



Anthropogenic disturbance effects remain visible in forest structure, but not in lemur abundances



de Winter Iris^{a,*}, Sebastiaan van der Hoek^{a,b}, Jeroen Schütt^{a,b}, Ignas M.A. Heitkönig^a, Pim van Hooft^a, Gerrit Gort^c, Herbert H.T. Prins^a, Frank Sterck^b

^a Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3A, 6708, PB, Wageningen, The Netherlands

^b Forest Ecology and Management Group, Wageningen University, Droevendaalsesteeg 3A, 6708, PB, Wageningen, The Netherlands

^c Biometris, Wageningen University, Droevendaalsesteeg 1, 6708, PB, Wageningen, The Netherlands

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ABSTRACT

The persistence of tropical rainforests, together with their flora and fauna, is highly threatened by anthropogenic disturbances. In this study, we investigate to what extent selective logging influences the structure and composition of a tropical rainforest in Madagascar and subsequently lemur encounter rates and cluster sizes. We quantified forest structure variables and conducted transect surveys of seven sympatric diurnal lemur species in five protected forest sites with different logging histories. We found that DBH, tree height, the interquartile ranges of DBH and tree height (measure of forest heterogeneity), tree species and family richness were relatively high and tree density was relatively low in less disturbed compared to disturbed sites. Although the disturbed forests have not fully recovered to previous conditions, they seem to have recovered from a functional perspective into suitable lemur habitat, as lemur encounter rates and cluster sizes were similar in disturbed and less disturbed sites. We only found slightly higher encounter rates for *Varecia variegata* ($P = 0.078$) and lower encounter rates for *Eulemur rufifrons* ($P = 0.059$) in less disturbed forests. This is one of the first studies that report the presence of *V. variegata*, a species characterised by its drastic decline, in previously logged sites. Lemurs travelling between disturbed and less disturbed sites disperse seeds and hereby facilitate forest regeneration. Therefore, we promote the need for better attention to the value of logged forests for biodiversity conservation in Madagascar and suggest that there is considerable potential for regenerating logged forests to support lemur communities.

1. Introduction

Tropical forests hold most of the earth's terrestrial biodiversity and provide important ecosystem services, such as nutrient cycling, soil formation and water retention and they provide habitat for a vast array of plants and animals (Gardner et al., 2009; Laurance, 2015). An increasing number of tropical forests have been disturbed by human activities, such as deforestation, logging and fragmentation and by the consequences of anthropogenic climate change (Bradshaw et al., 2008). These human-induced changes can disrupt forest stability and can have long-lasting impacts on forest structure and biodiversity (Laurance, 2015). In particular, intensive logging drastically changes the forest structure and can result in a structurally more homogeneous forest canopy (DeWalt et al., 2003). Fragmented or homogeneous tropical forests show a reduced diversity of mammal species (McElhinny et al., 2005; Michalski et al., 2007; Pardini et al., 2005) and are therefore a

primary concern for conservation scientists and practitioners worldwide (Ogrzewalska et al., 2011; Michalski et al., 2007).

The tropical rainforests of Madagascar are among the most biodiverse habitats on earth and are widely considered a global conservation priority (Brooks et al., 2006; Ganzhorn et al., 2014; Myers et al., 2000). Madagascar experiences high rates of deforestation and ongoing habitat loss (Scales, 2014), hereby threatening many endemic species, including lemurs, with extinction (Goodman and Jungers, 2014; Schwitzer, 2014). Many of the fruit trees important for lemur species' survival are hardwood species favoured by selective loggers, thereby affecting frugivore lemur populations (Wright et al., 2005). Nevertheless, not all lemur species are similarly affected by selective logging. Like in other primate species (e.g., Johns and Skorupa, 1987) as well as non-primate species (Bicknell and Peres, 2010), lemurs characterised as folivores generally show less negative responses to such disturbances compared to frugivores (Herrera et al., 2011; Lehman et al., 2006a).

* Corresponding author.

E-mail addresses: iris.dewinter@wur.nl (I. de Winter), ignas.heitkonig@wur.nl (I.M.A. Heitkönig), pim.vanhooft@wur.nl (P. van Hooft), gerrit.gort@wur.nl (G. Gort), herbert.prins@wur.nl (H.H.T. Prins), frank.sterck@wur.nl (F. Sterck).

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Bamboo is the almost exclusive food source for bamboo lemurs (Yamashita et al., 2009). The species is typically present in the dense understory of disturbed Malagasy forests in the proximity of human settlements (Olson et al., 2013). Although some lemur species seem to cope with human-induced forest alternations, habitat loss and fragmentation are among the most pervasive causes of declining lemur populations and biodiversity loss in Madagascar (Gardner et al., 2010; Irwin et al., 2010; Laurance et al., 2000).

In selectively logged forests, large mature trees of commercial value are usually removed (McElhinny et al., 2005). For that reason, past logging can result in a lower average tree diameter, tree height and crown volume, and higher tree densities due to the increased emergence of tree saplings (Gibson et al., 2011). The removal of such high-canopy trees also creates profound gaps in the upper forest canopy, thereby reducing canopy closure and consequently increasing light and reducing humidity (Van den Van den Meerschaut and Vandekerckhove, 2000). Within primate communities, species can react differently to such changes in habitat conditions. Primate species with specialised diets and characterised by slow reproduction are most affected by forest disturbances compared to more generalist species (Cowlshaw et al., 2009). In addition, small-scale disturbances can be beneficial for both folivorous and frugivorous species, as fruit production and leaf quality increase following increased sunlight exposure at the understory level (Ganzhorn, 1995). Furthermore, logging can lead to changes in forest heterogeneity (Swanson et al., 2011). Numerous studies have found a positive relationship between increasing heterogeneity in multiple forest characteristics after logging events and the diversity in potential habitats, essential food resources, and shelter for animal communities (e.g., Dunn, 2004; Yang et al., 2015). Heterogeneity in forest structure is associated with a high degree of biodiversity (McElhinny et al., 2005). The relations between logging, forest structure and primate densities are complex and reflect varying causalities (Lehman et al., 2006a). Anthropogenic disturbances typically reduce species diversity, but species responses to disturbance are poorly known and can be very different across ecoregions (Irwin et al., 2010). It is important to have a local understanding of the responses of forests and lemurs to disturbances for conservation actions, in example in defining new protected areas. Therefore, we aim to assess the variation in Malagasy rainforest structure at sites that have experienced different logging intensities in the past and link these differences to the encounter rates and cluster sizes of multiple sympatric lemur species.

Other studies have addressed both structural and compositional changes in forests and at the same time linked these differences to primate abundances (Herrera, 2016; Lehman, 2007; Lehman et al., 2006b). For example, in West Malaysia, frugivore and folivore primates slowly recovered after disturbance, as logging drastically reduced overall food availability (Johns, 1988). In West Kalimantan, logged areas had fewer large food trees and a greater number of canopy gaps, leading to reduced orangutan (*Pongo pygmaeus*) nests (Felton et al., 2003). Furthermore, nocturnal lemur encounter rates were higher in primary compared to disturbed forests (Sawyer et al., 2017). In contrast, Javan slow lorises (*Nycticebus javanicus*) showed high abundances in agricultural mosaic habitats (Rode-Margono et al., 2014). Also in a dry deciduous forest in western Madagascar, lemur sightings of both folivore and frugivore species increased compared to the pre-logging state of the forest (Ganzhorn, 1995). In Ganzhorn's study, small scale disturbances created gaps in the forest canopy, which increased sun exposure for some trees, leading to higher fruit production and protein concentration in leaves. However, results were not consistent across years and some species were probably not present during sampling due to hibernation. In addition, the increased sighting rate post-logging could be due to greater visibility through the vegetation (Ganzhorn, 1995). In a study on lemur density in response to human disturbances, it was found that many lemur species responded positively to such disturbances, despite the negative influence on lemur food trees (Lehman et al., 2006a). This study suggests that due to the lemurs'

tolerance for human disturbances, some lemur species can survive the extreme habitat loss and forest fragmentation throughout Madagascar. So, these previous studies revealed no clear patterns in primate abundances as a result of structural and compositional forest changes.

The distribution and quality of food patches can influence the size of primate social groups (Chapman and Chapman, 2000). The crown volume of trees in relatively less disturbed forests is usually larger than in disturbed forests (Balko and Underwood, 2005; Tecot, 2008), influencing the availability of resources. The smaller and more widely dispersed food patches in disturbed forests can lead to increasing travel costs, especially for relatively large primate groups (Chapman and Chapman, 2000; Majolo et al., 2008). Therefore, some primate species lower their group sizes in disturbed areas to reduce these costs as well as the costs of within-group competition (Chapman and Chapman, 2000; Isbell, 1991).

In this study, we hypothesize that lemur abundance and cluster size vary according to disturbance-induced forest structure characteristics. These disturbances are expected to result in smaller trees, higher stem densities, lower heterogeneity in tree height and diameter, as well as a lower diversity in tree species and families. In particular, we predict: (1) that in *Varecia variegata*, the association between encounter rate and tree size, reflecting lower disturbances, is positive because of the species' specialised frugivorous diet; (2a) that the smaller, more generalist (i.e., *Eulemur rufifrons* and *E. rubriventer*) and (2b) the more folivorous lemur species (i.e., *H. griseus*) in our study are encountered at a higher rate in forests with smaller trees compared to the forests with larger trees; (3) and finally, that lemur cluster size among our study species increases in forests with larger trees that reflect a low disturbance history. To determine the impact of selective logging on lemur communities, we quantified forest structure variables and conducted transects surveys to determine the encounter rates and group sizes of seven sympatric diurnal lemur species (i.e., *Varecia variegata editorum*, *Eulemur rubriventer*, *Eulemur rufifrons*, *Propithecus edwardsi*, *Hapalemur griseus ranomafanensis*, *Hapalemur aureus* and *Prolemur simus*) in five protected forest sites in Ranomafana National Park (RNP), Madagascar, that have been subjected to different intensities of logging in the past.

2. Materials and methods

2.1. Study area and species

This study was conducted in Ranomafana National Park (RNP, 43,500-ha), a mid-altitude (600–1500 m) rainforest, providing essential habitat to thirteen species of Strepsirrhini in southeast Madagascar, located within the following coordinates: 20°58'22" S, 47°26'13" E, 20°27'25" S, 47°23'5" E, 21°8'23" S, 47°35'32" E and 21°15'45" S, 47°17'54" E (Wright et al., 2012; Wright and Andriamihaja, 2002). Before the establishment of the National Park in 1991, the forest was subjected to different logging schemes, ranging from intensive commercial logging to gradual wood extraction for local subsistence (Wright and Andriamihaja, 2002). RNP currently comprises a mix of pristine, nearly pristine and regenerating rainforest. For this study, we selected five sites (ca. 1.5 km² each) within the park, where trails existed for following animals. These sites had been subjected to different intensities of anthropogenic disturbances nearly three decades ago and have been regenerating since (Wright et al., 2012; Wright and Andriamihaja, 2002). In our three disturbed sites, Talatakely (TALA), Sakarao (SAKA) and Vohiparara (VOHI), extensive clearing for agriculture and human habitation in the 1950s was followed by intensive commercial logging until the late 1980s. Much of the secondary growth is dominated by dense stands of introduced Chinese guava (*Psidium cattleianum*) as well as clumps of giant bamboo (*Cathariostachys madagascariensis*). In our less disturbed sites: Vatoharanana (VATO) and Valoahaka (VALO), commercial logging occurred in both sites, albeit with much lower intensity than our disturbed sites. However, many rosewood (*Dalbergia* spp.) stumps are present in these latter sites

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