar trends for stem density and species diversity were observed in a Cameroonian wet forest, with the highest basal area found on slopes (Chuyong et al., 2011). On the other hand, from a 600-m transect survey in a Japanese subtropical forest, Kubota et al. (2004) report that stem density, above-ground biomass, and species diversity were higher on ridges than on slopes and valleys. For shrubs and saplings with a diameter at breast height (DBH) <10 cm, Denslow (1995) reports that both stem number and species diversity were higher on slopes than on ridges along 600-m transects in a Costa Rican tropical wet forest. Perhaps, whether the topographical gradient has a positive or negative correlation with species diversity, stem density, and biomass depends on the range of elevation, climate, and soil types, which interactively determine water and nutrient availability. On limestone valleys to hills with elevations from 130 to 607 m in southern China, higher elevations mean greater drought and nutrient stress, which operate as environmental filters (Geekiyana et al., 2018).

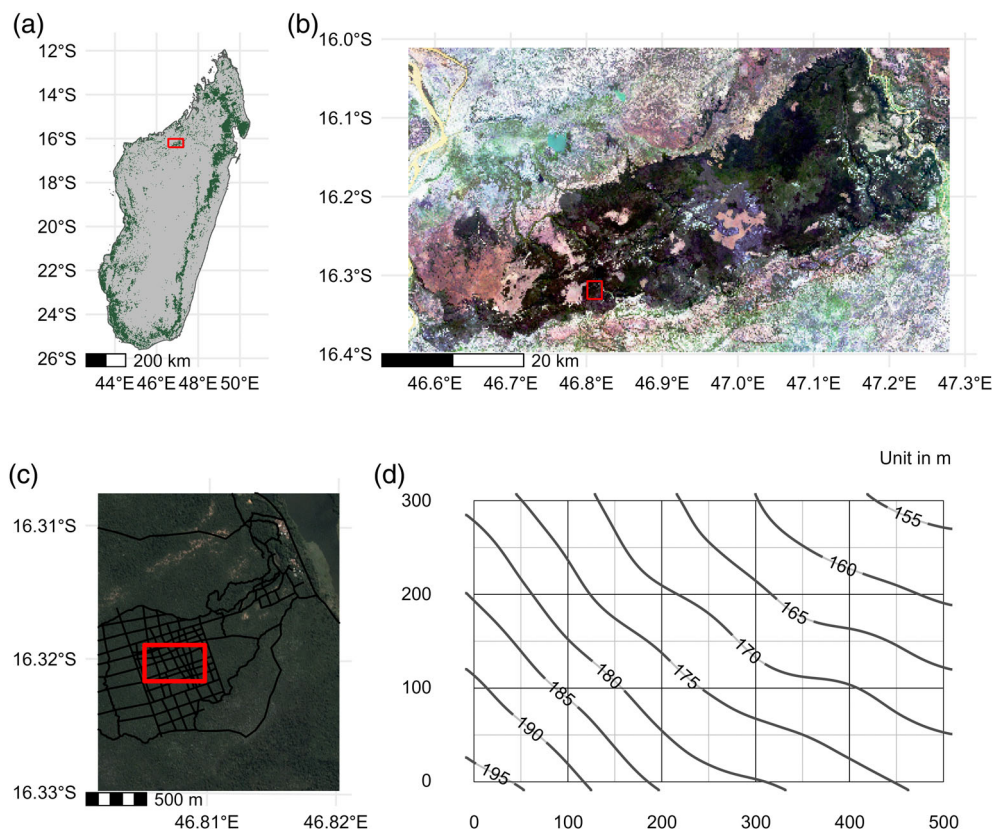
Although many studies compared topographic habitats such as ridges, slopes, and valleys, there may be significant variation even within a narrow elevation range over a gentle slope. In a 500 m × 500 m plot of a Sri Lankan mixed dipterocarp forest with an elevation range 425.3–571.9 m and a slope range 0.6°–36.5°, a high-elevation area had a higher stem density and a lower

species richness of trees with a DBH ≥1 cm than a mid-elevation area (Punchi-Manage et al., 2013). Valencia et al. (2004) also report a similar trend between upper and lower slopes within a 30-m elevational difference within a 500 m × 500 m plot. Small differences in elevation may result in large differences in hydrological regimes between upper and lower slopes. However, Johnson et al. (2021) did not find differences in tree species diversity in relation to small elevation differences between 35 and 50 m on a longleaf pine sandhill in Florida. This may be due to relatively small ranges in elevation within their 25-ha plot, as well as monodominance of longleaf pine and frequent fire, which were more influential upon competitive interactions and regeneration of tree species.

Here, we report the structure and diversity of a woody plant community in a 15-ha plot on a monotonous and gentle slope in a seasonally dry tropical forest in north-western Madagascar (Figure 1). In general, seasonally dry tropical forests contain many species adapted to the seasonal drought, either through drought avoidance or drought tolerance. Those forests tend to exhibit species richness of woody plants in Fabaceae, also often in Euphorbiaceae, Meliaceae, Myrtaceae, and Rubiaceae (e.g., Almulqu et al., 2018; Fernandes et al., 2020; Gillespie et al., 2000, 2011). The geological origin of Madagascar goes back to the breakage of eastern Gondwana from the African continent ca. 180 million years ago, followed by separation from the Australian–Antarctic subcontinent 120–140 million years ago, and finally from the Indian subcontinent 84–92 million years ago (Reeves, 2018; Torsvik et al., 1998). Due to this long isolation from the other land masses, unique and diverse ecosystems have evolved there, and more than 80% of vascular plant species in Madagascar are reported to be endemic (Callmander et al., 2011). These endemic species were largely of either Indian or African lineages (Warren et al., 2010; Yoder & Nowak, 2006).

Despite the uniqueness of natural ecosystems in Madagascar, we have limited knowledge about the community ecology of Madagascan woody plants (e.g., Abraham et al., 1996; Cadotte et al., 2002; Sussman & Rakotozafy, 1994). Deforestation rates in Madagascar have been high largely due to the expansion of agriculture, fire, and other anthropogenic drivers (Vieilledent et al., 2018a). Northwestern Madagascar, with a long dry season of 6–7 months, has experienced the highest rate of forest loss of 79% within Madagascar, most of which takes place during the dry season and not during the monsoon rainy season (Percival, 2024, updating the analysis of Vieilledent et al. (2018a) to 1953–2023). Ankarafantsika National Park, protected since 1927, has one of the rare examples of large stands of seasonally dry tropical forest in north-western Madagascar. In the forest stand on a hill dominated

FIGURE 1 Location of the Ankarafantsika 15-ha plot and its contour map. (a) Forest cover of Madagascar in 1990 (Vieilledent et al., 2018b) and the location of Ankarafantsika National Park, (b) satellite image of Ankarafantsika (from Landsat 8 imagery in 2021–2022) and the location of a trail system including the Jardin Botanique A (JBA), (c) satellite image (Planet Labs PBC, 2019) around JBA with the trail system visualized by black lines and the location of the 15-ha plot, (d) contour map of the 15-ha plot (300 m × 500 m; illustrated based on the digital elevation model provided by T. Kaneko, Y. Onoda, and J. Percival, unpublished data). The locations are indicated by red rectangles.



by white sand, we established the first large-scale plot in Madagascar to describe the structure and species diversity of the woody plant community, including trees and lianas with DBH ≥ 5 cm.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in a seasonally dry tropical forest on a white-sand hill in Ankarafantsika National Park (136,513 ha) in Boeny Region, northwestern Madagascar. This park has been protected since 1927, with several types of management zones: the core zone with full protection, the zone designated for academic research and eco-tourism, the zone used by local communities within the park, and the peripheral zone outside of the park boundary (Aymoz et al., 2013; Madagascar National Parks, 2017). We selected Jardin Botanique A (JBA, 16°19' S, 46°48' E; Figures 1 and S1) near the Ampijoroa Village and the park headquarters, within an area designated for scientific research. The annual mean temperature and annual precipitation in 4 years (2016–2019) are 25.5–26.1°C (Sato, 2022; H. Sato, unpublished data) and 1195–1615 mm, respectively, and the dry season (monthly precipitation <10 mm) typically occurs from May to October (rainfall data are provided by the Durrel

Wildlife Conservation Trust in Ampijoroa). Anthropogenic fires, mainly from slash and burn and field burning for cattle grazing, are common outside the park boundary, but some of them spread into the park and illegal fire episodes within the park boundaries are increasing. Satellite remote sensing data (MODIS) going back to 1984 show no fires in the area surrounding JBA, and only after 2014 did the area near JBA within the southern border of the park start to experience fire episodes (Percival et al., 2024). The topsoil within JBA is a quartz-rich white sand derived from Jurassic marine sediments, classified as Quartzipsamments by USDA (Soil Survey Staff, 1999; T. Nishigaki, personal communication).

2.2 | Plot establishment

Starting in July 2019, we gridded out a rectangular area of 15 ha (300 m north–south and 500 m east–west) with survey instruments, permanently marking every 5 m with a PVC pipe. Prior to our study, a trail system had been established by the national park for scientific monitoring studies, such as monitoring of a rich fauna, including mammals (e.g., Hakan et al., 2017; Ito et al., 2013; Levesque et al., 2012; Lobban et al., 2014; Marquès Gomila et al., 2023; Rasoloharjaona et al., 2003; Sato, 2013a, 2013b, 2022; Sato et al., 2014), birds (e.g., Asai et al., 2002; Hasegawa et al., 2009; Mizuta

et al., 2001; Nakamura et al., 2001, 2004; Rakotomanana et al., 2001), and reptiles (e.g., Hasegawa et al., 2009; Ikeuchi et al., 2005, 2012; Ikeuchi & Mori, 2014; Ito & Mori, 2010; Randriamahazo & Mori, 2005), all of which are endemic to Madagascar. Within the 15-ha plot, there is a gentle slope from the lowest corner in the northeast to the highest corner in the southwest (Figure 1d). While it is possible to analyze the spatial variation at various scales within the plot, we chose to analyze the spatial variation of forest structure in terms of variation among 50 m × 50 m quadrats, resulting in a sample size of 60 quadrats. We selected this quadrat size as optimal to avoid effects of treefall gaps and a walking trail system, but to yield sufficient sample size to test the relationship of forest structure and species diversity with the elevation gradient.

2.3 | Measurements of woody stems

In the 15-ha plot, all woody stems with DBH ≥ 5 cm were measured, mapped, identified to species, and tagged with aluminum numbered tags during the period from August 2019 to June 2020. Since seasonally dry forests are usually characterized by abundant lianas (DeWalt et al., 2010), we recorded lianas as well as trees. We measured the circumference of each stem at 1.3 m above the ground with measuring tape and converted it to DBH by dividing it by π (≈ 3.14). For stems that had a flat shape or were tightly attached to another stem, DBH was measured in two orthogonal directions with calipers. For multi-stemmed individuals, the stem with the largest DBH was designated as the main stem, while the other stems attached to the same base were also measured, tagged, and recorded if they had DBH ≥ 5 cm. Hence, the total number of stems is larger than the total number of individuals in the results. In addition, we measured the height of all free-standing trees in systematically selected eight areas (20 m × 20 m each) within the 15-ha plot. To record the x and y coordinates of each stem relative to the southwest corner of the plot (0–0), we mapped the location of each stem within each 5 m × 5 m grid on a sheet of paper pre-printed as a dot with stem ID adjacent to it. Each sheet was scanned, and digitized information was converted to x–y coordinate data.

All stems were classified into free-standing trees and lianas based on their gross morphology. For species identification, we made preliminary identification using an unpublished floristic list of local vascular plants provided by Ankarafantsika National Park and other floristic information (Schatz, 2001). We collected voucher specimens for confirmation by the local expert at the Botanical and Zoological Garden of Tsimbazaza and the Kew

Madagascar Conservation Centre. The endemism and extinction risk of each species were checked in the Catalogue of the Plants of Madagascar (Madagascar Catalogue, 2023) and the IUCN Red List (IUCN, 2023).

2.4 | Forest structure and taxonomic diversity

To describe the patterns of tree and liana species diversity for the entire 15-ha plot, we examined the species–area (rarefaction) curves using the 10 m × 10 m subplot information after 100-time permutation and generated the rank–abundance curves. To explore spatial variation of forest structure and species diversity, for each 50 m × 50 m quadrat, we calculated basal area (BA), the 95th percentile of DBH ($D_{\max}$), the median of DBH (D_{med}), the number of woody plant individuals (N_{ind}), the number of individuals with DBH of their main stem ≥ 30 cm (N_{large}), the number of species (N_{spp}), the ratio of N_{spp} to N_{ind} ($N_{\text{spp}}: N_{\text{ind}}$), Shannon's index $\exp(H')$, Simpson's index $1/D$, and Fisher's alpha. The mean elevation of each quadrat was obtained from a digital elevation model derived from drone photos (T. Kaneko, Y. Onoda, and J. Percival, unpublished data).

2.5 | Statistical analysis

All analyses, including linear regression and randomization, were conducted with the statistical software R ver.4.2.1 (R Core Team, 2022). To summarize the spatial variation of the forest structure, we used multi-dimensional scaling (MDS) with the Euclidean distance, using the following variables: BA , $D_{\max}$, D_{med} , N_{ind} , N_{large} , and N_{spp} . All the variables were standardized prior to the MDS. For multivariate analysis of species composition in 50 m × 50 m quadrats, we ran the non-metric multi-dimensional scaling (nMDS) with the Bray–Curtis dissimilarity. The permutational multivariate analysis of variance (PERMANOVA) was conducted to test whether forest structure and species composition differ significantly with elevation within the 15-ha plot.

3 | RESULTS

3.1 | Structure and diversity of the woody plant community

Within the 15-ha plot, we recorded 36,271 individuals (35,758 trees and 513 lianas) with DBH ≥ 5 cm, with the mean basal area (BA) of 19.6 m² per ha, the majority of

TABLE 1 Forest structure of the 15-ha plot in Ankarafantsika National Park for woody stems with a diameter at breast height ≥ 5 cm.

Area	Life form	Number of individuals	Number of stems	Basal area (m ²)	Number of species	Number of families	Fisher's alpha
15 ha	Tree	35,758	38,538	293.323	140	47	18.50
	Liana	513	553	1.600	20	14	4.14
	Total	36,271	39,091	294.924	160	53	21.54
1 ha	Tree	2384 $\pm$ 141	2569 $\pm$ 124	19.555 $\pm$ 1.156	89 $\pm$ 7	40 $\pm$ 2	18.31 $\pm$ 1.68
	Liana	34 $\pm$ 11	37 $\pm$ 12	0.107 $\pm$ 0.036	8 $\pm$ 3	7 $\pm$ 2	3.38 $\pm$ 1.51
	Total	2418 $\pm$ 144	2606 $\pm$ 126	19.662 $\pm$ 1.159	97 $\pm$ 8	43 $\pm$ 2	20.29 $\pm$ 2.12

Note: The upper half represents summed values of the whole 15-ha plot, and the bottom half represents mean values $\pm$ SD of 15 1-ha areas (100 m $\times$ 100 m each).

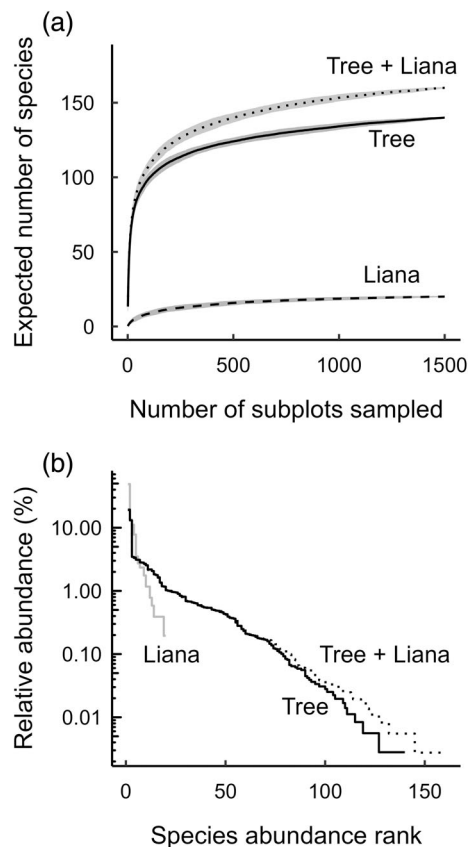


FIGURE 2 (a) Species–area curves and (b) species rank–abundance curves of a woody plant community in Ankarafantsika National Park. For the species–area curves, the unit of area is 10 m $\times$ 10 m subplot, and standard deviations are shown with shaded areas.

which was accounted for by trees (99.5%) and the rest by lianas (Table 1). We identified 160 species (140 tree species and 20 liana species) belonging to 53 families (47 families for trees and 14 families for lianas) (Tables 1 and S1). According to species–area curves (Figure 2a), the 15-ha plot sufficiently captured the diversity of tree and liana species, although only one individual was

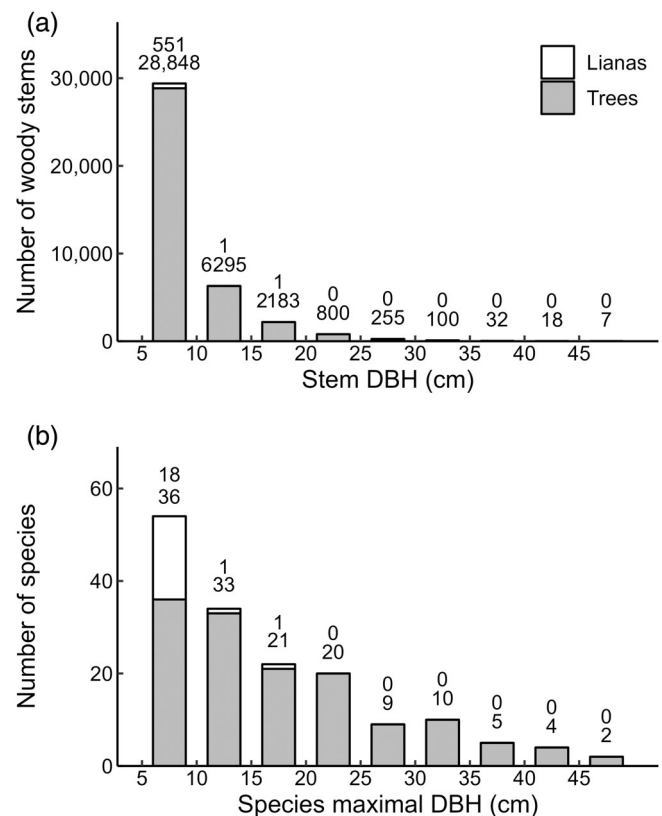


FIGURE 3 (a) Number of woody stems in different size classes and (b) the number of species of which a diameter at breast height (DBH) of the largest individual is in each size class. The size class intervals are left-closed and right-open, with the rightmost class including all the stems with DBH ≥ 45 cm. Two numbers above each bar indicate the stem or species numbers of lianas (upper) and trees (lower).

recorded for 14 tree species and 2 liana species (Figure 2b). The median and maximum of DBH were 7.3 and 68.9 cm, respectively. The mean and maximum of tree height were 8.8 and 15.6 m, respectively, within the selected areas for the height measurement. This forest was dominated by relatively small stems, as 75% of all

Family	Number of species	Number of individuals	Basal area (m ² /ha)
Rubiaceae	14	2484	0.9796
Fabaceae	13	3446	2.7160
Lamiaceae	8	1038	0.6688
Malvaceae	8	1464	0.9938
Anacardiaceae	6	1170	1.2583
Euphorbiaceae	6	581	0.1816
Meliaceae	6	1014	0.8740
Sapindaceae	6	251	0.0676
Apocynaceae	5	316	0.1364
Ebenaceae	5	565	0.1871
Annonaceae	4	312	0.1540
Phyllanthaceae	4	1292	1.0063

TABLE 2 Dominant families in the tree flora of the Ankarafantsika 15-ha plot, showing the 12 families with the highest number of species.

Note: See Table S2 for the full list of families.

woody stems were <10 cm in DBH (Figure 3a). A small number of species could become large-diameter trees, with only 21 and 6 species having individuals whose DBH reached 30 cm and 40 cm, respectively (Figure 3b).

In terms of the number of tree individuals, the three most abundant tree species were *Drypetes perrieri* (19.0% of all individuals), *Noronhia alleizettei* (12.9%), and *Rhopalocarpus similis* (3.4%). In terms of the tree BA, *D. perrieri* (18.1%) was the most dominant, followed by *N. alleizettei* (6.2%) and *Baudouinia fluggeiformis* (5.4%). The two most dominant species that together make up 29.7% of the stand BA were evergreen, whereas *R. similis* and *B. fluggeiformis* gradually become leafless late in the dry season. Rubiaceae and Fabaceae were the two most species-rich families (Tables 2 and S2). Within the liana community, a single species *Metaporana sericosepala* accounted for almost half of the individuals (48.9%) and BA (49.1%).

About 79% of the woody species (126 spp.) were endemic to Madagascar, including those belonging to 21 endemic genera and two endemic families (Sarcocaulaceae and Sphaerosepalaceae). According to the IUCN Red List, one species was “Critically Endangered,” 14 species were “Endangered,” 15 species were “Vulnerable,” and four species were “Near Threatened.” All these species, except for one, were endemic to Madagascar.

3.2 | Spatial variation in forest-structural and species-compositional variables

There were significant spatial variations among 50 m × 50 m quadrats in relation to elevation, with overall higher stem numbers and species diversity at higher elevations. The

number of woody plant individuals (N_{ind}) and the number of species (N_{spp}) were positively correlated with elevation, while the median of DBH (D_{med}) showed a negative correlation. Both BA and the 95th percentile of DBH (D_{max}) were marginally negatively correlated with elevation (Figure 4a–e). The number of individuals with the main stem DBH ≥ 30 cm (N_{large}) was not correlated with elevation (Figure S2). Since the number of species is expected to increase with the number of stems per quadrat, we examined the ratio of N_{spp} to N_{ind} ($N_{spp} : N_{ind}$), Shannon's index $\exp(H')$, and Fisher's alpha, which also increased with elevation, although Simpson's index $1/D$ had no significant trend (Figure 4f–i). Both the forest structure and species composition gradually changed along the elevational gradient (Table S3, Figures 5 and S3).

4 | DISCUSSION

This is the first study that evaluates the structure and diversity of a woody plant community with a sufficiently large contiguous plot to detect the spatial pattern in Madagascar. This forest seemed to be extremely biased toward small-diameter stems, based on a steep L-shaped size distribution (Figure 3a) and small maximal size for many species (Figure 3b). The overall small stature of trees likely reflected the limited availability of nutrients and dry season soil moisture from the white sand substrate (K. Oshima et al., unpublished data). Tree species with smaller adult stature and slower growth are reported to be more drought tolerant (Guillemot et al., 2022). Our site annually experiences pronounced seasonal drought for 6–7 months, and therefore, smaller size would be realized for surviving the dry season by evergreen species. Yet, the two most dominant species, both in terms of

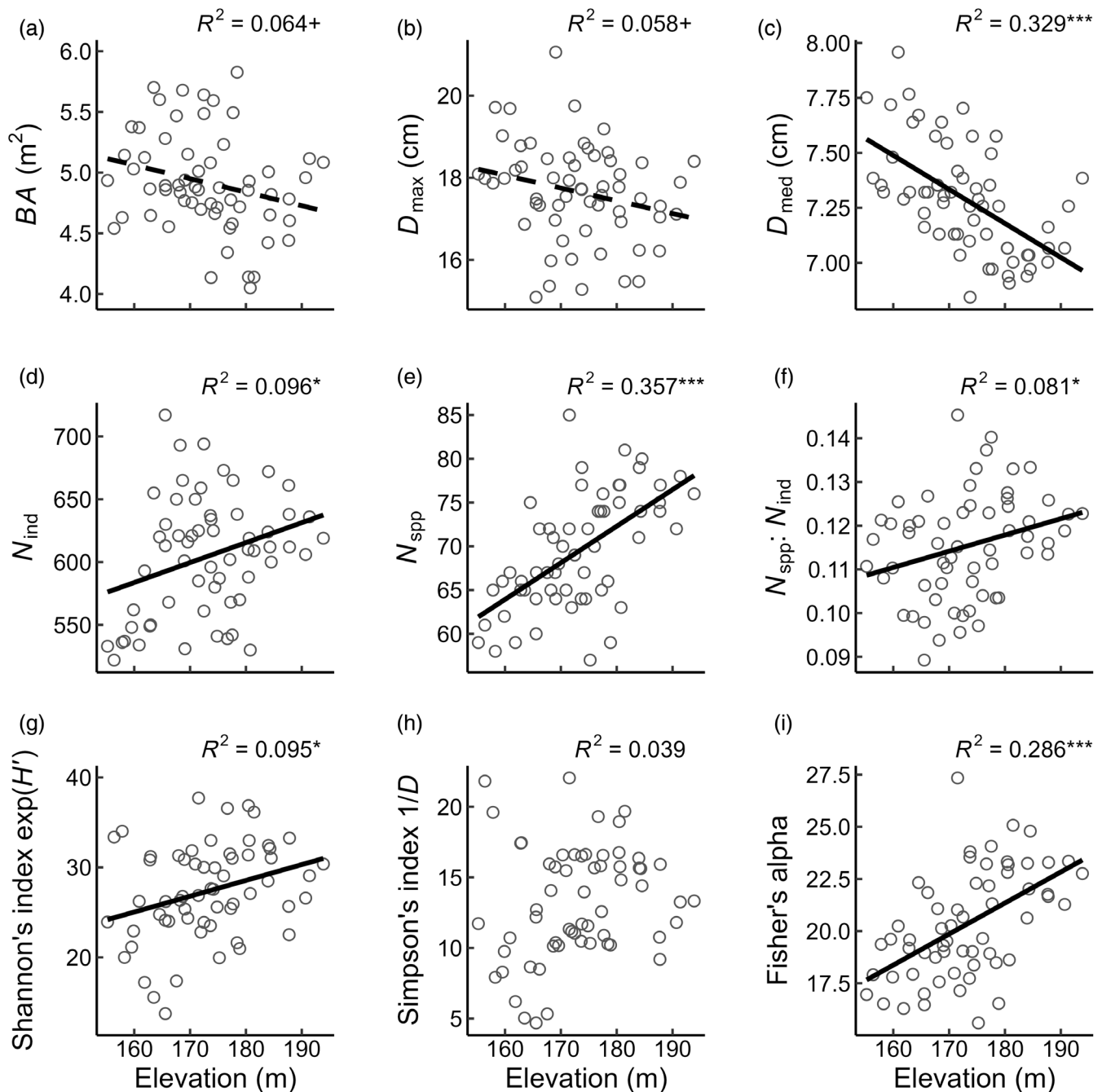


FIGURE 4 Variations of the forest structure and woody species diversity per 50 m × 50 m quadrat along elevation: (a) the basal area (BA), (b) the 95th percentile of diameter at breast height (DBH) ($D_{\max}$), (c) the median of DBH (D_{med}), (d) the number of woody plant individuals (N_{ind}), (e) the number of woody plant species (N_{spp}), (f) the ratio of N_{spp} to N_{ind} ($N_{\text{spp}}: N_{\text{ind}}$), (g) Shannon's index $\exp(H')$, (h) Simpson's index $1/D$, and (i) Fisher's alpha. Solid lines indicate significant correlations ($p < 0.05$) while a dashed line indicates marginal significance ($p < 0.1$). p values of regression slopes are indicated right after R^2 values: *** <0.001 ; ** <0.01 ; * <0.05 ; + <0.10 .

stem number and basal area, were evergreen. The evergreen habit is known as a nutrient conservation strategy (Aerts & Chapin, 1999; Monk, 1966).

The endemism of woody species in the Ankarafantsika plot (79%) was 5% lower than that of vascular plants in the whole of Madagascar (84% in Callmander et al., 2011). In our 15-ha plot, 88% of

abundant species with >500 individuals and 77% of rare species with <10 individuals were endemic to Madagascar. A total of 12 of these species are also listed by the IUCN as endangered species. Such a high level of endemism and the presence of endangered species imply a high conservational value of this forest. Many of the species-rich families in the plot, each including 6 to

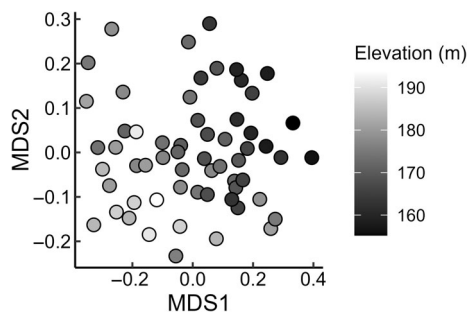


FIGURE 5 nMDS (non-metric multidimensional scaling) with the Bray–Curtis dissimilarity using species community data, which count the number of individuals for each species in each quadrat. Species community differed significantly with elevation by PERMANOVA ($p < 0.001$, Table S3 for further statistical details). [Correction added on 24 September 2024, after first online publication: the word ‘nMDS’ has been spelled out in this version.]

14 species (Table 2), were also reported to be common by other studies on the flora of western Madagascar, as well as in dry forests of other regions. Abraham et al. (1996) report Fabaceae, Meliaceae, and Rubiaceae as common in a western dry forest (700–800 mm annual precipitation and a 6–8-month-long dry season). Sussman and Rakotozafy (1994) report Malvaceae, Burseraceae, Fabaceae, and Euphorbiaceae from a transect survey in a dry forest of southwestern Madagascar with 750 mm mean annual precipitation (MAP) and a 7-month-long dry season.

In dry forests of other regions, Fabaceae and Rubiaceae are the most species-rich families, followed by Malvaceae, Meliaceae, and Moraceae in San Emilio, Costa Rica (MAP = 1565 mm; Enquist & Enquist, 2011), whereas Fabaceae, Moraceae, Euphorbiaceae, and Rubiaceae are the most species-rich families in Mudumalai 50-ha plot in India (MAP = 1200 mm; Sukumar et al., 1992). We found that these families were also species-rich in our 15-ha plot, except for Moraceae (Table S2).

Among the species-rich families in wetter forests of Madagascar, such as Clusiaceae, Lauraceae, and Rubiaceae in an eastern rainforest (1708 mm MAP and no pronounced dry season), and Anacardiaceae, Clusiaceae, and Lauraceae in a dry forest on the Central Highlands (1820 mm MAP and a 5-month-long dry season) as reported by Abraham et al. (1996), Clusiaceae and Lauraceae were each represented by only one species or were missing in Ankarafantsika, respectively.

The gradational changes of the forest structure and species composition with elevation (Figures 4 and 5) were somewhat surprising, as the topography created by deep white sand appeared flat and there was no apparent change in forest physiognomy until we actually measured them. The size of woody plants became smaller and the number of individuals per unit area (N_{ind}) increased with increasing elevation, similar to the pattern reported by

some other studies (Punchi-Manage et al., 2013; Valencia et al., 2004). Tree height also tended to decrease at higher elevations (Figure S4). In the soil survey by our team, coarse white sand was the homogeneous substrate for 1.2 to >3.5 m across the elevation range of 160–190 m (K. Oshima, T. Nishigaki, and K. Kitajima, unpublished data).

More surprising was that species diversity increased with increasing elevation because it was the opposite of a common pattern reported in other studies (e.g., Punchi-Manage et al., 2013; Valencia et al., 2004). The number of species (N_{spp}), the ratio of N_{spp} to N_{ind} , Shannon's index $\exp(H')$, and Fisher's alpha in 50 m $\times$ 50 m quadrats all increased with elevation. Simpson's index $1/D$ was the exception with no significant correlation, possibly because this index is greatly influenced by the relative abundance of common species: some quadrats at lower elevations had low relative abundances of common species (high evenness) with a relatively small number of species (low richness). The most abundant species, *D. perrieri*, decreased its relative abundance at higher elevations, while the second abundant species, *N. alleizettei*, increased it, with a slightly negative correlation between the sum of relative abundance of the two species and the elevation (Figure S5). Since *D. perrieri* is a canopy species and *N. alleizettei* is a subcanopy species, the spatial changes of their abundance may not be simply complementary to each other in terms of the forest structure. They are found throughout the 15-ha plot, and *D. perrieri* tended to be slightly smaller and shorter with elevation, whereas *N. alleizettei* did not change in size with elevation (Figure S6). This may suggest that size limitation on *D. perrieri* at higher elevations may create more niche space for *N. alleizettei*. The relative abundance of those two species partially influenced the species evenness. The ratio of N_{spp} to N_{ind} , Shannon's index $\exp(H')$, and Simpson's index $1/D$ were more strongly correlated with the relative abundance of these two species than with elevation, but Fisher's alpha was correlated with both elevation and the relative abundance of the two species (Table S4). There could be various possibilities for factors underlying these patterns, including environmental filtering and competitive interactions among neighbors.

In conclusion, our study revealed non-random spatial patterns in forest structure and local woody species diversity on a relatively homogeneous gentle slope in a seasonally dry forest in northwestern Madagascar. It remains unclear how elevation may be related to the environmental heterogeneity that likely drives the competitive interaction among the species, including the most abundant two species that clearly exhibit contrasting patterns of dominance. Such spatial patterns of tree species diversity could be demonstrated only in sufficiently large forest

dynamics plots. Our 15-ha plot is the first of such plots in Madagascar, and as such, it provides an important research infrastructure and insight into the community assembly process in the flora rich with endemism. This 15-ha plot within a primary stand of a seasonally dry forest is also a significant addition to the global network of large-scale forest monitoring plots which has few tropical dry forests. The future plan to monitor growth and survival with repeated censuses is promising in revealing forest dynamics that contribute to the spatial patterns of tree species diversity and forest structure, especially when we accumulate more data on environmental conditions including light, water, and nutrients. Such ecological knowledge of this woody plant community in Ankarafantsika National Park provides a critical foundation for the conservation and restoration of Madagascan dry forests.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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REFERENCES

- Abraham, J.-P., Benja, R., Randrianasolo, M., Ganzhorn, J. U., Jeannoda, V., & Leigh, E. G. (1996). Tree diversity on small plots in Madagascar: A preliminary review. *Revue d'Écologie (La Terre et La Vie)*, 51(2), 93–116. <https://doi.org/10.3406/rev.1996.2195>
- Aerts, R., & Chapin, F. S. (1999). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research*, 30, 1–67. [https://doi.org/10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1)
- Almulqu, A. A., Arpornpong, N., & Boonyanuphap, J. (2018). Tree species composition and structure of dry forest in Mutis Timau protected forest management unit of East Nusa Tenggara, Indonesia. *Biodiversitas Journal of Biological Diversity*, 19(2), 496–503. <https://doi.org/10.13057/biodiv/d190217>
- Asai, S., Mizuta, T., Eguchi, K., & Yamagishi, S. (2002). Environmental cues that initiate reproduction in the rufous vanga (*Schetba rufa*). *Journal of the Yamashina Institute for Ornithology*, 34, 232–239. <https://doi.org/10.3312/JYIO1952.34.232>
- Aymoz, B. G. P., Randrianjafy, V. R., Randrianjafy, Z. J. N., & Khasa, D. P. (2013). Community management of natural resources: A case study from Ankarafantsika National Park, Madagascar. *AMBIO*, 42(6), 767–775. <https://doi.org/10.1007/s13280-013-0391-9>
- Cadotte, M. W., Franck, R., Reza, L., & Lovett-Doust, J. (2002). Tree and shrub diversity and abundance in fragmented littoral forest of southeastern Madagascar. *Biodiversity and Conservation*, 11, 1417–1436. <https://doi.org/10.1023/A:1016282023542>
- Callmander, M. W., Phillipson, P. B., Schatz, G. E., Andriambololona, S., Rabarimanarivo, M., Rakotonirina, N., Raharimampionona, J., Chatelain, C., Gautier, L., & Lowry, P. P., II. (2011). The endemic and non-endemic vascular flora of Madagascar updated. *Plant Ecology and Evolution*, 144(2), 121–125. <https://doi.org/10.5091/plecevo.2011.513>
- Chuyong, G. B., Kenfack, D., Harms, K. E., Thomas, D. W., Condit, R., & Comita, L. S. (2011). Habitat specificity and diversity of tree species in an African wet tropical forest. *Plant Ecology*, 212(8), 1363–1374. <https://doi.org/10.1007/s11258-011-9912-4>
- Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R., & Turner, B. L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences*, 110(13), 5064–5068. <https://doi.org/10.1073/pnas.1218042110>
- Denslow, J. S. (1995). Disturbance and diversity in tropical rain forests: The density effect. *Ecological Applications*, 5(4), 962–968. <https://doi.org/10.2307/2269347>
- DeWalt, S. J., Schnitzer, S. A., Chave, J., Bongers, F., Burnham, R. J., Cai, Z., Chuyong, G., Clark, D. B., Ewango, C. E. N., Gerwing, J. J., Gortaire, E., Hart, T., Ibarra-Manriquez, G., Ickes, K., Kenfack, D., Macia, M. J., Makana, J.-R., Martinez-Ramos, M., Mascaro, J., ... Thomas, D. (2010). Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area: Climatic correlates of liana density. *Biotropica*, 42(3), 309–317. <https://doi.org/10.1111/j.1744-7429.2009.00589.x>
- Engelbrecht, B. M. J., Comita, L. S., Condit, R., Kursar, T. A., Tyree, M. T., Turner, B. L., & Hubbell, S. P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447(7140), 80–82. <https://doi.org/10.1038/nature05747>
- Enquist, B. J., & Enquist, C. A. F. (2011). Long-term change within a Neotropical forest: Assessing differential functional and floristic responses to disturbance and drought. *Global Change*

- Biology, 17(3), 1408–1424. <https://doi.org/10.1111/j.1365-2486.2010.02326.x>
- Fan, B., Tao, W., Qin, G., Hopkins, I., Zhang, Y., Wang, Q., Lin, H., & Guo, L. (2020). Soil micro-climate variation in relation to slope aspect, position, and curvature in a forested catchment. *Agricultural and Forest Meteorology*, 290, 107999. <https://doi.org/10.1016/j.agrformet.2020.107999>
- Fernandes, M. F., Cardoso, D., & De Queiroz, L. P. (2020). An updated plant checklist of the Brazilian Caatinga seasonally dry forests and woodlands reveals high species richness and endemism. *Journal of Arid Environments*, 174, 104079. <https://doi.org/10.1016/j.jaridenv.2019.104079>
- Geekiyana, N., Goodale, U. M., Cao, K., & Kitajima, K. (2018). Leaf trait variations associated with habitat affinity of tropical karst tree species. *Ecology and Evolution*, 8(1), 286–295. <https://doi.org/10.1002/ece3.3611>
- Gillespie, T. W., Grijalva, A., & Farris, C. N. (2000). Diversity, composition, and structure of tropical dry forests in Central America. *Plant Ecology*, 147, 37–47. <https://doi.org/10.1023/A:1009848525399>
- Gillespie, T. W., Keppel, G., Pau, S., Price, J. P., Jaffré, T., Meyer, J.-Y., & O'Neill, K. (2011). Floristic composition and natural history characteristics of dry forests in the Pacific. *Pacific Science*, 65(2), 127–141. <https://doi.org/10.2984/65.2.127>
- Guillemot, J., Martin-StPaul, N. K., Bulascoschi, L., Poorter, L., Morin, X., Pinho, B. X., Le Maire, G., Bittencourt, R. L., Oliveira, R. S., Bongers, F., Brouwer, R., Pereira, L., Gonzalez Melo, G. A., Boonman, C. C. F., Brown, K. A., Cerabolini, B. E. L., Niinemets, Ü., Onoda, Y., Schneider, J. V., ... Brancalion, P. H. S. (2022). Small and slow is safe: On the drought tolerance of tropical tree species. *Global Change Biology*, 28(8), 2622–2638. <https://doi.org/10.1111/gcb.16082>
- Harms, K. E., Condit, R., Hubbell, S. P., & Foster, R. B. (2001). Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, 89(6), 947–959. <https://doi.org/10.1111/j.1365-2745.2001.00615.x>
- Hasegawa, M., Mori, A., Nakamura, M., Mizuta, T., Asai, S., Ikeuchi, I., Rakotomanana, H., Okamiya, T., & Yamagishi, S. (2009). Consequence of inter class competition and predation on the adaptive radiation of lizards and birds in the dry forest of western Madagascar. *Ornithological Science*, 8(1), 55–66. <https://doi.org/10.2326/048.008.0108>
- Hokan, M., Strube, C., Radespiel, U., & Zimmermann, E. (2017). Sleeping site ecology, but not sex, affect ecto- and hemoparasite risk, in sympatric, arboreal primates (*Avahi occidentalis* and *Lepilemur edwardsi*). *Frontiers in Zoology*, 14(1), 44. <https://doi.org/10.1186/s12983-017-0228-7>
- Ikeuchi, I., Hasegawa, M., & Mori, A. (2012). Characteristics of sleeping sites and timing of departure from them in a Madagascar diurnal gecko, *Lygodactylus tolampyae*. *Current Herpetology*, 31(2), 107–116. <https://doi.org/10.5358/hsj.31.107>
- Ikeuchi, I., & Mori, A. (2014). Natural history of a Madagascan gecko *Blaesodactylus ambonihazo* in a dry deciduous forest. *Current Herpetology*, 33(2), 161–170. <https://doi.org/10.5358/hsj.33.161>
- Ikeuchi, I., Mori, A., & Hasegawa, M. (2005). Natural history of *Phelsuma madagascariensis kochi* from a dry forest in Madagascar. *Amphibia-Reptilia*, 26(4), 475–483. <https://doi.org/10.1163/156853805774806142>
- Ito, R., & Mori, A. (2010). Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri cuvieri* (Reptilia: Iguania). *Proceedings of the Royal Society B: Biological Sciences*, 277(1685), 1275–1280. <https://doi.org/10.1098/rspb.2009.2047>
- Ito, R., Rakotondraparany, F., & Sato, H. (2013). Non-flying mammalian fauna of Ampijoroa, Ankarafantsika National Park. *Madagascar Conservation & Development*, 8(1), 45–48. <https://doi.org/10.4314/mcd.v8i1.7>
- IUCN. (2023). *The IUCN Red List of Threatened Species*. Version 2022-2. <https://www.iucnredlist.org>
- John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard, R. F., Mirabello, M., Hubbell, S. P., Valencia, R., Navarrete, H., Vallejo, M., & Foster, R. B. (2007). Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences*, 104(3), 864–869. <https://doi.org/10.1073/pnas.0604666104>
- Johnson, D. J., Magee, L., Pandit, K., Bourdon, J., Broadbent, E. N., Glenn, K., Kaddoura, Y., Machado, S., Nieves, J., Wilkinson, B. E., Almeyda Zambrano, A. M., & Bohlman, S. A. (2021). Canopy tree density and species influence tree regeneration patterns and woody species diversity in a longleaf pine forest. *Forest Ecology and Management*, 490, 119082. <https://doi.org/10.1016/j.foreco.2021.119082>
- Kubota, Y., Murata, H., & Kikuzawa, K. (2004). Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. *Journal of Ecology*, 92(2), 230–240. <https://doi.org/10.1111/j.0022-0477.2004.00875.x>
- Kupers, S. J., Wirth, C., Engelbrecht, B. M. J., & Rüger, N. (2019). Dry season soil water potential maps of a 50 hectare tropical forest plot on Barro Colorado Island, Panama. *Scientific Data*, 6(1), 63. <https://doi.org/10.1038/s41597-019-0072-z>
- Lasky, J. R., Sun, I.-F., Su, S.-H., Chen, Z.-S., & Keitt, T. H. (2013). Trait-mediated effects of environmental filtering on tree community dynamics. *Journal of Ecology*, 101(3), 722–733. <https://doi.org/10.1111/1365-2745.12065>
- Levesque, D. L., Rakotondravony, D., & Lovegrove, B. G. (2012). Home range and shelter site selection in the greater hedgehog tenrec in the dry deciduous forest of Western Madagascar. *Journal of Zoology*, 287(3), 161–168. <https://doi.org/10.1111/j.1469-7998.2012.00899.x>
- Lobban, K. D., Lovegrove, B. G., & Rakotondravony, D. (2014). The energetics of a Malagasy rodent, *Macrotarsomys ingens* (Nesomyinae): A test of Island and zoogeographical effects on metabolism. *Journal of Comparative Physiology B*, 184(8), 1077–1089. <https://doi.org/10.1007/s00360-014-0853-9>
- Madagascar Catalogue. (2023). Catalogue of the plants of Madagascar. <https://www.tropicos.org/Project/Madagascar>
- Madagascar National Parks. (2017). *Plan d'aménagement et de gestion: Plan quinquennal de mise en œuvre 2017-2021, Parc National d'Ankarafantsika Région Boeny*. Ministère de l'Environnement, de l'Ecologie et des Forêts.
- Marquès Gomila, C., Kiene, F., Klein, A., Kessler, S. E., Zohdy, S., Rakotondravony, R., Durden, L. A., & Radespiel, U. (2023). Host-related and environmental factors influence long-term ectoparasite infestation dynamics of mouse lemurs in north-western Madagascar. *American Journal of Primatology*, 85(6), e23494. <https://doi.org/10.1002/ajp.23494>

- Mizuta, T., Nakamura, M., & Yamagishi, S. (2001). Breeding ecology of Van Dam's vanga *Xenopirostris damii*, an endemic species in Madagascar. *Journal of the Yamashina Institute for Ornithology*, 33(1), 15–24. <https://doi.org/10.3312/jyio1952.33.15>
- Monk, C. D. (1966). An ecological significance of evergreenness. *Ecology*, 47(3), 504–505. <https://doi.org/10.2307/1932995>
- Nakamura, M., Okamiya, T., & Yamagishi, S. (2004). The diet of adult and nestling sickle-billed vangas *Falcoelea palliata*, a species endemic to Madagascar. *Journal of the Yamashina Institute for Ornithology*, 35(2), 155–158. <https://doi.org/10.3312/jyio.35.155>
- Nakamura, M., Yamagishi, S., & Nishiumi, I. (2001). Cooperative breeding of the white-headed vanga *Leptopterus viridis*, an endemic species in Madagascar. *Journal of the Yamashina Institute for Ornithology*, 33(1), 1–14. <https://doi.org/10.3312/jyio1952.33.1>
- Percival, J. E. H. (2024). *Application of satellite remote sensing techniques to detect spatial and temporal patterns of fire and other deforestation drivers in NW Madagascar* [Doctoral thesis, Kyoto University, Kyoto, Japan].
- Percival, J. E. H., Sato, H., Razanapary, T. P., Rakotomamonjy, A. H., Razafiarison, Z. L., & Kitajima, K. (2024). Non fire-adapted dry forest of northwestern Madagascar: Escalating and devastating trends revealed by Landsat timeseries and GEDI lidar data. *PLoS One*, 19(2), e0290203. <https://doi.org/10.1371/journal.pone.0290203>
- Planet Labs PBC. (2019). *Planet application program interface: Space for life on earth*. Planet. <https://api.planet.com>
- Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Savitri Gunatilleke, C. V., Nimal Gunatilleke, I. A. U., Wiegand, K., & Huth, A. (2013). Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. *Journal of Ecology*, 101(1), 149–160. <https://doi.org/10.1111/1365-2745.12017>
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rakotomanana, H., Nakamura, M., & Yamagishi, S. (2001). Breeding ecology of the endemic hook-billed vanga, *Vanga curvirostris*, in Madagascar. *Journal of the Yamashina Institute for Ornithology*, 33(1), 25–35. <https://doi.org/10.3312/jyio1952.33.25>
- Randriamahazo, H. J. A. R., & Mori, A. (2005). Factors affecting the intra-population variation in dorsal color pattern of an iguanian lizard, *Oplurus cuvieri cuvieri*. *Current Herpetology*, 24(1), 19–26. [https://doi.org/10.3105/1345-5834\(2005\)24\[19:FATIVI\]2.0.CO;2](https://doi.org/10.3105/1345-5834(2005)24[19:FATIVI]2.0.CO;2)
- Rasoloharijaona, S., Rakotosamimanana, B., Randrianambinina, B., & Zimmermann, E. (2003). Pair-specific usage of sleeping sites and their implications for social organization in a nocturnal Malagasy primate, the Milne Edwards' sportive lemur (*Lepilemur edwardsi*). *American Journal of Physical Anthropology*, 122(3), 251–258. <https://doi.org/10.1002/ajpa.10281>
- Reeves, C. V. (2018). The development of the east African margin during Jurassic and lower cretaceous times: A perspective from global tectonics. *Petroleum Geoscience*, 24, 41–56. <https://doi.org/10.1144/petgeo2017-021>
- Sato, H. (2013a). Habitat shifting by the common brown lemur (*Eulemur fulvus fulvus*): A response to food scarcity. *Primates*, 54(3), 229–235. <https://doi.org/10.1007/s10329-013-0353-7>
- Sato, H. (2013b). Seasonal fruiting and seed dispersal by the brown lemur in a tropical dry forest, north-western Madagascar. *Journal of Tropical Ecology*, 29(1), 61–69. <https://doi.org/10.1017/S0266467413000011>
- Sato, H. (2022). Significance of seed dispersal by the largest frugivore for large-diaspore trees. *Scientific Reports*, 12(1), 19086. <https://doi.org/10.1038/s41598-022-23018-x>
- Sato, H., Ichino, S., & Hanya, G. (2014). Dietary modification by common brown lemurs (*Eulemur fulvus*) during seasonal drought conditions in western Madagascar. *Primates*, 55(2), 219–230. <https://doi.org/10.1007/s10329-013-0392-0>
- Schatz, G. E. (2001). *Generic tree flora of Madagascar*. Royal Botanic Gardens, Kew and Missouri Botanical Garden.
- Soil Survey Staff. (1999). *Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys* (2nd ed.). Natural Resources Conservation Service. U.S. Department of Agriculture Handbook.
- Sukumar, R., Dattaraja, H. S., Suresh, H. S., Radhakrishnan, J., Vasudeva, R., Nirmala, S., & Joshi, N. V. (1992). Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India. *Current Science*, 62(9), 608–616.
- Sussman, R. W., & Rakotozafy, A. (1994). Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. *Biotropica*, 26(3), 241. <https://doi.org/10.2307/2388845>
- Torsvik, T. H., Tucker, R. D., Ashwal, L. D., Eide, E. A., Rakotosolofo, N. A., & de Wit, M. J. (1998). Late cretaceous magmatism in Madagascar: Palaeomagnetic evidence for a stationary Marion hotspot. *Earth and Planetary Science Letters*, 164(1–2), 221–232. [https://doi.org/10.1016/S0012-821X\(98\)00206-4](https://doi.org/10.1016/S0012-821X(98)00206-4)
- Valencia, R., Foster, R. B., Villa, G., Condit, R., Svenning, J., Hernández, C., Romoleroux, K., Losos, E., Magård, E., & Balslev, H. (2004). Tree species distributions and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. *Journal of Ecology*, 92(2), 214–229. <https://doi.org/10.1111/j.0022-0477.2004.00876.x>
- Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T. F., & Achard, F. (2018a). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, 222, 189–197. <https://doi.org/10.1016/j.biocon.2018.04.008>
- Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T. F., & Achard, F. (2018b). *Output data from: Combining global tree cover loss data with historical national forest-cover maps to look at six decades of deforestation and forest fragmentation in Madagascar* (2.0) [dataset]. CIRAD Dataverse. <https://doi.org/10.18167/DVN1/AUBRRRC>
- Warren, B. H., Strasberg, D., Bruggemann, J. H., Prys-Jones, R. P., & Thébaud, C. (2010). Why does the biota of the Madagascar region have such a strong Asiatic flavour? *Cladistics*, 26, 526–538. <https://doi.org/10.1111/j.1096-0031.2009.00300.x>

- Webb, C. O., & Peart, D. R. (2000). Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, 88(3), 464–478. <https://doi.org/10.1046/j.1365-2745.2000.00462.x>
- Yoder, A. D., & Nowak, M. D. (2006). Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology, Evolution, and Systematics*, 37, 405–431. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110239>
- Zuleta, D., Russo, S. E., Barona, A., Barreto-Silva, J. S., Cardenas, D., Castaño, N., Davies, S. J., Detto, M., Sua, S., Turner, B. L., & Duque, A. (2020). Importance of topography for tree species habitat distributions in a terra firme forest in the Colombian Amazon. *Plant and Soil*, 450(1–2), 133–149. <https://doi.org/10.1007/s11104-018-3878-0>

SUPPORTING INFORMATION

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