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Source: Journal of East African Natural History, 87(1) : 85-89

Published By: Nature Kenya/East African Natural History Society

URL: https://doi.org/10.2982/0012-8317(1998)87[85:VCASAR]2.0.CO;2

Journal of East African Natural History **87**: 85–89 (1998)

VEGETATION, CLIMATE AND SOIL: ALTITUDINAL RELATIONSHIPS ON THE EAST USAMBARA MOUNTAINS, TANZANIA

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ABSTRACT

The floristic composition of forest on the East Usambara Mountains, Tanzania, changes steadily with increasing altitude. Conveniently, two altitudinal zones (lowland, submontane) can be recognised; the altitude between them lying at about 850 m, which is 550 m lower than the equivalent zonal boundary in central Africa. This depression is probably related to lower daytime temperatures, which are 4–5°C lower than in central Africa—attributed to the presence of persistent low-lying cloud at higher altitudes. There is a marked change in topsoil at about 850 m, with a sharp fall in pH and the presence of a thick mor-humus layer at higher altitudes. The vegetation/climate/soil system is dynamic. There is evidence of upward movement of vegetation zones and a warmer and less misty climate over the last 25 years. The mor-humus layer is lost in tree-fall clearings and under the invasive tree *Maesopsis eminii*; in the latter case (at least) topsoil pH acidity is over a pH point higher. This is a good site for further investigations of climatic, vegetation and soil changes. Forest persistence during the last ice age (assumed from the large number of endemic species) was probably facilitated by an even mistier (though probably otherwise drier) climate.

INTRODUCTION

The purpose of this contribution is to draw attention to some previously published (Hamilton & Bensted-Smith, 1989), interesting but widely overlooked findings relating to altitudinal changes in vegetation, climate and soils on the East Usambara Mountains, Tanzania. These mountains lie about 4.5° south of the equator and, at their nearest point, are only 40 km distant from the Indian Ocean. They rise abruptly from lowlands, at 150–300 m, to level off from escarpments on a dissected plateau at 900–1,050 m. There are a number of isolated marginal rocky peaks, the highest being Nilo (1,506 m).

VEGETATION AND ALTITUDE

The natural vegetation is forest. Floristic changes in more mature patches of forest were investigated along three transects spanning (altogether) the altitudinal range 290–1,220 m. Analysis of results shows that the main axis of variation in floristic composition is highly correlated with altitude. Floristic variation with altitude is continuous, without any abrupt changes. Forest changes in a similar way with altitude on other mountains in eastern Tanzania (Lovett, 1996).

Despite this altitudinal continuity, it is useful to recognise forest types for the purposes of description and comparison. Two main types can conveniently be recognised, the boundary between them lying at about 850 m. The lower altitude type (lowland forest) is semi-deciduous, with species of the families Moraceae, Sapotaceae and Ulmaceae being abundant. The higher altitude type (submontane forest) is evergreen and contains *Drypetes gerrardii, Parinari excelsa* and *Strombosia scheffleri*, among others. These two forest types have clear floristic equivalents in central Africa, but there the boundary between them is at higher altitude—1,400 m in the case of Uganda (Hamilton, 1984).

Isolated rocky summits on the East Usambaras carry a number of trees and shrubs typical of montane forest and ericaceous vegetation. The actual species present on any particular summit is apparently random, and would be an interesting field of investigation for further research. Species include *Agauria salicifolia* (on Mount Mtai), *Podocarpus latifolius* (on Mount Mlinga), *Rapanea melanophloeos* (on Mtai and Lutindi summit) and two species of shrubby Ericaceae (on Lutindi). Altitudes are: Mtai 1,060 m, Mlinga 1,069 m and Lutindi about 1,200 m. These altitudes are much lower than is typical for these taxa in central Africa, a depression in vegetational zonation as also shown by the altitude of the lowland/submontane forest boundary.

CLIMATE AND ALTITUDE

There are a number of meteorological stations on and near the East Usambara Mountains. Comparison of data for these with data for stations in other parts of Tanzania (Moffett, 1958; TWMP, 1976) shows that the climate at high altitude on the East Usambara Mountains is anomalous. In particular, mean maximum (*i.e.* daytime) temperatures are depressed by about 4–5 °C and mean temperatures (calculated as the average of mean maximum and minimum temperatures) by about 2–3 °C, compared with expectations based on normal temperature/altitude relationships in Tanzania as a whole. However, mean minimum (*i.e.* night-time) temperatures are essentially normal. It should be noted that these depressions in temperature are quite apart from a general lowering in maximum and mean temperatures associated with proximity to the sea (as shown, for example, by measurements from the low altitude station of Mlingano, which lies between the mountains and the coast).

Depression of the lowland/submontane forest boundary on the East Usambaras by about 550 m (compared to central Africa) is equivalent to depression in mean temperature by about 3.3 °C (given a lapse rate of temperature with altitude of 6 °C per 1000 m, as is typical for central Africa). It seems reasonable to postulate that reduced daytime temperatures are a major cause of depression of vegetational zones on the East Usambaras.

In turn, depression of day-temperatures on the upper slopes of the East Usambaras can almost certainly be attributed to persistent low cloud hanging around the upper slopes, as can often be observed especially during rainy seasons (such cloud was probably even commoner before about 1970—see later).

Unfortunately there is a shortage of temperature data from intermediate altitudes on the East Usambaras (between 210 and 910 m). However, it is predicted that mean maximum (and hence mean) temperatures do not change regularly with altitude, but rather at first fall steadily at the normal lapse rate and then drop abruptly from the level where the lower limit of the cloud deck frequently stands. This prediction could be tested by measuring soil temperatures at depth (these should approximate to annual means).

SOILS AND ALTITUDE

Topsoil samples (0–10 cm, below the litter) were collected at the sites of the plots used to study altitudinal change in floristic composition of the forests. These show a remarkable drop in acidity (water-based measurements) from about pH 6.5 at 850 m to below pH 5.0 at 900 m and then to about pH 4 at 1,050 m. In contrast, pH declines only gradually over the wide altitudinal range of 300 m (pH about 7) to 850 (pH 6.5). An obvious visual change in soils with altitude (but not revealed by the standard organic-matter measurements made in the laboratory) is that those at higher altitudes typically have a thick (up to about 10 cm) upper layer of mor-type humus underneath the litter. This is absent from lowland forest soils.

Examination of full soil profiles extending to depths of about 120 cm was made at three sites in lowland forest (altitudes 210–260 m) and three sites in submontane forest (920–980 m). Analysis of samples from these profiles showed that lowland soils tend to be more neutral at all depths (often about pH 6.0) than submontane soils (often about pH 4.5, but even more acidic in their uppermost layers).

Studies of the soils of the East Usambara plateau (Milne, 1937) made important historical contributions to development of the general theory that tropical forest soils are highly leached and inherently infertile. Milne (1937) postulated that the soils of the escarpment are less weathered because they are more subject to rejuvenation by material originating from exposed rock faces. However, this explanation is not supported by new observations and data: there are no obvious relationships between soil pH and occurrence of nearby rock outcrops and there is no overall correlation between soil acidity and angle of slope. In any case, slopes on the highly dissected plateau are just as steep as on the escarpment. Bedrock is similar at all altitudes.

It seems reasonable to postulate that the greater acidity of the submontane soils is due to the direct or indirect (through variations in litter quality) effects of the wetter climate. Soil data thus suggest that the base of the cloud deck typically stands at about 850 m (or, even more so, stood in the recent past).

A DYNAMIC SYSTEM

It is therefore suggested that there are causal relationships between the common occurrence of cloud above 850 m, and the presence of acidic soils and submontane forest. These relationships are likely to be complex and also not static.

A mor-humus layer is not universally present in soils above 850 m. In particular, it is absent from tree-fall gaps (which have changed microclimate and litter dynamics) and also from soils below forest rich in the invasive tree *Maesopsis eminii*. In feeding experiments, leaves of *Maesopsis* proved to be more palatable to diplopods (major litter feeders in these forests) than those of *Allanblackia stuhlmannii* (Macfadyen, 1989). The latter was chosen as a representative submontane forest species for the purposes of these experiments; unlike the relatively thin leaves of *Maesopsis*, the leaves of *Allanblackia* are thick and coriaceous, like those of many other submontane forest tree species in these forests. Topsoil samples under *Maesopsis*-rich forest are also typically over 1 pH point less acidic than those of neighbouring soils under mature submontane forest lacking *Maesopsis*. Thus, the nature of the litter is certainly a major factor influencing the acidity and organic matter characteristics of the topsoil.

There is evidence that both climate and vegetation on the East Usambaras are changing. Despite some problems with inaccurate readings, there is some evidence from meteorological data that rainfall has become less reliable since about 1960 not only on the East Usambara Mountains, but more widely in the whole East Usambara region (lowlands and highlands). Compared with earlier years, there have been an exceptional number of dry years interspersed with occasional very wet years. Long-term residents of the East Usambaras report that, since about 1970–1975, temperatures at higher altitudes have felt warmer, rainfall has become less predictable with rainfall events more concentrated in torrential episodes, and there has been less mist. Reports of biological changes include the up-slope movements of some crops (coconuts, citrus fruits, mangoes) and malaria, and decreased luxuriance of forest epiphytes. There is evidence for an increased incidence in tree-falls during the last 25 years at the one site at which change in the rate of tree-falls with time has been investigated (Binggeli, 1989). There is also a total failure of the canopy species *Ocotea usambarensis* to regenerate. This tree occurs only as large specimens on ridges at high altitudes on the East Usambaras, where it may well be at its lowermost altitudinal limit judging by its distribution elsewhere in East Africa. This is a species which could be on the margins of its climatic tolerance on the East Usambaras and hence particularly susceptible to climatic change.

The underlying causes of these climatic and vegetational changes could well be at least partly due to human activities, reducing forest and tree cover on and around the mountains. Possibly, greenhouse climatic change could also play a role, but it does not seem necessary to invoke this to explain the observed phenomena. The East Usambaras provide an excellent site at which to study recent (and on-going) climatic changes further, and the effects of these changes on biological systems. For example, it would be interesting to study whether there is an upslope movement of species within the forest; this might be established from a comparison of floristic composition in tree fall gaps of different ages (older gaps can often be mapped quite accurately in these forests, using methods developed by Binggeli, 1989).

Judging by the large number of endemic species on the East Usambara Mountains, it is very likely that forest has persisted on or very close to the mountains for a long time. The mountains must have been a Pleistocene refuge. How did forest survive here under the drier climate that seems to have characterised all of East Africa during the last ice age (Hamilton, 1982)? Judging by pollen and glacial evidence, temperatures were perhaps 6°C lower than now in East Africa; however, evidence from sediment cores from the Indian Ocean suggest that surface temperatures of the sea may not have been depressed to an equivalent extent. Even though direct rainfall on the East Usambaras was probably reduced, climatic conditions would appear to have been even more favourable for the formation of fog on the mountains than now, with a relatively warm ocean abutting a relatively cold hinterland. Thus, forest may well have been maintained largely by occult precipitation. Trees typical of submontane forest would have occurred at even lower altitudes than they do today. These predictions will be difficult or impossible to test directly, because of an apparent absence of suitable fossil sites.

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