Refuge theory and distribution patterns of land snails in Ugandan rain forests

Torsten Wronski[1] and Bernhard Hausdorf[1*]

[1]*Zoological Museum, University of Hamburg*

***Correspondence: Bernhard Hausdorf, Zoological Museum, University Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany. E-mail: hausdorf@zoologie.uni-hamburg.de**

INTRODUCTION

Refuge theory assumes that the recent distribution of organisms is influenced by past, usually Pleistocene, environmental changes resulting in the contraction of ranges into refugia or the expansion of ranges from refugia. Refugia are areas that are less affected by environmental changes than the surrounding regions so that organisms that become extinct elsewhere can survive there. The existence and importance of Pleistocene refugia in the northern continents that were heavily affected by Pleistocene glaciations is universally accepted. However, the existence and role of refugia in the tropics is still controversial.

Often the existence of refugia is inferred only from the recent distribution of species richness. However, several other patterns in the distribution of organisms are expected to originate, if retraction to refugia and expansion from refugia are processes that affect recent biogeography. Such patterns are nestedness of ranges (Hultén, 1937; Daubenmire, 1975; Hausdorf & Hennig, 2003a), clustering of ranges (***; Hausdorf & Hennig, 2004), and Rapoport effects (***; Pfenninger, 2004; Hausdorf, 2006).

It is a long standing question whether the recent distribution of organisms can be explained by current ecological conditions alone or whether it shows the imprint of historical events (Endler, 1982a,b; ***).

It has been assumed that the Pleistocene climatic cycles have resulted in cycles of retraction of ranges of organisms to refuges and expansions (***).

Such hypotheses have been tested mainly for temperate regions.

A retraction of biota into refugia and subsequent range expansions from such refugia will result is specific patterns in distribution data. Such processes should result in:

1. A decrease of species richness with increasing distance from the refuge;
2. Nestedness; that is the biota in regions more distant from the refuge will be subsets of the biota more closer to the refuge;
3. A Rapoport effect; that is the average range extension of the species belonging to a regional biota will increase with increasing distance from the refuge;
4. Clustering of ranges (biotic elements)

MATERIAL & METHODS

Study area and sampling

We sampled 60 plots, each 20 m x 20 m in 11 forests within protected areas along the Albertine Rift Valley and in the forest belt around Lake Victoria in western Uganda (Fig 1). Most plots were in primary forest that had no more than limited selective cutting. Sampling was carried out in March and April 2006 during the rainy season when snails and slugs are most active. At each station we collected all living slugs and snails as well as their empty shells for two hours. Additionally we sampled about 5l of surface leaf litter and soil from each plot into plastic bags. The litter samples were dried, fractioned by sieving and sorted. More details about the sampling stations and lists of the sampled species will be published elsewhere (Wronski & Hausdorf, in prep.).

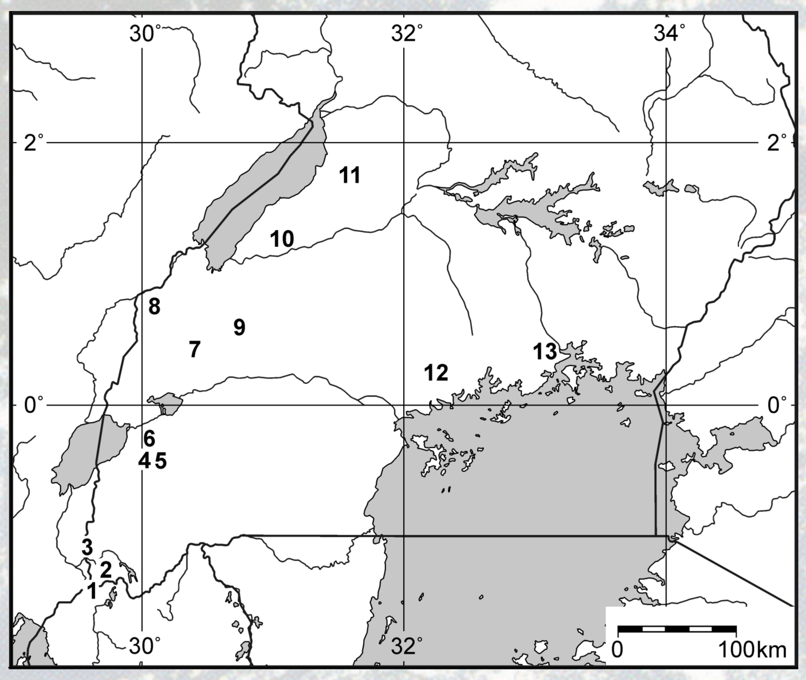

Figure 1 Map of Uganda showing location of the 13 forests studied: 1, Mgahinga; 2, Echuya, 3, Bwindi, 4, Kalinzu; 5, Kasyoha-Kitomi; 6, Maramagambo; 7, Kibale; 8, Semliki; 9, Matiri; 10, Bugoma; 11, Budongo, 12, Mpanga; 13, Mabira.

RESULTS & DISCUSSION

Gymnarion alloysii-sabaudiae (Pollonera, 1906), Urocyclidae, Pulmonata, Kibale Forest National Park

Oreohomorus nov. spec., Subulinidae, Pulmonata endemic to Matiri Central Forest Reserve

1. Relation between species richness and environmental parameters

Bivariate analyses revealed that the relative species richness (calculated using rarefaction) of Ugandan forests for land snails significantly increases with annual rainfall and altitude and decreases with evaporation and distance from the supposed East-Congolian refugia (Table 1). Moreover, there was an only marginally non-significant negative correlation with temperature and soil pH. However, only rainfall was included in the model in a stepwise multiple regression.

Table 1 Bivariate relationships between relative land snail species richness and abiotic variables of forests. *N* = 13 for all analyses

	r	*p*
mean annual rainfall (mm)	0.694	0.008
mean annual maximum temperature (°C)	-0.539	0.057
mean annual evaporation (mm)	-0.571	0.041
mean altitude (m)	0.598	0.031
acidity (pH)	-0.491	0.088
area (km²)[a]	0.141	0.645
distance from refugia (km)[a]	-0.563	0.045

[a]log_{10}-transformed

2. Tests for nestedness of distribution areas

There are 4495 cases in which a range of an Ugandan land snail species is a subset of the range of an other species. The observed number of supersets is significantly lower than those obtained in 1000 Monte Carlo simulations (2978-4899 supersets were observed, mean 3945.97). Thus, the test indicates that the ranges of the Ugandan land snail species are significantly nested (p = 0.031). The centre of the sets of nested subsets is in the Virunga mountains in the southwest of the study area, close to the putative East-Congolian refugia (Fig. 2). Nestedness remains significant, if the montane elements are omitted (p = 0.039; there are 2234 supersets in the real data, whereas 1357-2482 have been counted in 1000 Monte Carlo simulations, mean 1884.90).

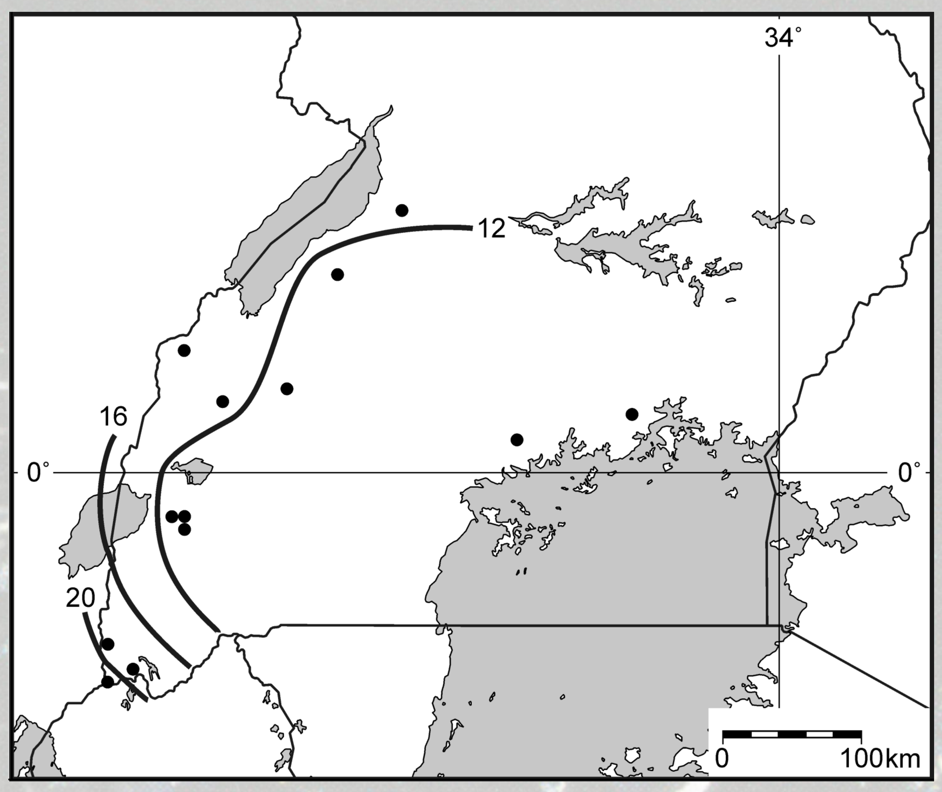

Figure 2 Distribution of sets of nested subsets in the land snail fauna of Uganda (sampling locations indicated by dots) as visualized by isolines of the index of nestedness n_j (the average number of supersets of ranges of species present in cell j; see text). n_j increases towards the geographic centre of sets of nested subsets in Congo.

3. Tests for nestedness of distribution areas

The cases in which the occurrences of a species in the 13 forests form a subset of the occurrences of an other species, i. e., the number of supersets, is used as test statistic following Hausdorf & Hennig (2003a). For n species all nx(n-1)/2 pairs are screened for supersets. If two ranges are identical, this is not counted as if one species range were a superset of the other. The distribution of the test statistic under the null hypothesis is approximated by a Monte Carlo simulation depending on some parameters estimated from the data. The null model should simulate the case in which all inhomogeneities of the data can be attributed to varying range sizes, to varying numbers of taxa per geographic unit and to the spatial autocorrelation of the occurrences of a taxon. We used a null model in which the all ranges are generated independently according to the same probabilistic routine. This routine yields ranges in such a way that their cell number distribution approximates the actual distribution of the number of cells per range, the richness distribution of the cells approximates the actual richness distribution of the cells, and the tendency to form disjunct areas is governed by a parameter which is estimated from the real data set. Computational details have been described elsewhere (Hausdorf & Hennig, 2003a; Hennig & Hausdorf, 2004). We used the index of nestedness (Hausdorf & Hennig, 2003a) to visualize the spatial distribution of the sets of nested subsets. The index of nestedness (n_j) is defined as the average of the p_i values of all species present in sample j, where p_i is the number of supersets, i.e., the cases in which the occurrences of a species i form a subset of the occurrences of an other species. Identical ranges are not counted as sub- or supersets of each other. The index of nestedness increases towards the geographic centres of the sets of nested subsets.

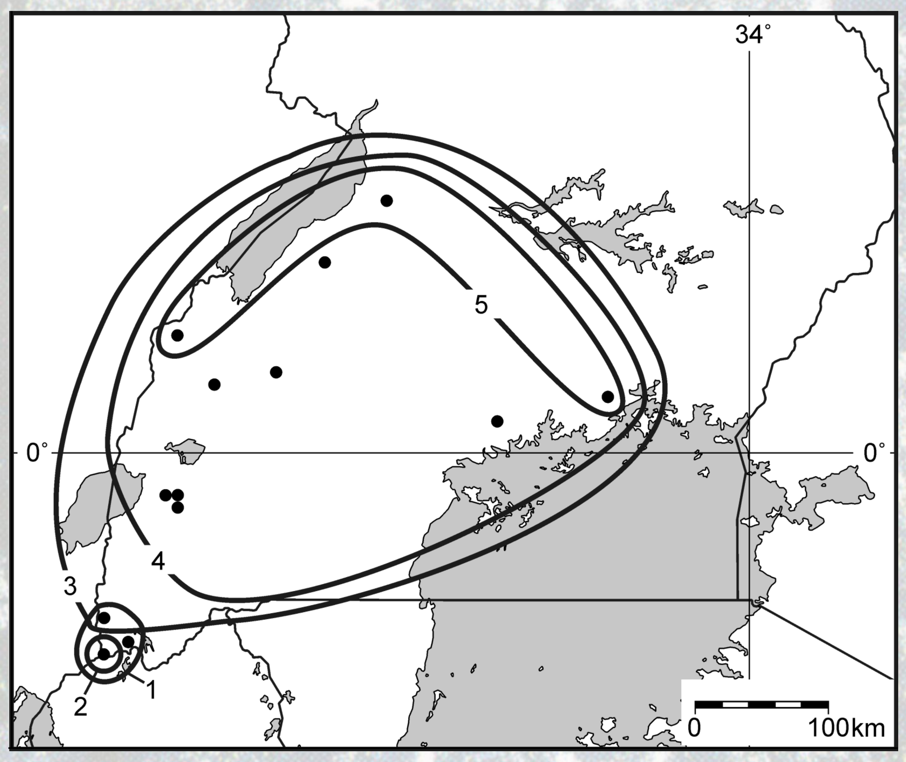

Figure 4 Distribution of biotic elements (1-2: montane elements; 3-4: lowland elements; 5 = northern element) of land snails in Uganda. The lines indicate the areas where more than 30% of the species of an element are present.

4. Tests for Rapoport effects

Mean range extension of land snail species increases with increasing distance from the putative East-Congolian refugia (Fig. ***a). There is also a significant positive correlation between range extension of land snail species in the direction away from the putative East-Congolian refugia and the midpoint of the ranges in the study area in western Uganda (Fig. ***b; Spearman´s rank correlation coefficient r_S = 0.803, two-sided, p = 0.000).

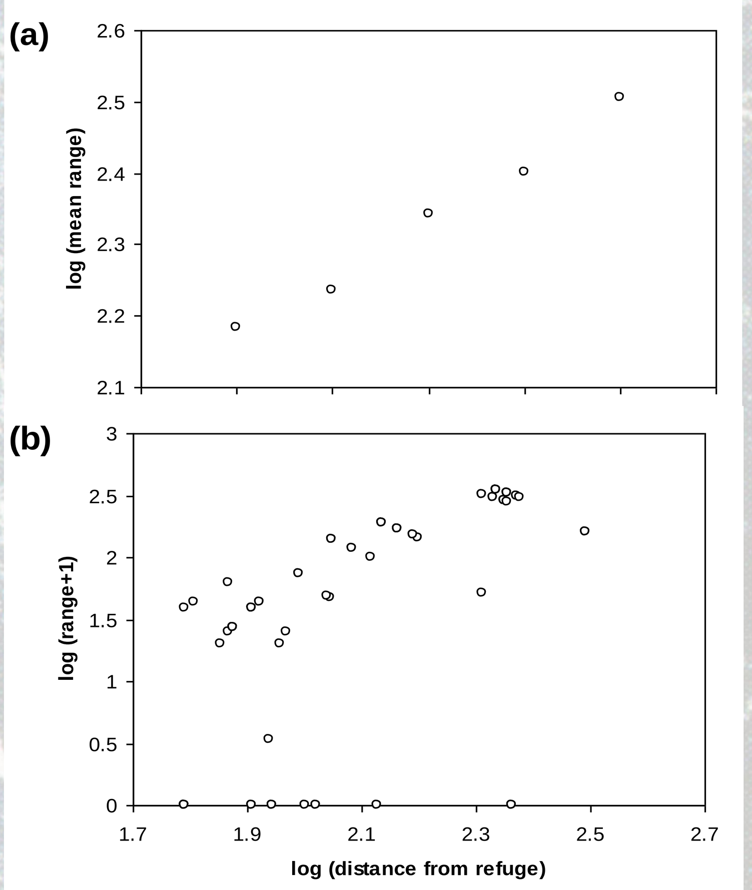

Figure 3 Rapoport effects with increasing distance from the supposed East-Congolian refuge. (a) Mean range extension of land snail species in zones in the direction away from the refuge, (b) correlation between range extension of land snail species in the direction away from the refuge and the midpoint of the ranges in the study area in western Uganda.

ACKNOWLEDGEMENTS

We would like to thank Paul Barugahare, the research assistant of the project, as well as Ann Apio, for rendering considerable support to our field work. We are further greatful to the Uganda Wildlife Authority, the National Forest Authority of Uganda and the Uganda Council for Science and Technology for permitting this research to be carried out. We further thank the German Research Council for financial support to this project.