Combining spatial and ecological approaches to describe the vegetation of the Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera

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Abstract

Established in 2015, the Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera is managed by the Association Fanamby, which aims to mitigate ecosystem degradation, promote biodiversity conservation, and restore ecological functions to its remaining natural vegetation. To support the advancement of their work, a study was conducted to characterize vegetation and generate essential land-use data to help inform conservation strategies and planning efforts. This work integrates landscape ecology and cartographic methods, drawing on multiple data sources including: satellite imagery, results from vegetation surveys, vegetation indices, environmental variables, and measures of human activities. The findings reveal that 75% of the landscape is dominated by anthropogenic vegetation, with the balance comprising natural vegetation, primarily dry deciduous forests and moist semi-deciduous forests. These natural vegetation types are confined to fragmented areas and are often situated away from populated areas. They are highly vulnerable in the level of degradation, with the main forest blocks of Antsahabe, Andavakoera, and Andrafiamena having become isolated from one another by extensive secondary grasslands and areas of cattle pasture. Dry deciduous forests exhibit distinctive variants associated mainly with limestone *tsingy* formations, but also lithosol complexes, weakly ferralitic soils, and ferrisols. The presence of moist semi-deciduous forests at Andrafiamena-Andavakoera, which include plant species characteristic of moist forests, suggests an ecological transition zone between the northern sector of the Western Domain and the Sambirano Domain. The two detailed maps produced in the context of our study represent a valuable tool and a key source of information for a range of purposes, including conservation and spatial planning.

Key words: vegetation, environmental factors, NDVI, Andrafiamena-Andavakoera

Résumé détaillé

Le Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera, situé dans le secteur nord du Domaine phytogéographique de l'Ouest, est l'une des plus récentes aires protégées de la région DIANA, gérée par l'Association Fanamby. Bénéficiant d'une position géographique stratégique à la frontière du Sambirano et à proximité du Domaine de l'Est, cette aire protégée est influencée par des facteurs climatiques combinés, notamment l'alizé et la mousson, qui lui confèrent une pluviométrie annuelle pouvant atteindre 1600 mm. Ces conditions, associées à des caractéristiques pédologiques et topographiques, permettent l'installation de divers types de forêts. Toutefois, ces forêts subissent une forte pression anthropique en raison d'activités telles que l'agriculture itinérante, la culture irriguée, l'élevage extensif et l'exploitation minière. La création de cette nouvelle aire protégée vise à freiner la dégradation de ces écosystèmes, préserver leur biodiversité et restaurer leurs fonctions écologiques.

Dans ce cadre, une étude a été menée fin 2023 avec pour objectifs d'améliorer la connaissance de la biodiversité d'Andrafiamena-Andavakoera, de décrire l'état actuel de ses habitats et de fournir des informations essentielles pour sa protection et sa valorisation. L'approche adoptée combine la télédétection, la cartographie et l'écologie du paysage par la superposition d'informations comme les données satellitaires, les relevés de végétation, les facteurs environnementaux, les données périodiques de l'indice de végétation et les données sur l'occupation humaine.

Les résultats montrent que 75 % du paysage est constitué de végétation transformée (prairies secondaires, zones de pâturage, formations secondaires, parcelles agricoles et zones habitées). Seuls 25 % sont couverts de végétation naturelle, sous forme des petits fragments forestiers abrités par les vallons, les vallées et quelques versants

Tahinarivony, J. A. & Gautier, L. 2025. Combining spatial and ecological approaches to describe the vegetation of the Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera. In A floral and faunal inventory of the Andrafiamena-Andavakoera protected area of northern Madagascar, eds. S. M. Goodman & J. A. Tahinarivony. *Malagasy Nature*, 19: 52-74.

des chaînes d'Andrafiamena et d'Andavakoera. Les forêts denses sèches caducifoliées sont présentes principalement sur roche calcaire (*tsingy*), mais on trouve également des variantes sur complexes de lithosols, ou encore sur sols faiblement ferralitiques et ferrisols. Les forêts denses humides semi-décidues, comprenant des espèces typiques des forêts humides, se trouvent sur les massifs gréseux d'Andavakoera-Andrafiamena, témoignant d'une transition écologique unique entre le secteur Nord du Domaine de l'Ouest et celui du Sambirano. Ces résultats mettent en évidence la richesse et l'hétérogénéité écologique d'Andrafiamena-Andavakoera, et témoignent de son importance pour la conservation. Pour décrire la structure du paysage, deux cartes présentant différents niveaux d'interprétation sont présentées. Elles constituent également un outil pour une meilleure planification et gestion des activités de conservation.

Mots clés: végétation, facteurs du milieu, NDVI, Andrafiamena-Andavakoera

Introduction

The northern region of Madagascar includes six terrestrial protected areas, among which are the Parc National de la Montagne d'Ambre, and the Réserve Spéciale d'Ankarana. Several of the regional protected areas, such as the Paysage Harmonieux Protégé de Montagne des Français and the Paysage Harmonieux Protégé d'Andrafiamena-Andavakoera (herein generally referred to as the Andrafiamena-Andavakoera protected area), were established after 2013. The latter, one of the 23 classified forests in the former Antsiranana Province formerly administered by the forestry department, was subsequently delegated to Association Fanamby for conservation management.

In Humbert's (1965) vegetation map, all the remaining forest of what is currently included in the Andrafiamena-Andavakoera protected area is classified as dry deciduous forests and associated degraded scrub and thicket formations. In the Kew vegetation atlas (Moat & Smith, 2007), most of the remaining forests are classified as western dry forest, with isolated pixels of humid forest (herein we use the term moist forest for this same formation), but restricted to the Andavakoera Range. However, these simplified views stem from large-scale cartographic projects based on aerial photograph and satellite imagery that often lacks ground-truthing. Soon after the Andrafiamena-Andavakoera protected area was established and field studies were initiated, it quickly became obvious that the reality of its vegetation types was more complex (Burivalova, 2011).

The region's ecosystems are actually highly diverse (Tahinarivony & Goodman, 2025, herein), shaped by their unique geographical location, soil complex composition, and regional climate influenced by the trade winds (alizé in French, *varatraza* in Malagasy). On the bioclimatic map of Cornet (1974), most of the area, including the Andavakoera Range is in his S1b zone, defined as having a dry season of seven months per year, annual cumulated hydric deficit between 300 and 400 mm, mean temperature of the coldest month between 16°C and 18°C. A SW-NE band roughly corresponding to the Andrafiamena Mountain range is classified as Hhd, defined as: no pronounced annual dry season, no hydric deficit, mean temperature of the coldest month between 10°C and 13°C. This complex environment is home to a range of vegetation types, including dry deciduous forests on limestone formations (known in Malagasy as *tsingy*), as well as variants on other substrates, moist semi-deciduous forests, and various secondary and degraded habitats (Burivalova, 2011; Gautier *et al*., 2018; Ranirison & Andriamiarantsoa, 2018). Additionally, the region is rich in non-renewable mineral resources, including gems and gold.

Anthropogenic impact on the landscape is probably ancient. On the 1954 aerial photographs (FTM, 1958a, 1958b, 1958c), the two main forest blocks of Andrafiamena and Andavakoera appear already separated by a non-forest environment. This disconnection is due to the ancient deforestation of the plain separating the two mountain chains, which is now covered with degraded secondary formations or utilized for agricultural purposes. This fragmentation has led to a notably heterogeneous landscape, shaped not only by the diversity of its natural formations but also by variations in the type, intensity, frequency, and duration of anthropogenic pressures. Currently, the protected area faces significant additional habitat fragmentation, primarily driven by pressures such as mining, agriculture, extensive livestock farming, bushfires, charcoal production, and logging. These observations highlight the vulnerability of the protected area, not only due to the fragmentation of its habitats but also because of the loss of ecological connectivity between its key forest areas.

In this context, a comprehensive assessment of the landscape's spatial and functional structure is essential to understand the characteristics of its vegetation and to analyze the diversity and composition of its biological richness, particularly regarding the local flora and fauna, in order to understand their relationships with anthropogenic-dominated environments.

The objective of this study is thus to describe the spatial structure of the Andrafiamena-Andavakoera protected area and to characterize its vegetation diversity, drawing on data from satellite imagery, vegetation indices, ecological variables, anthropogenic data, environmental metrics, and botanical surveys. Accordingly, it utilizes these different information sources to provide a detailed description of the landscape structure and to characterize the distinct habitats within the protected area.

Materials and methods

Study area

The circumscription of the Andrafiamena-Andavakoera protected area employed in this study is the one used in its official creation decree (2015-761). Situated between 12°47'42''S-13°11'38''S and 49°6'26"E-49°25'30"E, this 73,710 ha site is located in the middle of a complex of protected areas that include Montagne d'Ambre to the north, Ankarana to the northwest, Analamerana to the northeast, and Loky-Manambato to the east (Figure 1).

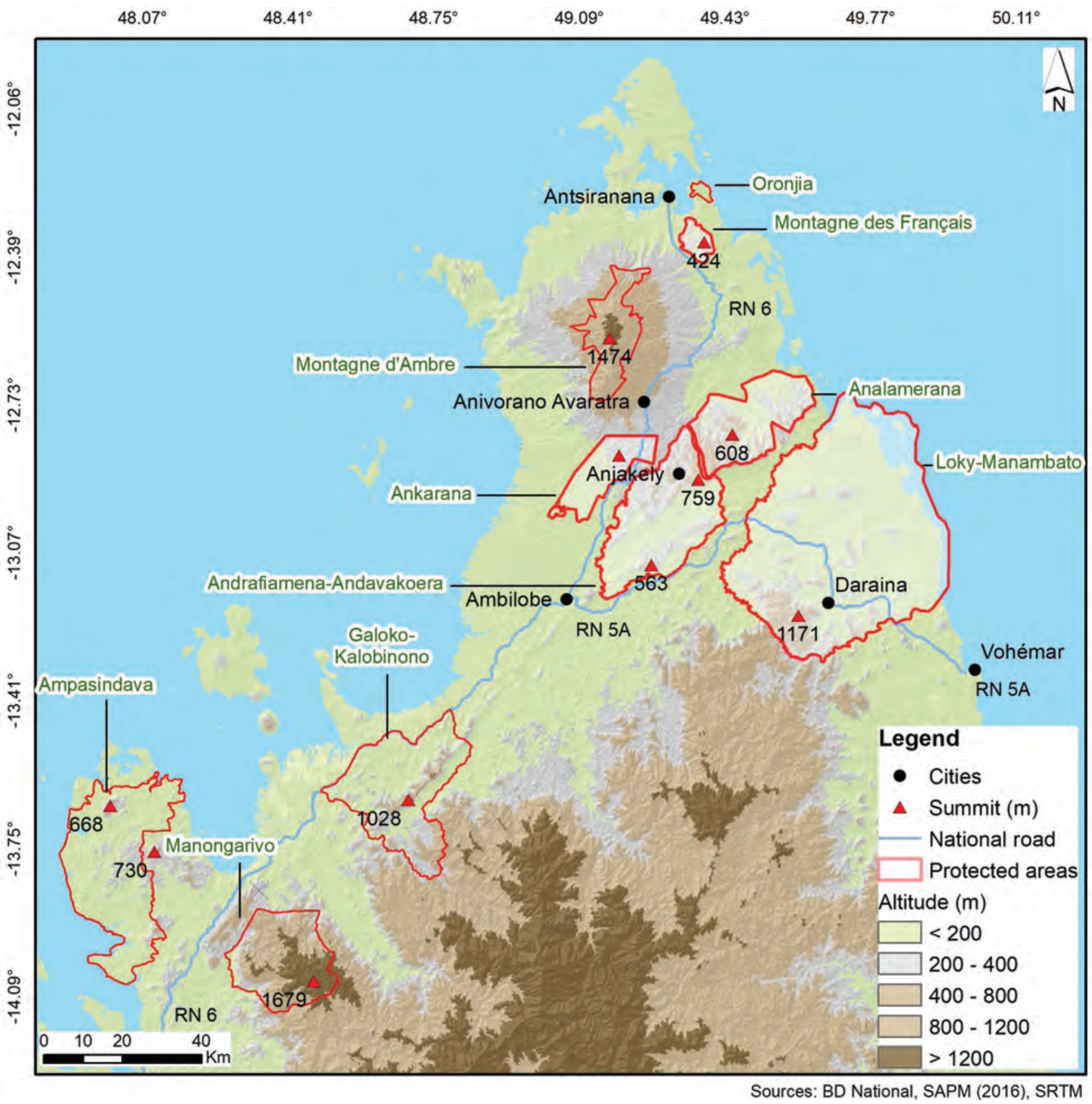

Figure 1. Location of the Andrafiamena-Andavakoera protected area and with respect to neighboring protected areas.

Physical environment

The region is characterized by an irregular topography, dominated by the Andrafiamena and Andavakoera mountain ranges (Figure 2). The Andrafiamena range stretches northeast from Tanambao-Marivorahona, including notable peaks such as Manahoro (604 m) and culminating at Ambatombazaha (760 m). In contrast, the Andavakoera Range sits at lower elevations, including the hills of Bobavato (308 m), with its highest point at Antongonaomby (551 m). Between these two prominent ranges lies a depression defined by a watershed located between Mahanoro and Ambohimanangarana through which flow several water sources. The eastern watershed encompasses an extensive area, including several small lakes scattered between Andrevokely and Tsaratanana that eventually join the Loky River. The

Figure 2. Topography of the Andrafiamena-Andavakoera protected area.

western watershed is drained by the Maharenina River, which flows southwesterly into the Mananjeba River.

Low hills punctuate the landscape to the northwest, occurring discontinuously and forming part of the broader topographic structure associated with the Ankarana Massif. Among the *tsingy* areas within the Andrafiamena-Andavakoera protected area are Antsahabe (554 m), situated west of Anjakely; Ampatsona (551 m), just north of Anjakely; and Antserasera (422 m), located 7 km to the southwest.

Located within the sedimentary Diego-Suarez Basin in the northernmost part of Madagascar (Besairie, 1972), the landscape of the Andrafiamena-Andavakoera protected area has been classified into two distinct geological units by Saint Ours (1958), Roig *et al*. (2012), and Crowley and Sparks (2018). The northern section predominantly consists of marine limestones deposited during the Middle Jurassic, along with clayey limestone and marl formations. These limestone deposits are largely continuous with those observed in the adjacent Ankarana and Analamerana reserves. The southern two-thirds of the Andrafiamena region exhibits a more complex geological composition, including outcrops of sandstone, sandy limestone, dolomite, marl, shale, and gypsum, primarily dating from the Middle Jurassic. These formations are interspersed with older strata composed of sandstone, shale, and conglomerates from the Triassic and Lower Jurassic. Geological surveys by Besairie (1968) revealed marked north-to-south variation in soil types. In the northern sector, soils are weakly ferrallitic, reddish-brown, and developed on basic rocks. By contrast, soils in the northeast sector are characterized by erosion, yielding sandy and rocky substrates. In the southern area, tropical ferruginous soils dominate; they are minimally leached, with reddish and yellow hues, and form from acidic rock substrates.

Based on the bioclimatic classification by Cornet (1974), the region falls within the dry ecological zone, with annual precipitation exceeding 1,400 mm and an average daily temperature ranging from 21.0 to 30.8°C. Minimum temperatures can drop to 17.4°C during the coldest season. Furthermore, data from NASA (https://power.larc.nasa.gov/) indicate irregular annual precipitation trends between 1990 and 2020. Notably, the maximum recorded precipitation of 1,498 mm in 2019 represents an unprecedented peak over the previous three decades.

Data collection

To investigate the origins and structure of the Andrafiamena-Andavakoera landscape, we utilized a wide array of spatial datasets, which offer a comprehensive understanding of the factors shaping the spatial organization and ecological functions for all vegetation types, whether human-modified or not. All datasets are standardized to a unified projection system (WGS 1984, UTM Zone 39S).

The first dataset group focuses on topographic features, including elevation, slope, and hydrology. Elevation data were derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model, which also facilitated the creation of slope and watershed maps using ArcMap 10.8. Rivers were mapped based on digitized topographic maps (FTM, 1958a, 1958b, 1958c).

The second dataset group comprises Normalized Difference Vegetation Index (NDVI) layers from the period ranging from December 2022 to November 2024 (Table 1). NDVI values were calculated using the red (B4) and near-infrared (B5) bands (Rouse *et al*., 1974) from 15 freely available multispectral Landsat 8-9 images (Table 1) that were obtained from the glovis.usgs.gov platform (path/row 158/69 and 159/69, spatial resolution: 30 m). They span different months of the year to capture the seasonal variation of the index. This index, sensitive to vegetation condition and biomass activity, reflects seasonal changes (wet vs. dry seasons) and vegetation types (primary, secondary, or degraded). Together, the absolute NDVI values and their temporal variations provide critical insights into the unique characteristics of each vegetation class. Additionally, multispectral bands from the Landsat 9image dated 14 October 2024 were used to generate color composites and classify land cover type based on pixel-level spectral properties.

The third dataset group incorporates environmental data, including soil types (Besairie, 1972) and vegetation height (Potapov *et al*., 2021). Furthermore, data on human settlements and infrastructure, sourced from CIESIN (2024), offer a preliminary indication of anthropogenic influence in the region. While these data provide information on the location of infrastructure and human habitations, they do not encompass data on active land-use zones, such as agricultural plots or mining sites.

The fourth and last dataset used to describe landscape structure comprises biological data collected during field inventories conducted in November and December 2023 by teams from

Table 1. Metadata of the images used for the analysis of NDVI periodic variation.

Date acquired	Path and Row	Landsat product ID
28/12/2022	158/69	LC09_L1TP_158069_20221228_20230316_02_T1
14/02/2023	158/69	LC09_L1TP_158069_20230214_20230310_02_T1
26/03/2023	158/69	LC08_L1TP_158069_20230326_20230404_02_T1
05/05/2023	158/69	LC09_L1TP_158069_20230505_20230505_02_T1
01/08/2023	158/69	LC08_L1TP_158069_20230801_20230805_02_T1
12/10/2023	158/69	LC09_L1TP_158069_20231012_20231012_02_T1
05/04/2024	158/69	LC09_L1TP_158069_20240405_20240405_02_T1
23/05/2024	158/69	LC09_L1TP_158069_20240523_20240523_02_T1
08/06/2024	158/69	LC09_L1TP_158069_20240608_20240608_02_T1
08/06/2024	158/69	LC09_L1TP_158069_20240608_20240608_02_T1
24/06/2024	158/69	LC09_L1TP_158069_20240624_20240624_02_T1
26/07/2024	158/69	LC09_L1TP_158069_20240726_20240726_02_T1
11/08/2024	158/69	LC09_L1TP_158069_20240811_20240811_02_T1
27/09/2024	159/69	LC08_L1TP_159069_20240927_20241005_02_T1
21/10/2024	159/69	LC09_L1TP_159069_20241021_20241021_02_T1
17/12/2024	158/69	LC08_L1TP_158069_20241209_20241217_02_T1

Association Vahatra and the Conservatoire et Jardin botaniques de Genève. Vegetation was surveyed using the linear transect method (Gautier *et al*., 1994), and floristic information was compiled through fertile herbarium specimens and a synthesis of all available floristic records, as reviewed in Gautier *et al*. (2025, herein). Eight vegetation plots were established across various forest sites within the Andrafiamena region to support vegetation mapping and spatial analyses. This dataset is further complemented by previous vegetation characterization carried out by Burivalova (2011), providing additional insights into the floristic composition and structural attributes of the area.

Data processing and classification

Landsat 9 satellite imagery, acquired on 14 October 2024 (at the end of the dry season), was utilized for land-use mapping, focusing on the green, blue, red, and near-infrared bands. The imagery was processed using an unsupervised classification approach, specifically the k-means algorithm (MacQueen, 1967). This method is widely applied in remote sensing and land-use mapping (Xie & Shao, 2016), as it groups pixels based on their spectral characteristics without the need for prior labeling. The algorithm initiates by randomly selecting ($k = 12$) initial cluster centroids. Each pixel is then assigned to the nearest centroid, forming distinct clusters. The centroids are subsequently recalculated as the mean of all points within each cluster, and the process iterates until convergence, at which point the cluster assignments stabilize. Following the classification, a smoothing analysis was performed to refine the results, removing isolated pixels and improving the spatial coherence of the final classification.

This layer with 12 classes was then cross-referenced with environmental data such as altitude, slope, and soil type to enhance the understanding and description of the attributes of each class. This integration resulted in the subdivision of certain initial classes, driven by the differentiation introduced by environmental factors. The intermediate classes were further combined with canopy height data (Potapov *et al*., 2021) to incorporate typological data into the vegetation cover classification. The nomenclature assigned to these intermediate classes synthesizes their typology (height), ecological characteristics, and dominant environmental factors, such as edaphic and topographic influences.

This process yielded a large number of classes but failed to separate objects differing by response to climatic variables, particularly precipitation regime, as described for the region's natural vegetation by Gautier *et al*. (2018) and Ranirison and Andriamiarantsoa (2018). This limitation was addressed by integrating seasonal data from NDVI.

The preprocessed NDVI maps were classified into seven categories based on attribute values (< 0; 0-0.15; 0.15-0.25; 0.25-0.35; 0.35-0.45; 0.45-0.55; < 0.55). Overlaying the preliminary classification with NDVI data provided critical insights into the vegetation mass characteristics of each class across seasons. For instance, a forest class was categorized as moist semi-deciduous if its NDVI values were high in the wet season (equal or above 0.48), with a moderate decrease in the dry season (not lower than 0.39). In contrast, dry deciduous forests exhibited similar NDVI values to moist semi-deciduous forests during the wet season but showed a significant decline during the dry season (equal or lower than 0.36). This approach was also applied to distinguish secondary

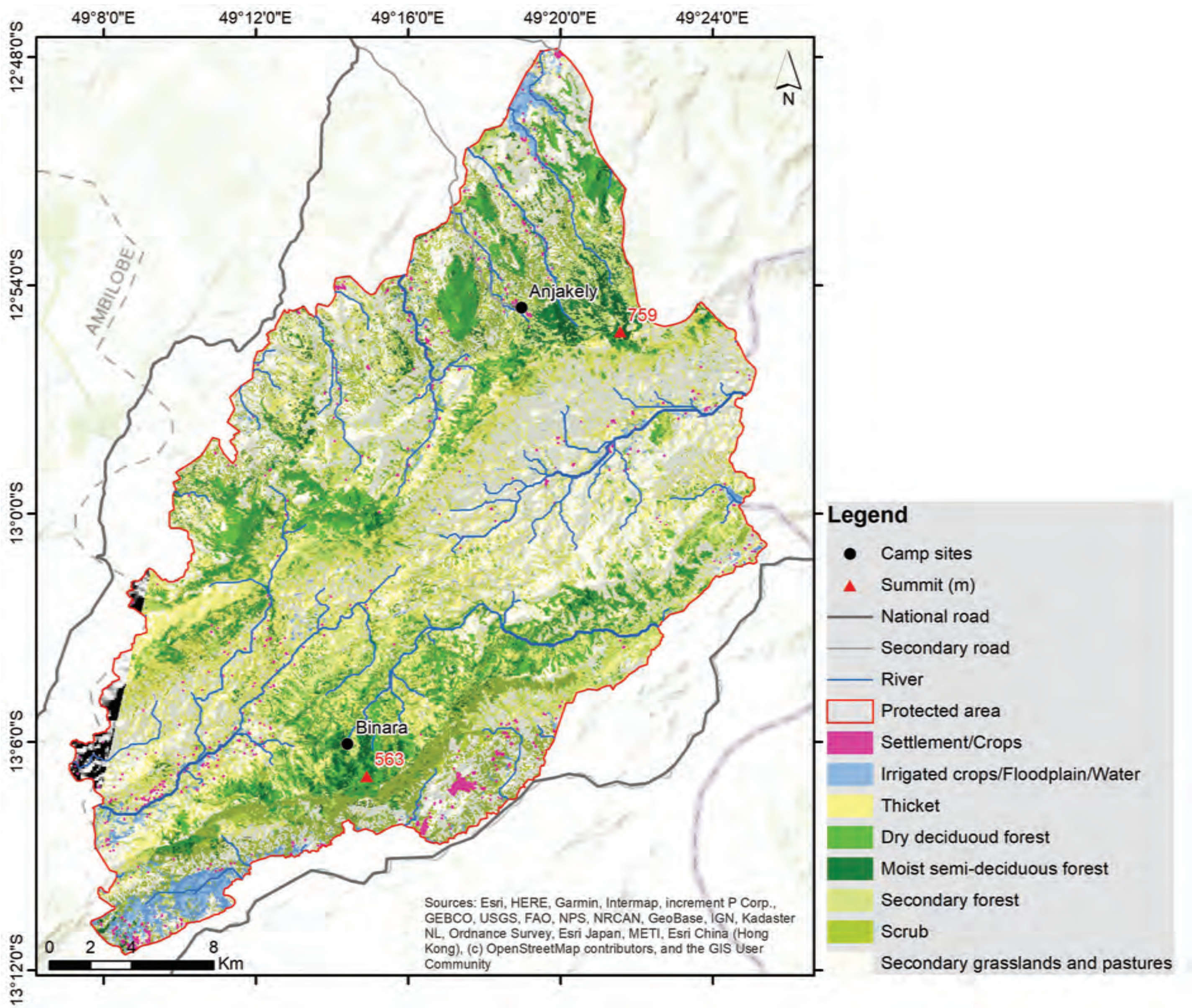

Figure 3. Land-use map of the Andrafiamena-Andavakoera protected area, derived from the combination of multispectral data, vegetation index, and vegetation survey data.

and degraded formations within the Andrafiamena-Andavakoera protected area. The resulting layer was further overlaid with infrastructure and human land-use data (CEISEN, 2024) to delineate anthropogenic zones and settlement areas.

To facilitate the interpretation of our results, two maps were produced. They were generated by grouping similar classes to highlight the characteristics of key vegetation types within the protected area. The first map (Figure 3) focuses on major natural and modified vegetation classes, as described by Gautier *et al*. (2018), offering a general depiction of the spatial structure at Andrafiamena-Andavakoera. Conversely, the second map (Figure 4) gives a finer level of detail, which distinguishing forest sub-classes based on their typology, is primarily influenced by edaphic factors and secondary succession processes. Taken together, these two maps provide a comprehensive view of the spatial and functional characteristics of the habitats within the protected area and their ecological integrity. The physiognomic characteristics and floristic composition of the classes were characterized based on field-collected vegetation data. Species naming and delimitation follow the Catalogue of the Plants of Madagascar (Madagascar Catalogue, 2025). Additionally, floristic and ecological data from Burivalova (2011) were incorporated, provided that most sampling sites studied had not undergone human transformations since their initial assessment a decade and a half ago

Results

Two interpretations of the spatial data offer a comprehensive understanding of the current landscape structure and provide critical insights into its degree of anthropogenic transformation of the protected area. Seven distinct classes were recognized in the first map (Figure 3), depicting the spatial distribution of natural vegetation remnants (dry deciduous forest and moist semi-deciduous forest) and the extent of modified vegetation formations within the landscape (secondary grassland and grazing areas, cropland, thicket, scrub, and secondary forest), as well as inhabited areas.

The second map (Figure 4), with 12 classes highlights the structure and diversity of natural vegetation as shaped by edaphic factors.

Main vegetation types

Figure 3 illustrates the spatial distribution of natural vegetation remnants of dry deciduous forest and moist semi-deciduous forest, as well as the extent of modified vegetation formations within the protected area's landscape, including secondary grasslands, grazing areas, croplands, thickets, scrubs, secondary forests, and human-inhabited zones. The classes of this map are illustrated by field images (Figures 5, 6 & 7), depicting the landscape structure of Andrafiamena-Andavakoera, highlighting the concentration of forests on the two main mountain ranges and the prominence of agricultural areas, secondary grasslands, and grazing zones in the valleys and plains.

In addition to being differentiated by their altitudinal distribution across the landscape, these classes differ by their structural characteristics, as defined by the indicators described in Table 2. Forest formations exhibit the greatest height, with moist semi-deciduous forests being denser and richer in woody species compared to dry deciduous forests, and containing more trees with a diameter at breast height greater than 10 cm. Woody species are mostly absent from flooded or agricultural areas but are represented in secondary grasslands and formations by *Albizia lebbeck* and *Tamarindus indica* (Fabaceae), *Ehretia cymosa* (Ehretiaceae), and *Mangifera indica* (Anacardiaceae). These fire-resistant species, which are edible or are used as fuelwood by the local population, can exceed 30 cm in DBH (Table 2).

In relation to these various characteristics, the physiognomy of these classes is also distinguished by the density of woody species, which is nearly zero in agricultural areas and does not exceed 10 individuals per 100 linear meters in secondary grasslands. However, this parameter alone is insufficient to distinguish scrub and thickets from secondary forests, just as it fails to separate the two forest types within the natural vegetation group.

In addition to structural data, the mean value of the vegetation index was calculated for each season, providing support for the description of the main land cover classes. Surface water, irrigated crop fields, and flooded areas are grouped into a single class comprising wetland zones. Permanent water exhibits a negative NDVI, whereas flooded areas and crop fields may have positive values when vegetation is emergent or when the area is temporarily dry. Moreover, accurately defining the boundary between

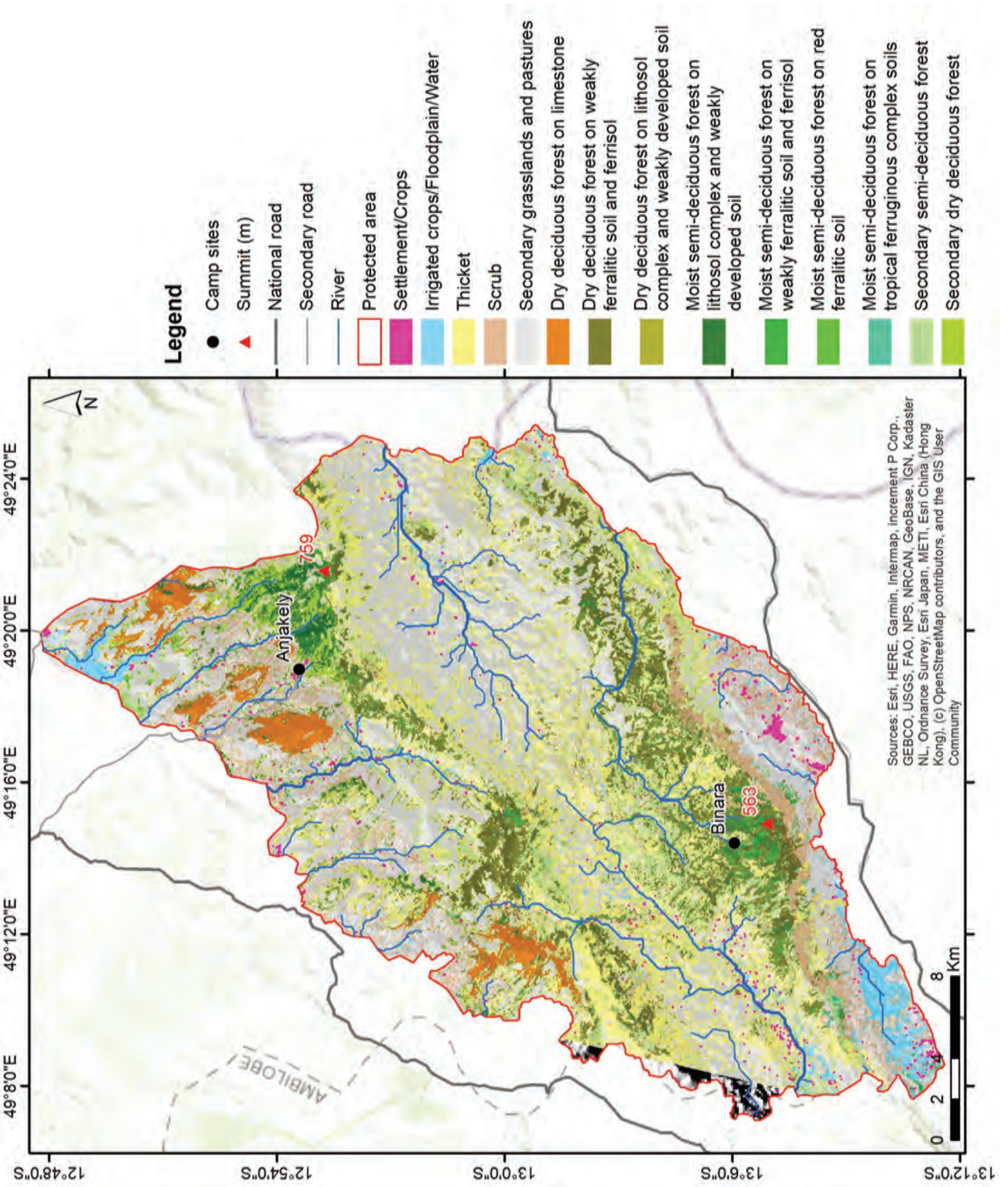

Figure 4. Map of the main forest types in the Andrafiamena-Andavakoera protected area and their edaphic variants.

Figure 5. Northwestern part of the Andrafiamena-Andavakoera protected area, as viewed from Anjakely, showcasing forests on limestone (*tsingy*) surrounded by secondary grasslands. (Photo by Jacquis Tahinarivony.)

Figure 6. The landscape viewed from National Road 5 (towards Betsiaka), with the Andavakoera Mountain range in the background. (Photo by Jacquis Tahinarivony.)

Figure 7. Moist semi-deciduous forest of Anjakely (Andrafiamena), located at the foothills near the Akiba Lodge. (Photo by Jacquis Tahinarivony.)

water and irrigated crop fields is challenging both in the dry and wet seasons.

Secondary grasslands and grazing areas consist of vegetation under 2 m in height with low to very low NDVI values during the dry season (0 to 0.15) due to the desiccation of herbaceous biomass. The NDVI can increase to 0.25 during the wet season as a result of regrowth of the hemicryptophytic perennials and Poaceae along with the emergence of annual species dominated by Cyperaceae and Fabaceae.

Thicket formations are also typically limited to 4 m in height. In contrast, they are relatively rich in woody vegetation, primarily shrubby species. The woody component can range from dense to extremely dense and is typically unstratified due to either high plant density or the bushy architecture of the vegetation.

Scrub, on the other hand, can reach heights exceeding 4 m associated with the growth of woody species of shrubs and bushes. This class also includes young *Eucalyptus* plantations, bamboo stands, and post-cultivation shrub formations dominated by pioneer species, both exotic and indigenous. NDVI values are higher than that of secondary grasslands but do not exceed 0.42, even during the peak of the wet season.

Secondary forests and scrub share similar characteristics in terms of height and vegetation indices. They range from 4 to 8 (-10) m in height, are dense to very dense and deciduous to evergreen, with average NDVI values ranging from 0.31 to 0.44.

Table 2. Structural parameter descriptions for the various land cover classes in the Andrafiamena-Andavakoera protected area.

Class	Surface (ha)	Mean NDVI - dry season	Mean NDVI - wet season	Height (m)	Density of woody species (per 100 linear meters)	Linear density of individuals with DBH ≥ 10 cm	Max DBH (cm)
Water/Flooded area/ Irrigated crop	10-630	0.25 (± 0.09)	0.23 (± 0.19)	< 1	0	0	-
Secondary grassland	10-750	0.21 (± 0.03)	0.30 (± 0.06)	< 2	< 10	< 5	30
Thicket	10-750	0.29 (± 0.03)	0.40 (± 0.04)	2-4	40-80	< 5	35
Scrub	10-730	0.31 (± 0.05)	0.41 (± 0.08)	4-8	120-200	10-30	25
Secondary forest	10-750	0.33 (± 0.03)	0.44 (± 0.04)	4-10	100-180	5-15	20
Dry deciduous forest	10-740	0.35 (± 0.04)	0.49 (± 0.04)	8-15	60-140	28-43	60
Moist semi-deciduous forest	10-700	0.39 (± 0.03)	0.49 (± 0.03)	12-25	110-205	40-52	78

However, these two classes are found in distinct conditions within the Andrafiamena-Andavakoera protected area:

- Scrub is generally found in rugged areas with slopes greater than 40%, such as the steep and narrow southern hills of Andavakoera, and is also observed along riverbanks or ridges with shallow soils. These formations can be primary or secondary but are classified as part of the modified vegetation group due to their floristic and ecological characteristics.
- Secondary forests are often situated adjacent to natural forest, either at their edges or isolated within the forest. They can reach heights of 8 m, with densities of up to 120 woody individuals per 100 linear meters. The largest individuals may exceed 15 cm in DBH.

Within the natural vegetation group, dry deciduous forests can range from 10 to 15 m in height, depending on environmental conditions (Table 2). Their NDVI values can reach up to 0.60 in March (maximum during the rainy season). These forests occur at various topographic levels, between 10 and 740 m of altitude, and form irregular patches. They can be found scattered in both the Andrafiamena and Andavakoera ranges as well as in larger stands on limestone, all as isolated forest patches surrounded by secondary grasslands, such as on the Antsahabe Massif. The mean NDVI of this forest type is 0.35 (± 0.04) in the dry season and 0.49 (± 0.04) in the wet season.

Moist semi-deciduous forest represents another class of natural vegetation, reaching 25 m high in certain areas. This vegetation type is dense to very dense and occurs at altitudes of up to 700 m, with large, well-preserved blocks mostly found in areas such as Anjakely, along the banks of the Ampantsona River, and within the valleys, slopes, and plateaus of Andavakoera. This forest type is dense, with a high proportion of large trees (DBH greater than 30 cm), and is therefore characterized by a high NDVI compared to other land cover classes. The mean dry season value of NDVI is 0.42 recorded in September, corresponding to period of leaf loss in a portion of the tree species, while the highest value, exceeding 0.61, is recorded in March, during the wet season.

Edaphic variants of the Andrafiamena-Andavakoera protected area

In order to develop a more detailed understanding of the natural vegetation within the Andrafiamena-Andavakoera protected area, we have taken into account substrate type, which provides a distinction among three types of deciduous forests and four types of moist semi-deciduous forests (Figure 4).

Dry deciduous forest is typically found on limestone (*tsingy*) formations, but can also occur on partially leached ferralitic soils and ferrisols or on complexes of lithosols and poorly developed soils (Table 3). Forests on *tsingy* formations are located in the northwestern part of the protected area, at altitudes ranging from 20 to 590 m, in patches surrounded by secondary grasslands. Due to the distribution of exposed rock, which impedes the progress of fire, the regular burning that occurs in the surrounding grasslands rarely penetrates into the forest. The forest height can exceed 15 m and the linear density of woody species, as well as the canopy cover, vary significantly depending on the extent and/or prominence of exposed limestone outcrops. NDVI values range from 0.33 to 0.48, with the highest values recorded in March and April (0.56 ± 0.05).

The two other edaphic types, found on partially leached ferralitic soils and ferrisols or on complexes of lithosols and weakly developed soils, are quite similar. These forests can exceed 14 m in height (Table 3) and have an average linear density of over 105 individuals per 100 linear meters, 35% of which have a DBH greater than 10 cm.

Moist semi-deciduous forests are distributed widely across the Andrafiamena and Andavakoera ranges, up to altitudes of 700 m. Among the variants, no major differentiation is revealed by satellite imagery. However, the vegetation index indicates that their biomass shifts differently across seasons. Forests on partially leached ferralitic soils and ferrisols (Andavakoera, Andrafiamena) and those on complexes of lithosols and weakly developed soils (Ampantsona basin) exhibit the highest and most stable NDVI values in the landscape, with seasonal averages ranging from 0.40 (± 0.03) to 0.49 (± 0.02). This vegetation type also includes the tallest forests in the region, reaching heights of over 20 m, with the largest tree recorded as having a DBH of 61 cm.

Only a small amount of moist semi-deciduous forest remains on complexes of red ferralitic soils. However, the relicts observed still retain the characteristics described in Table 3. The variant found on tropical ferruginous soil complexes with weak development is also of limited area, reduced to fragments in the southern valleys of Andavakoera, between 20 and 510 m in altitude. These forests are shorter in stature (14 m), dense, and have canopies ranging from partially closed (80%) to fully closed (90%).

Table 3. Edaphic variants of natural forests typology in the Andrafiamena-Andavakoera protected area.

Class		Average NDVI - dry Season	Average NDVI - wet Season	Height (m)	Density of woody species (per 100 m linear)	Linear density of individuals with DBH ≥ 10	Max DBH (cm)
Dry deciduous forest	On limestone	0.35 (± 0.03)	0.48 (± 0.03)	8-20	77	38	60
	On poorly leached ferralitic soils and ferrisoils	0.36 (± 0.03)	0.48 (± 0.03)	8-14	96	42	42
	On complexes of lithosols and poorly leached soils	0.35 (± 0.04)	0.49 (± 0.02)	10-16	80	48	44
Moist semi-deciduous forest	On complexes of lithosols and poorly leached soils	0.40 (± 0.05)	0.49 (± 0.03)	12-30	110	39	62
	On poorly leached ferralitic soils and ferrisoils	0.43 (± 0.03)	0.48 (± 0.03)	12-24	125	43	78
	On red ferralitic soils	0.39 (± 0.03)	0.49 (± 0.02)	12-24	82	32	35
	On tropical ferruginous soil complexes with poorly leached soils	0.39 (± 0.05)	0.49 (± 0.03)	12-30	107	40	52

Habitat typology

Transformed habitats

Of the 73,319 ha comprising the Andrafiamena-Andavakoera protected area, 74.5% is covered by modified vegetation, primarily consisting of agricultural plots and secondary grasslands (Figures 8 & 9). These formations extend from the valley bottoms, lowland areas, and up to the massif summits, in an elevational range from 10 to 750 m. Secondary grasslands and grazing areas, particularly susceptible to recurrent fires, can degrade into bare soil due to the erosion of its upper layers. In the southeastern part of the Andavakoera Range, these grasslands host scattered woody species (those

Figure 8. Agricultural plot at the beginning of the wet season, between the Andavakoera Range and the RN 5A road. (Photo by Jacquis Tahinarivony.)

Figure 9. Agricultural plots and secondary grasslands during the dry season, with the Andavakoera Range in the background. (Photo by Jacquis Tahinarivony.)

Figure 10. An example of a thicket in the Binara Forest. (Photo by Jacquis Tahinarivony.)

that are introduced to Madagascar are in bold, both here and below), including ***Albizia lebbeck*** (Fabaceae), ***Mangifera indica***, *Sclerocarya birrea* (Anacardiaceae), and *Mascarenhasia arborescens* (Apocynaceae). Between Anjakely and Marotaolana, some zones have been reforested with *Eucalyptus* plantations.

Thickets (Figure 10) are dominated by pioneer, pioneering, and exotic species. Notable taxa include ***Acacia mangium***, ***Albizia lebbeck***, *Chadsia salicina*, *Tamarindus indica* (Fabaceae), *Annona senegalensis* (Annonaceae), *Breonia* cf. *sambiranensis* and *Gardenia rutenbergiana* (Rubiaceae), ***Cordia myxa*** (Cordiaceae), *Hugonia* cf. *brewerioides* (Linaceae), ***Lantana camara*** (Lamiaceae), ***Mangifera indica***, *Sclerocarya birrea* (Anacardiaceae), *Mascarenhasia arborescens*, and *Strychnos madagascariensis* (Loganiaceae). These formations are generally low, ranging from sparse to moderately dense, and are found along riversides, ridges, and along forest edges. Scrub vegetation is often found at the forest edge, in confined environments with thin, sandstone-derived substrates such as those of Andavakoera and Andrafiamena, or within cliff interstices. It forms a dense to very dense woody assemblage with limited stratification, reaching heights of over 8 m. Its origin

Figure 11. Secondary forest on tropical ferralitic soil at Anjakely. (Photo by Jacquis Tahinarivony.)

Figure 12. Secondary forest at Binara on a sandstone plateau. (Photo by Jacquis Tahinarivony.)

can be anthropogenic, resulting from vegetation regeneration following forest loss due to fire or other human-induced disturbances. However, some scrub formations are naturally occurring, their structure and physiognomy shaped by the combined effects of edaphic factors, topography, and climate.

In contrast, the secondary forests (Figures 11 & 12) within the protected area are characterized by a high abundance of native, often woody species, often endemic to Madagascar, which result from stump regrowth or new growth from seed. Depending on their stage of development, these formations can range from dense to very dense (linear density of woody plants: 50-160 per 100 linear meters). Key species include *Leptolaena* spp., *Sarcolaena codonochlamys*, *Schizolaena viscosa*, and *Xyloolaena richardii* (Sarcolaenaceae), *Grangeria porosa* (Chrysobalanaceae), *Erythroxylum nitidulum* (Erythroxylaceae), and *Rinorea longipes* (Violaceae). On slopes with relatively fertile substrates, the floristic composition includes *Abrahamia* spp. (Anacardiaceae), *Aphloia theiformis* (Aphloiaceae), *Baudouinia* spp., and *Parkia madagascariensis* (Fabaceae), *Brachylaena ramiflora* (Asteraceae), *Danais fragrans*, *Gaertnera obovata*, *Gardenia rutenbergiana*, and *Mantalania sambiranensis* (Rubiaceae), *Ehretia cymosa* (Ehretiaceae), and *Paropsia grandiflora* (Passifloraceae). Depending on the site conditions and history of disturbance, these secondary forests may also be dominated by bamboo species (Poaceae).

Natural habitats

Moist semi-deciduous forests

The natural vegetation of the Andrafiamena-Andavakoera protected area is highly fragmented, covering only 25.5% of the total area. Within this, moist semi-deciduous forests occupy approximately 2,500 ha, representing 3.6% of the landscape. The best-preserved fragments, which retain the original characteristics of the formation, are found in Anjakely (Figures 13 & 14) and the valleys of Binara (Figure 15 & 16). These forests are dense, tall, multi-layered, and have a significant proportion of evergreen species, many of which also occur in the adjacent Sambirano Domain. The linear density of woody plants exceeds 125 individuals per 100 linear meters, with more than 40% of stems having a DBH greater than 10 cm. The understory is open, developing on a substantial layer of organic matter, which supports the growth of tree and shrub seedlings. This forest type, characterized by its tall, dense, multi-layered physiognomy and closed canopy, exhibits a unique

Figure 13. Moist semi-deciduous forest in the Andrafiamena-Andavakoera protected area dominated by *Labramia sambiranensis* in the vicinity of Ampantsona River. (Photo by Jacquis Tahinarivony.)

and heterogeneous flora with elements characteristic of both moist and dry forests. Its structure and composition are strongly influenced by topography, with the richest and most diverse forests, which include large trees, often occurring in valleys and on lower slopes. The upper canopy layer, ranging from 12 to 16 m in height, is closed to largely-closed. The large tree species characteristic of this formation are *Abrahamia sambiranensis*, *Ambavia gerrardii*, and *Xylopia ambanjensis* (Annonaceae), *Canarium multiflorum* (Burseraceae), *Euclinia suavissima* (Rubiaceae), *Hirtella thouarsiana* (Chrysobalanaceae), *Labramia sambiranensis* (Sapotaceae), *Parkia madagascariensis*, *Uapaca ferruginea* (Phyllanthaceae), and some taxa of Lauraceae.

Dry deciduous forests

This type is distinguished by its structure and flora, dominated by characteristic taxa of the Western Domain such as *Baudouinia fluggeiformis, Delonix boiviniana*, and *D. regia* (Fabaceae), *Givotia stipularis* (Euphorbiaceae), *Commiphora ankaranensis*, *C. arafy*, and *C. lasiodisca* (Burseraceae), *Hildegardia erythtosiphon* (Malvaceae), and others. Within the Andrafiamena-Andavakoera protected area, these forests can be found on limestone (*tsingy*) formations

Figure 14. Moist semi-deciduous forest in the Andrafiamena-Andavakoera protected area with *Pandanus*, found downstream of the waterfall along the Ampantsona River and in the upper portion of the Anjakely Forest. (Photo by Jacquis Tahinarivony.)

Figure 15. Understory structure of the moist semi-deciduous forest in the Andrafiamena-Andavakoera protected area, Andavakoera Range, Binara Massif. (Photo by Jacquis Tahinarivony.)

Figure 16. Closed canopy of a semi-deciduous forest in in the Andrafiamena-Andavakoera protected area, Andavakoera Range, Binara Massif. (Photo by Jacquis Tahinarivony.)

(Figure 17) or other types of substrate. The structure and floristic composition of the *tsingy* variant are shaped by the extent of limestone outcrops (Chatelain *et al*., 2013). In these environments, the tallest formations can reach up to 15 m in stature (Figure 18), featuring three or four strata and a canopy that ranges from relatively closed to fully closed. Characteristic large tree species include *Abrahamia* aff. *chapelieri* and *Poupartia chapelieri* (Anacardiaceae), *Baudouinia* spp. and *Delonix boiviniana*, *Breonia* aff. *perrieri*, *Givotia stipularis*, *Hildegardia erythrosiphon*, *Brachylaena ramiflora*, and *Stereospermum longiflorum* (Bignoniaceae). The crevices of the *tsingy* host short-lived herbaceous vegetation and notable perennial geophyte species such as *Amorphophallus hildebrandtii*, *A*. *ankarana*, and *Carlephyton glaucophyllum* (Araceae), and *Nervilia* sp. (Orchidaceae), as well as species of Acanthaceae and Fabaceae. A shorter variant, reaching 8 to 13 m, is found on continuous limestone plates that are less favorable for the development of deep root systems. This formation is more open, with medium stature trees that do not exceed 20 cm in DBH (Figure 19). Dominant species include *Albizia boinensis*, *Baudouinia* spp., *Parkia madagascariensis*, and *Xanthocercis madagascariensis* (Fabaceae), *Diospyros* spp. (Ebenaceae), *Khaya madagascariensis* (Meliaceae), *Strophanthus boivinii* (Apocynaceae), and *Paropsia grandiflora*. In some areas, these forests have been affected by fires or selective logging.

Another type of dry deciduous forest develops on complexes of lithosols and poorly evolved soils, as well as on tropical ferruginous complexes or poorly leached ferralitic soils and ferrisols (Figures 20 & 21). These two types do not show significant differences in terms of structure or floristic composition. The densest and tallest of these forests do not exceed 14 m in height and occur on poorly leached ferralitic substrates, ferrisols, or lithosol complexes. They consist of three or four strata, with an open understory and a relatively closed canopy. Characteristic species include *Cynometra ankaranensis* and *Xylia hoffmannii* (Fabaceae), *Grangeria porosa*, *Schizolaena viscosa,* and *Leptolaena cuspidata*, as well as *Stereospermum hildebrandtii*.

Figure 17. *Tsingy* dry deciduous forest on the exposed limestone Antsahabe Massif in the Andrafiamena-Andavakoera protected area. (Photo by Jacquis Tahinarivony.)

Figure 18. The largest tree found during the work in the *tsingy* forest of Antsahabe, a specimen of *Rhopalocarpus undulatus* with a DBH of 62 cm. (Photo by Jacquis Tahinarivony.)

Figure 19. Variant of dry deciduous forest on limestone (*tsingy*) on the Antsahabe Massif in the Andrafiamena-Andavakoera protected area, an example of the open and moderately low forest structure. (Photo by Jacquis Tahinarivony.)

Figure 20. Understory of a dry deciduous forest in the Andrafiamena-Andavakoera protected area on poorly leached ferrallitic soils and ferrisols. Andavakoera Range, Binara Massif. (Photo by Jacquis Tahinarivony.)

Figure 21. Understory of a dry deciduous forest in the Andrafiamena-Andavakoera protected area on complex of lithosols and poorly leached soils. Andavakoera Range, Binara Massif. (Photo by Jacquis Tahinarivony.)

Discussion

The Andrafiamena-Andavakoera protected area, situated at the interface between the Sambirano Domain and the northern sector of the Western Domain, with Ankarana, Montagne d'Ambre, and Loky-Manambato protected areas in close vicinity, serves as a critical node of ecological connectivity between various biomes and protected areas in northern Madagascar. Given the site's geographic position, it is a key component for maintaining ecological continuity in the natural habitats of the region, supported by an exceptional floristic diversity (Gautier *et al*., 2025, herein) and complexity of forest types. Indeed, the Andrafiamena-Andavakoera landscape encompasses a variety of habitats, including dry deciduous forests on *tsingy* similar to those of Ankarana, and dry deciduous forests akin to those found in parts of Daraina (Loky-Manambato) and Analamerana, as well as moist semi-deciduous forests sharing taxa with those of the Sambirano and with the medium altitude moist evergreen forests of the Loky-Manambato (separate areas form those in Andrafiamena-Andavakoera and also known as Binara and Antsahabe Massifs) and of Montagne d'Ambre.

This remarkable ecological diversity makes the Andrafiamena-Andavakoera protected area a zone of exceptional richness. However, the impact of anthropogenic activities on the environment has led to the degradation and fragmentation of its original forests. The landscape is now mostly dominated by secondary formations and modified vegetation, which directly affects the site's ecological connectivity. An assessment of the current state of the landscape revealed a marked precariousness of its forest relicts, with clear signs of fragmentation. Floristic data collected from the three study sites (Binara, Antsahabe, and Anjakely) suggest a historical connection between the *tsingy* forest and the subhumid forest type of Andrafiamena that has now been lost.

Among natural vegetation classes, dry deciduous forest occupies a larger area than the moist semi-deciduous forest, although originally the situation was presumably reversed. This can be explained as follows:

- The environments originally occupied by the moist semi-deciduous forest are much more prone to transformation by shifting agriculture than the dry forests, due to differences in both soil and microclimate.

A smaller proportion of the dry deciduous forest has been exploited, resulting also in lower losses in terms of both surface and quality. Among its edaphic variants, the forest on *tsingy* has probably experienced the least amount of surface loss due to its bare rock substratum, which is unsuitable for agriculture, and a resulting vegetation structure that impedes the propagation of uncontrolled fires. It is, however, exploited for its timber.

Conclusion

The influences of environmental, climatic, and edaphic factors determine the biological and ecological specificity of the Andrafiamena-Andavakoera protected area. However, the current state of natural ecosystems, coupled with the area's conservation status (IUCN Category V), requires that the manager rigorously assess conservation actions and ensure the protection of this forest relic. These relics, fragmented into unconnected forest blocks, limit both biological and genetic exchanges for plant and animal species. In this context, the maps presented herein serve as a valuable tool for planning conservation and ecological restoration activities for these ecosystems.

The areas where characteristic species are concentrated are primarily located within the three main remaining forest blocks, which are surrounded by secondary formations and human-impacted areas. According to the current management plan (Fanamby, 2023), the Andrafiamena and Andavakoera forest blocks are designated as conservation zones, while Antsahabe is classified as a sustainable use zone. This categorization, although formally established, may still lead to a reduction in forest area, particularly due to the degradation or loss of the *tsingy* forests of Antsahabe, which have already suffered significant deterioration, as shown by recent observations. However, it should be stressed that these *tsingy* dry deciduous forests are in close proximity to the protected Ankarana Special Reserve (the closest point is the Mahory Forest, less than 3.5 km west of Antsahabe), and that we have no evidence of any plant species (Gautier *et al*., 2025, herein) or forest type unique to the Antsahabe Forest. In contrast, the moist semi-deciduous forests of the Andrafiamena and Andavakoera ranges are exceptional, representing a northeastern drier extension of the moist evergreen forests of the Sambirano. They host several very rare Sambirano plant species, as well as local endemics, whose distribution is restricted to the Andrafiamena-Andavakoera protected area.

Currently, the forest area within the Andrafiamena-Andavakoera protected area may not be sufficient to support the richness and abundance of the plant and animal species that remain. All of the populations of the emblematic lemur species *Propithecus perrieri* are found exclusively in fragments of moist semi-deciduous forests, as are locally endemic and threatened tree species of Sapotaceae, such as *Capurodendron andrafiamenae* and *Donella ranirisonii* (Gautier *et al*., 2025, herein). Consequently, it is essential to rely on up-to-date information such as vegetation cover maps to prioritize conservation actions within the protected area and to develop an ecological restoration action plan, which should aim not only to increase forest cover but also to maintain or restore habitat connectivity for characteristic plant and animal species.

Acknowledgements

We are grateful to the Ministère de l'Environnement et du Développement Durable (MEDD) for granting us the research permit (No. 08/23/MEDD/SG/DGGE/DAPRNE/SCBE.Re, dated 19 September 2023). We also sincerely thank two reviewers of an earlier version of this contribution, Cyrille Chatelain and Porter Prescott Lowry II, for their constructive feedback, which helped improve the manuscript. Lastly, we acknowledge Fanamby, the protected area manager, and the KOBABY project for their financial support of this study.

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