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Abstract

Understanding how biocultural landscapes, as a result of human-nature interactions, have emerged and will evolve seem to us a fundamental pre-requisite to better anticipate and understand the new ecological dynamics at work in Madagascar. This may help to better implement biodiversity conservation measures within and outside protected areas.

In this contribution, we present several biocultural landscapes on the island, providing examples in contrasting ecological situations. These range from relatively old agricultural and agroforestry landscapes that continue to evolve today, which in turn make up relatively densely wooded landscapes without natural forests in an agroforestry landscape entirely formed by farmers. These cultivated landscapes, rich in cash crops, provide significant income to farmers, which makes such regions some of the most economically productive on the island. In contrast, the dry spiny thicket in the extreme south, provides an example with rather different dynamics. Here, the combination of the local cultural groups relying on agricultural activities (*hatsaky* or swidden agriculture) and hunting-gathering live in a rather ecologically extreme ecosystem. In the following sections, we present several biocultural landscapes and place each in its historical, biogeographical, human, and economic context. Further, we sometimes consider the consequences of these activities in terms of the non-native forest landscapes,

including the effects of human practices on ecological processes of forest regeneration, biodiversity dynamics, and sometimes both.

Introduction

If Madagascar's biodiversity, originality, and threats are recognized worldwide associated with its forested ecosystems, this is not the case for a diversity of non-forested landscapes that human activities have produced over the course of centuries (Carrière-Buchsenschutz 2007; Amelot et al. 2011). These current Malagasy landscapes are the result of both old and more recent exploitation of ecosystems by humans and have generated some of the renowned agricultural systems that contribute to both Malagasy livelihoods and heritage. These agricultural diverse landscapes are not only the image of treeless homogeneous landscapes distributed by the media as well as certain non-governmental organizations (Figure 1A). As in many other regions of the world, on Madagascar in addition to the important diversity of climate and soil conditions that shape the different natural ecosystems, there are indigenous knowledge and practices associated with ecosystem usage. Further, there is a diversity of relationships that humans maintain with their environment, considered herein as cultural diversity, ultimately leading to a range of socio-spatial contexts, that we refer to herein as biocultural landscapes.

As we can be found in the literature from a few decades ago (e.g., Goodman and Benstead 2003), a large portion of research during that period in ecology, botany, and zoology concerned natural ecosystems with low human disturbance, and focused on inventory, description of biodiversity and biogeography, ecosystem dynamics, genetic diversity, and evolution and history. This is still true today, but more recently Malagasy and international research programs have shed light on new aspects and areas concerning biodiversity on Madagascar. This research focused in part on spaces that can be referred to as the so-called "anthropised" and "cultivated", or open spaces (Carrière and Bidaud 2012). These human-modified areas, dominated by exotic species, depleted in native and endemic species form new species assemblages, called "novel ecosystems" (Hobbs et al. 2006), which are the baseline of tomorrows ecosystems and ecological process in open landscapes on the island. As is the case of protected areas (Janzen 1983), these "novel ecosystems" are not closed in that the species they contain disperse and interact with other ecosystems, modifying native and endemic Malagasy species distribution and dynamics. Thus, understanding how biocultural landscapes, as a result of humannature interactions, have emerged and will evolve seem to us a fundamental pre-requisite to better anticipate and understand the new ecological dynamics at work. This may help to better implement biodiversity conservation measures within and outside protected areas.

In this contribution, we present several biocultural landscapes on the island, providing examples in contrasting ecological situations. For example, these range from relatively old agricultural and agroforestry landscapes that continue to evolve today, which in turn make up relatively densely wooded landscapes without natural forests in an agroforestry landscape entirely formed by farmers. These cultivated landscapes, rich in cash crops, provide significant income to farmers, which makes such regions some of the most economically productive on the island. In contrast, the dry spiny thicket in the extreme south, provides an example with rather different dynamics. Here, the combination of the local cultural groups relying on agricultural activities (*hatsaky* or swidden agriculture) and hunting-gathering live in a rather ecologically extreme ecosystem. In the following sections, we present several biocultural landscapes and place each in its historical, biogeographical, human, and economic context. Further, we sometimes consider the consequences of these activities in terms of the non-native forest landscapes, including the effects of human practices on ecological processes of forest regeneration, biodiversity dynamics, and sometimes both.

Clove agroforestry dynamics in Vavatenina region (Analanjirofo Region): Transition from shifting cultivation to complex agroforestry systems

On Madagascar, as compared to the pantropics in general (Jose 2009; Tscharntke et al. 2012), agroforestry has not been the subject of much research. A wide range of agroforest types adapted to a variety of biophysical environments and socio-economic conditions are observed across the island, with sometimes high levels of plant species richness (Arimalala et al. 2019), comprising both introduced and native plants. By comparing the current landscape to that described in the 1960s

(Dandoy 1973), the area of Vavatenina, located along the central part of the eastern coast, provides an illustrative case study of agroforestry diversification and complexification trajectories.

The Vavatenina area presents a tropical humid climate with two seasons, with average annual rainfalls of about 2000 mm, mostly falling between November and April (Dandoy 1973). The landscape is topographically complex, with successions of hills (*tanety*) and valleys (*horaka*) oriented along a north-south axis, presenting altitudes ranging from about 150 m in the Iazafo floodplain located in the east to about 600 m in the mid-hills in the west. The commune of Vavatenina that includes the main town of the district and surrounding villages includes about 37,240 inhabitants, mostly of the Betsimisaraka cultural group.

There is some evidence that this area has been deforested for some time. According to Dandoy (1973) the area was named "pays de Ghalemboule" – meaning 'bamboo forest country' - by the first European explorers who crossed the region during the 17th century (e.g., Etienne de Flacourt), which indicates that it was already largely covered by secondary vegetation at this time. In 1953, based on a map derived from aerial images from Humbert (1965), the Vavatenina area appears almost fully deforested. Deforestation of the area was probably the result from earlier occupation and the high population density, which was estimated as one of the highest of the eastern coast in the 1950s with about 14 inhabitant/km² in comparison to the average in the Toamasina Province as 9.9 (Gourou 1967). A reason of this especially high population density in Vavatenina may be related to its location along the former Fenoarivo-Imerimandroso road, which was an important commercial conduit connecting the coast to the Lake Alaotra region.

The in-depth study of Dandoy (1973), conducted in 1966 in the Vavatenina area, provides a valuable baseline to monitor local landscape evolution. He provided a detailed land-use map of a village located about 5 km north to Vavatenina town showing that only small fragments of natural forest, including native biodiversity, remained on the hill tops and along rivers. Most of the hills were covered by shrubby and herbaceous secondary fallow vegetation (with native, endemic, and introduced species), as local populations largely relied on shifting cultivation of rain fed hill rice, or tavy, which covered about 30% of the cultivated area and is the classical agricultural system of the Betsimisaraka (Aubert et al. 2003). Monospecific coffee (Coffee arabica) plantations during this period covered about the same surface area as it was the main cash crop up to the 1980 and 1990s, until global prices decreased dramatically. Further, monospecific clove tree (Syzygium aromaticum) plantations covered about 15% of the cultivated area. Cloves were a secondary cash crop on the east coast at that time, for which the planted surface area increased considerably after the coffee crisis. In the 1990s, it became the first cash crop income for Madagascar, along with vanilla (Vanilla planifolia) (Danthu et al. 2014). Clove trees were introduced in the Vavatenina area around 1930 and by the 1960s they covered about 8000 ha and accounted for about 20% of the production at the country level (Dandoy 1973). In the late 1980s, clove was the most important cash crop of the area (Blanc-Pamard and Ruf 1992).

Nowadays, landscapes in this area are different from those described about 50 years ago by Dandoy, reflecting major recent agricultural changes. The most striking one is the increase in tree cover – mostly introduced species - related to the development of agroforestry. Agroforests nowadays cover about 20% of the village territory, while these were limited to home gardens in the 1970s (Mariel 2016). These systems can be classified in two main types: "parks" with scattered trees and annual crops or pastures beneath, and complex multispecific and multilayered-agroforests called *tsabo* (Arimalala et al. 2019; Figure 1B).

A wide range of *tsabo* occur in the area in combination with different ligneous and nonligneous plants either planted, encouraged or tolerated, native and introduced. *Tsabo* trees include cash crops collected by local economic operators and then exported, such as introduced cloves, vanilla, and litchi (*Litchi chinensis*), but also in a lesser extent other spices such as cinnamon (*Cinnamomum verum*) and pepper (*Piper nigrum*). A range of fruit trees are grown for local consumption or sold in local markets, the most common include the families of Annonaceae (anona, *Annona muricata*, *A. reticulata*, and *A. squamosa*), Rutaceae (citrus), Moraceae (jackfruit, *Artocarpus heterophyllus*), Musaceae (banana and plantain), and Bromeliaceae (pineapple, *Ananas comosus*). Third, starchy food (*bomafana*) includes all crops that complement rice, especially during the hunger gap, mainly plantain banana, cassava (*Manihot esculenta*), breadfruit (*Artocarpus altilis*) and yams (Dioscoreaceae). Last, timber trees (*hazotrano*) or those for firewood (*kitay*) are also frequent in agroforests. The need for this latter product being especially important as clove leaf distillation requires a lot of combustible energy, and species used for these purposes are mainly eucalyptus (*Eucalyptus robusta* or *E. camaldulensis*), *Grevillea banksii*, and bamboo (*Bambusa* spp.). Several introduced fruit trees such as jackfruit or mango (*Mangifera indica*) are also used as firewood, as well as Fabaceae such as *Albizzia lebbeck* and *A. chinensis* that were initially used as shade trees for coffee. Other nitrogen-fixing species are used as stakes for vanilla or as living fences, mainly *Gliricidia sepium* and *Pachira aquatic*. Last, scattered coffee trees are also frequently found in *tsabo*, reflecting the progressive conversion of the former coffee plantations toward agroforests. Coffee production in this area of Madagascar is now mostly dedicated to self-consumption, as its sale price remains low.

In this region, the diversification of tree production, is a widespread strategy developed by households to increase their resilience to the different ongoing economic and climatic changes, in a context of decreasing land availability and increasing monetarization of household's economy (Dandoy 1973: Mariel 2016). Indeed, a certain portion of local households are not able to fulfill their food self-sufficiency and they rely on the sale of agricultural products such as clover, clove essential oil, or fruits, and on the production of complementary food crops such as cassava or breadfruit. Furthermore, the price of cash crops varies considerably over years, and cyclones frequently hit the area, which makes agricultural specialization a risk. Diversification also allows stabilizing the income and food production over the year, as the different productions become available during different season, as observed in Foulepointe (Mahavelona) (>30 km east of Vavatenina site; Blanc-Pamard and Ruf 1992) in the late 1980s. Clove essential oil especially plays a key role in the economy of local households as it can be produced throughout the year, can be easily stored, and sold at any time.

The different diversification strategies implemented by farmers in Vavatenina led to the emergence of different types of agroforests, the distribution of which in the landscape is not random. Fruit trees, coffee, breadfruits, banana, and yams for households and animal consumption are planted in home gardens and fertilized by different forms of compost. These types of plant associations are also found in the humid valleys (*vavasaha*) and in old coffee plantations that were progressively enriched with other plants. Litchi and banana are also frequently planted on the border of irrigated rice plains, while clove trees are planted on hill slopes and often associated with pineapple, cassava, and some fruit and firewood trees. Woodlots are also located on hill tops and sometimes associated with various woody and non-woody native and introduced tree species; hence, constituting complex and species-rich agroforests.

Most of the clove complex agroforests occurring near Vavatenina are recent, that is to say planted in the last 20 years, while the old clove and coffee plantations were mostly monocultures. Indeed, the cultivation of cloves by smallholders was supported by the French colonial administration that provided advice, and recommended growing this species in monospecific stands. Cloves progressively supplanted coffee, and its cultivation expanded in multi-specific stands associating introduced and native plant species. An important motivation for planting cloves on savoka (postagricultural secondary forests) was also probably to secure individual property tenure (Aubert et al. 2003). According to village elders, the local hills were covered with clove plantations before the cyclone Honorine hit the area in 1986, causing major damage to trees. They report that "people were discouraged of planting" after Honorine, and in the 1990s this problem combined with low prices of export products and decreasing soil fertility led many people to move elsewhere to find salaried job. Many of these individuals moved further north to the Mananara-Nord area, where clove and vanilla production was less affected by the cyclone. This probably played a major role in the emergence of clove agroforests in Vavatenina, which probably started around 2000 when people returned to the area and started to plant again, encouraged by the increased market value of cloves, the absence of cyclones for about a decade, and inspired by the clove agroforests they observed in Mananara-Nord. Vanilla cultivation also started in those years, but augmented significantly around 2010 when prices increased.

Nowadays, farmers still refer with some nostalgia to the time when Betsimisaraka planted their crops in the forest and where crops "grew by themselves", despite the forest having disappeared probably long before the 1950s. Indeed, Betsimisaraka lived at the forest margin, practicing *tavy* shifting cultivation and gathering (Aubert et al. 2003). Even though the forest disappeared several generations ago in the Vavatenina area, people appear deeply imprinted by the forest and this lasting memory may partly explain the return of a notable diversity and density of trees in the landscape. These agroforestry dynamics may open perspectives for enhancing agricultural production in a

sustainable way, and for contributing to the conservation of biodiversity outside of the protected area system as suggested by a recent study in the Andapa region (Hending et al. 2018). Research is now needed to investigate how the spread of trees in the agricultural landscapes of Vavatenina affects biodiversity, in particular animal species. Indeed, studies conducted in different regions of the tropics over the last decades provide multiple evidence that agroforests enhance biodiversity, even though they are dominantly composed of introduced tree species (Tscharntke et al. 2015).

The humid forest fragments of the Atsinanana Region: The case of the villages of Beforona (Moramanga) and Ranomafana-Est (Brickaville)

The forest fragments in these areas represent relics of the moist evergreen forests of eastern Madagascar. The village of Beforona (Moramanga District) is located on the national road connecting Antananarivo to Toamasina where large forested areas co-exist with a belt of open areas and forest fragments. The village of Ankorabe (commune of Ranomafana-Est, Brickaville District) is located along the same road. In the Ranomafana-Est area, there are forest fragments including the Vohilahy Forest (145 ha) near the village of Ankorabe.

For these two study sites, the elevation varies from 20 to 340 m. The relief is dissected with V-shaped valleys, rice fields are rare in the low-lying areas, and most agricultural production is cultivated on slopes in the form of swidden agriculture (*tavy*), including at inclines of > 40%. This area is influenced by a tropical and per-humid climate, characterized by two alternating seasons: 1) hot and rainy season from October to March, and during this season, the temperature varies from 17 to 30°C, and 2) dry season from June to September, when the rains are less regular and average temperatures cooler. The wind is dominated by trade winds, which generally blow from the southeast towards the northwest. The average rainfall is 3000 mm per year. The general soil type is a yellow-red ferralitic type, resting on the crystalline base. Hydromorphic soils are found in the lowlands where rice growing is practiced.

The vegetation is made up of relict patches of lowland moist evergreen forests, a form of grasslands, and post-agricultural regrowth in fallows (Figure 1C). The different types of vegetation found in the landscape are: (1) forests (*atiala*), which are multi-layered natural woody forests with 20 to 25 m high trees; (2) post-agricultural regrowths (savoka) and their physiognomy and floristic composition vary according to the age of the fallow and the past cultivation intensity, crops, and practices (*tavy*, fallow period length, and tillage intensity). For example, one can find young shrubby regrowths with native species such as *Psiadia* spp. and *Harungana madagascariensis*, and introduced species such as Rubus moluccanus and Clidemia hirta, but also shrubby regrowths dominated by the introduced Lantana camara and native Psiadia altissima with dense growths of native ferns (Pteridium aquilinum); (3) pseudo-steppe (roranga alafamafa), composed of a herbaceous carpet essentially of Aristida similis in discontinuous mats (the last stage of natural forest conversion); (4) tanety crops which consist essentially of rain-fed rice fields and cassava. The landscape is also formed of orchards (jackfruit, coffee, banana trees, and cinnamon apple) around the villages and where exotic species such as Grevillea banksii and eucalyptus form small plantations; and (5) riparian forests or shrubby vegetation that develop on the edges of rivers where frequent introduced species is Eugenia and the native Pandanus used for basketry.

Archeological excavations carried out in Antongombato near the Vohilahy Forest, within 5 km of Ankorabe indicate the area has been occupied by humans since at least the 14th century (Randrianasolo 2014). Thus, these biocultural landscapes have probably been shaped by the exploitation of the forest for centuries. The intact forest, therefore, probably disappeared a long time ago even if the "mature" or old secondary forests still persist today in some places. Likewise, the Beforona region experienced an occupation by Arab colonists in the 10th or 11th century (Pfund 2000). Currently, the population consists mainly of the local cultural group Betsimisaraka and migrant groups of Merina, Antesaka, and Antemoro. The dominant traditional farming system is *tavy*. According to Althabe (1982), this practice is part of the Betsimisaraka ethnic identity, as mentioned above for the Vavatenina region.

In this portion of central eastern Madagascar, swidden agriculture is one of the main causes of landscape degradation and deforestation (Styger et al. 2007). It is the main form of land-use in this area to produce rain-fed rice, crops such as cassava and sweet potatoes, without tillage, on a portion of cleared and then burned lowland moist evergreen forests at different stages (mature forest, secondary

forest or forest regrowth). A multidisciplinary research program on alternatives to swidden cultivation linking social and biophysical issues was launched in 1994 in the Beforona area (Pollini 2009) and agroforestry was proposed as a possible solution to reduce deforestation, but this was not achieved. In 10 years, half of the land of Ambinanisahavolo (Beforona), in particular the hills, were cultivated and thus cleared, which is one of the important highlights of the landscape degradation dynamics in this region (Styger et al. 2007).

With regards to Ranomafana-Est Commune, natural relatively intact forest cover in 2018 was about 3560 ha. Despite the creation of community based management initiatives (called COBA) established in 2001, annual natural forest loss of 3.28% was recorded between 1990 and 1998 and 2.82% from 1998 to 2018 (Rasoanaivo et al. 2019). To give a greater general context, in the eastern part of Madagascar between 2010 and 2015, annual deforestation rates fell within the range between 0.93 to 2.33% per year (Grinand et al. 2013). Currently, in the Beforona and Ranomafana-Est areas, forest relicts are mainly found on hill slopes, which correspond to what Green and Sussman (1990) mentioned as where remnant natural forests would remain in 35 years to come, if deforestation continued.

In this area with deforestation dating from several centuries ago and more recently, agricultural practices related to *tavy* and other types of resource exploitation had direct and indirect effects on forests successions and dynamics. Different authors have tried to describe the ecosystems trajectories in this area following agricultural land-use. Pfund (2000) proposed a five-step ecosystem change characterized by different types and stages of vegetation: from natural forest, to fallows with forest components (peri-forest fallows and shrubby fallows), then to mixed fallows (densely populated with exotic invasive species such as Lantana and Rubus), and finally grassland vegetation. A decrease in the plant biomass in secondary vegetation is recorded after the first two crops and followed by radical changes in floristic composition. The study by Styger et al. (2007) in Vohidrazana (Beforona) located on the edge of the Ankeniheny-Zahamena forest corridor, has also shown that in the past 30 years the period plots lay as fallow have been shortened from 8 to 15 years to 3 to 5 years. This decrease has resulted in shorter and shorter crop cycles and fallow periods during which no vegetation regeneration occurs. This induces a "vicious circle" which jeopardizes the possible sustainability of this form of swidden agriculture. According to some authors, this is caused by the lack of land, at least in part associated with population growth reinforced by immigration (Pfund 2000). Given this situation and these agricultural practices, it takes 15 to 20 years for the trees to regenerate within herbaceous vegetation dominated by Imperata and by ferns (Styger et al. 2007). As lengthened fallow periods are not practiced, there is a need to intensify upland systems based on improved nutrient cycling, targeted inputs, less use of fire in land management, and diversification of land use (Styger et al. 2009) and agrobiodiversity diversification.

How agricultural practices have shaped native biodiversity in mid-altitude landscapes at the margin of the Ranomafana National Park

The biocultural landscapes located in the region of Haute-Matsiatra, included in west of COFAV (Corridor Forestier Ambositra-Vondrozo, a protected forest corridor area which links Ambositra to Vondrozo), illustrate a very different socio-ecological situation in comparison to the other examples presented herein. The COFAV, as one of the few remaining extensive tracts of forest in this portion of Madagascar, is by law under strict conservation regulations since a 2014 as a NAP (nouvelle aire protégée or new protected area) and include preexisting protected areas such as Ranomafana and Andringitra. This biocultural landscape seeks to maintain both the forest's highly endemic biodiversity, and its alleged ecological corridor function between the two national parks (Goodman and Razafindratsita 2001; Carrière-Buchsenschutz 2007). Located in Betsileo, which is part of the Central Highlands, the village of Ambendrana (at the edge of the forest) in the commune of Androy, is part of the peripheral zone of the Ranomafana National Park. In the surroundings of this village, conservation measures, which rely on the participation of populations (community based management projects known as COBA (Blanc-Pamard and Ramiarantsoa 2007), were implemented when the COFAV was initiated.

Ambendrana is located at around 1100 m above sea level and has a range of topographic factors and forest vegetation cover (Blanc-Pamard and Rakoto-Ramiarantsoa 2014). The climate is tropical, with considerable rainfall (1300-1400 mm per year) with maximum precipitation from

January to March and a drier period from May to September. Temperatures are temperate and cool, especially during the southern winter, when the area can experience frost. The forested corridor is mainly composed of a dense, medium altitude moist evergreen forest dominated by *Weinmannia* spp. and *Tambourissa* spp. (Koechlin et al. 1974). This area is densely populated and mostly inhabited by the Betsileo ethnic group (Serpantié et al. 2007). Most of local activities and forms of resource exploitation take place in the forest and at its margins (swidden agriculture, lowland rice farming, animal husbandry, hunting, fishing, and gathering) (Carrière et al. 2005). Paddy rice is the staple food and the heart of social exchanges (Le Bourdiec 1978).

The village of Ambendrana dates back to about 1790, created by the Zafindrareoto people, a clan originated from the "eastern forest" (Dubois 1938). There are still remnants of old abandoned villages in the forest, perhaps dating from this approximate period, but also more recent areas of refuge where one can still find planted trees from the period of the 1947 rebellion (Solondraibe 1991-92; Carrière et al. 2007a). The forest is not intact in such areas, there are many traces of villages, different symbolic markers, long-lived pioneer tree species, and plantations such as banana and avocado trees (Goodman and Rakotoarisoa 1998; Carrière et al. 2007a). It would appear that the previous strong link between the Betsileo and the forest has been gradually weakened, notably by the transition to agriculture and more precisely to rice growing (Kottak 1980; Moreau 2002). During this period, land conquest for cultivation has been an important local demographic pressure and has extended into previous forested areas. This pressure on the remaining forest, particularly by young households, is still active, with the creation of small secondary hamlets, along the valleys moving away from the central valleys (Blanc-Pamard and Rakoto-Ramiarantsoa 2014; Figure 1D).

The current structure of the landscapes in this area follows these various historical processes of population establishment associated with the conversion of bottom lands into paddy fields (Figure 1E). In addition to a wide variety of natural forest types (medium altitude moist evergreen forest, old and medium-aged secondary forests, wood-exploited forests, riparian forests, Carrière et al. 2007a), this agricultural landscape is currently notably heterogeneous (Martin et al. 2009, 2012). It consists of a fine-grained mosaic of cultivated and non-cultivated habitats, including medium altitude moist evergreen forest fragments called songon'ala (Figure 1E), secondary medium altitude forest at different succession ages (kapoaka), eucalyptus and other tree and crop plantations, swidden agricultural fields on slopes, and paddy fields in valley bottoms. In a sampled reference surface of 3320 ha (2004), habitat patches included dry crops 23.7%, herbaceous recruits 10.7%, irrigated rice fields 14.2%, reforestation areas 7.4%, medium altitude natural forests 2.1%, and shrubby recruits 41.8%. Open areas occupy 48.6% of these habitats (Martin et al. 2009), which are defined as areas either without dense vegetation cover, or where the height of dense vegetation is less than 1 m. The various ecological studies in this area showed that relative to the low intensity of agricultural and natural forest uses, forest-dependent animals (endemic bat and birds; Picot 2005; Picot et al. 2007; Martin et al. 2009, 2012) and forest plants (trees, lianas, shrubs, and herbaceous species; Randriamalala et al. 2007, 2012; Rakotoarimanana et al. 2008), native and endemic, are present. This is due to the diversity of ecological habitats (from secondary forests to shrubby and herbaceous vegetation types), with marked levels of habitat heterogeneity across the landscape, the high density of isolated trees of some value (Ficus spp., eucalyptus, fruit trees, Harungana, and Anthocleista spp.) (Martin et al. 2009; Rafidison et al. 2020) and exotic tree plantations, to the plant diversity found in various ecological habitats and in particular the close proximity of the site to the forest corridor (Randriamalala et al. 2015a; Figure 1E).

The dispersal of different plant and animal species in these landscapes, specifically at the edges of the natural forests patches and corridor, have also made possible the advancement of new ecological processes, which include, for example, afforestation processes or native forest species regeneration in cultivated spaces, which are useful for restoration of forests on Madagascar (Gérard et al. 2015). Studies have shown that artificial plantations of exotic species (such as *Pinus* and *Acacia*), which were originally planted in grassland areas, can act as a catalyst for the regeneration of native Malagasy and endemic plant species if in close proximity to natural forest parcels (Randriambanona et al. 2019). In this area, which has been affected by various disturbances (e.g., cyclones, logging, cultivation), *Pinus* plantations have become environments conducive to the regeneration of native species. A total of 125 species, 34 of which are endemic, from 46 families were inventoried in disturbed *Pinus* plantations in approximately 200 plots of 100 m² at Ambendrana. These results also

suggested that a low level of disturbance, such as that resulting from selective *Pinus* tree logging, can act as a catalyst for the establishment of native woodlands. However, excessive disturbance from sylvicultural and agricultural practices, such as frequent burning, heavy tillage, and high number of crop/fallow cycles, may hinder, but does not block, the establishment of native woodlands (Randriambanona et al. 2019).

These heterogeneous landscapes show successional stages through time (Carrière et al. 2007b; Martin et al. 2012): (1) the landscape fragmentation and heterogeneity may be a consequence of the increase human population density in Ambendrana and (2) in Sahabe, in the southwestern part of the corridor, the gradual replacement of a forested matrix by grasslands. First in Ambendrana, based on 15 categories of ecological habitats listed for an area of 3300 ha, the landscape and its evolution was described between 1954, 1991, and 2004. The landscape structure in 1954 consisted of a mosaic of large, more or less homogeneous forest, agricultural, and grassland plots. In 1991, the mosaic was more complex. The plots of each category were smaller (on average 400 plots in 1954 and 750 in 1991) and the landscape was essentially open and made up of cultivated areas (rice fields and food crops). The landscape structure in 2004 was more complex than during the previous two periods and with a mosaic of small heterogeneous plots (960 in total). By 2004, many habitat types such as natural moist evergreen forests, grasslands, woody fallows, and reforestation plots were highly fragmented (Carrière et al. 2007b).

Over time, the increase in the heterogeneity of this biocultural landscape was linked to the landscape complexification, resulting from an increase in the variety of habitats, as well as to a fragmentation of each of the habitats types which induces a larger number of habitat patches. Thus, a transition occurred, from a landscape dominated by forest plantations, crops, and pseudo-steppes associated with cattle pastoralism in 1954, towards a fine landscape mosaic resulting from changes in agricultural uses (reduction of pastoralism and increased rice cultivation), forest regeneration and recolonization processes which induced a diversity of forest regrowth stages. Many social, economic, and political factors were behind this dynamic shift since 1954. Indeed, population density has more than tripled in 50 years in this region and the commune (Gourou 1967; Blanc-Pamard and Rakoto-Ramiarantsoa 2014), leading to an increase in the occupation of the lowland rice areas. In addition, changes in household strategies, the constraints linked to the development of new value-chains (food, fruit, alcohol, wood, etc.), access to land, fire and access bans to forests due to conservation measures, as well as insecurity, have led to a decrease in livestock grazing in the forest and therefore fire use (Serpantié et al. 2007). Finally, successive reforestation, disturbance, and afforestation lead to the installation of native and introduced pioneer species establishment in former herbaceous habitats (Randriambanona et al. 2019). In addition, on a finer scale, heterogeneity changes were amplified by isolated tree plantations for social, economic, and symbolic purposes (Martin et al. 2009; Rafidison et al. 2020).

Second, the pattern of forest regeneration after clearing for swidden agriculture seems to be similar throughout the forest corridor, but we observe that a provisional herbaceous state (observed at low rate in Ambendrana, locally called *kilanjy*), gradually become more common near Sahabe village, a mostly herbaceous matrix containing some forest fragments (Randriamalala et al. 2007, 2012). This situation is becoming widespread, near the Andringitra National Park, specifically near Sahabe (Figure 1F).

The comparison of this different areas near the villages of Ambendrana and Sahabe, between 1999 and 2009, illustrates some peculiarities of these landscapes. They changed from a natural medium altitude evergreen moist forest matrix, cleared for areas to cultivate hill rice then to *tanety* which, once cultivated, is first covered with shrubby and woody fallows, then gave rise to a herbaceous matrix. This matrix is dominated by plantations of introduced eucalyptus, or by native medium altitude evergreen moist forests that have withstood fires when the zones include grasslands (Hervé et al. 2010). In Sahabe, the diversity of landscape patches is the same as in the Ambendrana area, but the proportions are different. This herbaceous matrix landscape, subject to an annual and therefore regular fire regime, dominates further south in the area of Andringitra National Park.

How agricultural practices may influence dry spiny thicket vegetation recovery

This case-study concerns human activities held in a special type of dry ecosystem and known as dry spiny thicket. It is a low-growing open dry ecosystem, located in the most arid part of lowland

southwestern Madagascar (Randriamalala et al. 2016). This vegetation covers approximately five million hectares and is the oldest and most arid biome of Madagascar (Wells 2003). This area accounts for the highest known proportion of endemic plants in the island (classified as very high level), reaching up to 90% of the documented 1100 plant species (Burgess et al. 2004). Most of plant species of dry spiny thicket vegetation present adaptations to store moisture efficiently and to minimize water loss (Gautier and Goodman 2003). Spiny thicket is also classified as an 'endemic bird area' (Stattersfield et al. 1998), and is home to nine endemic threatened lemur species (IUCN 2003). This formation occurs on two main soil types: calcareous rocky soil and yellow sand soil. The plant community on calcareous soil is more resistant to drought than that on yellow sand soil, where water availability is higher (Koechlin et al. 1974).

The vegetation of dry spiny thicket provides several goods and ecosystem services such as: timber for building houses and pirogues, medicinal plants, food (tubers, honey, and meat from hunted animals), fuelwood and charcoal, and land for agricultural use or goat pastures (Randriamalala et al. 2016, 2017). Due to the multiple uses by human populations, conservation of its biodiversity remains difficult. Swidden agriculture, charcoal production and at a lesser extent, grazing of goats are the main human practices that impact this vegetation type, which is undergoing degradation and deforestation (Casse et al. 2004; Randriamalala et al. 2015b, 2016; Figure 1G). Furthermore, these thickets are described as being less resilient to human disturbance as compared to dry and moist evergreen forests because forest recovery is slow, as is regrowth of shrubs (Gaspard et al. 2018; Randriamalala et al. 2019).

On the Belomotse Plateau, although agriculture is not the main activity of people living in and around the dry spiny thicket, a form of swidden cultivation (*hatsaky*) is practiced to grow staple foods (Randriamalala et al. 2019) and is the main cause of deforestation (Randriamalala et al. 2015b). Swidden cultivation consists of cutting all trees and shrubs in the plot during the dry season (November-December), before the first rains, letting them dry out during 2-10 days, and then burning the lot. Maize, peas, and cucurbitaceous plants are sown together after the first clearing, and then during the first two to three cropping periods. Plots on calcareous soils are abandoned after two to three years of cropping, while plots on yellow sand soils may be exploited for a longer period with cassava and/or sweet potato and sometimes with groundnuts after manual soil ploughing (Randriamalala et al. 2019). Overstory floristic composition of post-cultivation dry spiny thickets on both two soil types do not vary based on secondary succession stages. However, structure parameters (height and basal area) increased significantly with age of abandonment, while diversity (species richness and evenness index) did not. Poor regeneration (Randriamalala et al. 2016, 2019) and the slow growth of shrub species (Gaspard et al. 2018) found after cultivation in this formation can explain the lack of change in diversity and floristic composition during secondary succession stages (Figure 1H).

The production of charcoal, derived from spiny thicket trees, and breeding of goat are the main income sources of local people (Raoliarivelo et al. 2010; Hänke and Barkmann 2017). The diet of goats is essentially formed by shrub leaves and shoots of more than 100 shrubby and herbaceous species (Randriamalala 2014; Feldt et al. 2017). Charcoal production reduces shrub density and biomass and affects species composition (Randriamalala et al. 2016). It is an unsustainable activity that in certain circumstances results in the local loss of mature hardwood species. In contrast, goat grazing alone did not significantly affect the diversity, mean height, stem and leaf biomass or species composition of dry spiny thicket growing on calcareous soil. Goat grazing at a moderate stocking rate (~1 head per hectare) does not leave significant footprint on the dry spiny thicket communities in terms of plant diversity, biomass, and regeneration rates (Randriamalala et al. 2016).

Dry spiny thicket vegetation is not resilient to cultivation and charcoal extraction. Furthermore, cultivation and charcoal production, combined with goat production, are antagonist activities because they exploit the same thicket habitat. Indeed, sustainable wood harvesting is difficult in this ecosystem. Consequently, sustainable management will necessarily require the reduction of pressures from cultivation and charcoal production by reducing the natural resource dependence of local communities through alternative income generating activities, such as goat breeding (Randriamalala et al. 2016, 2019). The regular sale of goats maintains low stocking densities and avoids overgrazing. Further, this regular sale also enters greater income to families breeding of these animals as compared to charcoal production. However, in order to better understand the impact of goat foraging on dry spiny thicket vegetation additional research is needed and should examine the impact of inter-annual rainfall variability on plant regeneration and diversity. Further, the carrying capacity of dry spiny thicket related to local goat populations needs to be properly measured in order to evaluate the optimal size of goat herds.

Conclusion

Madagascar is well known for its ecological specificities and unique biodiversity. As elsewhere in the world, the island has many biocultural landscapes in which people live, such as the Betsimisaraka vanilla and clove agroforestry systems, and the famous Betsileo rice-terrace agricultural landscapes. Faced with the evolution of socioeconomic, political, and demographic contexts, each of these cultural groups and their associated lifestyles are no longer able to provide well-being and sufficient food to the local population. Because of these changes, associated with advancing problems of global warming, the ecological sustainability of agricultural systems is no longer guaranteed. Outside of biodiversity conservation that tends to focus on species, habitat and ecosystem levels, biocultural landscapes, which are present in many areas of the tropics, should be considered in greater detail to understand recent local and global change and environmental issues on biodiversity loss (Hong 2014). In particular, it would be important to understand which practices and in which social and ecological conditions allow to best achieve the needed levels of social (in terms of equity and justice), economic (with acceptable way of life and well-being), and ecological sustainability (with the maintenance of ecological functions essential to the functioning of ecosystems).

Biocultural agricultural landscapes of Madagascar, which have a strong traditional component, are composed of different ecological habitats and ecosystems that comprise a mosaic of small-scale fields for crops; herbaceous, shrubby and woody fallows; natural tropical forest patches at different levels of secondarization; and permanent agricultural cultivations, such as flooded paddy fields, orchards, and simple or complex agroforestry systems. As illustrated by the examples presented in this contribution, in these landscapes, one can find patches of natural ecological habitats and cultivated areas where native biodiversity and introduced agrobiodiversity co-exist and interact.

These landscapes are poorer in endemic biodiversity than forests or natural ecosystems. They are spatially notably heterogeneous, with many various patches of vegetation types, they may serve as habitats or corridors for many native non-specialist species and to some forest mammal and bird species. They also contain a diversity of plants ranging from endemics to introduced and invasive species. In these landscapes, there is also an important level of agrobiodiversity, cultivated or uncultivated, which is essential to local communities and allow local people different means to advance on different aspects of their lives - feeding themselves, medicines, building materials, and handcraft production. Combating deforestation and finding solutions so that these landscapes remain biodiversity useful to all of the constituent organisms, is also to ensure a good future for these human communities and proper buffer zones to protected areas. These biocultural landscapes represent the base of future agro-ecological sustainable landscapes pathways on Madagascar.

In examples presented in this contribution, such as in the Vavatenina region and the Ranomafana-Andringitra forest corridor, spatial mosaics may form unique islands of species-rich communities in agricultural landscapes. The diversity of biocultural landscapes, which reflect a diversity of human-nature interactions on Madagascar, represent examples of different nature-based solutions to improved cultivation systems, inspired by both traditional and modern practices, which when combined may contribute to form more sustainable agricultural systems. More incentives and innovative policies for sustainability, with the consideration of social, economic, and cultural agents in the biocultural landscape, should be combined to ensure proper traditional and modern approaches for food security without compromising biodiversity in agricultural landscapes and sustainability (Liu et al. 2014). With the respect and recognition of these biocultural landscapes and associated diversity, it will also be easier to work with communities for biodiversity conservation in protected areas but also in cultivated landscapes. In order to find solutions, research and policy must adopt a new paradigm that recognizes the differences in the perceptions and priorities of the various actors (Scales 2014), such as those of researchers working with communities to improve the biocultural landscapes

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Figure caption

Figure 1. Different views of biocultural landscapes of Madagascar. A) A biocultural landscape in the Central Highlands and north of Ambalavao; B) Vavatenina complex multispecific and multilayered agroforests called *tsabo*; C) overview of the landscape at Ranomafana-Est and relicts of forest on hill top surrounded by *savoka* (post-agricultural secondary forests; D) land colonization along valley for rice cultivation; E) ecological habitats diversity in Fandriana-Vondrozo corridor; F) Sahabe biocultural landscape near Andringitra dominated by land cover with herbaceous vegetation; G) agriculture established in dry spiny thicket in the Toliara region; and H) dry spiny thicket in the southwest. Photos A, B, D, E, F, and G by S. M. Carrière; C by H. Randriambanona; and H by J. Randriamalala.

