An appraisal of biodiversity conservation in the littoral zone of Sainte Luce, southeastern Madagascar

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Abstract

The littoral forests of Madagascar represent a distinct phytogeographic habitat and support a diverse assemblage of plants and animals. Now largely confined to a series of small, isolated fragments along the eastern side of the island, littoral forest biodiversity is greatly imperilled. Sainte Luce (also known as Manafiafy), in the extreme southeast, represents one of the most intact littoral regions, yet is subject to a range of intense anthropogenic pressures. With mineral mining operations now imminent in the area, the appraisal presented herein sets out a new baseline for biodiversity conservation efforts and describes a series of specific recommendations and actions to minimise anticipated losses. This paper explores in detail each of the major local threats and provides an up to date review of most major vertebrate groups. Based on genetic evidence, long-term monitoring and developments in forest management and community use over two decades, this account makes explicit the loss of several key species and highlights a number of taxonomic groups and research topics that require further attention. Using this synergistic approach and a range of relevant criteria, a list of 21 priority species is presented. Finally, the work highlights several on-going local conservation initiatives, and reflects on the progress made towards earlier conservation recommendations and goals. Local managers and stakeholders must now consider all available conservation tools if current levels of biodiversity are to be maintained in the long-term. The preservation of largely intact standing forest should be prioritised, augmented by carefully considered restoration and afforestation initiatives. Forest habitat connectivity and the protection of key frugivore-plant interactions remains crucial. If efforts to conserve local biodiversity are to succeed, communications and knowledge sharing between all invested groups is essential.

Keywords: endangered species, forest fragmentation, hunting, mining, zoochory

Résumé détaillé

Les forêts littorales de Madagascar représentent un habitat phytogéographique distinct et supportent un assemblage riche et diversifié de plantes et d'animaux. Aujourd'hui largement confinée à une série de fragments isolés, la biodiversité forestière littorale est en grande danger. Sainte Luce, au Sud-est, représente l'un des écosystèmes littoraux les plus intacts, mais soumise à des pressions anthropiques intenses. En conséquence, la région perdra de nombreuses espèces végétales et animales au cours des prochaines décennies. Les opérations minières sont désormais imminentes dans la région ; cette évaluation établit ainsi une nouvelle base de référence pour les efforts de conservation de la biodiversité et décrit une série de recommandations et d'actions spécifiques pour faire face aux menaces actuelles et minimiser les pertes anticipées. Ce travail explore en détail chacune des principales menaces locales, en mettant en évidence les espèces vulnérables. La plus importante d'entre elles est l'exploitation minière, qui représente une menace globale pour la biodiversité locale. Les opérations devraient toucher plus de 50 % de la couverture forestière existant ainsi que d'importants habitats conjonctifs et aquatiques. De nombreux fragments de forêt dans la zone minière contiennent d'importantes populations d'espèces menacées. De telles modifications environnementales à grande échelle menacent directement la persistance des espèces, mais exacerbent également les effets négatifs de la fragmentation et de l'isolement de l'habitat, ce qui a une incidence sur les relations entre les espèces et les zones, les modèles de dispersion et la dynamique des populations.

En parallèle, la dépendance locale aux ressources naturelles limitées menace de saper la stratégie environnementale à long terme, mettant directement en danger d'importantes espèces socio-économiques et mettant en péril les moyens de subsistance traditionnelle. Alors que l'exploitation minière promet

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une croissance économique et une diversification indispensables, le développement pose des défis supplémentaires à la biodiversité grâce à un accès accru. Cette étude aborde en outre la menace que représente la chasse pour les espèces clés (ex. les frugivores) et les processus écologiques (interactions plantes-animaux) et examine les pratiques et les impacts locaux. Les méthodes agricoles destructrices et les incendies sont également pris en compte, de même que les menaces émergentes des espèces envahissantes. Cette évaluation fournit en outre un examen opportun de l'état taxonomique actuel de la plupart des groupes de vertébrés et de plusieurs assemblages d'invertébrés. Depuis la première évaluation de la faune, la biodiversité littorale a manifestement augmenté en termes de diversité et d'importance. Les stratégies de gestion doivent être adaptées pour refléter ces connaissances. Sur la base d'approches génétiques modernes et des études approfondies sur le terrain, les estimations de cette richesse ont augmenté au sein des principaux groupes taxonomiques. De manière cruciale, la comparaison avec des travaux antérieurs révèle explicitement la perte de plusieurs espèces clés de Sainte Luce. Cette perte fournit un exemple frappant de déclin des écosystèmes et souligne la nécessité d'initiatives de reboisement, de protection élargie de l'habitat et d'intervention en conservation.

A partir de cette approche synergique, combinant une évaluation contemporaine des menaces et avec un examen actualisé de la biodiversité, une série de recommandations en conservation seront fournies. Une liste de 21 espèces prioritaires est présentée, sur la base d'une série de critères pertinents, y compris la classification dans la Liste rouge de l'UICN, l'aire de répartition des espèces, l'utilité écologique, l'abondance et l'importance économique, et surtout sans aucun doute la présence de nombreux taxons non décrits à Sainte Luce. Parmi les éléments majeurs de la stratégie de conservation, il faudrait viser à maintenir des populations saines et résilientes d'espèces clés. L'expansion des zones de conservation en incluant les zones forestières centrales actuellement dans l'empreinte minière pourrait apporter des avantages considérables en matière de conservation et d'écologie. Enfin, cette évaluation décrit plusieurs efforts de conservation majeurs en cours dans la région et réfléchit aux progrès réalisés par rapport aux recommandations antérieures. En fin de compte, les efforts des gestionnaires locaux et des intervenants doivent devenir plus intégrés et transparents. Une vision et une stratégie à long terme pour la biodiversité qui vont au-delà de l'exploitation minière sont nécessaires si l'on veut préserver la biodiversité littorale au cours du siècle prochain. A court terme, la préservation des forêts existantes et intactes devrait être une priorité, complétée par des initiatives de reboisement et de restauration soigneusement réfléchies. La connectivité de l'habitat et la protection des interactions entre les frugivores et les plantes demeurent aussi une priorité de conservation.

Mots clés : espèces menacées, fragmentation forestière, chasse, exploitation minière, zoochorie

Introduction

Madagascar supports a globally important biodiversity characterized by extensive species richness, high levels of endemicity, and broad phylogenetic clustering within a limited range of taxonomic groups. Some of the families of plants and animals represented on the island reflect its ancient origin and long isolation from other landmasses (Vences, 2004; Yoder & Nowak, 2006; Upchurch, 2008). New species are still regularly described across multiple taxa (e.g., mammals, amphibians, palms) (Hotaling *et al*., 2017; Eiserhardt *et al*., 2018; Scherz *et al*., 2019), whilst certain groups remain relatively unstudied (e.g., freshwater fish, arachnids, moths). With such high species level diversity across its varied environments, Madagascar is considered one of the world's great biodiversity hotspots. However, the island has experienced dramatic environmental change over the past century (Harper *et al*., 2007; Gorenflo *et al*., 2011; Vieilledent *et al*., 2018) and the burgeoning threats posed to its native flora and fauna mark Madagascar as a global conservation priority (Myers *et al*., 2000).

Against the backdrop of widespread national deforestation and habitat change, littoral forests stand out as a national priority (Green & Sussman, 1990; Ganzhorn *et al*., 2001; Consiglio *et al*., 2006). Once believed to occupy much of the coastal fringe of eastern Madagascar, these forests now persist only in small, isolated fragments (de Gouvenain & Silander, 2003). Despite their greatly reduced extent, littoral forests harbour approximately 13% of Madagascar's total native flora and support important and distinct plant and animal assemblages (Dumetz, 1999; Schatz, 2000; Ganzhorn *et al*., 2007). Yet scant littoral habitat exists within the current protected area network (Goodman *et al*., 2018).

In the extreme southeast, the littoral forests of Sainte Luce (sometimes referred to as Ste. Luce or Manafiafy) are considered among the most intact (Rabevohitra *et al*., 1996; Bollen & Donati, 2006; Temple *et al*., 2012). Although the site shares many similarities with nearby forests at Mandena, and to a lesser extent Petriky, the plant and animal communities differ in both composition and abundance (Lowry & Faber-Langendoen, 1991; Lewis Environmental Consultants, 1992; Ganzhorn *et al*., 2007). The Sainte Luce formation comprises 17 forest fragments, ranging in size from 6 to 350 ha, covering an estimated 1500 ha (Figure 1); herein the term Sainte Luce is used as a reference to these different forest blocks. Forest fragments vary in condition, largely due to their proximity to human communities. The major Sainte Luce forests are in close proximity to three main hamlets (Ambandrika, Ampanasatomboky, and Manafiafy) with a combined human population of ca. 2727 (Berina, pers. comm. 2022), all reliant on natural forest resources. The forests also support the communities of Ebakika to the north and Mahatalaky and Tsiharoa Ampasy to the west. Significant pressure is exerted on forest resources for livelihoods, food, medicine, and construction materials (Vincelette, 2003; Rasolofoharivelo, 2007; Račevska *et al*., 2022).

The area is also subject to a well-documented, but controversial mining operation managed by QIT Madagascar Minerals (QMM). Currently active in Mandena, the mine exploits the mineral rich sand substrate to extract titanium- iron oxide (ilmenite), zircon, and monozite (QMM, 2001). Operations are expected to progress to Sainte Luce ca. 2027 (Kluge, pers. comm. 2022). Prior to the outset of mining, the southern littoral region was subject to an extensive environmental impact assessment (EIA), and the flora and fauna were well characterised (summarised in Ganzhorn *et al*., 2007). As part of plans to minimise biodiversity losses (Temple *et al*., 2012), several forest fragments in Sainte Luce have been designated as 'Conservation Zones' or 'Avoidance Zones' (NAP Ambatoatsinanana, decree of 28 April 28 2015, no. 2015-778) (Figure 1). The site is also recognised as a Key Biodiversity Area (KBA).

The appraisal presented herein is an update of the earlier conservation focused review of Bollen and Donati (2006), but with specific emphasis on Sainte Luce. Given that over 30 years have now passed since the initial environmental impact assessment (Lowry & Faber-Langendoen, 1991; Lewis Environmental Consultants, 1992) and mining operations are now imminent in the Sainte Luce block, a re-examination of the challenges and threats facing littoral forest biodiversity is needed. Furthermore, our understanding of littoral forest ecology and biodiversity has developed considerably as technology and scientific tools have advanced. Earlier workers (Ganzhorn *et al*., 2001; Bollen & Donati, 2006; Consiglio *et al*., 2006) forecasted the loss of numerous endemic plant and animal species from littoral forests within the coming decades. Thus, it is now important to reflect on these earlier predictions and reassess conservation strategies (Ganzhorn *et al*., 2007; Temple *et al*., 2012) in light of our current knowledge.

Major threats

The general threats facing biodiversity in Sainte Luce are largely unchanged from those outlined by Bollen and Donati (2006). Unsustainable use of natural resources and a reliance on swidden agriculture (*tavy*) pose a significant challenge, whilst the overarching threat from mining is increasingly tangible. Additional threats include hunting, climate change, and the developing problem of introduced species that in certain cases, become invasive. Whilst most threats are inherently linked to human population growth and socio-economic drivers, each is considered here in the specific context of biodiversity conservation. The broad topic of climate change is largely beyond the scope of this review.

Mining

Although many questions remain unanswered regarding the operation in Sainte Luce, mining works are anticipated to begin within the next decade (Gaylord, pers. comm. 2019; Kluge, pers. comm. 2022). Based on satellite imagery (CNES / Airbus 2020) and the projected mining footprint (Temple *et al*., 2012), an estimated 822 ha of littoral forest will be lost in Sainte Luce, including the clearance of 12 existing fragments. Thus, the scale of environmental modification presents a substantial threat to local biodiversity and cultural customs that rely on natural resources (livelihoods and medicines) (Ganzhorn *et al*., 2001; Consiglio *et al*., 2006; Watson *et al*., 2010; Goodman *et al*., 2018; Račevska *et al*., 2022).

Numerous threatened plant and animal populations exist within the mining footprint and a range of mitigation strategies will be required to prevent the expected biodiversity losses (Ganzhorn *et al*., 2001; Consiglio *et al*., 2006; Bollen & Donati,

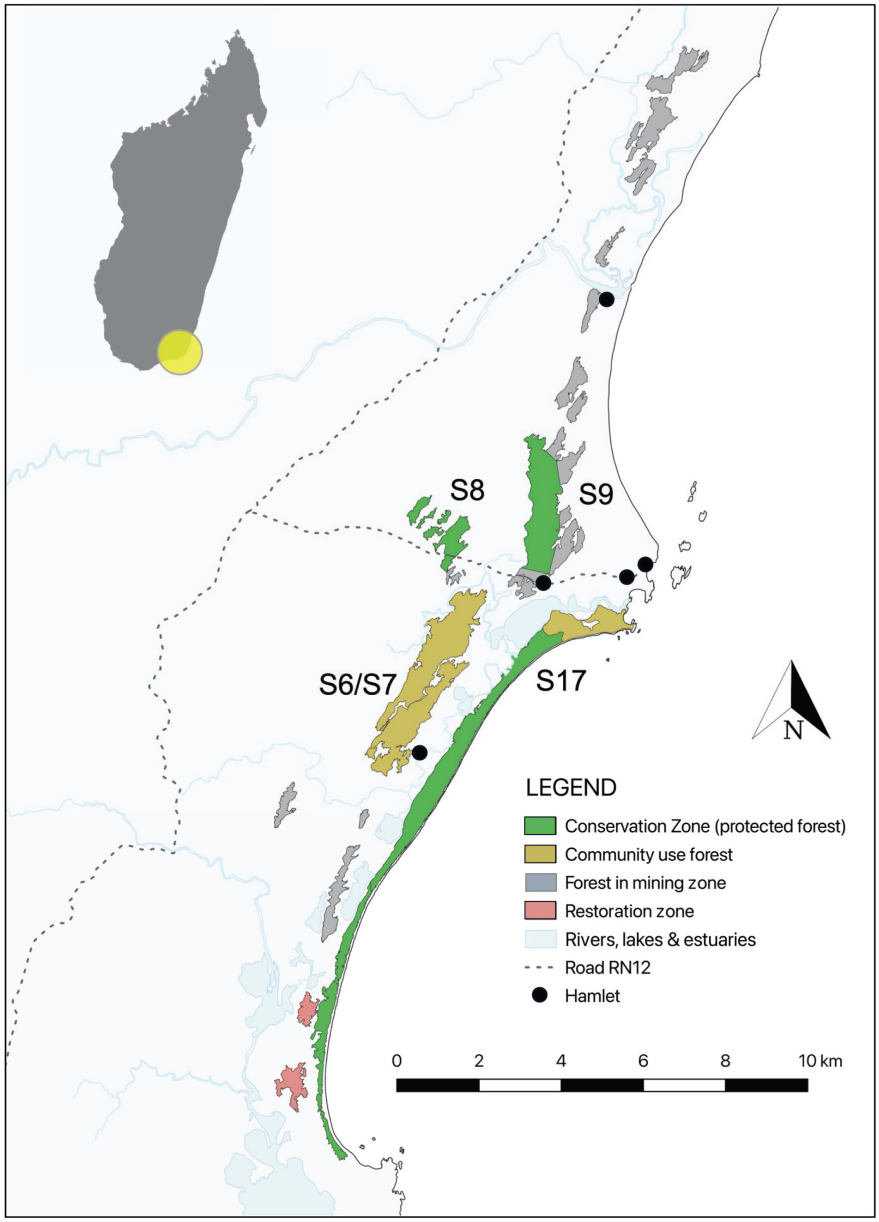

Figure 1. The relative position of the Sainte Luce Forest fragments, with the protected Conservation Zones (CZ's) and Community Resource Zones (CRZ's) highlighted. Fragments S1 + S2 are earmarked for restoration and S6 + S7 occur within the projected mining footprint.

2006; Watson *et al*., 2010). A group of 10 Endangered Brown Lemurs (*Eulemur collaris*) inhabit forest fragment S12 and the three Endangered nocturnal lemur species (*Avahi meridionalis*, *Cheirogaleus thomasi*, and *Microcebus tanosi*) occupy at least five fragments in the mining path (Hyde Roberts, unpublished data). A large population (ca. 490 individuals) of Dwarf Lemur (*C. thomasi*) inhabit fragment S7 and similar numbers likely occur in S6 (Ganzhorn *et al*., 2007; Hyde Roberts *et al*., 2021). The single Flying Fox (*Pteropus rufus*) (Vulnerable) colony in Sainte Luce is also situated in S6 and represents one of only a handful in the general Taolagnaro area occupying intact native forest (Jenkins *et al*., 2007; Hyde Roberts *et al*., 2016). Fragment S7 also supports an important population of the Critically Endangered *Phelsuma antanosy* (Ramanamanjato, 2007; Hyde Roberts, unpublished data), considered one of the world's rarest gecko species, whilst 14 of the 18 known observations of the Data Deficient ghost gecko *Matoatoa spannringi* also originate from the S6/S7 forest block (Hyde Roberts, unpublished data).

Almost 80% of the 66 known remaining adult *Chrysalidocarpus saintelucei* palms (Endangered) exist inside the mining zone, whilst just 16 remain

inside the protected fragments (Hyde Roberts *et al*., 2020). Bird diversity inside the main protected forest fragment S9 also appears reduced compared to that inside the Community Resource Zones (Hyde Roberts, unpublished data), potentially the result of years of dead wood collection impacting trophic dynamics. Thus, forests within the mining zone, and particularly the twin fragments S6 and S7, support notable biodiversity and a range of threatened species.

Mining operations are further expected to drastically alter the wider Sainte Luce landscape, impacting both connective forest and aquatic habitats. Dredge mining is recognised as a major threat to aquatic biodiversity in Madagascar, increasing water pollution, turbidity, siltation, and eutrophication (Máiz-Tomé *et al*., 2018). Whilst the local freshwater fish fauna requires further study, the area is considered an important Odonata hotspot, supporting noteworthy species richness and a high number of threatened and Data Deficient species (Schütte & Razafindraibe, 2007). Wetland areas are also important to several bird species (e.g., *Gallinago macrodactyla*, *Nycticorax nycticorax*, *Porphyrio madagascariensis*), although the wider landscape can likely accommodate these.

The impact of mining on local economic resources such as the grey sedge (*Lepironia articulata* or *mahampy*) are also unclear, as are the effects on proximal coastal environments such as mangroves, lagoons, and fisheries, which may be sensitive to unmitigated operational effects (Harris, 2011). The mine in Mandena is accused of exceeding its legal footprint, encroaching into sensitive aquatic buffer zones (Swanson, 2019) and has been linked to increased environmental radionuclide exposure, contaminating potable water sources. However, lessons from the environmental initiatives at Mandena, including the damming of the Anony River (Réville *et al*., 2007) and the effects on the wider aquatic ecosystem, are potentially transferable to Sainte Luce.

Whilst the mine undoubtedly offers much-needed local economic development and growth, the associated investment in road infrastructure may further threaten the littoral zone biodiversity. Roads are widely recognised as drivers of global deforestation (Fahrig & Rytwinski, 2009; Poor *et al*., 2019) and facilitated the extensive logging seen in Madagascar during the 1990s (Gorenflow *et al*., 2011). The development of the RN12A, will improve access to Sainte Luce but may potentially catalyse commercial extractive enterprises and illegal wildlife trafficking.

To offset anticipated biodiversity losses, QMM propose a range of measures. Several key forest fragments (Figure 1) are now protected (IUCN Category V) 'Conservation Zones', with resource collection by the community forbidden without specific permission. Similarly, QMM are committed to restore 225 ha of littoral forest post mining (Temple *et al*., 2012). The location of the proposed new forest, re-established from a preserved seed/soil layer, is unclear but is expected to be positioned strategically to maximise natural regeneration and forest connectivity. In addition, large biodiversity offset sites have been established away from Sainte Luce (e.g., in the rainforest sites of Mahabo, Bemangidy, and Tsitongambarika), with the specific objective of preserving forest habitat and decreasing pressure on threatened species, many of which, but not all, are shared with the littoral forests. Whilst these measures are welcome from a conservation perspective, the offsets have proved controversial in local communities, although appear to benefit some species (Seagle *et al*., 2012; Campera *et al*., 2019).

Despite the considerable contribution to research in the local area (Lowry & Faben-Langdoen, 1991; Lewis Environmental Consultants, 1992; Ganzhorn *et al*., 2007), conclusions drawn on the effectiveness of operational environmental proposals are mixed. Whilst some local initiatives in both Sainte Luce and Mandena are considered a success (Donati *et al*., 2007a; Campera *et al*., 2014; Andriamandimbiarisoa *et al*., 2015), numerous studies conclude that current strategies are insufficient to fully preserve the area's rich biodiversity and functional ecology on the long-term (Ganzhorn *et al*., 2001; Bollen & Donati, 2006; Watson *et al*., 2010).

Resource use

Since the initial review by Bollen and Donati (2006), the human population in Sainte Luce has increased substantially (from 1238 in 2006 to 2727 in 2022) (Berina, pers. comm. 2019), driving increased demand for food and natural resources (Račevska, 2020). Illustrating this growth, a new community comprising around 30 houses and entirely dependent on the Community Resource Zones has appeared on the southeastern border of fragment S6. Likewise, the Ambandrika hamlet is also rapidly expanding in size. Rural communities around Taolagnaro attain an estimated 90% of their energy needs from firewood (Vincelette, 2003), emphasising

the great pressure placed on remaining regional forests. Satellite imagery reveals that forest cover in Sainte Luce declined between 2000 and 2010, losing approximately 220 ha and mirroring national deforestation trends (Vieilledent *et al*., 2018).

Logging is now chronic inside the Community Resource Zones, and in most areas beyond the protected area boundaries (Figure 1). Forests are being rapidly degraded and changes to forest structure and composition are evident. The accelerated resource use is partly a consequence of greater community need, but is also being catalysed by the lack of an effective resource management system and a tacit understanding that mining activity will consume large areas of standing forest. Moreover, a sense of community powerlessness to the ultimate fate of the local forests is driving an insouciant approach to resource use (Holloway, 2013).

In the short-term, utilitarian species are most at risk from direct over-harvesting, and in Sainte Luce, many of these are directly related to fisheries livelihoods. Roughly 80% of households rely on fisheries (Holloway, 2013) and, as a result, materials such as vines and palms (e.g., *Flagellaria indica*, *Chrysalidocarpus saintelucei*, *C. prestonianus*) used in the manufacture of fishing gear and lobster traps have become rare (Hogg *et al*., 2013; Hyde Roberts *et al*., 2020). Sub-optimal species for these purposes (e.g., *Bambusa multiplex*, *Beccariophoenix madagascariensis*) are increasingly substituted; however, durability is often compromised, and alternative resources are themselves now becoming scarce.

A recent assessment of the eponymous Endangered palm *Chrysalidocarpus saintelucei* revealed a 64% reduction in the adult population over an eight-year period, with only 66 known adults remaining (Hyde Roberts *et al*., 2020). However, the species is now known from other scattered sites along the east coast. Similarly, there are no longer any sufficiently large and suitable trees (*Calophyllum pervillei*) in Sainte Luce for the construction of pirogues (dugout canoes), with new vessels now being constructed at considerable cost in the distant Vohimena Mountains. The unsustainable use of natural resources within the local fisheries industry is likely to have major implications for the local economy in coming years.

At present, the commercial exploitation of resources from the littoral forest zone from Sainte Luce to Taolagnaro is rare, although several incidences have been reported in the past few years. Commercial extraction was previously considered a major issue in Sainte Luce, complicit in dramatic forest clearance (Bollen & Donati, 2006). The rapid clearance of large areas of standing forest in Manangotry (Andohahela National Park), driven by demand in Taolagnaro during the Covid-19 pandemic, highlights the speed and severity of this threat. In Sainte Luce, as well as in many other Malagasy forests, hardwoods favoured by selective loggers also comprise important dietary resources for frugivorous lemur species, with potential implications for reproductive success and persistence (Wright *et al*., 2005; Donati *et al*., 2007b; Račevska *et al*., 2022). The overlap between community resource use and the ecological requirements of key vertebrate species warrants careful attention as demand for resources increases.

In general, the major threat to standing forest has seemingly shifted from large scale clearance for agricultural purposes (Bollen & Donati, 2006), to a rapid reduction in forest quality, particularly outside of the protected fragments. Unsustainable resource extraction and the selective removal of particular species is having serious ecological and socio-economic effects (Thompson, 2011; Alroy, 2017; SEED Madagascar, 2019). Furthermore, rapid changes in forest composition and structure impacts both microhabitat and microclimate variables and the capacity for forests to sustain biodiversity (Gardner, 2009; Strier, 2021).

Forest fragmentation and habitat connectivity

Habitat fragmentation and isolation impacts species-area relationships, dispersal patterns, and population dynamics of numerous threatened species (Marsh *et al*., 2013). Such trends are known to elicit negative population responses in lemurs (Balestri *et al*., 2014; Kling *et al*., 2020), forest dependent birds (Langrand & Wilmé, 1997), insectivorous mammals (Goodman & Rakotondravony, 2000), and amphibians (Vallan, 2000; Riemann *et al*., 2022). Isolation is also known to impact key ecological services and processes like seed dispersal and pollination (Bodin *et al*., 2006; Kindlmann & Burrel, 2008), disrupt predator-prey dynamics (Terborgh *et al*., 2001; Estes *et al*., 2011), and affect species' long-term persistence in fragments (Gould *et al*., 2020; Strier, 2021).

Several animal assemblages occurring in Sainte Luce are considered highly nested, with smaller fragments supporting non-random subsets of the communities in larger, more intact forests (Ganzhorn

& Eisenbeiß, 2001; Lehtinen & Ramanamanjato, 2006; Ganzhorn *et al*., 2007). Whilst species diversity is lower in smaller fragments, some species appear more extirpation prone than others. A species' ability to withstand the effects of habitat degradation and fragmentation to a large extent depends on their ecological flexibility, a range of specific functional traits (e.g., size, vagility, fecundity, rarity, ranging behaviour) (Terborgh, 1974; Donati *et al*., 2020; Eppley *et al*., 2020) and landscape level variables (Gould *et al*., 2020). Thus, it is clear that preserving core areas of mature forest and improving habitat connectivity is paramount to the long-term survival of many forest-dependent, specialist species (Bodin *et al*., 2006; Chapman *et al*., 2020).

All remaining forest in Sainte Luce is now within ~350 m of a sharp habitat edge, where it abuts anthropogenic grasslands. Thus, all remaining forest is exposed to edge effects, where outside conditions permeate and affect forest interior composition and structure (Laurance *et al*., 2000). Edge effects may have critical long-term implications for species persistence (Lehman *et al*., 2006; Campera *et al*., 2022) and particularly for those species that require specific microhabitat conditions (e.g., hibernators) (Lehtinen & Ramanamanjato, 2006; Dausmann *et al*., 2009; Norscia *et al*., 2012).

Hunting, persecution, and illegal trade

Bushmeat consumption in Sainte Luce is considered moderate relative to other inland forest sites on the island (Bollen & Donati, 2006), due to the availability of animal protein from oceanic resources. However, hunting pressure has been high historically (ca. 2000) and the legacy of past practices remains, reflected in the distributions and abundances of target species (e.g., *Eulemur collaris* and the introduced *Potamochoerus larvatus*) (Hyde Roberts *et al*., 2020). The disappearance of two duck species (*Anas melleri* and *Sarkidiornis melanotos*), are attributed to over-harvesting (Solo, pers. comm. 2019). Whilst the hunting of lemurs outlined in Randriamanalina *et al*. (2000), and Bollen and Donati (2006) had been considered a thing of the past, strictly prohibited under local law (*dina*), numerous reports and observations over the past few years (2016-2022), indicate that such practices continue, and may be on the rise again (Longosoa, pers. obs.).

In May 2022, a series of lemur traps were observed in the protected fragment S9. On two further occasions, living *Eulemur collaris* have been seen with snares attached to their limbs (Figure 2H). Snares, specifically targeting this species, are set along deliberately felled trees that span forest clearings (a technique known as *tandraho*), whilst traps set along forest paths target ground birds (e.g., *Coua gigas*, *Lophotibis cristata*). *Eulemur collaris* groups in S9 also now exhibit fleeing behaviours, a tell-tale signature of recent hunting pressure. *Tandraho* may have further implications for long-term population structure and growth, inadvertently selecting group leading females (Bollen & Donati, 2006). Traps, when encountered are destroyed by local guides and forest police.

The extent of hunting for nocturnal lemurs is unknown. In early 2022, active hunters were encountered in the north of S9 and discarded a basket containing slingshot ammunition and corpses of *Microcebus tanosi* and *Tenrec ecaudatus*. In 2017, a sharpened skewer was found in S9, left in place deep inside a tree hole where it had been used to check for sleeping lemurs. In 2016, a tree was felled in S7 with a hole in the trunk enlarged with an axe, a technique used to extract nocturnal lemurs from sleeping sites. Anecdotal evidence, obtained during environmental education sessions at Ambandrika school, along with an independent household survey in 2019 (SEED Madagascar, 2019; Račevska, 2020) revealed that between 5-10% of the community had eaten lemur. That school children, mostly aged between 6 to 14 years old, had consumed lemur suggests that bushmeat consumption persists in the community, and although extremely difficult to monitor, presumably remains an important threat.

Other documented hunting incidents include two shooting events at the Madagascar Flying Fox (*Pteropus rufus*) roost in S6, a man observed with a dog hunting *Tenrec ecaudatus* in S9, the discovery of a cache of shaped stones (slingshot ammunition), and the remains of multiple *Setifer setosus*, the animals skinned in the forest. Slingshots are commonly carried to opportunistically subdue quarry (e.g., fruit pigeons *Treron australis* and *Alectroenas madagascariensis*) whilst dogs are trained to locate terrestrial species (e.g., *Tenrec ecaudatus* and *S. setosus*). Clearly, these fragmentary accounts represent only a portion of the hunting activity that occurs, seemingly even in the Conservation Zones. The situation in the more remote and less well monitored fragments is unknown. Hunting can be particularly adverse in small, isolated forest fragments (Golden, 2009) and focused measures are urgently required to prevent practices spiralling to the levels of previous decades.

Figure 2. A series of photographs depicting the threats facing littoral forest biodiversity in Sainte Luce. **A**) Forest fragmentation and agriculture plots to the northwest of fragment S8. **B**) Burnt ground between two forest remnants in the north of fragment S8. **C**) Cassava cultivation on the forest edge of S7, with an exposed *Beccariophoenix madagascariensis* palm. **D**) Resources collected from S7 entering Sainte Luce. **E**) Swidden agriculture (*tavy*) in the north of fragment S8. **F**) Effects of fire in the southern area of S9. **G**) *Tenrec ecaudatus* killed for bushmeat in S9. **H**) *Eulemur collaris* (female) with snare attached to hand in protected forest S9. **I)** *Coua gigas* being released after being caught in a snare in S9. **J**) *Dermochelys coriacea* captured by fishermen in Manafiafy. **K**) A skewer inside a tree hollow, used to extract nocturnal lemurs. **L**) The QMM/RioTinto mine at Mandena. Photographs by Sam Hyde Roberts and SEED Madagascar, except for **L**, from Google Images

A small number of species (primarily snakes, birds of prey, and crocodiles) experience high levels of persecution in an around Sainte Luce. Since predatory species largely occur at low density, persecution poses a notable threat. The Nile Crocodile (*Crocodylus niloticus*) population in Sainte Luce is small and reported attacks on humans are unverified. In response, several local hunters are considered crocodile specialists and often trap and kill crocodiles using large, baited hooks (Longosoa, pers. comm. 2018). Other persecuted species are often killed opportunistically, in part out of fear, or in response to a perceived threat to children and livestock. Snakes (e.g., *Acrantophis madagascariensis, Leioheterodon madagascariensis*, *Sanzinia madagascariensis*) are frequently killed,

and large individuals of these snakes, particularly *L. madagascariensis* are now extremely rare. The displayed remains of a Madagascar Long-eared Owl (*Asio madagascarensis*) were also recently observed within the protected forest fragment S8.

The threat of wildlife trafficking and the pet trade remains plausible in Sainte Luce, given the illegal collection of rare herpetological species, including *Phelsuma antanosy*, from nearby forests (Schneider, pers. comm. 2020). However, there is no such known evidence from Sainte Luce, for either the international animal trade or national markets. Only a single case of a lemur (*Cheirogaleus thomasi*) being kept as a pet has been documented since 2014, and it was quickly released after pressure from community members. Infrequently, birds of prey (e.g., *Buteo brachypterus*, *Falco newtoni*) are captured and kept captive.

In Manafiafy, marine turtles are commonly captured by fishermen and eaten throughout the year (Figure 2J), and *Caretta caretta*, the only species known to nest at Sainte Luce, is traditionally harvested during egg-laying season (November-February). This species has experienced heavy mortality rates over previous decades and the local nesting population, which was previously large, appears on the verge of extirpation (Solo, pers. comm. 2018). During the 2018 breeding season, only a single nest of this species was observed along 6.5 km of monitored beach (Neaves, pers. comm. 2018).

In recent years, an increasing number of elasmobranchs are also being harvested, including numerous Endangered, Critically Endangered, and Data Deficient species (e.g., *Isurus oxyrinchus, Rhinobatus* spp., *Sphyrna lewini*). A total of 430 elasmobranch landings (~30 species) were recorded between September 2019 and February 2020, with a further 300 landings between January and March 2021 (SEED Madagascar, 2021). Whilst the majority were guitarfish, 23.9% (n=174) of total catch comprised of Critically Endangered Scalloped hammerhead sharks (*Sphyrna lewini*), a species considered particularly vulnerable to overfishing (IOTC, 2015). Allegedly, elasmobranchs are captured for a growing external Chinese market (Ralaitiany, pers. comm. 2019) and roughly 20% (from a select range of taxa) had or would have their fins removed for sale. However, the meat of many captured sharks is consumed locally.

Agricultural expansion and fire

Whilst the Sainte Luce community is largely fisheries based, its reliance on agriculture is noticeably increasing, with cassava, a hardy, drought-tolerant crop now widely cultivated. Roughly 85% of households engage in agricultural practice, although it comprises the primary means of income for only 4% (Holloway, 2013). The borders around some forest fragments (notably S6 and S8) are being rapidly transformed into agricultural plots and in some areas, these encroach into standing forest. In nutrient-poor areas such as Sainte Luce, forested land is often cleared to access the richer soils. The locally preferred method of clearance, *tavy*, is notoriously destructive and unsustainable (Styger *et al*., 2007), with repeated episodes of burning impeding soil recovery and contributing to rapid soil erosion, and forest loss (Jarosz, 1993).

Control of *tavy* fire is also problematic, particularly in windy months (September and October). In 2019, an uncontrolled fire devastated an area of ca. 375 ha of grassland and swamp to the east of S9. In 2015, another *tavy* fire resulted in the loss of 6 ha of standing forest in S7. Fires have destroyed several small mixed plantations in Sainte Luce (Bass, pers. comm. 2018) along with habitat corridors and entire small forest fragments in Mandena (Bollen & Donati, 2006). Fires can evidently cause rapid and extensive habitat loss, destroy vital connective habitats exacerbating the effects of forest fragmentation (Bodin *et al*., 2006), and directly impact wildlife communities.

Invasive and exotic species

The spread of non-indigenous species into insular, highly endemic communities is a global conservation concern (Kolar & Lodge, 2001; Donlan & Wilcox, 2008), with degraded and fragmented habitats particularly affected (Joshi *et al*., 2015). Whilst the floral community of Sainte Luce naturally contains many cosmopolitan species due to its coastal nature (e.g., *Cocos nucifera*, *Ficus reflexa*, *Hibiscus tiliaceus*), many exotic tree species (e.g., *Acacia mangium*, *Eucalyptus* spp.) have been introduced for plantation purposes. Most are thought to pose little risk; however, introduced *Melaleuca quinquenervia* has become invasive in swampy areas (Eppley *et al*., 2015) and *Grevillea robusta* has proliferated greatly in grassland areas (Hyde Roberts, unpublished data).

By contrast, the vertebrate fauna contains relatively few alien species. Of these, the Black Rat (*Rattus rattus*) is the most problematic (Goodman, 1995; Varnham, 2010; Shiels *et al*., 2014). Whilst widespread across Madagascar, it thrives in highly fragmented landscapes (King *et al*., 2011). There is

currently little evidence to indicate that it competes directly with endemic rodent, tenrec, or lemur species (Ganzhorn, 2003), although diets overlap extensively. However, as omnivores, *R. rattus* consume a diverse range of plants and animals and likely pose a direct threat to a range of species (Harper & Bunbury, 2015). Invasive rats can disrupt ecosystem function, affect trophic pathways, and even drive environmental collapse (Athens, 2009; Kaiser-Bunbury *et al*., 2010; Hilton & Cuthbert, 2010). *Rattus rattus* is ubiquitous throughout Sainte Luce and further research is required to understand its ecological impact and possible importance for the transmission of zoonotic diseases.

The two introduced insectivorous shrew species, *Suncus murinus* and *S. etruscus*, are both relatively uncommon in Sainte Luce. Generally considered a human commensal, *S. murinus* has been observed in core areas of S9, although again is not thought to be a direct competitor of endemic species (Goodman & Rakotondravony, 2000). *Suncus etruscus,* a predominantly forest dwelling species, feeds on invertebrate prey and is presumably has little impact on the local mammal community. Of the avifauna, the Common Mynah (*Acridotheres tristis*) has established a permanent breeding presence in recent decades, particularly around fragments S8 and S9 and near villages where this notably aggressive species has become dominant. Its presence may be linked with a decline of native bird species (Ellis, 2003), and groups have been seen harrying Lesser Vasa Parrot (*Coracopsis nigra*).

Domestic animals pose a noteworthy threat near villages and forest edges. Although cats are not abundant in Sainte Luce, they are often kept by shopkeepers to control rodent populations. In Sainte Luce, cats have been observed predating nocturnal lemurs (*Cheirogaleus thomasi*), rodents (*Rattus rattus*), snakes (*Liophidium torquatum* and *Thamnosophis lateralis*), chameleons (*Furcifer lateralis* and *F. oustaleti*), skinks (*Trachylepis gravenhorstii*) and assorted invertebrates (Anostostomatidae spp., Blaberidae spp.) (Hyde Roberts, pers. obs.). Whilst they do not typically enter the forest, one cat was observed several hundred metres inside fragment S9, 2 m high in a tree (Račevska, pers comm.). Dogs are uncommon in Sainte Luce and considered *fady* or taboo by most of the community. However, a small number of dogs are kept for security and hunting. The impact of dogs on the native carnivoran community is unclear.

Current status (new species and taxonomic updates).

Since the earliest biodiversity studies in Sainte Luce dating from the late 1980s, advances in molecular techniques have led to remarkable refinements in gene-based investigative approaches. Consequently, many species formerly classified based on general morphological characters have been taxonomically updated, with implications for littoral biodiversity and conservation. The summaries herein are based on published works and personal projects conducted since 2014.

Invertebrates

Only a small number of invertebrate taxa have been well studied in Sainte Luce to date – the Coleoptera, Diplopoda, Odonata, Lepidoptera, Mantodea, and Phasmatodea (Ganzhorn *et al*., 2007). The terrestrial invertebrate fauna appears to be rich, containing many new undescribed forms. Unpublished baseline surveys of invertebrate diversity in forest remnants suggests high arachnid, hemipteran, and orthopteran richness (Hyde Roberts, unpublished data). A unique and diverse community of millipede species, containing a number of forest dependent, microendemic forms is documented (Wesener & Wägele, 2007). Sainte Luce also supports the greatest diversity of Mantodea and Phasmatodea species in the southern littoral forests, with both groups similarly encompassing a large number of undescribed forms (Schütte, 2007). Work to assess the diversity of the coleopteran community is currently underway, following a significant collection made in 2016 (SEED Madagascar, unpublished data).

The only flying taxa to be well studied (Odonata and Lepidoptera), appear more cosmopolitan but include a number of important taxa. Since 2015, 11 additional odonate species have been added to the initial inventory of Schütte and Razafindraibe (2007), including the notable re-discovery of *Libellulosoma minutum* (Hyde Roberts *et al*., 2019). The local dragonfly community (37 species) contains an as yet undescribed Gomphiidae species (*Isomma* sp. nov.), seven Data Deficient and two Endangered species (*Acisoma* cf. *ascalaphoides* and *Teinobasis alluaudi*) (IUCN, 2022), several forest dependent species, and others that require specific aquatic conditions to reproduce. The butterfly community of Sainte Luce stands at 56 documented species (Hyde Roberts, unpublished data). Most are widespread and no littoral forest endemics are known. Very few

Malagasy butterfly species are currently assessed by the IUCN. Moth diversity remains almost entirely unexplored and will undoubtedly reveal many new forms. Of the very few specimens collected, a new syntomine species is notable. Further work is required to fully characterise invertebrate diversity in littoral forest habitats.

Amphibians and reptiles

Among vertebrates, the greatest number of taxonomic amendments and revisions have taken place in these two groups. Prior to 2015, the majority of herpetofauna species in Sainte Luce were identified solely based on morphological characters. The inventory provided by the initial EIA (Lewis Environmental Consultants, 1992) was further developed by Ramanamanjato (2007) and the number of observed species in the area increased from 55 to 69. However, given that many reptile and amphibian species are highly cryptic, numerous taxa required further study. A community wide barcoding project began in 2015 (Hyde Roberts, unpublished data) with the aim of characterizing all local species and providing a reliable platform for future conservation efforts. Genetic tools have led to an array of species corrections, new records, and to the identification of new candidate species.

Based on available evidence, the amphibian fauna in Sainte Luce is represented by 22 species. One species fewer than presented by Ramanamanjato (2007) since the earlier inclusion of *Madecassophryne truebae* is considered highly dubious. The revised inventory includes seven candidate species, three of which are included for the first time (*Boophis* sp. aff. *pauliani*, *Boophis* sp. aff. *picturatus*, and *Mantidactylus* sp. nov.). In addition, the tiny microhylid formerly considered a *Stumpffia* is now recognised as part of a newly established genus, *Mini* (Scherz *et al*., 2019). Three further species have also since been subject to recent taxonomic revisions (Bellati *et al*., 2018). The elevated number if *Mantidactylus* species listed in previous works are likely misidentifications based on unconfirmed morphological characters. The validated amphibian community now includes one Critically Endangered (*Guibemantis diphonus*), three Endangered (*Anodonthyla nigrigularis*, *Guibemantis annulatus*, and *G. wattersoni*), a single Near Threatened species, nine of Least Concern, one Data Deficient species and a further seven that are not yet formally evaluated (IUCN, 2023).

The reptile fauna proved similarly in need of revision, with eight candidate species identified across four families (Chamaleonidae, Gekkonidae, Lamprophiidae, and Scincidae), four new distributional records (*Pelomedusa subrufa*, *Dermochelys coriacea*, *Liophidium vaillanti*, and the non-native *Indotyphlops braminus*), and numerous taxonomic clarifications diagnosed (e.g., *Liophidium kely* and *Pseudoxyrhopus* sp. aff. *tritaeniatus*). The total number of confirmed reptile species in Sainte Luce is 53; however, older unverified records could push the figure to 55 if confirmed. Of the validated species, three are classified as Critically Endangered (*Dermochelys coriacea*, *Eretmochelys imbricata*, and *Phelsuma antanosy*), two as Endangered (*Chelonia mydas* and *Liophidium kely*), four as Vulnerable (*Caretta caretta*, *Pseudoxyrhopus sokosoko*, *Zonosaurus anelanelany*, and *Zonosaurus maximus*) and two as Data Deficient (*Madascincus ankodabensis* and *Matoatoa* cf. *spannringi*) (IUCN, 2023). A further 34 species are considered Least Concern and eight are Not Evaluated as they represent candidate species. Generally, the fauna is similar to that of the eastern humid forests yet includes several microendemic species found only in littoral habitat. The community includes a large number of forest dependent species with specific habitat requirements. Given that forests over 300 ha appear necessary to sustain current herpetological diversity (Ramanamanjato, 2007), and many species possess limited dispersal capacity, several populations may already be under great pressure.

Birds

To date, five major bird studies have been conducted in Sainte Luce, including both the initial mine EIA (Lewis Environmental Consultants, 1992) and the ongoing work of the author (Goodman *et al*., 1997; Ellis, 2003; Watson *et al*., 2005; Hyde Roberts, unpublished data). Each study has produced a thorough species inventory, although different methodologies have been adopted and study aims vary. The combined results offer a fascinating insight into littoral forest avian diversity and importance of habitat heterogeneity. When observational records are combined (adjusted for taxonomic changes), a total of 117 species have been reported in the Sainte Luce area. Although no species is considered endemic to littoral forest and aquatic habitats, some 41% are unique to Madagascar. Of the 117 species, 36 species are considered forest dependent, 24 utilise a mixture of both forest and open areas, 24 are associated with aquatic systems, 23 show preference

for open grassland areas, and 10 with coastal or oceanic environments.

Although general avian abundance is low and many species are rare, littoral forests contain a unique avian assemblage and provide important links between humid and dry spiny forests (Watson *et al*., 2005). Whilst a number of observations seem anomalous, and many species have not been seen in the most recent studies, they cannot be discounted. When all records are considered, a single species (*Anas melleri*) is classified as Endangered, four are Vulnerable (*Charadrius thoracicus*, *Falco concolor*, *Gallinago macrodactyla*, and *Glareola ocularis*), three Near Threatened (*Accipiter henstii*, *A. madagascariensis*, and *Lophotibis cristata*), and 107 Least Concern. A further two species (*Porphyrio madagascariensis* and *Saxicola sibilla*) are not recognised by the IUCN (2022).

Small mammals, carnivorans, and bush pigs

The small mammal community comprises four tenrec species (*Microgale pusilla*, *Tenrec ecaudatus*, *Setifer setosus*, and *Oryzorictes hova*), two rodents (the endemic *Eliurus webbi* and the invasive *Rattus rattus*) and two introduced insectivores (*Suncus murinus* and *S. etruscus*). Species identities are genetically confirmed in each case, with the exception of *Microgale pusilla*, which was confirmed in the field ca. 1990 (Goodman, pers. comm. 2022). The record of *O. hova* in S9 represents a new area record (Hyde Roberts, unpublished data). Both *T. ecaudatus* and *S. setosus* are known from both S9 and S8, although likely have a wider distribution in Sainte Luce. All species are considered Least Concern (IUCN, 2023).

The introduced bush pig (*Potamochoerus larvatus*) (Lee *et al*., 2020) has returned to Sainte Luce in recent years and has been observed in the north of forest fragment S9. Local guides attribute its return to a series of large fires, driving the pigs south towards Sainte Luce. Prior, this species had been absent from the area for decades after a prolonged period of effective hunting (Longosoa, pers. comm. 2019). The ecological impact of bushpigs in small forest fragments is unknown. The carnivoran fauna consists of two species, the endemic Spotted Fanaloka (*Fossa fossana*) and the introduced Small Indian Civet (*Viverricula indica*). Both have been observed at night near forest edges and in cassava plantations, with identifications confirmed using camera trap images. This Vulnerable *F. fossana* (IUCN, 2023) is thought to rely on intact and undisturbe areas of forest and is considered threatened by habitat loss and hunting. The larger Fosa (*Cryptoprocta ferox*) has not been observed in Sainte Luce for several decades (Lewis Environmental Consultants, 1992).

Bats

The insectivorous bat community in Sainte Luce requires review. The only previous published study (Jenkins *et al*., 2007) recorded 10 species using a combination of mist nets and acoustic detectors. The study reports an unknown Vespertilionidae species and a further Hipposideridae species whose vocalisations were previously unrecorded. Of those species identified, *Macronycteris commersoni* is considered as Near Threatened (IUCN, 2022). Further species are known to inhabit nearby areas and additional survey effort may increase the bat inventory for Sainte Luce. The Madagascar flying fox (*Pteropus rufus*) is the only pteropodid bat species in Sainte Luce, represented by a single colony (~450 individuals). Numbers have increased in recent years following conservation initiatives by SEED Madagascar. Bollen and Donati (2006) highlighted the importance of the species as a key seed dispersal agent, able to carry small seeds over large areas (Bollen *et al*., 2004; Gérard *et al*., 2015). However, fragment S6 is now experiencing heavy logging pressure and the future of the colony, also inside the mining zone is uncertain. Presently classified as Vulnerable, there have been recent calls to reassess its conservation status nationwide (Brook *et al*., 2019).

Lemurs

Perhaps the most consequential taxonomic changes have occurred within the lemur community of Sainte Luce, with all four species having undergone revision since the initial faunal studies. The three nocturnal species were each elevated from existing cryptic species complexes, whilst *Eulemur collaris* was promoted to full species status from being a subspecies of *E. fulvus* (Mittermeier *et al*., 2021). The community of lemurs present in Sainte Luce now comprises one Lemuridae species, *E. collaris*, one Indriidae, *Avahi meridionalis*, and two Cheirogaleidae, *Cheirogaleus thomasi* and *Microcebus tanosi*. These revisions have direct implications and consequences for conservation and biodiversity management. All four lemur species are classified as Endangered (IUCN, 2022). The three nocturnal lemurs are likely present in each of the suitable remaining fragments (Hyde Roberts *et al*., 2021), whilst with the majority

of *E. collaris* exist in fragments S9 and S17. A recent unpublished census suggests that the total *E. collaris* population at Sainte Luce stands at ca. 500 individuals, with a number of sub-populations remaining vulnerable to hunting and long-term isolation (Hyde Roberts, unpublished data).

Key ecological species

Zoochory and the importance of conserving key frugivores-plant interactions were specifically highlighted by Bollen and Donati (2006). Whilst Madagascar supports a rich and varied flora (Schatz, 2000), the diversity of frugivore species is limited. Many taxa that provide important ecological services in other tropical forests are not represented on the island. Relatively few of Madagascar's bird species are frugivores (8%) and the majority of bats are insectivorous (Wright *et al*., 2005). Thus lemurs, often as keystone mutualists, stand out as being essential to Malagasy forests (Ganzhorn *et al*, 1999; Bollen *et al*., 2004; Wright *et al*., 2005; Chapman *et al*., 2020).

All four lemur species in Sainte Luce exhibit relatively broad diets and undoubtedly fulfil important ecological roles (Bollen *et al*., 2004; Lahann, 2007; Chapman *et al*., 2013; Ramananjato *et al*., 2020). However, *Eulemur collaris* is the only species able to consume and disperse species with large seeds (Bollen *et al*., 2004; Sato, 2022). Whilst it is apparent that *E. collaris* groups can occasionally travel between fragments (Bertoncini *et al*., 2017; Hyde Roberts *et al*., 2020), a number of tree species, and particularly those with larger diaspores (e.g., *Canarium boivinii*, *Diospyros* sp., *Hypercanthus mandenensis*), now have extremely limited means to be dispersed between forest fragments.

Several further species known from the Sainte Luce area facilitate seed dispersal and occupy important pollination roles, including birds (*Alectroenas madagascariensis*, *Coracopsis nigra*, *C. vasa*, *Coua gigas*, *Hypsipetes madagascariensis*, *Nesoenas picturata*, and *Treron australis*), fruit bats (*Pteropus rufus*), rodents (*Eliurus webbi* and *Rattus rattus*), and potentially even some reptiles (*Zonosaurus* spp.) (Bollen *et al*., 2004; Lahann, 2007; Račevska, 2020). However, despite notable overlap in the diets of frugivorous species (Bollen *et al*., 2004), contributions vary greatly according to key functional traits (e.g., specific diet, vagility, and seed predation) (Bollen & Donati, 2006). Volant taxa (e.g., birds and fruit bats) are better able to disperse seeds across the landscape, with implications for the functional ecology of large-seeded tree species. Thus, the hunting of frugivorous species poses a direct threat to species persistence and frugivore-plant relationships (Golden, 2009; Estrada *et al*., 2017; Borgerson *et al*., 2022).

Missing species and impacts on local biodiversity

Several important species appear to have vanished from Sainte Luce since the biodiversity assessments three decades ago (Table 1). Whilst some small or rare species with cryptic lifestyles may go undetected for long periods (e.g., *Amphiglossus astrolabi*, *Guibemantis* cf. *pulcher*, *Flexiseps* cf. *macrocercus*), more conspicuous species (e.g., *Cryptoprocta ferox*, *Galidia elegans*, *Hapalemur meridionalis*) should have been detected given the consistent research effort and the size of remaining forest fragments. Whilst it is possible that some species persist in the wider environment beyond the main study forests (S7, S8, S9, and S17), many of these more remote fragments are smaller in size, highly degraded, and are considered unlikely to support viable populations of rare forest dependent animals (Lehtinen & Ramanamanjato, 2006; Strier, 2021).

The loss of larger species from the protected areas, and particularly those that provide key ecological functions (seed dispersers, pollinators, and carnivores), is a real concern (Chapman & Onderdonk, 1998; Bollen *et al*., 2004; Colman *et al*., 2014). Whilst difficult to diagnose, such losses may represent the extirpations predicted by previous studies (Ganzhorn *et al*., 2001; Bollen & Donati, 2006). Carnivores such as *C. ferox*, which naturally occur at low densities and require large territories, are particularly vulnerable in fragmented habitats (Hawkins & Racey, 2005) and may be amongst the first species to vanish from disturbed forests. Such species likely also experience significant human pressure, being considered a threat to domestic fowl. The potential disappearance of *H. meridionalis* appears to have coincided with the large-scale reduction of fragment S8 in the early 2000s. The last conceivable sighting was made in this area in 2002 (Ellis, 2003), although focused surveys in 1999 had failed to find the species, concluding that the species was likely already extirpated or had never occurred in Sainte Luce (Donati, pers. comm. 2017). The loss of important food resources combined with the high hunting pressures may have attributed to its disappearance (Johnarson, pers. comm. 2015).

Similarly, the absence of *Cheirogaleus major* is puzzling. The species persists in smaller and

Table 1. Vertebrate species not observed in Sainte Luce since at least 2010, with IUCN RedList conservation statutes (LC = Least Concern, VU = Vulnerable, EN = Endangered, DD = Data Deficient, NA = Not Assessed) and last known records. * = Reports of both lemur species are contested and may derive from early misidentifications. ** = Avian species restricted to forest dependent species and ducks. Bat not included due to lack of search effort.

Order	Family	Species	Common Name	Status	Last Record
Primates*	Lemuridae	*Hapalemur meridionalis*	Eastern Bamboo Lemur	VU	Ellis, 2003 (S8)
	Cheirogaleidae	*Cheirogaleus major*	Greater Dwarf Lemur	DD	Ganzhorn *et al*., 2007
Carnivora	Eupleridae	*Cryptoprocta ferox*	Fossa	VU	Lewis Environmental Consultants, 1992
		Galidia elegans	Ring-tailed Vontsira	LC	Lewis Environmental Consultants, 1992
Aves**	Accipitridae	*Aviceda madagascariensis*	Madagascar Cuckoo-hawk	LC	Watson, 2007
	Anatidae	*Anas melleri*	Meller's Duck	EN	Ellis, 2003
	Cuculidae	*Coua reynaudii*	Red-fronted Coua	LC	Watson, 2007
	Falconidae	*Falco concolor*	Sooty Falcon	VU	Watson, 2007
		Falco eleonorae	Eleonora's Falcon	LC	Ellis, 2003
	Vangidae	*Cyanolanius madagascarinus*	Blue Vanga	LC	Watson, 2007
		Leptopterus chabert	Chabert's Vanga	LC	Watson, 2007
		Schetba rufa	Rufous Vanga	LC	Watson, 2007
Squamata	Lamprophiidae	*Micropisthodon ochraceus*		LC	Azafady, unpublished data, 2010 (S8)
	Scincidae	*Amphiglossus astrolabi*	Diving Skink	LC	Ramanamanjato, 2007
		Flexiseps cf. *macrocercus*	Black-lined Skink	LC	Ramanamanjato, 2007
	Matellidae	*Guibemantis cf. pulcher*		NA	Ramanamanjato, 2007

less intact littoral forest fragments further south (Mandena), and in the rainforests of the Vohimena Mountains, immediately to the west. In this instance, early misidentification and confusion with *C. thomasi* must be considered a real possibility.

Of the avifauna, 35 bird species recorded in previous studies have not been reported or seen since 2010. Whilst many bird species may be rare visitors to Sainte Luce, both *Anas melleri* and *Sarkidiornis melanotos* were considered resident but were known to have been under severe threat from the local community who hunt waterfowl (Ellis, 2003).

The loss of vertebrate species provides a stark example of littoral forest ecosystem decline and the conservation challenges ahead. It remains evident that even the largest forest fragments in Sainte Luce are unlikely sufficient in size to support a truly natural vertebrate community. The losses highlight the necessity to expand existing forests and preserve functional habitat connectivity (Kindlmann & Burel, 2008; Marsh *et al*., 2013). Furthermore, whilst the species outlined in Table 1 deal largely with the more obvious vertebrate taxa, the impact of the combined threats on the invertebrate and botanical communities needs further attention (Laurance *et al*., 2000; Hyde Roberts *et al*., 2020). It has long been known that important botanical resources in these forests are under great pressure (Consiglio *et al*., 2006) and that some utilitarian species (e.g., *Calophyllum pervillei*) are already lost from the area.

Conservation recommendations

With the protected areas and mining footprint now established (Temple *et al*., 2012), solutions are urgently needed to mitigate foreseeable biodiversity losses. Protected forest fragments will require considerable management and monitoring if they are to maintain current vertebrate diversity (Ganzhorn *et al*., 2001; Watson *et al*., 2010). Local area managers now have the opportunity to align environmental strategy with ambitious global biodiversity targets, such as those set out by the Convention on Biological Diversity (2021). Post mining (ca. 2045), the largest remaining forest blocks will be S9 and S17 at an estimated 190 ha and 237 ha, respectively (QMM, 2001). Given that ca. 800-1000 ha appear necessary to maintain viable vertebrate assemblages long-term (Ganzhorn *et al*., 2001; Marsh *et al*., 2013), the importance of reforestation efforts and habitat connectivity cannot be overstated. Targets should further aim to halt species loss, safeguard the genetic diversity of key plant and animal populations, and recognise and protect important ecosystem services.

Currently, the protected forest block S8 represents a priority area for such efforts, given its position beyond the mining area and within the KBA

zone. Opportunities to expand fragment S9 will be restricted during mining operations, whilst S17 is naturally isolated by aquatic systems (Figure 1). The successful restoration of the degraded fragments S1 and S2 may improve connectivity with the southern portion of S17, although current initiatives in the area are focused on *Acacia* plantations for community resource purposes (Randriatafika, pers. comm. 2022) rather than supporting biodiversity. Prioritising habitat connectivity will be essential for long-term biodiversity conservation (Kindlmann & Burel, 2008) and even small, seemingly insignificant vestiges of connective habitat should be regarded as important. Improving habitat connectivity increases resilience to severe weather events and climate change effects (Wright *et al*., 2005) and can ameliorate the effects of food patchiness for key frugivores (Irwin *et al*., 2010; Campera *et al*., 2014). Moreover, small forest remnants may further serve as temporary biodiversity reservoirs, facilitate dispersal, and maintain ecological services (Bodin *et al*., 2006).

The rapid environmental modifications rendered by mining will necessitate the movement of myriad animals from the exploitation zones. Whilst most flying taxa are likely able to autonomously relocate, at least over short distances, a strategy to minimise the loss of terrestrial species and reluctant volant species must be developed. During mining operations at Mandena, a series of habitat corridors helped to facilitate animal movements ahead of the mine dredge (Andriamandimbiarisoa *et al*., 2015); however, this method has limited utility in Sainte Luce given the greater isolation of fragments and challenging terrain between forested areas. Proposals to reconnect the protected littoral forest fragments of Sainte Luce should be considered as part of a longer-term strategy. Consequently, management must consider all appropriate conservation tools (e.g., species translocation, habitat corridors, forest expansion, remote sensing, *ex-situ* initiatives) within a robust monitoring, evaluation, and learning framework.

Given that Sainte Luce supports numerous species with specific microhabitat requirements (e.g., *Cheirogaleus thomasi*, *Guibemantis wattersoni*, and *Phelsuma antanosy*), the translocation of animals into the protected fragments is problematic, with existing habitats unlikely able to support increased populations. Important fossorial species (e.g., *Liophidium kely*, *Oryzorictes hova*, and *Pseudoxyrhopus sokosoko*) must also be considered. Likewise, the propensity for *C. thomasi* to hibernate underground (Blanco *et al*., 2011) remains unclear and operations should carefully consider operational timing. In addition, botanical species that constitute major dietary resources for key frugivores, and those with limited natural dispersal capacity should be included in reforestation efforts, to account for broader loses (Bollen & Donati, 2006; Chapman *et al*., 2020).

The integration of core areas of fragments S6 and S7 into the protected Conservation Zone could provide great conservation benefits and should be considered. Such a scheme could protect the *Pteropus rufus* colony and further safeguard a number of priority species (e.g., *C. thomasi*, *Phelsuma antanosy*, *Chrysalidocarpus saintelucei*), whose principal populations exist in the area. Furthermore, it could stimulate increased community responsibility in these forests. Besides acting as an important additional reservoir for biodiversity throughout the mining process, these core areas could expedite future reforestation works and act as vital connective forest post-mining. Additionally, the proposed 225 ha forest (part of QMM's environmental commitment) (Temple *et al*., 2012), must be positioned strategically to maximise habitat connectivity between protected forests and facilitate animal dispersal.

Alternatives to key natural resources must be developed in coming years to prevent a future dependence by local communities on protected forests. An urgent appraisal of projected community needs is required (e.g., for livelihoods, construction, ceremonial materials, medicines) (Vincelette *et al*., 2006; Račevska, 2020). Several plantations, comprised of fast-growing introduced species (e.g., *Acacia mangium*, *Eucalyptus citriodora*, *E. robusta*, *Grevillea robusta*) are now maturing in Sainte Luce. Notably, *G. robusta* plantations have self-seeded and spread over large areas, particularly around S8, and are developing rapidly into thick monoculture forest. These new forests may provide in coming years a valuable future fuelwood resource. Whilst existing reforestation initiatives need to be scaled up, a robust sustainability mechanism needs to be incorporated into the local resource management structure to ensure proper governance.

Whilst plantations are known to provide important refuge for many species globally (Brockerhoff *et al*., 2008), including some lemur species (Ganzhorn, 1987; Eppley *et al*., 2015), they generally support an impoverished biodiversity (Lindenmayer & Hobbs, 2004; Yue *et al*., 2015; Braun *et al*., 2017). Plantations should not be considered a substitute for natural forest and initiatives to protect and expand

mature standing forest must be prioritised (Barlow *et al*., 2007; Watson *et al*., 2018; Chapman *et al*., 2020). However, plantations can provide a vital role in preserving littoral forest biodiversity by reducing anthropogenic pressure on threatened species and resources in natural forest areas (Konersmann *et al*., 2022). Interestingly, the maturing *G. robusta* plantations appear highly attractive to dwarf lemurs (*Cheirogaleus thomasi*) who consume the flower nectar on emergence from hibernation. Such plantations may therefore have a direct conservation application.

The specific placement of plantations is also contested, with some researchers recommending they be positioned adjacent to existing forests to facilitate animal dispersal (Bollen & Donati, 2006). However, contrary evidence suggests plantations support a greater abundance of invasive species

Figure 3. A range of priority species in Sainte Luce. **A**) *Eulemur collaris* (♀), **B**) *Avahi meridionalis*, **C**) *Cheirogaleus thomasi*, **D**) *Microcebus tanosi*, **E**) *Pteropus rufus*, **F**) *Fossa fossana*, **G**) *Caretta caretta*, **H**) *Liophidium kely*, **I**), *Phelsuma antanosy*, **J**) *Matoatoa* cf. *spannringi*, **K**) *Guibemantis diphonus*, **L**) *Anodonthyla nigrigularis*, **M**) *Chrysalidocarpus saintelucei*, **N**) *Dypsis brevicaulis*, **O**) *Panulirus homarus*, and **P**) *Lepironia mucronata*. (Photos by Sam Hyde Roberts except for **C** and **F** by Elena Račevska, **N** by John Dransfield, and **O** and **P** courtesy of SEED Madagascar.)

(Ramanamanjato & Ganzhorn, 2001; Silmi *et al*., 2013), undermining adjacent natural habitats. Linking plantations to protected forests could further blunt the effectiveness of conservation measures. Whilst some non-native species (e.g., *Acacia mangium*) can initially improve local edaphic conditions (Corlett & Hau, 2000), evidence from mixed plantations suggests several commonly utilised non-native species ultimately reduce the growth and survival rates of endemic species (Vincelette *et al*., 2007). Furthermore, certain *Eucalyptus* spp. exude natural chemical products which may negatively impact local invertebrate diversity (Samways *et al*., 1996; Wang *et al*., 2008). Thus, plantations require considerable planning, albeit accessibility to the local community is perhaps the most salient factor.

Beyond the much-needed afforestation and alternative resource initiatives, the issue of illegal hunting, particularly of key frugivore and Endangered vertebrate species, must be firmly addressed. The upskilling and empowerment of local community agencies needs committed investment. A formal monitoring (e.g., following a SMART approach) and reporting system should be adopted (Andrianambinina *et al*., 2022), with all incidents systematically recorded. Not only would this provide evidence for local enforcement but would also provide much needed data on hunting in the area. Reporting could be expanded to include a range of activities (e.g., illegal logging, agricultural encroachment). Presently, the familial and close-knit nature of community life often forestalls prosecution, thus, diversification of this enforcement mechanism is essential. The presence of researchers also appears to have a positive impact on hunting prevalence and encouraging researcher led community education schemes may provide additional value.

Fires remain a considerable threat to standing forest and restorative projects. Current fire management policy in Sainte Luce is to clear firebreaks around protected forests, biannually (Solo, pers. comm. 2020). This policy should be

Table 2. A list of 21 priority species in Sainte Luce. IUCN conservation statutes as of August 2022. The list does not include species listed in Table 1, and such species should be considered as high priorities if re-discovered. IUCN RedList statutes (LC = Least Concern, VU = Vulnerable, EN = Endangered, CR: Critically endangered, DD = Data Deficient, NA = Not Assessed).

Order	Family	Species	Common or Vernacular Name	Primary Reason	IUCN STATUS
Arecales	Arecaceae	*Dypsis brevicaulis*		Conservation	CR
Arecales	Arecaceae	*Chrysalidocarpus saintelucei*	*Telopoloambilany*	Conservation / Utilitarian	EN
Malpighiales	Calophyllaceae	*Calophyllum pervillei*	*Vitano*	Utilitarian / Conservation	NA
Myrtales	Myrtaceae	*Eugenia cloiselii*	*Ropasy / rotra*	Utilitarian	EN
Poales	Cyperaceae	*Lepironia mucronata*	*Mahampy*	Economic / Ecological / Utilitarian	NA
Decapoda	Palinuridae	*Panulirus homarus*		Economic / Conservation	LC
Odonata	Corduliidae	*Libellulosoma minutum*		Conservation	DD
Carcharhiniformes	Sphyrnidae	*Sphyrna lewini*	Scalloped hammerhead Shark	Conservation	CR
Anura	Mantellidae	*Guibemantis diphonus*		Conservation	CR
Anura	Microhylidae	*Anodonthyla migrigularis*	Black-throated Climbing Frog	Conservation	EN
Squamata	Gekkonidae	*Matoatoa* cf. *spannringi*		Conservation	DD
Squamata	Gekkonidae	*Phelsuma antanosy*		Conservation	CR
Squamata	Pseudoxyrhophiidae	*Liophidium kely*		Conservation	EN
Testudines	Cheloniidae	*Caretta caretta*	Loggerhead Turtle	Conservation	VU
Chiroptera	Pteropodidae	*Pteropus rufus*	Madagascan Flying Fox	Ecological / Conservation	VU
Carnivora	Eupleridae	*Fossa fossana*	Spotted Fanaloka	Ecological / Conservation	VU
Primates	Cheirogaleidae	*Cheirogaleus thomasi*	Thomas' Dwarf Lemur	Conservation	EN
Primates	Cheirogaleidae	*Microcebus tanosi*	Anosy Mouse Lemur	Conservation	EN
Primates	Lemuridae	*Eulemur collaris*	Red-collared Brown Lemur	Ecological / Conservation	EN
Primates	Indriidae	*Avahi meridionalis*	Southern Woolly Lemur	Conservation	EN

reviewed as it may be possible to maintain firebreak effectiveness and allow natural forest succession by incrementally stepping out the firebreaks. Although without precedent, the adjustment could provide a cost-effective alternative to laborious restoration efforts. Crucially though, communication between the numerous invested stakeholders needs to be improved and actions more integrated if conservation efforts are to be successful. An open forum where stakeholders and researchers can discuss project ideas, share findings, access information on previous work, and reflect on the successes and failures of past interventions could provide great value. Furthermore, such a forum could be extended to include other organizations working in non-regional littoral forests, who surely face similar challenges and yet presently work in isolation.

Whilst there are many undescribed and threatened taxa in Sainte Luce, a number of species require specific monitoring and management. A list of priority species, earmarked for special measures was initially proposed by QMM (reproduced in Temple *et al*., 2012), including 10 vertebrates, 26 invertebrates, and 90 plant species. However, due to financial constraints, the list has since been reduced leaving it unclear which species are now priorities (QMM Stakeholder Meeting, 2018). Thus, a new and independent list of 21 priority species is presented in Table 2, based on a number of criteria: IUCN RedList status, species range, ecological utility, local abundance, and economic importance.

Conservation actions

In line with earlier recommendations (Bollen & Donati, 2006), several interventions focusing on frugivore conservation and natural resource sustainability have been implemented by local stakeholders. The quasi protection of the *Pteropus rufus* colony in S6 by SEED Madagascar has seen a rapid increase in bat numbers (~150% in five years) (Hyde Roberts, unpublished data). The colony in July 2023 supported ca. 400-450 bats. The demarcation of a community-backed, 38 ha no-disturbance zone, alongside a community education program has proven extremely effective. The scheme also supports local resource management bodies by providing funds generated through research and eco-tourism. However, the long-term future of the roost remains uncertain as mining operations likely supersede local protection.

Efforts to improve habitat connectivity in the protected region of S8 are underway, with five short habitat corridors (max = 245 m) under development. The project, again developed by SEED Madagascar, aims to reunite isolated nocturnal lemur populations by reconnecting four satellite remnants to the main forest fragment using a mixture of introduced and endemic tree species. Similar initiatives have proven successful at facilitating lemur movement in Mandena (Andriamandimbiarisoa *et al*., 2015). The scheme aims to increase connected forest habitat from 40 to 70 ha and learn lessons for similar initiatives in the future. Given the projected loss of forest cover in coming years, expanding and connecting protected forests is a vital strategy for conserving biodiversity and ecological function in the long-term. Intervention may be particularly necessary, since littoral forest regeneration is notably slow (Lowry & Faber-Landoen, 1991; Vincelette *et al*., 2007) and both fire prevention policy and agriculturally practices currently prevent natural expansion.

Numerous further actions are similarly underway in Sainte Luce, driven by a range of invested local stakeholders, largely aimed at protecting important cultural and economic resources, diversifying economic opportunities, and bolstering sustainability mechanisms. Activities range in scale from taxa-specific projects (e.g., focusing on the *in-situ* conservation of threatened palm species), to larger sustainable fisheries schemes, and working to protect important marine resources tied to local livelihoods. Ancillary projects have also been developed in parallel to increase the availability of important fisheries related materials, particularly those used in the construction of lobster traps (e.g., *Flagellaria indica*, *Bambusa multiplex*), albeit with mixed results (Solo, pers. comm. 2022).

Conclusion

Littoral forests represent Madagascar in a microcosm, bearing a wide range of exigent environmental threats that leaves the long-term future of many species uncertain. Simultaneously, our understanding of the biodiversity they support continues to increase in terms of diversity and importance. Richness estimates in the Sainte Luce area have increased across all major taxonomic groups (mammals from 17 to 24 recognised species, birds from 77 to 117, amphibians and reptiles from 55 to 76), whilst several vertebrate taxa require urgent attention (e.g., insectivorous bats, freshwater fish). Our knowledge of numerous important and speciose groups is largely missing (e.g., arachnids, fungi, moths). This appraisal aims to help focus conservation efforts on the Sainte Luce region. Given that several charismatic species

have seemingly already disappeared, further losses will only serve to diminish the areas future prospects and increase the costs of restoration.

Over coming decades, mining operations stand to dramatically alter the remaining littoral forest landscape of Sainte Luce. Important biodiversity evidently resides within the mining footprint, and considering the substantial difficulties associated with mitigation (temporal, ecological, financial, and logistical), preserving additional strategic habitats (mature forests, connective habitats, and aquatic systems) may provide a prudent solution to minimising long-term impacts (Watson *et al*., 2005; Bodin *et al*., 2006, Bollen & Donati, 2006; Strier, 2021). Given the mine's commitment to biodiversity conservation (QMM, 2001; Temple *et al*., 2012), set out at the 2004 IUCN World Conservation Congress, and the efforts invested in securing a net positive environmental outcome, it seems pertinent to review its strategy in light of these updates.

Although deforestation in Sainte Luce remains severe, the rapid clearance of standing forest for agricultural use that marked earlier decades has largely stopped. However, extensive selective logging continues to drive a dramatic reduction in forest quality, particularly in the community resource forests. Navigating a sustainable future for both the local communities and biodiversity remains the Holy Grail in conservation, and although many tree plantations are now maturing across Sainte Luce, further efforts are required to replace key resources and to encourage communities away from unsustainable practices. The regeneration of littoral forest is very slow (Vincelette, 2007) and the restoration of functional ecological assemblages may take many decades (Mansourian *et al*., 2018). Thus, the decisions made in the coming years will have great consequences for the future of the Sainte Luce forests and its biodiversity.

Despite the obvious environmental impacts, the mine promises much needed economic growth. It is clear that economic diversification is vital if local communities are to break their dependence on dwindling forest resources, although development can bring its own challenges (e.g., pollution and increased human access). The creation of industrial employment may also reduce pressure on protected forests, as in nearby Mandena (Donati *et al*., 2020); however, the net loss of forest calls in to question the long-term conservation vision (Watson *et al*., 2010). Whilst proposals to establish vast mixed community use tree plantations in the future are welcome from a biological perspective, albeit with caveats, such endeavours may prove difficult to achieve in practice. Furthermore, efforts to support more environmentally harmonious initiatives such as eco-tourism, a promising economic sector prior to the Covid-19 pandemic, should be supported. If biodiversity can be sustained and the community continues to benefit from its rich natural heritage, there is still cause for optimism.

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