ARTICLE

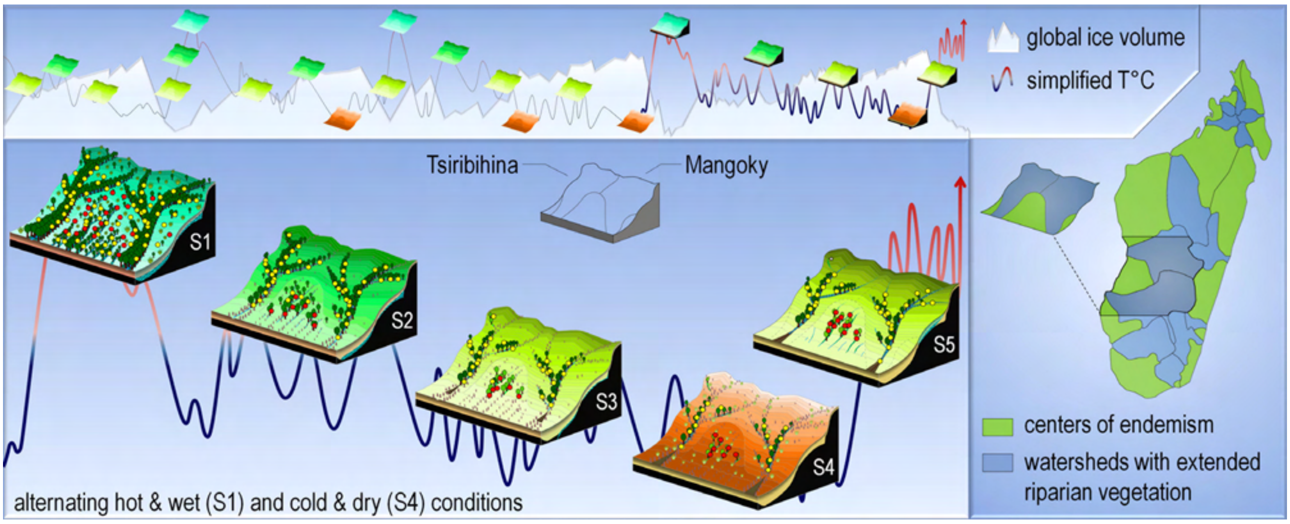
http://dx.doi.org/10.4314/mcd.v8i2.3

The Eco-Geo-Clim model: explaining Madagascar's endemism

Jean-Luc Mercier[I] and Lucienne Wilmé[II]

Correspondence:
Lucienne Wilmé
Missouri Botanical Garden, Madagascar Research & Conservation Program, BP 3391, Antananarivo 101, Madagascar.
E-mail: lucienne.wilme@mobot-mg.org

ABSTRACT



Paleoclimatic oscillations (top left) driving tropical island endemism by producing alternating wet (S1) and dry (S4) conditions (bottom left), with Madagascar's centers of endemism (right panel, green) located between watersheds with headwaters at high altitude and extended riparian forest (right, blue).

RÉSUMÉ

Les oscillations paléoclimatiques au cours du Pléistocène ont influencé tous les termes du bilan d'énergie stationnel (rayonnements, flux de chaleur latente, flux de chaleur dans le sol et flux de chaleur sensible). Associées aux précipitations, ces fluctuations ont contrôlé les bilans hydriques stationnels. Les bilans hydrologiques des bassins versants sont l'intégration spatiale et temporelle de ces bilans hydriques. La végétation et plus généralement la biomasse végétale sont dépendantes de ces deux types de bilans. L'interface entre l'atmosphère et la végétation est occupée par les sols et les formations superficielles, celles-ci sont le résultat de la dégradation des roches et de l'érosion des versants. Lorsqu'ils existent, ces sols ou géosols sont hérités de périodes humides antérieures.

La disponibilité en eau est l'élément majeur de la vie végétale et animale, or celle-ci a fluctué au cours du Pléistocène ; lors de périodes sèches, les bilans sont déficitaires, la biomasse diminue, l'érosion hydrique domine l'altération, le paysage entier évolue d'amont en aval. Lors des bilans hydriques humides le retour vers un état voisin de l'actuel n'a pas été immédiat car chaque composante du milieu naturel possède une résilience temporelle propre. La proximité d'un bilan hydrique stationnel positif est indispensable à la survie de la faune et de la flore sylvicoles. Dans le cas de l'endémisme à Madagascar, cette difficulté a été résolue de deux manières opposées et a produit deux types d'endémisme. D'une part par l'existence de cours d'eau prenant leurs sources à haute altitude, d'autre part par certains reliefs résiduels dans lesquels l'eau libre existe exceptionnellement. 1) Au cours du Pléistocène, les hauts reliefs ont eu une alimentation permanente en précipitations, les sources et les cours d'eaux ont été alimentés, les ripisylves sont restées humides. À l'opposé, lors des périodes sèches, l'aval des bassins versants a été sec, les écoulements discontinus, les forêts ont reculé, les animaux associés ont disparu. Ce n'est pas

---

[I] Université de Strasbourg, UFR de Géographie, 3 rue de l'Argonne, 67083 Strasbourg Cedex, France.
[II] Missouri Botanical Garden, Madagascar Research & Conservation Program, BP 3391, Antananarivo 101, Madagascar.

VOLUME 8 ISSUE 2 NOVEMBER 2013

MADAGASCAR CONSERVATION & DEVELOPMENT

INVESTING FOR A SUSTAINABLE NATURAL ENVIRONMENT FOR FUTURE GENERATIONS OF HUMANS, ANIMALS AND PLANTS OF MADAGASCAR

IN THIS ISSUE

Farmers' preferences

Eco-Geo-Clim model

Two new *Mimusops* L.

Madagascar Conservation & Development is the journal of Indian Ocean e-Ink. It is produced under the responsibility of this institution. The views expressed in contributions to MCD are solely those of the authors and not those of the journal editors or the publisher.

All the Issues and articles are freely available at
http://www.journalmcd.com

Contact Journal MCD
info@journalmcd.net for general inquiries regarding MCD
funding@journalmcd.net to support the journal

Madagascar Conservation & Development
Institute and Museum of Anthropology
University of Zurich
Winterthurerstrasse 190
CH-8057 Zurich, Switzerland

io@i

Indian Ocean e-Ink
Promoting African Publishing and Education
www.ioeink.com

MISSOURI BOTANICAL GARDEN

Missouri Botanical Garden (MBG)
Madagascar Research and Conservation Program
BP 3391
Antananarivo, 101, Madagascar

le cas de sous bassins versants dans lesquels un écoulement a été pérenne et où la forêt et sa faune associée ont pu subsister. 2) Dans certaines parties basses, profitant de spécificité géologiques et géomorphologiques, des milieux exceptionnels ont facilité la conservation, la transformation et l'évolution de certaines espèces endémiques. Ce processus est dénommé modèle Eco-Geo-Clim.

INTRODUCTION

The main features used to explain the current distribution of many endemic taxa in the flora and fauna of Madagascar include its topographic asymmetry, with a narrow eastern slope (27 % of the total area) and a broad western slope (73 %), and its climate, with the eastern windward slope uplifting the humid trade winds from the south-east and the leeward western slope in the rain shadow of the highlands receiving rain only during the austral summer (Cornet 1974, Donque 1975, Lourenço 1996, Dewar and Richard 2007). These features have often been used in various phytogeographical classifications of the island (Baron 1890, Perrier de la Bâthie 1921, Humbert and Cours Darne 1965, Moat and Smith 2007), in which most of the area was classified as forest of various kinds, where the majority of endemic taxa occur (Goodman and Benstead 2005). These endemic taxa are not distributed randomly on the island, but the climatic zones recognized today are not sufficient, by themselves, to explain, for example, the current distribution pattern of Malagasy lemur taxa. The phyto- and zoogeographical classification systems proposed during the 20th century are consistent with the contemporary distribution of taxa or forest types, without considering the conditions under which these ecosystems evolved; they do not, however, take into account changes in these ecosystems during recent geological time.

The Earth's surface is a complex interface between (i) the atmosphere, i.e., the climate with its radiative and advective components, (ii) the biosphere, and more specifically its floral and faunal elements, and (iii) the topography, with its soils, surface formations, and rocks, including their historical dimension, which determines their physical characteristics, i.e., the functional characteristics described by the hydrodynamic and thermal equations. These biological and physical elements interact and adapt in a nonlinear manner through time and space. Earth's climate varies with its orbital parameters (Hays et al. 1976), and the resulting Milankovitch periodicities have characterized the last three million years of comparatively rapid climate shifts (Rahmstorf 2009), i.e., mainly during the Pleistocene (2.6 Ma), as recently circumscribed (Leigh Mascarelli 2009). During colder phases, more of the Earth's water is stored as ice (especially at higher latitudes) and sea level is lower. For example, sea level was as much as 120m lower than today during the Last Glacial Maximum (LGM) ca. 20,000 years ago (Church and Gregory 2001, Milne et al. 2009). In cooler times of low sea level and extended drought, less water is in circulation and river courses are longer, while the total quantity of circulating water is reduced on the continents, and there is a greater number of rivers and streams with discontinuous flow. Climate change has influenced the geomorphology of entire landforms as well as biological evolution and extinction (Jansson and Dynesius 2002, Rabosky et al. 2012, Blois et al. 2013). During colder phases, when icecaps extended to lower latitudes, at times reaching ca. N and S 40°, the climate at tropical latitudes is drier and colder, and forests recede. When the climate is again warmer, lower latitudes experience hotter and more humid conditions, and forests expand (e.g., Assi-Kaudjhis et al. 2010).

One recent hypothesis to explain the current distribution of endemic taxa in Madagascar, the centers of endemism hypothesis, sensu Wilmé et al. (2006, 2012), considers (i) Quaternary climate oscillations, (ii) the extent of forest, and (iii) rivers and their ability to maintain riparian vegetation and their associated fauna during the driest climatic events, and in particular those with headwaters at high altitude. According to this hypothesis, these riparian forests functioned as dispersal corridors during periods when the climate became wet (Wilmé et al. 2006). The underlying mechanistic model proposed by Wilmé et al. (2006, 2012) specifically compares rivers with headwaters at high altitude, which drain most orographic rainfall, with those whose headwaters are situated at mid- or low altitude. In the present article, we summarize the biotic factors and the main abiotic factors of this model, which we refer to as the 'Eco-Geo-Clim' model. More specifically, the climatologic, geomorphologic, and hydrologic features involved are detailed, highlighting their influence on ecological processes. The way in which recent paleoclimatic oscillations have driven local endemism in forest taxa is also illustrated.

FRAMEWORK

The conceptual framework of the Eco-Geo-Clim model is biogeographically defined, i.e., it considers geographical phenomena occurring in a given area as causal factors leading to the spatial and temporal distribution of species. Specifically, it addresses two questions: How are the distributions of faunal and floral species influenced by the dynamics of abiotic factors? How have these factors been shaped by paleoclimatic oscillations through time? The model also considers vegetation and the fact that it relies intimately on water, whether by intercepting rainfall, which is sufficient for certain vegetation types, or by uptake of water directly from unsaturated soil layers or the saturated phreatic zone below the water table. Riparian vegetation found along streams and rivers uses groundwater to grow. At the scale of a catchment or watershed, the vegetation cover is usually denser in places where the water table is shallow, e.g., typically close to rivers and streams. When trees don't suffer from water stress, they have higher aboveground productivity and can support higher animal biomass. Not only is the vegetation denser in areas with more available water, but species diversity can also be higher (e.g., Dorman et al. 2013a, b and references therein). Riparian forests are known to have higher levels of diversity than the surrounding vegetation, especially in the drier regions of Madagascar, but also in areas of humid rainforest (Langrand and Wilmé 1997).

GEOGRAPHICAL CONTEXT. The model illustrated here considers two major watersheds (drainage basins) on Madagascar's western slope that have tributaries at high altitude: the Mangoky to the south, with its headwaters on Andringitra mountain, culminating at the island's second highest summit (2658m); and the Tsiribihina watershed, whose headwaters lie below Madagascar's third highest summit (2642m). Both the Mangoky and the Tsiribihina flow throughout the year. The area situated between the lower portions of these large watersheds, the Central Menabe, is composed itself of the smaller watersheds and interfluves of rivers with headwaters at mid- or low altitude. The basins of these intermittent rivers receive little orographic rainfall, have only seasonal flow, and dry out for several months during the year (dry season), especially in situations where the headwaters are at lower altitudes.

MODEL TIME SCALE. Recent climatic oscillations that occurred in Madagascar during the Pleistocene are considered, i.e., over a total period of several hundred thousand years. The most reliable information on temperature variation during this period is based on data obtained from the northern hemisphere and the Antarctic, and there is a considerable paucity of comparable data from Madagascar; pollen analyses from the island are sparse and only available for the last 40,000 years (e.g., Gasse and Van Campo 2001, Virah-Sawmy et al. 2009). Here the last global climatic oscillation is illustrated, i.e., over a period of a little more than 100 millennia, from the graphics presented in Elderfield et al. (2012), to include the LGM and the preceding warm maximum, during which maximum deglaciation took place.

GEO-ECOLOGIC FACTORS. The model presented by Wilmé et al. (2006, 2012) emphasized the importance of rivers and the altitude of their headwaters in explaining the current distributions of some narrow-ranged endemic species. Here further detail is introduced, using a number of geomorphological and hydrologic features, including additional aspects of rivers and the water in the unsaturated upper soil layers, the water-saturated phreatic zone, and their evolution during periods of climatic change. Groundwater recharge from rainfall involves two main mechanisms: (i) slow infiltration through the unsaturated soil horizons, old geo-soils and superficial formations, to the water table below, and (ii) rapid recharge through sinkholes, which are typically found in sedimentary formations such as karstic residual landforms (e.g., *tsingy* limestone formations in western Madagascar). The geomorphologic and hydrologic evolution on limestone areas is understood as karstic landforms where water is absent on the surface but is maintained in caves, avens and subterranean hydrologic systems (e.g., Veress et al. 2008, Kaufmann 2009).

Geologically, the Menabe is a monoclinal sedimentary formation dipping towards the Mozambique Channel. Most landforms found in the region date from wetter periods than the present, as shown by its surface lithology, with dissected sand cover, resulting mainly from the evolution of the hydrologic system in western Madagascar. The Menabe is situated within a dry region; perennial moisture exists only where groundwater is available. Examples of landforms that can capture and maintain soil moisture in an otherwise dry environment include various areas as the Makay sandstones in the lower portion of the Mangoky watershed and upper valleys of the Menabe, as well as other Menabe sandstones. The landforms of Makay quartz sandstones resemble karstic limestone formations found in some tropical areas; the lithology and both the tectonic and geomorphologic evolution have sculpted a relief with convex summits, steep lower slopes and faulted valleys. In the resulting deep gorges, evapotranspiration is reduced and underground water is maintained in their alluvial sand filled lower portions. This exemplifies the Eco-Geo-Clim model, which applies equally well in all of Madagascar's sedimentary basins.

BIOTIC FACTORS. The extent and persistence of riparian forests are linked to perennial water availability, and for some species, to the presence of adaptations to floods and/or the capacity to produce roots that can reach the water table (Naiman et al. 1993). Riparian forests are found in both dry and humid areas in Madagascar, but are most prominent in the driest environments, such as along the Mandrare and Onilahy rivers in southern Madagascar, where *Lemur catta* and *Propithecus verreauxi* occur in high densities. The mid- and lower portions of these large rivers are located in dry environments; in this region precipitation is low and unpredictable, while evapotranspiration is high (cf. Dewar and Richard 2007). Riparian forests are denser than the surrounding drier, more open formations because trees have access to water from a shallow phreatic zone, allowing higher levels of transpiration, and the production of greater biomass, including leaves, flowers and fruits. A forest cover can be maintained along the river course even when it is extremely narrow or in some places runs underground during certain season.

ASSUMPTIONS. Water availability is the only abiotic factor acting at the same spatial scale as the biotic factors invoked in the Eco-Geo-Clim model. As biotic factors respond to water availability, they act at the same spatial scale, although their spatial and temporal resilience is different (cf. Moritz and Agudo 2013). In Figure 1, the spatial and temporal availability of water is considered for forest ecosystems, along with the responses to these changes of two hypothetical forest taxa that differ in their tolerance to a drying environment; species Y (yellow) has low tolerance to dry conditions and is assumed to disappear with increasing drought; species R (red) can cope with aridification and can thus survive longer under increasingly dry environmental conditions. In a situation where the two species are in competition with one another, e.g., over food resources, species Y has a competitive advantage over species R. Figure 1 also refers to 'niche conservatism', defined as the retention by a species over time of ecological traits related to its niche (i.e., the set of biotic and abiotic conditions in which the species can persist (Wiens et al. 2010)). Such taxa could be illustrated by the Gray mouse lemur (*Microcebus murinus*), corresponding to the yellow species in Figure 1, and Madame Berthe's mouse lemur (*M. berthae*) as the red taxon, which is endemic to the Central Menabe. The underlying assumption in the model is that forest taxa that cannot persist under dry conditions would be confined to riparian forests during drier periods, while those that exhibit more plasticity with regard to aridification would be able to persist in drier forests.

ECO-GEO-CLIM: A MODEL THAT CONSIDERS ECOLOGICAL, GEOMORPHOLOGICAL AND CLIMATOLOGICAL FEATURES

Three scenarios of Quaternary paleoclimatic oscillation are presented to illustrate the mechanisms of the Eco-Geo-Clim model (Figure 1):

(I) A humid period during which precipitation is abundant (Figure 1, relief S1). The soils are humid, groundwater is abundant, rivers are flowing all the time, and forest cover is expanding.

(II) A humid to dry period during which precipitation decreases (Figure 1, reliefs S2, S3, S4). Rivers with headwaters at high altitude are able to capture moisture in the form of orographic precipitation. Soils on slopes and around springs are initially moist but as the climate dries and precipitation decreases, they become more dry and water flow in rivers decreases. Rivers and streams with headwaters at lower altitudes experience intermittent flow and can totally dry out, seasonally or even permanently. Some rivers with headwaters at higher altitudes will maintain flow in the middle portion of their courses, where the surface layers are humid and groundwater is still abundant, but forest will recede where water disappears.

(III) A dry to humid period during which precipitation increases (Figure 1, relief S5). The flow of rivers with headwaters at higher altitude increases, whereas those with lower altitude headwaters where groundwater is fed by precipitation will remain isolated from adjacent watersheds for extended periods of time.

CENTERS OF ENDEMISM

Using the mechanism summarized in Figure 1, the group of small watersheds and interfluves present between the lower portions of the Tsiribihina and Mangoky watersheds comprise a center of endemism (Wilmé et al. 2006) in which some species have become isolated and evolved in pockets of remaining vegetation found on residual landforms. Several geological formations found in the Central Menabe could have retained such pockets of vegetation, in particular limestone formations with subterranean water circulation, as found along the lower portion of the Kirindy River, or sandstone formations where deep canyons maintain a comparatively high amount of moisture in their lower portions (Waeber et al. In press).

The alternating wet and dry periods of the Pleistocene were variable in time and space, but regardless of their dura-

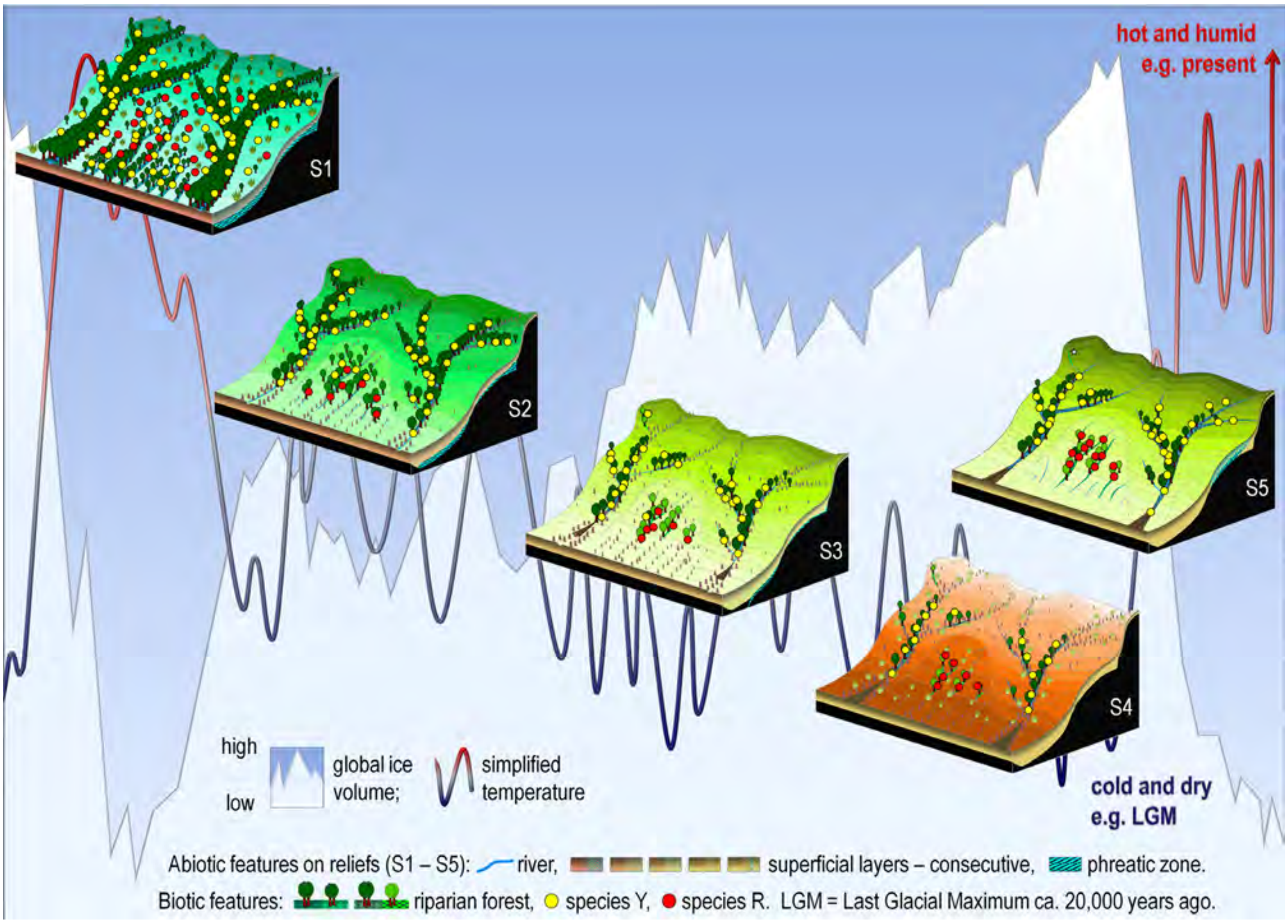


FIGURE 1. Evolution, during paleoclimatic oscillations, of abiotic factors, including surface layers, slope, phreatic zone, and rivers, and of biotic features, including riparian forest and two hypothetical forest species. (altitude not to scale).

S1: Situation during a humid phase: rainfall is abundant and river flow is high and continuous; the surface layers are moist and the phreatic zone is well fed; forest cover is expanding. Species Y (yellow) is abundant in riparian and other forest formations; species R (red) is more common in other (non-riparian) forests as a consequence of competition with Y in riparian forests. S2: Situation as the climate becomes drier: rainfall decreases, evaporation is higher, rivers with headwaters at lower altitudes dry up, and rivers with headwaters at higher altitudes are fed intermittently, at least along their mid-portions. The site-specific hydrologic balance decreases, surface layers dry up, and the water table drops. Slope instability increases as erosion becomes more widespread. Forests recede, disappearing from drier areas but persisting along rivers where the water table remains close to the surface. Species Y disappears from the driest areas but is able to survive in riparian forest where conditions remain suitable; species R survives in drier forests, but suffers from increased competition with species Y in riparian forest. S3: Situation as the climate dries further: river flow decreases and becomes sporadic; river courses become longer as sea level drops; slopes are more unstable with increased erosion and river sedimentation; an alluvial fan appears at the knick point. The site-specific hydrologic balance decreases further, surface layers become drier, and water table drops further. Forests recede even more. Species Y disappears from dry forests, reduced populations survive in riparian forest only along larger rivers with higher altitude headwaters; species R survives in the remaining pockets of dry forest. S4: Situation during the most arid phases: soil horizons are dry, the phreatic zone is discontinuous except below the mid-portion of rivers with high altitude watersheds and in isolated pockets within residual reliefs (e.g., karsts). Forests recede further, becoming limited to the riparian zone, which is drier along the small rivers. Species Y is restricted to riparian forest along rivers with high altitude headwaters, while species R is limited to watersheds with headwaters at low altitude, within the last remaining pockets with adequate moisture to maintain a forest cover. S5: Situation after a dry phase, when the climate becomes wet again: rainfall and river flow increase, surface layers become wet, the phreatic zone is once again fed. Some tributaries reconnect to the main rivers. Forests expand along these tributaries. Species Y disperses along the expanding riparian forest as tributaries aggregate to the re-establishing river system; species R is a narrow-ranged taxum endemic to the Central Menabe.

tion and extent, similar causes (i.e., a climatic oscillation) are likely to have had similar effects on the abiotic and biotic features considered in our model, allowing some forest taxa, as the climate became more humid, to expand and disperse along tributaries in systems with high altitude watersheds, while populations in isolated forest fragments may have diverged, leading to speciation, in watersheds whose headwaters are at low altitude. Although a single climatic oscillation may only bring about speciation in a limited number of groups, it could lead to the loss of one or more local populations, as in lemurs and birds, or even to extinction of species, as documented in the recent subfossil record (e.g., Burney et al. 2004), whereas other species may have experienced contraction of their range, as in *Hypogeomys antimena* (Crowley 2010).

CONCLUSION

During the Pleistocene, riparian forests in Madagascar acted during dry periods as refugia for forest-dwelling fauna and flora, and functioned as dispersion corridors during wetter periods, allowing species to extend their ranges along tributaries when orographic rainfall was sufficient for runoff to reach low-lying areas. The Eco-Geo-Clim model holds that the main factors involved in the maintenance of forests species include the availability and accessibility of water. During drier periods, forest species occurring in centers of endemism survived in refugia, typically found among residual reliefs where water storage capacity was higher. Given the hydrologic balance of the rivers flowing through these centers of endemism, riparian forests, and their capacity to act as dispersal corridors, were limited compared to those encountered in watershed with headwaters at high altitude.

The Eco-Geo-Clim model suggests that any geosystem able to store water and make it available to trees can be regarded as a potentially key element for the survival of forest taxa in Madagascar, and any place where this process operated during the driest phases of past climatic oscillations may have served as a refuge for forest taxa. The local topography, the superficial formations and the biota – each with its own velocity and resilience – are the end products of the impacts that Quaternary climate and its changes have had on the evolution of landscapes. The endemism generated in this manner can thus be regarded as resulting from the transformation of a landscape in time in conjunction with climatic change.

The model proposed here may be helpful to understand and explain how local endemism in Madagascar has been shaped and driven by paleoclimatic oscillation, although it provides little insight regarding the possible future of the island's endemic biodiversity in the face of current anthropogenic climatic change. The Eco-Geo-Clim model does, however, reveal one certainty: any site with a positive hydrologic balance, including those where riparian forests occur, must be taken into consideration for ensuring that Madagascar's unique biodiversity will be protected in the changing climate of the coming centuries.

ACKNOWLEDGEMENTS

We wish to acknowledge three anonymous reviewers for their constructive comments, which greatly improved this contribution, as well as Pete Lowry for his invaluable corrections on a previous version of the manuscript.

REFERENCES

Assi-Kaudjhis, C., Digbehi, B. Z., Roche, E. & Lezine, A.-M. 2010. Synthèse sur l'évolution des paléoenvironnements de l'Afrique occidentale atlantique depuis la fin de la dernière période glaciaire. Influences climatiques et anthropiques. Geo-Eco-Trop 34: 1–28.

Baron, R. 1890. The flora of Madagascar. Journal of the Linnean Society, Botany 25: 246–294.

Blois, J. L., Zarnetske, P. L., Fitzpatrick, M. C. and Finnegan, S. 2013. Climate change and the past, present, and future of biotic interactions. Science 341: 499–504. (doi:10.1126/science.1237184)

Burney, D. A., Pigott Burney, L., Godfrey, L. R., Jungers, W. L., Goodman, S. M., Wright, H. T. and Jull, A. J. T. 2004. A chronology for late prehistoric Madagascar. Journal of Human Evolution 47: 25–63. (doi:10.1016/j.jhevol.2004.05.005)

Church, J. A. and Gregory, J. M. 2001. Sea level change. In: Encyclopedia of Ocean Sciences. J. H. Steele, S. A. Thorpe and K. K. Turekian (eds.), pp 2599–2604. Elsevier Science Ltd. (doi:10.1006/rwos.2001.0268)

Cornet, A. 1974. Essai de cartographie bioclimatique à Madagascar. Notice explicative N° 55. ORSTOM, Paris.

Crowley, B. E. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. Quaternary Science Reviews 29: 2591–2603. (doi:10.1016/j.quascirev.2010.06.030)

Dewar, R. E. and Richard, A. F. 2007. Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences of the United States of America 104, 34: 13723–13727. (doi:10.1073/pnas.0704346104)

Donque, G. 1975. Contribution à l'Étude du Climat de Madagascar. Nouvelle Imprimerie des Arts Graphiques, Tananarive.

Dorman, M., Svoray, T., Perevolotsky, A. and Sarris, D. 2013a. Forest performance during two consecutive drought periods: diverging long-term trends and short-term responses along a climatic gradient. Forest Ecology and Management 310: 1–9. (doi:10.1016/j.foreco.2013.08.009)

Dorman, M., Svoray, T. and Perevolotsky, A. 2013b. Homogenization in forest performance across an environmental gradient – The interplay between rainfall and topographic aspect. Forest Ecology and Management 310: 256–266. (doi:10.1016/j.foreco.2013.08.026)

Elderfield, H., Ferretti, P., Greaves, M., Crowhurst, S., McCave, I. N., Hodell, D. and Piotrowski, A. M. 2012 2012. Evolution of ocean temperature and ice volume through the Mid-Pleistocene climate transition. Science 337: 704–709. (doi:10.1126/science.1221294)

Gasse, F. and Van Campo, E. 2001. Late Quaternary environmental changes from a pollen and diatom record in the southern tropics (Lake Tritrivakely, Madagascar). Palaeogeography, Palaeoclimatology, Palaeoecology 167: 287–308. (doi:10.1016/S0031-0182(00)00242-X)

Goodman, S. M. and Benstead, J. P. 2005. Updated estimates of biotic diversity and endemism for Madagascar. Oryx 39(1): 73–77. (doi:10.1017/S0030605305000128)

Hays, J. D., Imbrie, J. and Shackleton, N. J. 1976. Variations in the Earth's orbit: Pacemaker of the ice ages. Science 194: 1121–1132. (doi:10.1126/science.194.4270.1121)

Humbert, H. & Cours Darne, G. 1965. Carte Internationale du Tapis Végétal et des Conditions Écologiques à 1/1.000.000. Notice de la Carte de Madagascar. Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry Hors série 6, 165 pp.

Jansson, R. and Dynesius, M. 2002. The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. Annual Review of Ecology and Systematics 33: 741–777. (doi:10.1146/annurev.ecolsys.33.010802.150520)

Kaufmann, G. 2009. Modelling karst geomorphology on different time scales. Geomorphology 106: 62–77. (doi:10.1016/j.geomorph.2008.09.016)

Langrand, O. and Wilmé, L. 1997. Effects of forest fragmentation on extinction patterns of the endemic avifauna on the Central High Plateau of Madagascar. In: Natural Change and Human Impact in Madagascar. S. M. Goodman & B. D. Patterson (eds.), pp 280–305. Smithsonian Institution Press, Washington, D. C.

Leigh Mascarelli, A. 2009. Quaternary geologists win timescale vote. Nature 459: 624. (doi:10.1038/459624a)

Lourenço, W. R. (ed.) 1996. Biogéographie de Madagascar. Biogeography of Madagascar. Éditions de l'ORSTOM, Paris. 589 pp.

Milne, G. A., Gehrels, W. R., Hughes, C. W. and Tamisiea, M. E. 2009. Identifying the causes of sea-level change. Nature Geoscience 2: 471–478. (doi:10.1038/ngeo544)

Moat, J. and Smith, P. 2007. Atlas of the Vegetation of Madagascar. Kew Publishing, Royal Botanic Gardens, Kew.

Moritz, C. and Agudo, R. 2013 The future of species under climate change: Resilience or decline? Science 341: 504–508. (doi:10.1126/science.1237190)

Naiman, R. J., Decamps, H. and Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3, 2: 209–212.

Perrier de la Bâthie, H. 1921. La végétation malgache. Annales du Musée Colonial de Marseille série 3, 9: 1–273+i–vi.

Rabosky, D. L., Slater, G. J. and Alfaro, M. E. 2012. Clade age and species richness are decoupled across the Eukaryotic tree of life. PLoS Biol 10(8): e1001381. (doi:10.1371/journal.pbio.1001381r)

Rahmstorf, S. 2009. Rapid climate change. In: Encyclopedia of Ocean Sciences (Second Edition). J. H. Steele, S. A. Thorpe and K. K. Turekian (eds.), pp. 1–6. Elsevier Science Ltd. (doi:10.1016/B978-012374473-9.00710-4)

Veress, M., Lóczy, D., Zentai, Z., Tóth, G. and Schläffer, R. 2008. The origin of the Bemaraha tsingy (Madagascar). International Journal of Speleology 37, 2: 131–142. (doi:10.5038/1827-806X.37.2.6)

Virah-Sawmy, M., Willis, K. J. and Gillson, L. 2009. Threshold response of Madagascar's littoral forest to sea-level rise. Global Ecology and Biogeography 18, 1: 98–110. (doi:10.1111/j.1466-8238.2008.00429.x)

Waeber, P. O., Wilmé, L., Ramamonjisoa, B., Garcia, C., Rakotomalala, D., Rabemananjara, Z. H., Kull, C., Ganzhorn, J. U. and Sorg, J.-P. 2013 (In press). Dry Forests in Madagascar, neglected and under pressure. International Forestry Review.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13, 10: 1310–1324. (doi:10.1111/j.1461-0248.2010.01515.x)

Wilmé, L., Goodman, S. M. and Ganzhorn, J. U. 2006. Biogeographic evolution of Madagascar's micro-endemic biota. Science 312: 1063–1065. (doi:10.1126/science.1122806)

Wilmé, L., Ravokatra, M., Dolch, R., Schuurman, D., Mathieu, E., Schuetz, H. and Waeber, P. O. 2012. Toponyms for centers of endemism. Madagascar Conservation & Development 7, 1: 30–40. (doi:10.4314/mcd.v7i1.6)

SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

FIGURES S1 to S6. Evolution, during paleoclimatic oscillations, of abiotic factors, including surface layers, slope, water table, and rivers, and of biotic features, including riparian forest and two hypothetical forest species.

TABLE S1. Glossary.