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Assessing the drivers of biodiversity in Madagascar by quantifying its hydrologic properties at the watershed scale

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ABSTRACT

Motivated by a theory developed by Wilmé et al. (2006) according to which, watersheds of Madagascar with headwaters at high altitude respond differently to drought from those with headwaters confined to relatively low elevations, with possibly profound effects on the biodiversity patterns of the island, we analyzed multi-year basin-specific observations of soil moisture and vegetation water content (derived from NRL's WindSat radiometer) and their response to precipitation departures (derived from TRMM 3B42 V7) from its local mean. These datasets were analyzed to investigate the hydrologic properties at the basin scale, including the speed with which vegetation and soil moisture respond to precipitation anomalies. We also looked at the basin-specific normalized radar surface-backscattering cross-sections from NASA's QuikSCAT Scatterometer, to obtain information on the vegetation regimes of the various Malagasy basins. Finally, we correlated the basin response to the precipitation forcing, and compared the amplitude and time lag of the correlations across watersheds with high elevation headwaters versus those with low elevation headwaters in the aim of evaluating the drought-response hypothesis of Wilmé et al. (2006). Our results indicate that the vegetation water content time series exhibit several features that are consistent with those of the majority of the bioclimatic zones of the island. Specifically, although the speed of the response of the vegetation water content varies significantly among the different basins, it is inter-annually consistent for each watershed, while the soil–moisture time series are less consistent than the vegetation water content time series. This study is a first step in the quantification of the hydrologic properties derived from microwave remote sensing, and which could potentially shed new light on the different intra-annual responses of watersheds to precipitation anomalies. Furthermore, this analysis offers important insights into the hydro-geomorphologic drivers associated with biodiversity patterns in Madagascar, contributing to a better understanding of the mechanisms that determine biotic diversification across the various bioclimatic regions of the island.

1. Introduction

Totally cut-off from the rest of the world, situated in the south-western Indian Ocean and east of Africa, about 400 km off the coast of Mozambique, lies the world's fourth largest, and potentially oldest island, Madagascar. Often characterized as “a place of biological wonder”, this island attracts a lot of attention by researchers of various fields, such as geologists, biogeographers, and biologists. Madagascar comprises one of the world's hottest biodiversity hotspots, as it hosts one of the unique biotas on Earth. There is an astonishing range of landscapes that host a huge number of different species of flora and fauna, 80% of which are found nowhere else on Earth (Goodman, Ganzhorn, & Rakotondravony, 2003; Yoder & Nowak, 2006). Moreover, its topography is so unique, with substantial environmental gradients and very diverse climates along both its latitudinal and longitudinal axes, thus making the island “the climatologist's promised land”. The heterogeneous landscape of Madagascar with its complex climatic profile and its immense endemic species richness, all occur within a limited landmass area. The combination of its long isolation and varied landscapes, that have created its eccentric diversity of wildlife, is what makes this island the only region in the world that can provide us with such a wealth of information; if used appropriately, this information can contribute significantly to the challenging task of investigating the forces that have resulted in the complex biodiversity patterns of the island.

Our hypothesis is based on a theory developed by Wilmé, Goodman, and Ganzhorn (2006) according to which, river catchments with their headwaters located in the highland areas, surrounding the three summital regions of the island (all at altitudes above 2000 m), serve as routes of retreat into refugia and subsequent dispersion, while river catchments with headwaters at relatively low elevations act as zones of isolation. This speculation is based on the different responses of the basins to sustained precipitation deficits during climatic shifts in the

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late Tertiary and the Quaternary periods. Specifically, during periods of glaciations, when the climatic conditions were colder and drier, natural habitats at low elevations experienced more pronounced arid conditions than did zones at higher elevations. Orographic precipitation played a key role in this differentiation, as it allowed the continuous flow of river systems with headwaters at higher elevations, and the stability of the associated habitats, despite the climatic shift. Therefore, basins with their sources at higher elevations maintained more mesic conditions, and thus acted as buffers for fauna and flora species, by providing potential routes for retreat toward higher altitudinal zones. However, basins with headwaters at low elevations were subject to lesser amounts of rainfall, resulting in the creation of intervening arid areas that would fragment existing forests; these arid areas in turn, acted as barriers to gene flow. As a result, contrary to basins with their sources at high elevations, those with headwaters at relatively lower elevations experienced greater levels of habitat isolation, thus leading to the speciation of locally endemic taxa, and in this way exhibiting higher levels of microendemism.

To date there have only been a few attempts to validate Wilmé's theory, and all of them have been phylogenetic studies. Pearson and Raxworthy (2009) tested coincidence between lemurs', geckos', and chameleons' distributions and areas of endemism predicted by the watershed hypothesis, and found that although extant distributions of the aforementioned species reveal patterns that are significantly coincident with the watershed hypothesis, the hypothesis alone cannot fully account for the biodiversity patterns of the island. Craul, Zimmermann, Rasoloharijaona, Randrianambinina, and Radespiel (2007) tested predictions derived from the Wilmé biogeographic model by exploring the genetic and morphological divergence among populations of a widely distributed lemur genus; they found several discrepancies between the model and their findings. Similarly, Olivieri et al. (2007) conducted phylogenetic and morphometric analyses using mouse lemurs, which were systematically sampled in various areas of the island, while Wollenberg et al. (2008) combined spatial and phylogenetic analyses for a specific species of frogs in Madagascar. Finally, another study by Vences, Wollenberg, Vieites, and Lees (2009) offers a review of the existing diversity models, including Wilmé's hypothesis; they suggest the need for detailed phylogeographic case studies in combination with the application of novel statistical approaches and spatial modeling that can address the severe gaps of existing diversification mechanisms.

The current study uses earth observations to assess the hydro-geomorphologic drivers of the biodiversity patterns over Madagascar, by validating the Wilmé et al. (2006) hypothesis according to which, microendemism basins (low-elevation-headwaters river catchments) respond differently to sustained precipitation deficits than retreat-dispersion basins (high-elevation-headwaters river catchments), with possibly profound effects on the biodiversity patterns of the island. The validation is performed against basin-specific observations of two major hydrologic attributes, namely soil moisture and vegetation water content, and the response of these variables to prolonged departures (i.e. anomalies) of the precipitation from its local mean value. Observations of the normalized radar cross section $\sigma°$ (i.e. percentage of electromagnetic radiation reflected back to its source from within a specified area) at the watershed level are also being analyzed to better understand the spatially and temporally varying patterns of the surface hydrologic properties, that are characteristic of each basin and for each season. Overall, hydrologic attributes for each basin are being fastidiously examined for identifying consistent discrepancies among the predictions derived from Wilmé's biogeographic model. To this end, multi-year satellite remote-sensing data of precipitation, soil moisture, vegetation water content, and normalized radar cross section ($\sigma°$) were used for the analyses. To our knowledge, this is the first eco-hydrological study for which remote-sensing observations are utilized on a watershed-by-watershed basis, in the aim of assessing the differences in the hydrologic properties of the various basins on the island. The goal of this study is to provide insight into the hydro-geomorphologic processes that have resulted into the existing complex bioclimatic zonation of Madagascar, and thus to enhance our understanding of the island's current biodiversity patterns, through a unique approach to validating the watershed-based mechanism of its species diversification. In the next section, we will discuss the study region and its hydro-climatic characteristics, and in Section 3 we analyze the data and methodology used for the watershed-by-watershed satellite data analysis. In Section 4 we present and discuss the results, while in Section 5 we summarize our major findings.

2. Study region

2.1. Topography and climatology of Madagascar

Extending 1570 km from 11° 57′ S to 25° 32′ S and 560 km from 43° 14′ E to 50° 27′ E off the south-eastern coast of Africa, Madagascar has an area of ca. 590,000 km^2 (Ingram & Dawson, 2005). Along its longer latitudinal axis, the island is (asymmetrically) split in two by a spine of mountains that runs its entire length; the highest altitudes of this mountain chain are located on the eastern side of the island, and as such the eastern escarpment of the island is significantly steeper than the western one, as western Madagascar is characterized by moderate sloping relief. A highland plateau rises to elevations of at least 1000 m a.s.l.; this plateau extends through most of the interior part of the island, with three major massif systems whose summits reach up to almost 3000 m a.s.l. The three major massifs are located in the north (Tsaratanana), center (Ankaratra), and south (Andringitra). This complex topography characterized by varied relief within short distances and in close proximity to the ocean has an enormous effect on the island's climatology.

The climatologic landscape of Madagascar is no less variable than its topography. By and large, the island has two seasons: a hot, rainy season from November to April and a cooler, dry season from May to October. However, during the rainy season, rainfall patterns and magnitude vary significantly across the island. More specifically, the island exhibits a remarkable east–west precipitation gradient, which is due to the orographic effect of the highland plateau located on the eastern side of Madagascar; this is because of the island's steep eastern escarpment, which forces much of the humidity transported by the Indian Ocean trade winds to precipitate on the eastern side, and thus rendering the west side subject to drier conditions. This orographic effect results in a substantial discrepancy in the total annual precipitation between the west (400 mm) and the east (3700 mm). Even more extreme cases in the annual precipitation amounts can be found in the south–west and north–east tips of the island, with the total annual precipitation in the former being barely measurable, while that of the latter exceeding 5 m (Wright, 2007). The east coast has a subequatorial climate and is notorious not only for a hot and humid climate, but also for the destructive cyclones that occur during the rainy season. Moreover, the east coast is also characterized by a high interannual variability in the rainfall patterns. Also, in the north and the south, Madagascar exhibits high interannual variability in total precipitation (Dewar & Richard, 2007), with the south being much drier than the north. Evidently, precipitation amounts diminish to the west and south, leaving the southwest and extreme-south the driest parts of Madagascar, which are ranked as subarid climatic zones (Koechlin, 1972). The north and south have yet another considerable difference; there is a strong seasonal temperature-variation gradient between the two; more specifically, the north, being closer to the equator, experiences very little variation in temperature year-round, having a mean annual temperature of 27 °C. On the contrary, the south exhibits a greater range of temperatures on a yearly basis, with a mean annual temperature of 23 °C. Regions located in the central interior parts of the island are cooler because of their higher elevations, and characterized by moderate rainfall. Overall, the climate of Madagascar is