



Land-snail faunas of afro-montane forests of Mount Kenya, Kenya: ecology, diversity and distribution patterns

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Abstract

Aims To (1) describe the distribution patterns of land-snails occurring in afro-montane forest habitats on Mount Kenya, in relation to elevation and aspect; (2) explore the relations between the land-snail faunas and environmental conditions within the forests.

Location Mount Kenya, Kenya.

Methods Molluscs were sampled using standardized direct search and litter sieving methods in a total of sixty-four replicated plots along four elevational transects spanning an altitudinal range from 1782 to 2851 m on the east, west, south and north-northwest sides of Mount Kenya. Elevation, vegetation type, forest structure, soil calcium, soil pH, mean annual rainfall and other environmental variables were measured on each plot. Correlation and joint regression analysis, and canonical correspondence analysis (CCA) were used to relate snail diversity and abundance, and faunal composition, to site elevation and other environmental variables.

Results Sixty-eight mollusc species were recorded during the study with transect totals between thirty-four and fifty-three species. Mean number of species and mean snail abundance ranged from 6.75 to 23.0 and 19 to 348 per plot, respectively. Overall, species richness and Shannon diversity index declined with increasing elevation. Snail abundance declined with increasing altitude along three transects and was positively related to soil pH and soil calcium, but species richness was not. Several species exhibited clear altitudinal distribution patterns. Mean annual rainfall varies greatly around the mountain and tends to decrease with altitude over the elevational range studied. Soil calcium and pH were negatively related to annual rainfall. Estimated mean annual rainfall accounted for the greatest variation in the mollusc fauna around the mountain. Faunas in forests on the drier, western side of Mount Kenya contained higher numbers of species in families that are characteristic of temperate latitudes, whereas tropical families were more prevalent on the wetter, south and east sides.

Main conclusions Land-snail diversity in Mount Kenya's forests declines with elevation and thus follows the widespread pattern shown by most groups of organism. However, faunal variation appears to be more closely related to rainfall levels, than to altitude *per se* or the other environmental variables examined. The effects of rainfall on snails could either be direct, or indirect via its effects on soils or vegetation, but the study suggests that direct effects are more important. Indirect effects mediated by changes in soil chemistry appear to be less important because lower altitude sites with more strongly leached and acidic soils tend to have richer and more abundant snail faunas. The reason for the association of temperate latitude mollusc families with forests on the drier, western sides of the mountain is not clear. The number of mollusc species present in

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Mount Kenya's forests is broadly comparable with that reported elsewhere in East African forests. However, overall, the data from this study and elsewhere in East Africa may provide tentative evidence for a maximum level of land-snail richness at intermediate elevations of about 1000–1500 m.

Keywords

Land-snails, Mount Kenya, afro-montane forest, biodiversity, national park, altitudinal variation, biodiversity, Kenya, rainfall patterns, molluscs.

INTRODUCTION

The land-snails of Mount Kenya have been reasonably well documented (Verdcourt, 1983; Warui, 1998; Warui *et al.*, 2001) compared with those of the other high East African mountains. However, the systematic position of many species is still uncertain, and this means that there are significant problems associated in dealing with the fauna for ecological studies. A recent review and checklist of the land-snail fauna of Mount Kenya (Warui *et al.*, 2001), based on published records, museum material and information obtained during the study reported in this paper, has shown that at least 100 terrestrial species are present. These include at least seven that are probably endemic to Mount Kenya or nearby ranges, and several others that may be currently undescribed. A small number of species appear to be restricted to higher altitude heathland and alpine plant communities, but the majority of the fauna is found in the montane forest belt. Germain (1931) reviewed Mount Kenya's mollusc fauna using published information, and was able to identify species associated with high and low altitudes. However, the detailed patterns of species distribution, and the nature of faunal variation in relation to altitude or other factors, have not been examined.

Vegetation on high African mountains is strongly zoned in relation to altitude (Hedberg, 1951; Boughey, 1955a; Langdale-Brown *et al.*, 1964; Chapman & White, 1970; Hamilton, 1974). In general, three broad belts of montane vegetation (the montane forest, ericaceous and alpine belts) can be recognized (Hedberg, 1951; Chapman & White, 1970; Hamilton, 1974) although the definition, delineation and nomenclature of the variation has been the subject of debate (Hedberg, 1951; Hamilton & Perrott, 1981). Some studies have suggested that there is zonation within the forest belt (e.g. Boughey, 1955b; based on work on Mount Cameroon), whereas others have indicated that vegetation changes more gradually along an altitudinal continuum (Hamilton, 1975; Lovett, 1996). Lovett *et al.* (2001) have demonstrated that many endemic tree species in the Eastern Arc mountains, Tanzania have narrow elevational ranges.

This paper presents an analysis of the patterns of geographical variation in the land-snail fauna in Mount Kenya forests, and its relationship with altitude and a range of other abiotic parameters. The height and conical shape of the mountain make it particularly useful for studying the contrasting effects of aspect (and thus climate) and altitude.

As far as we are aware, it is the first detailed examination of the ecological and geographical patterns in a mollusc fauna on an African mountain, and their relationship with environmental factors.

MOUNT KENYA

Mount Kenya is the second highest mountain in Africa (5199 m) and forms an isolated conical massif with a basal diameter of about 120 km in central Kenya (Fig. 1), about 180 km north of Nairobi on the east side of the African Rift Valley just south of the equator. It was formed by volcanic activity in the Tertiary and Quaternary, mainly between 2.6 and 3.1 Myr BP although there have been more recent eruptions on the eastern side of the mountain until about 1 Myr BP (Bussman, 1994). A belt of forest encircles the mountain (except for a gap on the north side) in a band which currently extends from about 1800 to 2800 m altitude. The prevailing rainfall originates from the east and south-east with a pronounced maximum from April to May, and a lesser maximum from November to December (see Coetzee, 1967). Climatic factors define the upper tree limit, although forest clearance has substantially raised the lower limit of forest and most of the lower parts of the mountain, which formerly supported forest, are now either under cultivation or have been planted with mostly exotic fast-growing softwoods (Bussmann, 1994). Above the tree line the vegetation consists of heathland, afro-alpine vegetation and semi-desert.

Mount Kenya Forest Reserve was gazetted in 1932 and at that time covered an area of 228,340 ha (KIFCON, 1994). In 1949, the land above 3200 m plus the Naro Moro and Sirimon salients were designated as the Mount Kenya National Park. The result of this plus subsequent excisions and additions has had the net effect of reducing the area of the Forest Reserve by some 2.3% compared with the area originally gazetted. According to Wass (1995), the current gazetted Mount Kenya Forest Reserve, when combined with the protected areas of Mount Kenya National Park and other adjacent gazetted forests, covers an effective area of 213,000 ha.

The Mount Kenya forests are surrounded on all sides by densely populated farmland and this has put pressure on the Forest Reserve through activities such as illegal livestock grazing, uncontrolled logging and shamba agriculture involving localized clearance and temporary cultivation within

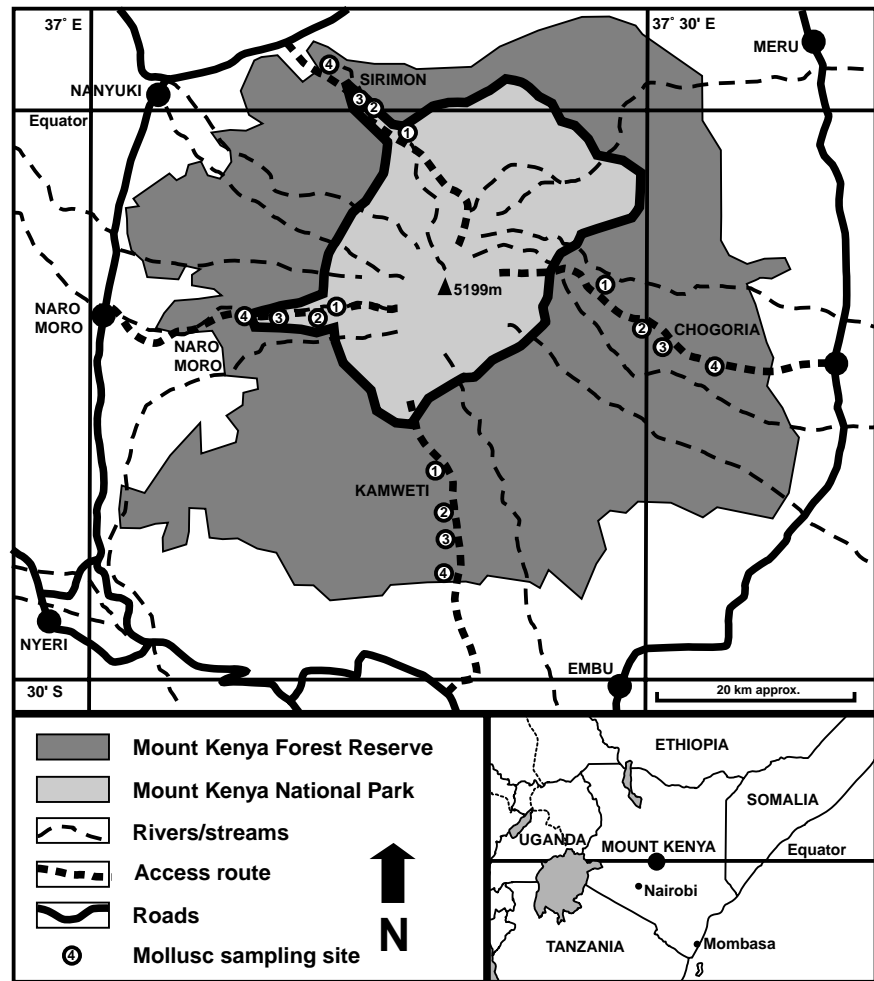


Figure 1 Location of Mount Kenya and the 16 land-snail sampling sites aligned along the Kamweti, Chogoria, Naro Moro and Sirimon access routes up the mountain.

the forest. In some areas, indigenous forest has been cleared and replanted with fast-growing softwood plantations. At present, agriculture and agroforestry extend up to 1800, 2400 and 2900 m on the south, west and east sides of the mountain, respectively (KIFCON, 1994). Further information on these and other pressures on Mount Kenya can be found in Wass (1995), Kenya Wildlife Service (1999) and Lockwood (1995).

METHODS

Survey design and the sampling sites

Four replicate plots were sampled at four sites on each of four altitudinal transects through the forest zone; locational data for the sites are given in Table 1. The transects were aligned along major access routes up the mountain (Fig. 1) with different aspects and overall spanned an altitude range of 1782–2851 m. These routes are known as the Naro Moro (referred to as N, with a west aspect), Sirimon (S, north-northwest), Kamweti (K, south) and Chogoria routes (C, east); they are shown on most maps of the mountain

(e.g. Wielochowski & Savage, 1988). Site 1 was located within bamboo forest and was the highest on each transect; site 4 was the lowest on each route. The four replicate plots sampled at each site are referred to as A–D. Thus, C4B refers to plot B on the lowest site on the Chogoria Route transect.

Bamboo (*Arundinaria alpina* K. Schumann) dominated the vegetation on each of highest altitude sites (S1, N1, C1 and K1). On the north and western transects, juniper (*Juniperus procera* Hochst. Ex Endlicher) was the dominant tree species on S2. *Podocarpus* species, which are characteristic trees of afro-montane forest communities, occurred on N2 and in parts of S3. Site N4 consisted of an approximately 70-year-old juniper plantation, which also contained a non-indigenous *Grevillia* species. The lowest site on the Sirimon route (S4, 2368 m) differed from the other forest sites because it supported highly fragmented vegetation and a very sparse litter layer with rocks; it was classified as bushland. The Chogoria and Kamweti sites contained mixed forest communities, with *Ilex europaea* ssp. *mitis* (L.) Radlk., *Albizia gummifera* (J.F. Gmel.), *Croton* spp., *Ocotea* sp. (on Chogoria but logged), *Ficus* sp., *Olea africana* (Miller) P.S. Green and *Teclea nobilis* Delile.

Table 1 Locations of the sampling sites and values of environmental values recorded at each of the sites

	Site latitude decimal degrees (negative south)	Site longitude decimal degrees east	Altitude (m)	Interpolated annual rain- fall (mm)	Frost sites	Mean soil pH	Mean soil calcium (meq)	Mean rela- tive canopy cover*	Bussman (1994) forest type	Minimum degrees from SE
Kamweti										
K1	-0.3311	37.3018	2545	1382	1	3.5	0.46	3.5	B	45
K2	-0.3446	37.3032	2288	1474	0	3.4	0.18	3.5	D	45
K3	-0.3671	37.3072	2138	1519	0	2.9	0.24	4	BL	45
K4	-0.3874	37.3063	1825	1601	0	3.1	0.25	4	BL	45
Chogoria										
C1	-0.1712	37.4572	2750	1147	1	3.7	9.58	NR	B	30
C2	-0.2297	37.5248	2252	1373	0	2.9	0.14	NR	O	30
C3	-0.2365	37.5405	1985	1472	0	2.7	0.11	NR	O	30
C4	-0.2365	37.5788	1782	1556	0	3.6	0.12	NR	BL	30
Sirimon										
S1	-0.0068	37.2725	2851	735	1	4.5	9.99	3.5	B	150
S2	0.0000	37.2523	2673	770	1	5.1	20.06	3.5	O	150
S3	0.0045	37.2477	2605	783	1	5.6	20.83	4	X	150
S4	0.0315	37.2320	2368	794	0	5.9	36.00	4	X	150
Naro Moro										
N1	-0.1703	37.1992	2822	942	1	4.5	9.36	4	B	130
N2	-0.1724	37.1810	2523	943	1	4.7	14.51	2.5	X	130
N3	-0.1724	37.1495	2432	986	0	5.1	11.53	2.75	X	130
N4	-0.1818	37.1045	2162	878	0	6.3	28.98	2	J	130

B, bamboo; BL, broad-leaved; D, deciduous; J, juniper; O, *Ocotea*; X, xeromorphic. NR: not recorded.

*Canopy cover ranked from 1: 0–20% cover to 5: 80–100% cover.

Mollusc sampling and identification

Molluscs were sampled in 1996 and 1997 in plots of approximately 70 × 70 m in visually homogeneous forest vegetation. The mollusc sampling on the Naro Moro transect was undertaken just before the short autumn rainfall season in November 1996, whereas the other transects were sampled during the dry season in late February and March 1997. Edge effects were minimized by locating plots away from the forest edges or other habitat boundaries and from access tracks, etc. Molluscs were sampled by direct searching for 2.5 h, plus collecting and subsequently drying and sieving 4 L of soil and litter samples to extract litter-dwelling micro-snails. All the plots were thus sampled with equal levels of 'effort'. Accessible molluscan microhabitats, including dead wood and rocks, tree trunks and living vegetation, and amongst leaf litter were searched and all molluscs located were collected. Other researchers (Emberton *et al.*, 1996; Tattersfield, 1996; Emberton, 1997; De Winter & Gittenberger, 1998; Tattersfield *et al.*, in press) have used similar methods, which have been found to provide reasonably consistent estimates of relative species richness. Emberton *et al.* (1996) recommend a similar approach to this consisting of combined, timed direct-search and litter/soil sieving to quantitatively sample molluscs in Madagascar rainforests. Fifty-three (78%) of the sixty-eight mollusc taxa recorded have been identified to species level; the remaining fifteen taxa have been assigned to a provisional genus and a morphospecies (e.g. *Punctum* sp. A, B,

etc.) based on external, mainly conchological, characters. Further notes on mollusc identification, the definition of morphospecies and the nomenclature used for mollusc taxa in this paper are provided in Warui *et al.* (2001).

Environmental variables

A range of habitat and abiotic environmental variables, including soil pH and calcium content, was recorded on each plot (Table 2). Habitat structure was assessed by visually estimating canopy cover, understorey density and tree/shrub height. Further information about vegetation and forest types has been obtained from Bussmann (1994). The values of the environmental variables are given in Table 1.

Spatial interpretation of rainfall

Mean annual rainfall totals for 102 rain gauges having eight or more years of records in 1961 were obtained from Trapnell & Brunt (1976). All of the rainfall gauges were located within a radius of about 150 km to the west and 70 km to the east of the summit of Mount Kenya; the original source of the information was the East African Meteorological Department. Overall, the altitude of the rain gauges ranged from 1124 to 4200 m, with the highest being at Teleki Camp; seventy-seven stations lay within the altitude range of the mollusc sampling sites. However, the majority of rainfall stations are located at lower altitudes in the populated areas around the mountain.

Table 2 Environmental variables and other information recorded on each plot

Environmental variable	Method
Altitude	Hand-held GPS and altimeter, and 1 : 50000 scale topographic maps
Soil calcium	Several subsamples of surface soil (upper 5 cm) taken and bulked up from each plot. Determined using atomic absorption spectrophotometry
Soil pH	As calcium but assayed in aqueous 0.01 M calcium chloride using an electronic probe
Mean annual rainfall	See text
Canopy cover	Percentage estimated visually – each plot allocated to one of five 20% bands (0–20, 20–40%, etc.)
Inclination	Estimated by eye
Aspect	Aspect from 135°N (SE), which is the direction of prevailing rainfall
Frost sites	Bussman (1994) states that frost can be expected above 2500 m. The sites above this altitude are defined as frost sites for the purpose of the analysis
Forest vegetation type	Six types were classified using Bussman (1994): bamboo, xeromorphic forest, <i>Ocotea</i> , deciduous forest, and broad-leaved forest and plantation

Rainfall data were imported into ArcView GIS 3.2 (ESRI, 1992–1999) for further analysis and integration with the existing data set. A separate interpolation tool was then used to generate a rainfall total surface for the Mount Kenya region. The interpretation algorithm consisted of generating a Triangular Irregular Network (TIN) or Delauney Triangulation model of the rainfall values, and then interpolating values for each position on the TIN lattice according to some weighted average of rainfall values adjacent to the point. This method allows the form of the rainfall surface to be well represented, resulting in relatively accurate estimates of rainfall. The TIN surface generated showed the expected pattern (e.g. Hedberg, 1951; Bussmann, 1994), with the highest values to the south and east of the mountain, especially between the towns of Chogoria and Kerugoya. Total rainfall was lower to the north and west, with a rain shadow effect apparent north of the mountain, aligned roughly along the Sirimon Route. A query procedure was then used to extract the interpolated rainfall values for each of the sampling locations (Table 1). These data were then used with altitude, aspect and other environmental variables to investigate the relationships between climate, altitude and mollusc diversity and abundance across the mountain.

Interpolated total rainfall declines with altitude on the Chogoria and Kamweti transects but apparently not on the Sirimon and Naro Moro transects (Fig. 2). Similar decreases in rainfall with altitude have been reported previously on tropical African mountains (Coetzee, 1967; Taylor, 1996). Lauscher (1976; cited by Taylor, 1996) states that tropical mountains exhibit precipitation maxima at 1500 m, above which levels can decline rapidly. Coetzee (1967) shows that on the southern slope of Mount Kenya, an average maximum of about 2340 mm occurs at an altitude of about 1830 m, in the lower part of the forest, above which the decline is rather steep. It is not certain whether rainfall does not similarly vary with altitude on the north and west facing sides of the mountain, or whether the generated TIN is inadequate to detect such a pattern. However, Coetzee (1967) suggested that maximum precipitation on the Sirimon and Naro Moro routes occurred in the bamboo zone at 3048 m altitude. Hedberg (1951) commented that on the NE

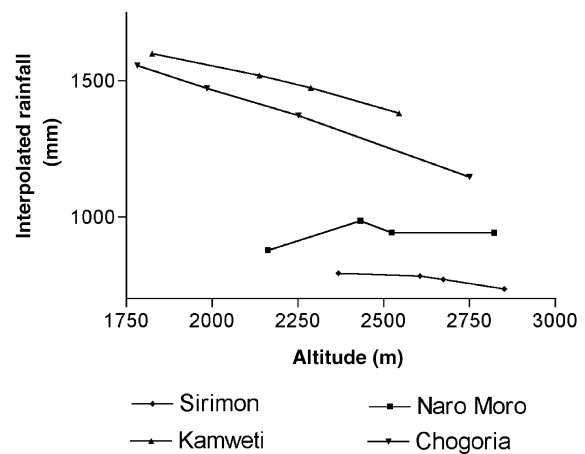


Figure 2 Relationship between interpolated mean annual rainfall (mm) and altitude (m) on the Kamweti, Chogoria, Naro Moro and Sirimon transects.

side of Mount Kenya, maximum rainfall was 2700 mm at an elevation of about 1700 m in the forest belt.

Methods of analysis

Three measures of site mollusc diversity/richness have been adopted (Cameron, 1992; Tattersfield, 1996). S is the total number of species recorded at a site and represents a measure of overall species richness. α is the mean number of species per plot or an estimate of point diversity and H' is the Shannon Index (e.g. Magurran, 1988). The Shannon evenness index, which is H'/H'_{max} , has also been computed and represents the degree to which faunas are dominated by a small number of species. Differences in the values of these parameters have been tested using ANOVA. Magurran (1988) has shown that samples of H' can be expected to be normally distributed and therefore that analysis of variance is an appropriate test. The mean number of specimens collected per hour provides a relative measure of mollusc abundance. Species-replacement effects along the

altitudinal transects have been explored using β -2 index by Harrison *et al.* (1992) which has been adjusted to accommodate variation in the altitudinal span of the transects. β -2 is defined by Harrison *et al.* (1992) as

$$\beta-2 = \{([S/\alpha_{\max}] - 1)\} \times 100$$

where α_{\max} is the maximum value of α diversity in the collection of N sites.

This index has been divided by the altitude range of the transect and does not therefore range from 0 to 100 as does β -2. It provides a measure of species turnover along a gradient (the β diversity of Whittaker, 1960) that is insensitive to trends in species richness (α). Harrison *et al.* (1992) recommend its use as a measure of the amount by which regional diversity exceeds the maximum diversity attained locally. Canonical correspondence analysis (CCA) has been applied using the CANOCO 3.12 package (Ter Braak, 1991) to explore faunal groups and their relations with environmental variables.

Pearson correlation coefficients have been calculated to explore the relations between snails, environmental variables and the CCA products. The relationships between species richness, snail abundance and altitude have been investigated by using joint regression analysis to test for differences in slopes between transects. The joint regression analysis has been applied to all species combined and to subgroups of taxonomically or biogeographically distinct species. These subgroups include a suite of species in the families Vertiginidae, Endodontidae *sensu lato* (especially the Punctidae) and Valloniidae that are more frequent and speciose in 'temperate' latitudes, although not confined to them. Other separately analysed subgroups consist of the Streptaxidae, Urocyliidae, and superfamily Achatinoidea (including both the Subulinidae and Achatinidae); these three subgroups have been further combined to form a further subgroup of 'tropical' species. Patterns have also been explored in the helicid family Bradybaenidae, and the remaining species, which have not been assigned to one of the above subgroups. This last subgroup of 'other species' includes the Euconulidae, Enidae, three species of prosobranch, the two species of *Kaliella* and *Vitrina cf. lactea*. Slopes that differ significantly from zero can be interpreted as indicating variation in respect of altitude. Variation in species richness amongst transects has been interpreted over the altitudinal range

studied, as it is not appropriate to extrapolate to the intercept.

RESULTS

The total species \times sites data matrix is given in Appendix 1; live and dead specimens have been combined. A total of 7486 specimens of sixty-eight species/morphospecies were collected during the sampling. Sixty-six specimens (0.88% of the total) could not be identified or confidently assigned to morphospecies because of juvenile or inadequate material. These have been included in the analysis of abundance but not diversity. Correlation coefficients between the environmental variables and snails, with data from all four transects combined, are shown on Table 3.

Levels of diversity and abundance

Table 4 gives the mollusc diversity and abundance statistics for the sixteen sites. Overall, total species number was fifty-three, forty-nine, forty-six and thirty-four on the Naro Moro, Kamweti, Chogoria and Sirimon transects, respectively. Site species richness S varied from thirteen species on Sirimon site S4 to thirty-eight on Kamweti K4. The abundance of snails collected at the sites also varied greatly, from seventy-six specimens on C2 to 1395 on S3. Neither diversity nor abundance estimates appear unusual on the N4 juniper plantation compared with the indigenous forest sites on this transects. Shannon and evenness indices are low on S1, S2 and S3, relative to S4 and sites on the other transects. S1, S2 and S3 support the highest abundance levels, but their faunas are dominated by three species (see below) and this accounts for the low evenness indices. Site S4 supports fewer species and individuals than the other Sirimon sites, and thus appears to be anomalous along this transect. S4's soils do not have markedly different levels of pH or calcium compared with the other Sirimon sites, but the highly degraded and fragmented structure of the bushland vegetation, the lack of large canopy trees and the presence of heavy grazing on S4 may have influenced species richness and abundance. Three species, *Punctum* sp. C, *Lauria desiderata*, '*Vitrina*' *baringoensis* account for 76 or 77% of the total sample on S1, S2 and S3 whereas the comparable proportion for the three most abundant species on S4 is 40%. On other sites on the

Table 3 Pearson correlation coefficients between environmental variables and snail diversity and abundance

Variable	Altitude	Rainfall	Soil pH	Log soil calcium	Canopy cover	No. species	No. specimens
Rainfall	-0.725***						
Soil pH	0.363**	-0.805***					
Log soil calcium	0.645***	-0.914***	0.812***				
Canopy cover	0.048	0.242	-0.335*	-0.324*			
No. species	-0.325**	0.080	0.194	0.043	-0.442**		
No. specimens	0.293*	-0.601***	0.577***	0.531***	-0.121	0.372**	
Shannon Index	-0.506***	0.488***	-0.189	-0.355**	-0.250	0.689***	-0.241

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Others not significant $P > 0.05$. $n = 64$ for all coefficients except for canopy cover comparisons where $n = 42$.

Table 4 Estimates of mollusc diversity and abundance for the sixteen sampling sites on Mount Kenya

Site	Altitude (m)	<i>S</i>	α	SE	<i>H'</i> *	<i>J</i>	Total specimens (incl. unidentified)	Mean specimens/plot	SE
Kamweti									
K1	2545	26	13.5	1.5	2.84	0.87	155	38.75	4.29
K2	2288	25	12.3	1.2	2.66	0.83	162	40.5	7.31
K3	2138	26	14	1.2	2.70	0.83	178	44.5	10.4
K4	1825	38	22.3	3.8	2.94	0.81	427	106.75	14.3
Chogoria									
C1	2750	15	8	1.1	1.74	0.64	166	41.5	6.18
C2	2252	15	8	1.6	2.43	0.90	76	19	5.61
C3	1985	24	12	0.8	2.71	0.85	112	28	6.56
C4	1782	30	17	1.4	2.26	0.66	424	106	13.7
Sirimon									
S1	2851	16	12.3	0.9	1.60	0.58	904	226	44.2
S2	2673	19	12.3	1.7	1.59	0.54	1055	263.75	14.3
S3	2605	23	14.3	1.9	1.83	0.58	1395	348.75	34.9
S4	2368	13	6.8	0.6	2.12	0.83	226	56.5	11.8
Naro Moro									
N1	2822	23	11.8	0.9	2.43	0.77	202	50.5	12
N2	2523	29	18.5	2.2	2.50	0.74	595	148.75	32.9
N3	2432	36	23	2.1	2.80	0.78	719	179.75	34.6
N4	2162	34	21.3	1.8	2.47	0.70	690	172.5	46.1

*Shannon Index *H'* (base e) calculated from combined data set from all four replicates (excl. unid. specimens).

other transects, the three most abundant species also contribute about 40% to the total sample and thus it is not certain whether it is S4 or the three higher Sirimon sites that are unusual relative to the faunas elsewhere on Mount Kenya. Removal of the S4 plots from the correlation analysis shown in Table 3 results in the correlations coefficients between soil pH and *S*, *H'* and abundance, and canopy cover and rainfall becoming statistically not significant ($P > 0.05$); however, these changes do not affect the overall conclusions from the study. The Shannon evenness index (Table 4) is highest on the four Kamweti sites and on Chogoria C2 and C3; it is generally lower on the Sirimon and Naro Moro transects (apart from S4, see above).

Total species number and total specimen number correlate weakly but significantly when data from all the transects (i.e. sixty-four plots) are combined (Table 3). Species richness and Shannon Index decline with increasing altitude, but snail abundance (mean specimens per plot) tends to increase at higher altitudes (Table 4). However, the relationship between abundance and altitude is possibly distorted because of the large number of individuals collected on the relatively high altitude Sirimon sites (S1, S2 and S3). Snail abundance correlates significantly and positively with soil pH and calcium, but species richness does not. Within the Naro Moro, Kamweti and Chogoria transects, *S*, α and mean snail abundance all tend to decrease at higher altitudes (Table 4). Apart from snail abundance on Chogoria, regression coefficients for species richness and abundance on altitude are all negative and significant for these three transects (Figs 3 & 4; Table 5).

Snail richness and altitude are positively related on the Sirimon transect (Table 5a).

Altitudinal variation in species number and abundance in the subgroups is shown in Table 5 and Figs 3 and 4. Species richness in the group of unassigned 'other species' declines with altitude on the Kamweti and Chogoria transects, but not on the Naro Moro or Sirimon transects. There are significant ($P < 0.05$) but weak negative relationships between altitude and Achatinoidea and 'helcid' richness on the Kamweti and Chogoria transects, respectively, but otherwise, subgroup richness does not show strong altitudinal variation. The positive relationship between tropical species and altitude on the Sirimon transect is probably anomalous (see above). The Sirimon transect has been excluded from the joint regression analyses between the routes. Interpretation of Fig. 3 suggests that there is some variation in subgroup species richness among the three transects. Temperate species are richer on the Naro Moro and Sirimon transects; there are more helicids and Achatinoidea on the Kamweti transect and streptaxids are richer on the Naro Moro route. Overall snail abundance (Table 5b and Fig. 4) declines with altitude on the Kamweti, Naro Moro and Chogoria routes, although the relationship does not achieve formal statistical significance on the Chogoria route ($P = 0.07$). Temperate species abundance declines with altitude on the Naro Moro transect, as does the abundance of the 'other species' subgroup on both Naro Moro and Chogoria. The number of specimens in the Achatinoidea and tropical subgroups decline with increasing altitude on the Kamweti route. Among the transects,

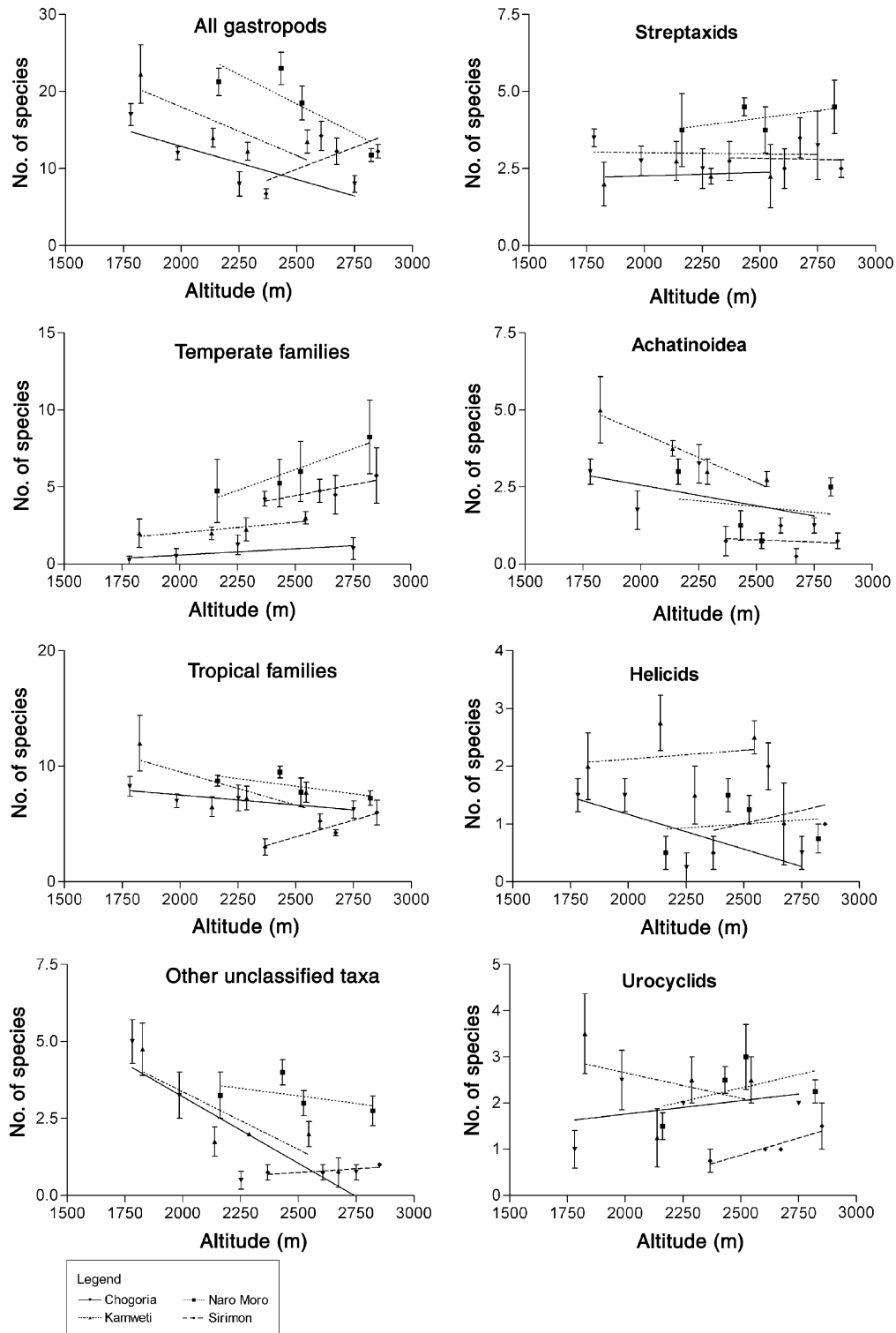


Figure 3 Altitudinal variation in mean species richness of total gastropods, species in tropical and temperate families and a variety of taxonomic groups on Mount Kenya.

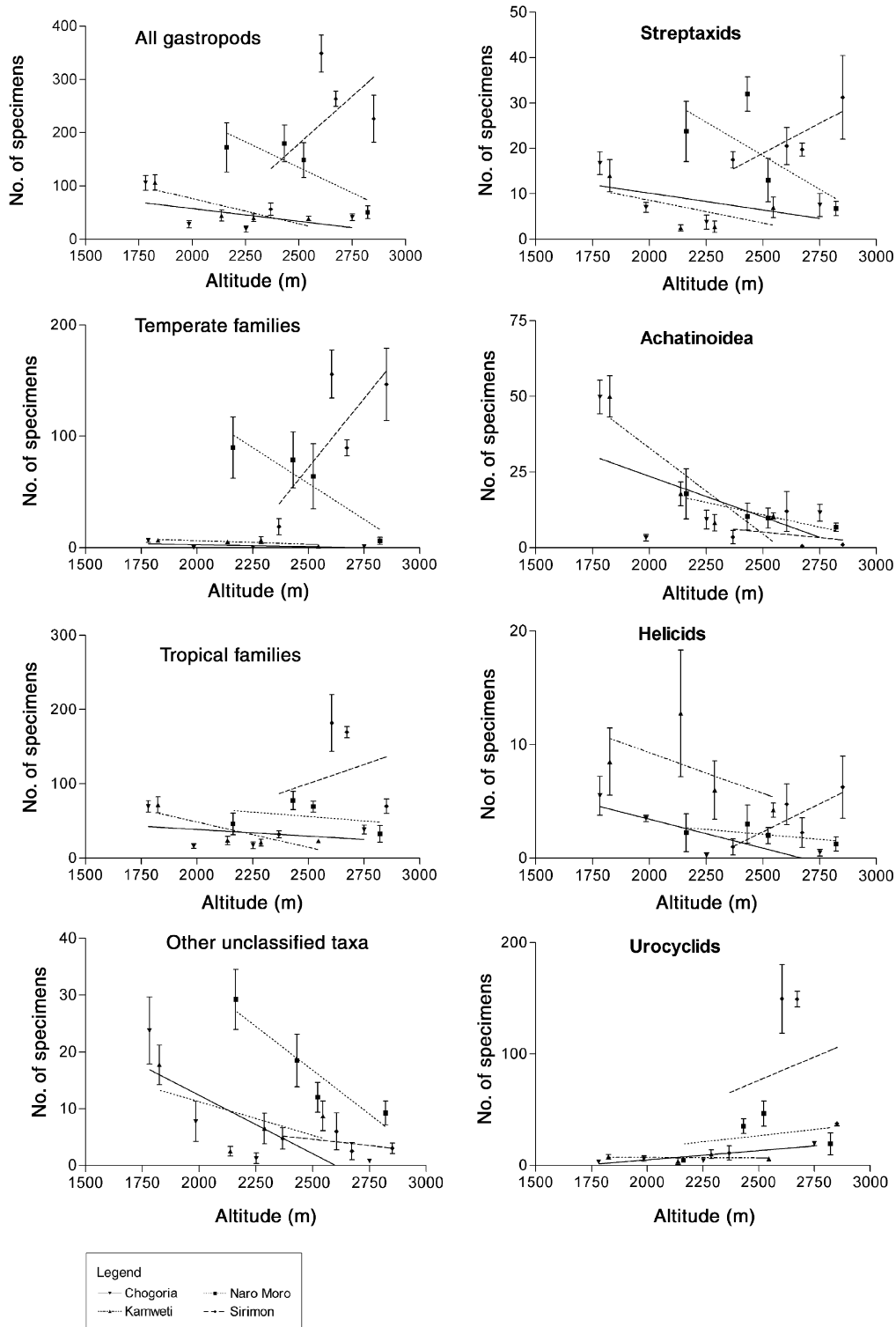


Figure 4 Altitudinal variation in mean abundance of total gastropods, species in tropical and temperate families and a variety of taxonomic groups on Mount Kenya.

Group/subgroup	Within transects				Between aspects (excluding Sirimon) Slope
	Naro Moro	Sirimon	Kamweti	Chogoria	
(a) Species number					
All gastropods	--	+	-	--	ns
Temperate species					ns
Tropical families		+			ns
Other species			--	---	ns
Streptaxids					ns
Achatinoidea			-		ns
Helicids				-	ns
Urocyclids					ns
(b) Abundance					
All gastropods	-	+	---		ns
Temperate families	-	++			**
Tropical families			-		ns
Other species	--			--	ns
Streptaxids	-				ns
Achatinoidea			---	-	ns
Helicids				--	ns
Urocyclids				+++	ns

Significance levels indicated by + or - symbols, showing the nature of relationship on the transect. Probability levels: ns or blank $P > 0.05$; */+/- $P > 0.05$; **/+ +/- $P > 0.01$; ***/+ + +/- $P > 0.001$.

streptaxids and helicids appear to be (see Fig. 4) more abundant on Naro Moro and Kamweti, respectively.

Many individual species show associations with either the wetter Chogoria/Kamweti routes, or forests on the drier, west and northern sides of the mountain along the Naro Moro/Sirimon routes (Table 7). Over 80% of the species listed in Table 7 that are associated with the Chogoria and Kamweti transects are in the tropical pulmonate families Streptaxidae and Subulinidae. In contrast, 55% of those on the Naro Moro and Sirimon routes are in the 'temperate' subgroup. Several species also show strong associations with high or low altitude sites (Table 8). Four of the higher altitude species are in temperate genera – *Truncatellina*, *Lauria*, *Acanthinula* and *Punctum*.

Relations amongst the abiotic variables

Several of the environmental variables are strongly correlated (Table 3). Overall, the low rainfall sites are associated with higher soil calcium levels and higher soil pH. The soils on the Naro Moro and Sirimon routes have much higher soil calcium levels than sites on the Chogoria and Kamweti routes. Such patterns are consistent with more severe soil nutrient leaching effects under the higher rainfall conditions on the east and south-east slopes of the mountain. Soil calcium and pH are also negatively associated with the extent of canopy cover.

Equivalent patterns in soil chemistry in relation to altitude along individual transects are less clear. The low rainfall on site C1 (Fig. 5) may help account for this site's high soil calcium levels compared with the other Chogoria sites. However, both soil pH and soil calcium decline with

increasing altitude within the Sirimon and Naro Moro transects. Interpolated annual rainfall for these two transects suggests that there is relatively little variation between the upper and lower sites, so it is possible that other types of precipitation at higher elevations, especially mist, maybe having a significant soil leaching effect. Alternatively, it is possible that the rainfall model used is not sufficient to describe the rainfall gradient on the drier side of the mountain.

Species turnover with altitude

Table 6 shows that species replacement, as expressed by the adjusted β -2 index, is highest on the Sirimon and Naro Moro routes. These two transects also have the shortest altitudinal ranges (Table 1). The lowest species turnover is along the altitude gradient on the Kamweti transect. Most species have large altitudinal ranges based on the combined records from all four transects. Forty-two species (61% of the total fauna) have ranges of at least 500 m, and fifteen of these (22% of

Table 6 Index of species turnover in relation to altitude gradients – β -2, altitudinal range and adjusted β -2 (see text) for the four transects

Transect	β -2	Altitude range (m)	(β -2/altitude range) \times 100
Kamweti	14.5	720	2.01
Chogoria	26.7	968	2.76
Sirimon	23.9	483	4.95
Naro Moro	23.6	660	3.58

Table 7 Species associated with particular routes

	Naro Moro	Sirimon	Kamweti	Chogoria	P
Species associated with Chogoria and Kamweti routes					
<i>Nothapalus doherlyi</i>	0	1	95	181	***
<i>Curvella</i> nr. <i>elgonsensis</i>	0	0	124	1	***
<i>Vicariihelix gregorii</i>	0	7	66	32	***
<i>Gulella pervitrea</i>	0	0	0	33	***
<i>Subulona egregia</i>	0	0	8	20	***
<i>Gulella pretiosa pretiosa</i>	0	0	20	6	***
<i>Oreohomorus</i> cf. <i>nitidus</i>	0	0	5	9	**
<i>Tayloria</i> near <i>marsabitensis</i>	0	0	0	14	**
<i>Gonaxis</i> cf. <i>innocens</i>	0	0	2	10	*
<i>Trochozonites</i> sp. A	0	0	6	4	*
<i>Gulella pilula</i>	0	0	6	3	ns
Species associated with Naro Moro and Sirimon routes					
<i>Lauria desiderata</i>	205	660	0	0	***
<i>Punctum</i> sp. C	55	632	1	0	***
<i>Pupisoma renschi</i>	283	20	0	0	***
<i>Trachycystis lamellifera</i>	172	88	0	0	***
<i>Streptostele</i> cf. <i>exasperata</i>	76	153	4	0	***
<i>Kaliella iredalei</i>	58	62	5	5	***
<i>Truncatellina pygmaeorum</i>	5	82	0	0	***
<i>Acanthinula expatriata</i>	25	61	2	0	***
<i>Halolimnolix</i> cf. <i>iredalei</i>	0	43	1	3	***
<i>Gulella columella</i>	13	10	0	0	***
<i>Hydrocena kenya</i>	14	0	0	0	**
<i>Truncatellina</i> sp. A	5	4	0	0	ns
<i>Punctum</i> sp. D	9	0	0	0	ns
<i>Truncatellina arboricola</i>	3	4	0	0	ns
<i>Punctum ugandanum</i>	7	0	0	0	ns
<i>Subuliniscus adjacens</i>	2	4	0	0	ns
<i>Limicolariopsis verdcourti</i>	4	0	0	0	ns
<i>Pupisoma</i> sp. B	3	0	0	0	ns
<i>Trochonanina</i> sp. B	3	0	0	0	ns
<i>Elgonocyclus koptawelilensis</i>	2	0	0	0	ns

Probability levels as in Table 5, based on comparison of combined data from Sirimon plus Naro Moro and Kamweti plus Chogoria transects. Chi-square tests (1 d.f.) with Bonferroni adjustment for multiple tests. Data are total number of specimens (live plus dead) recorded from the four sites on each transect.

the fauna) have ranges that exceed 1000 m. Ten of the twenty-five species with relatively small altitudinal ranges of less than 500 m are in the temperate families subgroup.

Canonical correspondence analysis

The CCA analysis was performed on the abundance of each species (combined live plus dead) at each site in relation to five environmental variables – interpolated annual rainfall, degrees from SE (i.e. the prevailing weather), frost sites, soil pH and Bussman's (1994) forest types. Species abundance was logged before analysis. Canonical correspondence analysis is designed for the analysis of species along environmental gradients. The different forest types are categorical rather than gradient variables and have been incorporated into the analysis as dummy variables. Site N4 was excluded from the analysis because it contains plantation rather than indigenous forest. The additional omission of bushland site S4 from the analysis makes little difference to the results of

the CCA. The CCA was initially run using all the environmental variables but altitude and soil calcium were subsequently excluded because they were so strongly correlated with other variables.

The sum of all unconstrained eigenvalues for the species data is 3.408. Axis 1 has an eigenvalue of 0.55 and accounts for 16.1% of the variance in the species data. Axes 2, 3 and 4 account for 5.5, 4.5 and 3.5% of the variance, respectively. The proportion of the variance in the species data explained by the environmental variables can be estimated as 35.9%, by dividing the total canonical eigenvalue (1.223) by the total unconstrained eigenvalue (3.408) (see Cowie *et al.*, 1995); 60.3% of this variation in the species abundance by site is explained by the first two axes, as constrained by the environmental variables included in the analysis. The inter-set correlations (Table 9) indicate the strength of association of the axes with the environmental variables. Axis 1 is strongly correlated with rainfall (Fig. 6) and other variables that are correlated with rainfall (Table 3), especially the

	Altitude group			
	Below 2162 m	2163–2368 m	2369–2605 m	> 2605 m
(a) Species more frequent at high altitudes				
<i>Vitrina' baringoensis</i>	39	79	913	880
<i>Lauria desiderata</i>	0	1	326	538
<i>Punctum</i> sp. C	1	46	377	228
<i>Streptostele</i> cf. <i>exasperata</i>	2	45	63	60
<i>Gulella simplicima</i>	1	2	47	79
<i>Acanthinula expatriata</i>	0	8	43	37
<i>Truncatellina pygmaeorum</i>	0	0	8	77
<i>Ptychotrema uniliratum</i>	3	0	57	16
<i>Gulella insolita</i>	3	1	31	17
<i>Halolimnobelex</i> cf. <i>iredalei</i>	2	3	10	32
<i>Hydrocena kenyana</i>	0	0	6	8
(b) Species more frequent at lower altitudes				
<i>Nothapalus dohertyi</i>	270	6	1	0
<i>Curvella</i> nr. <i>elgonensis</i>	108	16	0	1
<i>Vicariibelix gregorii</i>	67	22	16	0
<i>Streptostele</i> sp. C	39	28	0	0
<i>Halolimnobelex planulata</i>	32	1	7	1
<i>Gulella pervitrea</i>	33	0	0	0
<i>Subulona egregia</i>	25	3	0	0
<i>Gulella pretiosa pretiosa</i>	26	0	0	0
<i>Pupisoma orcula</i>	19	0	4	1
<i>Afroconulus iredalei</i>	14	2	1	0
<i>Pupisoma harpula</i>	14	0	0	0

All species shown show highly significant variation across the altitude classes (all $P < 0.001$, based on chi-square with Bonferroni adjustment for multiple tests). Data are number of specimens recorded in four altitude groups; each group consists of data from four sites.

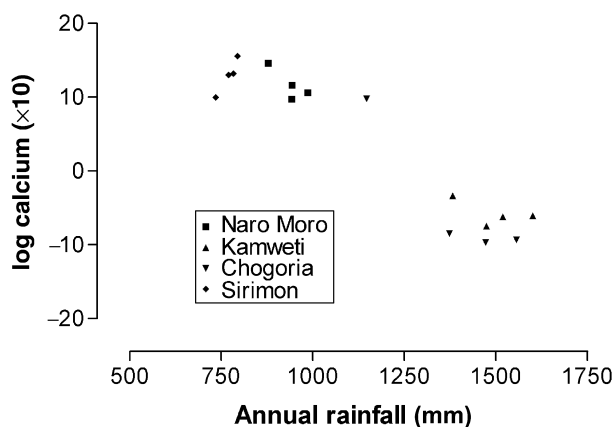


Figure 5 Relationship between mean soil calcium and estimated mean annual rainfall.

strong negative relationships with minimum degrees from south-east, and soil pH. The axis 1 site scores correlate more strongly with interpolated rainfall ($r^2 = 0.924$), soil calcium ($r^2 = 0.757$) and soil pH ($r^2 = 0.619$) than altitude ($r^2 = 0.604$). Axis 2 is much weaker and only accounts for 5.5% of the variation in the species data. It is less straightforward to interpret and appears to reflect variation

Table 8 Species showing associations with (a) high or (b) low altitude sites

Table 9 Interset correlations of CCA environmental axes generated by CANOCO

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Rainfall	975	-20	32	-2
Degrees SE	-823	-174	-90	-100
Frost	-641	197	-290	119
Soil pH	-782	-155	75	-176
Bamboo	-146	465	-705	143
Xeromorphic forest	-536	-97	332	-613
<i>Ocotea</i> forest	-75	224	519	600
Deciduous forest	166	-30	-105	21
Broad-leaved forest	735	-519	-74	42

in the snail fauna in relation to forest community type, especially as defined by Bussman's (1994) forest categories. These forest types are partly related to altitude, but altitude *per se* does not correlate significantly with the axis 2 scores ($r^2 = 0.069$). The high altitude bamboo forest makes the strongest contribution to axis 2. Examination of a biplot of species and sites (not shown) allows a group of species associated with the wetter Chogoria and Kamweti transects to be identified, including *Nothapalus dohertyi*, *Curvella* near *elgonensis*, *Vicariibelix gregorii* and *Kaliella barrakporensis*. A similar suite of species associated with the Naro

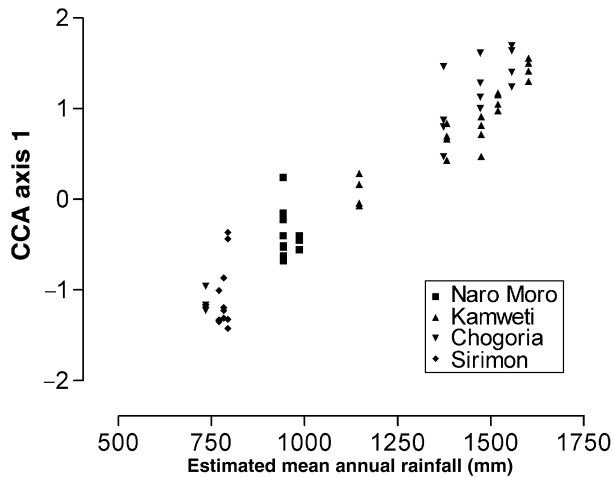


Figure 6 Relationship between estimated mean annual rainfall and CCA axis 1 scores.

Moro and Sirimon routes includes *Lauria desiderata*, *Truncatellina pygmaeorum* and *Trachycystis lamellifera*.

DISCUSSION

The results are discussed in the context of elevational gradients and climatic variation on Mount Kenya, the diversity of the fauna in an African context, the environmental determinants and origins of the faunas and biodiversity conservation planning.

The CCA must be interpreted cautiously because of the low proportion of the variation in mollusc abundance that is explained by the ordination. However, it suggests that annual rainfall is the most important factor (amongst those studied) influencing the mollusc faunas of Mount Kenya's forests. Most variation in the snail faunas studied appears to be associated with the large, aspect-related rainfall patterns, which are caused by the prevailing, easterly weather systems and the resulting rain-shadow effect on the west and north-west side of the mountain. The faunas are more strongly associated with rainfall than to either altitude, the other environmental variables, or the forest community types classified here. Plant communities on Mount Kenya and other high African mountains show similar aspect-related variation, which has also been attributed to local rainfall and climatic patterns (Hedberg, 1951; Coetzee, 1967). Rainfall could affect snail faunas in several ways; either directly by influencing moisture and humidity levels, or indirectly, via effects on vegetation or soils. Rainfall and its secondary effects have previously been suggested as important influences on land mollusc faunas. In a review of what was then known about land-snail diversity in different biomes worldwide, Solem (1984) commented on the probable effects of both the level and seasonality of rainfall on land-snail faunas. He considered that 'rain forests, suffer from an overabundance of rain, which leaches nutrients' and that the seasonality of rainfall in monsoon forests 'necessitates

diapause in snails'. Cameron (1978) suggested that the relationship between land-snail richness and altitude in the English Pennines might be influenced by the local climate.

The inverse relationships reported here between rainfall, and soil pH and soil calcium levels suggest that strong soil-leaching processes are operating under high rainfall conditions on Mount Kenya. These patterns are apparent mainly in respect of the aspect-related climatic gradients. Milne (1937) has shown that tropical rainforest soils are often highly leached, and Richards (1996) has commented that at higher altitudes, many tropical mountain soils resemble leached and wet temperate soils. Mist is a major source of precipitation in the higher altitude forests on Mount Kenya and rainfall estimates may not fully reflect this source of moisture. This factor might account for the altitudinal declines in soil pH and calcium on the drier side of the mountain although the influence of mist and incipient precipitation on soil chemistry on Mount Kenya is not known. Hamilton (1998) has suggested that there is a causal relationship between the common occurrence of cloud above 850 m in the East Usambaras, Tanzania and the presence of acidic soils. Several studies, mostly in temperate zones, have reported positive relationships between snail abundance and/or richness and soil pH and/or calcium levels (Warebörn, 1969; Bishop, 1977; Waldén, 1981; Coney *et al.*, 1982; Nekola & Smith, 1999). However, in some situations the species composition (rather than the richness and abundance) of land mollusc communities can be related to soil conditions. For example, in woodlands in a geographically restricted area of northern Britain, Tattersfield (1990) reported different mollusc faunas on acidic and calcareous substrates, but accounted for the differences in terms of site drainage characteristics; several individual species were associated with either the acidic or calcareous conditions. Bishop (1977) found that variation in the land-snail faunas of acidic Irish woodlands was most closely related to litter composition, especially calcium and nitrogen levels.

The forest classification (Bussman, 1994) and description of habitat structure used in this study were relatively simple and rather imprecise, and it is therefore perhaps not surprising that no strong relationships were found with the mollusc faunas. More detailed botanical information would be needed to explore relationships between vegetation and snails. Other studies have, however, suggested that vegetation and molluscs may sometimes not be closely related (Bishop, 1977; Cowie *et al.*, 1995) and that relationships between soils, vegetation and mollusc faunas can be complex (Warebörn, 1969).

The decline in mollusc species richness with elevation on Mount Kenya is consistent with the general patterns widely seen in most groups of animal and plant (Rahbek, 1995), including those on tropical African mountains (e.g. Hawkins, 1999 on Malagasy birds; Hamilton, 1975 – trees on Mount Elgon). However, the small number of sites sampled on each transect do not allow the nature of the altitude-related variation to be established (Rahbek, 1995). Variations in soil pH and calcium levels do not appear to account for this decline, as the soil-leaching effects of rainfall decline with

altitude on Mount Kenya, at least on the wetter sides of the mountain across the altitudinal range studied. There have been few similar studies on tropical molluscs but Emberton (1997) found that Madagascan lowland forests were richer than highland forests (maximum range 100–860 m) in total, endemic and rare mollusc species. In contrast, Emberton *et al.* (1997), reported high mollusc diversities at both ends of an altitudinal transect extending over a range of 900 m from coastal forest to East Usambaran submontane forests in north-east Tanzania, although the presence of limestone probably explained the increased diversity in the lowest coastal forest site. No evidence of an association between endemic species and lower altitude sites has been found in this study, although Mount Kenya supports relatively few endemic mollusc species and the lowest forests studied are still afro-montane rather than true lowland types (see below). Seven of the species recorded in this study are probably endemic or nearly endemic to Mount Kenya (Warui *et al.*, 2001). Three of these (*H. kenyana*, *L. verdcourti* and *T. arboricola*) were only found in the drier forest communities along the Naro Moro and/or Sirimon transects whereas the other 4 (*N. suturalis*, *H. planulata*, *V. cf. lactea* and *G. princei*) are more widely distributed on the mountain. Elsewhere, Cowie *et al.* (1995) has reported a 'tentative overall association of the Hawaiian mollusc fauna with altitude' over an elevational range of 1500–2100 m, and Cameron (1978) found impoverished mollusc faunas at higher altitudes in his study over a range from 230 to 590 m, in various habitats in the English Pennines.

The sites examined in this study can be classified as afro-montane forests. White (1983) defines the Afro-montane Region, on the basis of floristic composition, to describe the disjunct and distinct upland forests of intertropical Africa and separate them from the lowland Guineo-Congolian forests that predominate in western and central Africa. Chapman & White (1970) regarded 1370 m to be the boundary of the lowland/afro-montane boundary in East Africa, but other authors have considered this division to be variously between 1300 and 2000 m (see Hamilton, 1975 and Hamilton & Perrott, 1981 for reviews). There has also been considerable debate as to whether the transition between lowland and montane forests is gradual or abrupt (e.g. Hamilton, 1975; Lovett, 1996; Poynton & Boycott, 1996). Different mollusc faunas have been reported at high and low altitude sites in this study, but the small number of sampling sites on each transect means that it is not possible to establish the nature of the transition along the altitude gradient. However, the wide altitudinal ranges exhibited by most species might suggest that variation is gradual, or that any zonation present within the forest belt is poorly defined. Some species in this study exhibit local 'blooms' in abundance, like those described by Emberton (1997) in Madagascar. These patterns are not related to specific altitudes, but rather appear to be responses to local conditions.

Germain (1931) concluded that the mollusc faunas of the high East African mountains (Rwenzori, Kilimanjaro, Elgon, etc.) were essentially equatorial African in character,

although he also noted the occurrence of a small number of Palaearctic elements. The information available to Germain suggested that Palaearctic taxa were unusual on East African mountains, and were almost confined to Mount Kenya, although this is now known to be incorrect because genera, including *Lauria* and *Columella*, have been found on several of the other high mountains (Verdcourt, 1983; Tattersfield *et al.*, 2001). Further analysis of the relationships between the 'temperate' components of Mount Kenya's land snail fauna and their relations with taxa elsewhere in the world would be interesting, but is unfortunately not currently possible because of the inadequate state of knowledge on the taxonomy and systematics of most groups. Few of the taxa have been explored anatomically, which is essential before robust phylogenetic hypotheses can be formulated. Scharff (1992) has made the point that biogeographical interpretation needs to be based on a sound understanding of phylogeny. However, several of the species present on Mount Kenya are clearly allied to those found at higher latitudes, both to the south and north of the tropics. Verdcourt (1972) considered that the generic status of *Hydrocena kenyana* required confirmation but Connolly (1929) seemed certain the species was allied to the South African *H. noticola*. *Lauria* is probably an ancient genus (Verdcourt, 1972) whose range is restricted to the Palaearctic and Ethiopian Regions, including the Atlantic islands. The occurrence of these species on Mount Kenya is consistent with the suggestion that long range dispersal, via the chain of other mountains and high ground in East Africa, may explain the occurrence of species more characteristic of higher latitudes on high African tropical mountains (see Taylor, 1996). However, this explanation for the occurrence of temperate species does not account for their unexpected association with forests on the drier (west and north-west) rather than wetter (south and east) sides of the mountain. The reason for this pattern is currently unknown, although variation in mean temperatures or perhaps the seasonality of rainfall patterns, might be relevant.

Germain (1931), Verdcourt (1983) and Pickford (1995) have published lists of land-snails recorded from Mount Kenya, and Verdcourt (1998) and Tattersfield (1995) have added supplementary records. Preston (1911) and Connolly (1922) described a substantial number of new species from the mountain and more recently, Warui *et al.* (2001) have reviewed this literature and compiled a checklist of the mountain's mollusc species including the data presented here. The study reported here has added up to about twenty species to the list of terrestrial mollusc for the mountain. These include eight mostly small species, which have, as yet, not been identified or may have not been formally described. They also include several named minute species such as *Elgonocyclus koptawelilensis* and *Punctum ugandanum*, and widespread species (e.g. *Maizania volkensis*, *Afroguppya quadrisculpta*) which do not appear previously to have been specifically listed for Mount Kenya.

Direct comparisons of the diversities reported here with other studies in East African forests are complicated because of variations in sampling methodologies and other

factors such as seasonal variation (e.g. de Winter & Gittenberger, 1998). However, Tattersfield (1996, 1998) and Tattersfield *et al.* (1998) used broadly similar methods involving direct search and litter sieving techniques in Kakamega Forest, Kenya, and several coastal forests and four Eastern Arc mountain ranges in Tanzania, although the duration of the direct search and volume of litter searched varied. Mollusc species richness at the individual sampling sites on Mount Kenya does not approach the totals of forty-five, fifty and fifty-seven species recorded, respectively, from the single altitude sites of the limestone forest at Kimboza in the Ulugurus (350 m altitude) in Tanzania, Kakamega Forest (1600 m) in western Kenya or Bomole Forest (1000 m) in the East Usambaras, Tanzania. These three sites may be exceptional in an East African context although it should be noted that they were also sampled more intensively than those on Mount Kenya. Elsewhere in East Africa, overall species richness appears to be lower (Tattersfield *et al.*, 1998) and more comparable with, or lower than, that found on Mount Kenya. The lowest levels of diversity were reported in the Nguru Mountains of northern Tanzania (Tattersfield *et al.*, 1998). There, totals of only eight, ten and thirteen species were found in three forests at 1040, 740 and 540 m altitude, respectively, using sampling methods very similar to those applied here. In contrast with the altitudinal decline in species richness reported here, data of Tattersfield *et al.* (1998) from the West and East Usambaras and Nguru mountains, tentatively suggest that mollusc richness may increase with elevation at lower altitudes in these ranges, from roughly 500 to 1500 m. Although associated with mountainous areas, in phytogeographical terms most of these lower altitude forests have affinities with the Zanzibar-Inhambane forests (White, 1983) of the East African coast (Burgess *et al.*, 1998). Overall land-snail richness is also relatively low in other Zanzibar-Inhambane forests along the East African coastal belt (Tattersfield, 1998 for Tanzanian forests, and Lange (unpublished) for Arabuko Sokoke Forest in Kenya). The consequences of such contrasting patterns in altitudinal variation in the afro-montane and Zanzibar-Inhambane forests, could result in a peak in species richness at an elevation of 1000–1500 m. However, lower altitude forests have also generally been more intensely exploited than montane areas in East Africa, and resulting changes, for example in forest structure, could reduce molluscan richness in such areas. Similarly, the exceptionally rich fauna in Kakamega Forest, west Kenya may reflect the mixing of Guineo-Congolian and afro-montane elements. White (1983) notes the transitional nature of the Kakamega Forest plant communities, which include both afro-montane and lowland Guinea-Congolian species. Species diversity in other groups is not evenly distributed in some Eastern Arc mountain ranges. It has previously been noted that in the East Usambara Mountains, using data from birds (Stuart, 1983) and plants (Iversen, 1991), that the biologically richest zone lies between 800 and 1200 m. If these patterns for molluscs are confirmed by further study, they may thus mirror those already reported for

other groups. In KwaZulu-Natal, South Africa, Eeely *et al.* (1999) has noted that species from both higher elevation afro-montane and lowland coastal forests mingle in the intermediate elevation scarp forests, and Lawes *et al.* (2000) has noted higher levels of species richness in these scarp forests.

Bussman (1994) suggests that there was formerly a corridor of forest connecting the lower slopes of Mount Kenya with the Aberdare Range to the west, before a period of large-scale forest clearance during early colonial times. Despite the high level of protection, there is evidence that the forests on Mount Kenya are still decreasing and being exploited in an unsustainable manner (e.g. Kenya Wildlife Service, 1999). Such activities may lead to changes in habitat structure, which can result in changes in microclimates at forest edges. These effects may influence mollusc faunas (Tattersfield, 1996; Tattersfield *et al.*, in press) and lead to the loss of sensitive, litter-dwelling microsnails. The findings reported here emphasize that Mount Kenya's forest mollusc fauna can only be satisfactorily conserved if areas of forest reflecting both altitudinal and climatic/rainfall gradients are retained. Unlike many vertebrate species, it is likely that the majority of the forest mollusc fauna may be conserved in relatively small blocks of forest.

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REFERENCES

- Bishop, M.J. (1977) The Mollusca of acidic woodland in west Cork and Kerry. *Proceedings of the Royal Irish Academy B*, **13**, 227–244.
- Boughey, A.S. (1955a) The nomenclature of the vegetation zones of the mountains of Africa. *Webbia*, **11**, 413–423.
- Boughey, A.S. (1955b) The vegetation of the mountains of Biafra. *Proceedings of the Linnean Society of London, Session 165, 1952–53, Part 2*, pp. 144–150.
- Burgess, N.D., Clarke, G.P. & Rodgers, W.A. (1998) Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biology Journal of the Linnean Society*, **64**, 33–367.

- Bussmann, R.W. (1994) *The forests of Mount Kenya (Kenya). Vegetation, ecology, destruction and management of a tropical forest ecosystem*. PhD Thesis, Bayreuth University, Germany.
- Cameron, R.A.D. (1978) Terrestrial snail faunas of the Malham area. *Field Studies*, **4**, 715–728.
- Cameron, R.A.D. (1992) Land snail faunas of the Napier and Oscar Ranges, western Australia; diversity, distribution and speciation. *Biology Journal of the Linnean Society*, **445**, 271–285.
- Chapman, J.D. & White, F. (1970) *The evergreen forests of Malawi*. Commonwealth Forestry Institute. University of Oxford, Oxford, UK.
- Coetzee, J.A. (1967) Pollen analytical studies in East and South Africa. *Palaeoecology of Africa and of the surrounding islands and Antarctica* (ed. E.M. van Zinderen Bakker) pp. 1–145. A.A. Balkema, Cape Town and Amsterdam.
- Coney, C.C., Tarpley, W.A., Warden, J.C. & Nagel, J.W. (1982) Ecological studies of land snails in the Hiwassee River Basin of Tennessee, USA. *Malacological Review*, **15**, 69–106.
- Connolly, M. (1922) Notes on non marine Mollusca with description of many new species. *Annals and Magazine of Natural History Series 9*, **59**, 485–517.
- Connolly, M. (1929) Notes on non marine Mollusca with description of many new species (concluded). *Annals and Magazine of Natural History Series 10*, **3**, 165–179.
- Cowie, R.H., Nishida, G.M., Basset, Y. & Gon, S.M. (1995) Patterns of land snail distribution in a montane habitat on the island of Hawaii. *Malacologia*, **36**, 155–169.
- De Winter, A.J. & Gittenberger, E. (1998) The land snail fauna of a square kilometer of rainforest in SW Cameroon: high species richness, low abundance and seasonal fluctuations. *Malacologia*, **40**, 231–250.
- Eeely, H.A.C., Lawes, M.J. & Piper, S.A. (1999) The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. *Journal of Biogeography*, **26**, 595–617.
- Emberton, K.C. (1997) Diversities and distributions of 80 land-snail species in southeastern-most Madagascan rainforests, with a report that lowlands are richer than highlands in endemic and rare species. *Biodiversity and Conservation*, **6**, 1137–1154.
- Emberton, K.C., Pearce, T.A. & Randalana, R. (1996) Quantitatively sampling land-snail species richness in Madagascan rainforests. *Malacologia*, **38**, 203–212.
- Emberton, K.C., Pearce, T.A., Kasigwa, P.F., Tattersfield, P. & Habibu, Z. (1997) High diversity and regional endemism in land snails of eastern Tanzania. *Biodiversity and Conservation*, **6**, 1123–1136.
- ESRI (1992–1999) *ArcView GIS 3.2*. Environmental Systems Research Institute Inc. Redlands, California, USA.
- Germain, L. (1931) La faune malacologique des hautes montagnes de l'Afrique orientale. *Mémoires Société de Biogéographie, Paris*, **2**, 337–356.
- Hamilton, A.C. (1974) Distribution of patterns of forest trees in Uganda and their historical significance. *Vegetatio*, **29**, 21–35.
- Hamilton, A.C. (1975) A quantitative analysis of altitudinal zonation in Ugandan forests. *Vegetatio*, **30**, 99–106.
- Hamilton, A.C. (1998) Vegetation, climate and soil: altitudinal relationships on the East Usambara mountains, Tanzania. *Journal of East African Natural History*, **87**, 85–89.
- Hamilton, A.C. & Perrott, R.A. (1981) A study of altitudinal zonation in the montane forest belt of Mt. Elgon, Kenya/Uganda. *Vegetatio*, **45**, 107–125.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta diversity on geographical gradients in Britain. *Journal of Animal Ecology*, **61**, 151–158.
- Hawkins, A.F.A. (1999) Altitudinal and latitudinal distribution of east Malagasy forest bird communities. *Journal of Biogeography*, **26**, 447–458.
- Hedberg, O. (1951) Vegetation belts of the East African mountains. *Svensk Botanisk Tidskrift*, **45**, 140–202.
- Iversen, S.T. (1991) The Usambara Mountains, NE Tanzania: phytogeography of the vascular plant flora. *Acta Universitatis Upsaliensis, Symbolae Botanicae Upsalienses*, **29**, 3.
- Kenya Wildlife Service (1999) *Aerial survey of the destruction of Mt. Kenya, Imenti and Ngare Ndare forest reserves*. Forest Conservation Programme Report, August 1999.
- KIFCON (1994) *Forest inventory report no. 6. Mount Kenya and Thunguru Hill*. Kenya Indigenous Forest Conservation Programme, Nairobi.
- Langdale-Brown, I., Osmaston, H.A. & Wilson, J.G. (1964) *The vegetation of Uganda*. The Government Printer, Entebbe, Uganda, 159 pp.
- Lauscher, F. (1976) Weltweite Typan der Hohenabhanm gigkeit des Niederschlags. *Wetter und Leben*, **28**, 80–90.
- Lawes, M.J., Eeley, H.A.C. & Piper, S.E. (2000) The relationship between local and regional diversity of indigenous forest fauna in KwaZulu-Natal Province, South Africa. *Biodiversity and Conservation*, **9**, 683–705.
- Lockwood, L. (1995) Mount Kenya under threat. *Swara*, **18**, 5.
- Lovett, J.C. (1996) Elevational and latitudinal changes in tree associations and diversity in the Eastern Arc mountains of Tanzania. *Journal of Tropical Ecology*, **12**, 629–650.
- Lovett, J.C., Clarke, G.P., Moore, R. & Morrey, G.H. (2001) Elevational distribution of restricted range tree taxa in eastern Tanzania. *Biodiversity and Conservation*, **10**, 541–550.
- Magurran, A.E. (1988) *Ecological diversity and its measurement*. Croom Helm, London.
- Milne, G. (1937) *Essays in applied pedology, 1. Soil type and management in relation to plantation agriculture in East Usambara*. *East African Agricultural Journal*, **3**, 7–20.
- Nekola, J.C. & Smith, T.M. (1999) Terrestrial gastropod richness patterns in Wisconsin carbonate cliff communities. *Malacologia*, **41**, 253–269.
- Pickford, M. (1995) Fossil land snails of East Africa and their palaeoecological significance. *Journal of African Earth Sciences*, **20**, 167–226.
- Poynton, J.C. & Boycott, R.C. (1996) Species turnover between Afromontane and eastern African lowland faunas: patterns shown by amphibians. *Journal of Biogeography*, **23**, 669–680.
- Preston, H.B. (1911) Description of thirty-six new species of land and freshwater shells from British East Africa, chiefly from Mt. Kenya and the neighbouring district. *Annals and Magazine of Natural History, Series 8*, **7**, 463–476.

- Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200–205.
- Richards, P.W. (1996) *The tropical rain forest*, 2nd edn. Cambridge, CUP.
- Scharff, N. (1992) The linyphiid fauna of eastern Africa (Araneae: Linyphiidae) – distribution patterns, diversity and endemism. *Biology Journal of the Linnean Society*, **45**, 117–154.
- Solem, A. (1984) A world model of land snail diversity and abundance. *World-wide Snails. Biogeographical studies on non-marine Mollusca*. (eds A. Solem and A.C. van Brugger) pp. 6–22. E.J. Brill, Leiden.
- Stuart, S.N. (1983) *Biogeographical and ecological aspects of forest bird communities in eastern Tanzania*. PhD Thesis, Cambridge University, UK.
- Tattersfield, P. (1990) Terrestrial mollusc faunas from some south Pennine woodlands. *Journal of Conchology*, **33**, 355–374.
- Tattersfield, P. (1995) A new species of *Truncatellina* (Gastropoda: Vertiginidae) from Mount Kenya and new distributional records of *Truncatellina ninagongonis* (Pilsbry) from East Africa. *Journal of Conchology*, **35**, 243–247.
- Tattersfield, P. (1996) Local patterns of land snail diversity in a Kenyan rainforest. *Malacologia*, **38**, 161–180.
- Tattersfield, P. (1998) Patterns of diversity and endemism in East African land snails, and the implications for conservation. *Journal of Conchology, Special Publication No. 2*, 77–86.
- Tattersfield, P., Seddon, M.B., Meena, C., Kayumbo, N. & Kasigwa, P. (1998) Ecology and conservation of the land-snails of the Eastern Arc Mountains. *Journal of East African Natural History*, **87**, 119–138.
- Tattersfield, P., Paul, C.R.C. & Allen, J.A. (2001) *Columella* in sub-Saharan Africa: a range extension of over 4000 kilometres? *Journal of Conchology*, **37**, 281–284.
- Tattersfield, P., Seddon, M.B. & Lange, C. (in press) Land-snail faunas in indigenous rainforest and commercial forestry plantations in Kakamega Forest, Western Kenya. *Biodiversity and Conservation*, in press.
- Taylor, D. (1996) Mountains. *The physical geography of Africa* (eds W.M. Adams, A.S. Goudie and A.R. Orme). pp. 287–306. Oxford University Press, Oxford, UK.
- Ter Braak, J.F. (1991) *CANOCO Version 3.12*. Agricultural Mathematics Group, Wageningen, The Netherlands.
- Trapnell, C.G. & Brunt, M.A. (1976) *Climate map to accompany 1:250,000 Kenya Vegetation Map Sheet 2, D.O.S. (L.R.) 3006*. Directorate of Overseas Surveys, UK.
- Verdcourt, B. (1972) The zoogeography of the non-marine Mollusca of East Africa. *Journal of Conchology*, **27**, 291–348.
- Verdcourt, B. (1983) Checklist of non-marine molluscs of East Africa. *Achatina*, **11**, 200–239.
- Verdcourt, B. (1998) *Subuliniscus adjacens* Connolly (Gastropoda, Pulmonata, Subulinidae) on Mount Kenya, East Africa. *Basteria*, **62**, 123–124.
- Waldén, H. (1981) Communities and diversity of land molluscs in Scandinavian woodlands. 1. High diversity communities in taluses and boulder slopes in SW Sweden. *Journal of Conchology*, **30**, 351–372.
- Warebörn, I. (1969) Land molluscs and their environments in an oligotrophic area in southern Sweden. *Oikos*, **20**, 461–479.
- Warui, C.M. (1998) *Diversity, species composition and some ecological aspects of terrestrial molluscs in Mt. Kenya National Park, Kenya*. MSc Thesis, University of Nairobi, Kenya.
- Warui, C.M., Tattersfield, P. & Seddon, M.B. (2001) Annotated checklist of terrestrial molluscs of Mount Kenya, Kenya. *Journal of Conchology*, **37**, 291–300.
- Wass, P. (ed.) (1995) *Kenya's indigenous forests: status, management and conservation*. IUCN, Gland, Switzerland, and Cambridge, UK.
- White, F. (1983) *The vegetation of Africa*. UNESCO, Paris.
- Whittaker, R.M. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.
- Wielochowski, A.L. & Savage, M. (1988) *Mount Kenya 1:50,000 map and guide*. West Col Productions, UK.

BIOSKETCHES

Charles Warui recently completed his MSc at Nairobi University and currently works in Invertebrate Zoology at the National Museums of Kenya, where he is compiling inventories of soil invertebrates in Kenyan forests and savannas, and curating mollusc and spider collections.

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Appendix I Matrix of species morphospecies (with family names and sites)

Species	Kamweti transect				Chogoria transect				Sirimon transect				Naro Moro transect			
	K1	K2	K3	K4	C1	C2	C3	C4	S1	S2	S3	S4	N1	N2	N3	N4
Hydrocenidae																
<i>Hydrocena kenyana</i> Connolly	0	0	0	0	0	0	0	0	0	0	0	0	8	2	4	0
Cyclophoridae																
<i>Elgonocylus koptawelilensis</i> (Germain)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Maizaeniidae																
<i>Maizania volkensis</i> (von Martens)	16	0	4	9	0	0	3	40	0	0	0	0	2	19	17	0
Vertiginidae																
<i>Lauria desiderata</i> (Preston)	0	0	0	0	0	0	0	0	487	42	130	1	9	86	110	0
<i>Negulus kenianus</i> (Preston)	2	3	6	8	0	0	0	2	0	0	0	0	0	11	18	0
<i>Truncatellina arboricola</i> Tattersfield	0	0	0	0	0	0	0	0	0	0	4	0	0	1	2	0
<i>Truncatellina pygmaeorum</i> (Pilsbry and Cockerell)	0	0	0	0	0	0	0	0	14	63	5	0	0	1	2	2
<i>Truncatellina</i> sp. A	0	0	0	0	0	0	0	0	0	4	0	0	0	0	5	0
Valloniidae																
<i>Acanthinula expatriata</i> Preston	2	0	0	0	0	0	0	0	2	34	17	8	1	18	6	0
<i>Pupisoma</i> sp. A	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Pupisoma</i> sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
<i>Pupisoma barpula</i> (Reinhardt)	0	0	0	8	0	0	0	6	0	0	0	0	0	0	0	15
<i>Pupisoma orcula</i> (Benson)	0	0	4	1	0	0	0	14	0	1	0	0	0	0	4	8
<i>Pupisoma renschi</i> K.L. Pfeiffer	0	0	0	0	0	0	0	0	0	0	13	7	0	31	34	218
Enidae																
<i>Edonardia turricola</i> Preston	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Rhachidina chiradzuluensis</i> (E.A.Smith)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Subulnidae																
<i>Curvella</i> nr. <i>elgonensis</i> Connolly	0	16	25	83	1	0	0	0	0	0	0	0	0	0	0	0
<i>Curvella delicatosa</i> Preston	1	0	0	0	0	0	0	1	0	0	0	0	11	0	1	0
<i>Nothapalus dobertyi</i> (E.A.Smith)	0	6	26	63	0	0	0	181	0	0	1	0	0	0	0	0
<i>Nothapalus suturalis</i> (Preston)	17	5	2	34	45	0	0	0	0	0	0	11	2	0	0	0
<i>Oreohomorus</i> cf. <i>nitidus</i> (von Martens)	3	0	1	1	0	8	1	0	0	0	0	0	0	0	0	0
<i>Pseudopeas</i> sp. A	1	0	0	1	0	5	2	0	0	0	40	3	0	0	0	52
<i>Pseudopeas</i> sp. B	17	5	14	4	0	18	7	2	0	2	7	0	13	39	39	0
<i>Subuliniscus adjacens</i> Connolly	0	0	0	0	0	0	0	0	4	0	0	0	1	0	0	1
<i>Subulona egregia</i> (Preston)	0	0	0	8	0	3	3	14	0	0	0	0	0	0	0	0
Achatinidae																
<i>Limicolariopsis inepta</i> (Preston)	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0	3
<i>Limicolariopsis keniana</i> (E.A.Smith)	3	0	3	6	0	0	0	1	0	0	0	0	0	0	1	11
<i>Limicolariopsis verdcourti</i> Crowley and Pain	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Endodontidae <i>sensu lato</i>																
<i>Punctum</i> cf. <i>pallidum</i> Connolly	1	21	8	0	4	0	0	0	18	14	52	0	14	41	31	25
<i>Punctum</i> sp. C	0	0	1	0	0	0	0	0	65	163	358	46	0	13	6	36
<i>Punctum</i> sp. D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
<i>Punctum ugandanum</i> (E.A.Smith)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
<i>Trachycystis ariel</i> (Preston)	0	0	0	7	0	0	1	2	0	0	0	0	0	0	1	2

<i>Trachycystis iredalei</i> Preston	0	3	1	2	0	0	0	0	2	0	0	0	0	6	0	0	0	0	0	5	5
<i>Trachycystis lamellifera</i> (E.A.Smith)	0	0	0	0	0	0	0	0	0	0	37	38	13	0	0	0	0	0	0	54	90
Virimidae																					
<i>Vitina cf. lactea</i> Connolly	18	20	5	15	3	4	17	27	0	0	0	0	0	0	0	13	3	6	0	0	0
Helicariionidae																					
<i>Kaliella barrakaporensis</i> (Pfeiffer)	1	1	0	28	0	0	2	9	0	3	0	0	0	0	0	0	0	0	0	0	29
<i>Kaliella iredalei</i> Preston	0	3	0	2	0	0	0	5	12	7	24	19	19	11	17	26	4				
Euconulidae																					
<i>Afrocnulus iredalei</i> (Preston)	0	2	1	6	0	0	5	2	0	0	0	0	0	0	0	1	0	1	0	0	1
<i>Afrognypya quadrisculpta</i> (Connolly)	0	0	0	10	0	1	4	11	0	0	0	0	0	0	0	6	18	80			
<i>Afrognypya numurutensis</i> (Preston)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	2	3			
Urocyclidae																					
<i>Shelled urocyclid</i> sp. A *	0	3	2	5	0	3	3	3	0	0	0	0	0	0	0	1	7	7	0	0	0
<i>Trochonanina</i> sp. A *	4	1	1	16	3	5	3	0	1	0	0	0	0	0	3	2	0	2			
<i>Trochonanina</i> sp. B *	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0			
<i>Trochozonites</i> (<i>Zonitotrochus</i>) sp. A	4	1	0	1	0	0	1	3	0	0	0	0	0	0	0	0	0	0			
<i>Trochozonites medjensis</i> Pilsbry	0	8	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	2			
<i>Trochonanina</i> sp. C *	2	0	0	1	6	1	0	0	2	0	0	0	0	0	6	2	4	0			
' <i>Vitina</i> ' <i>baringoensis</i> E.A.Smith	13	27	12	5	69	8	16	6	147	597	598	44	67	172	130	14					
Bradybaenidae																					
<i>Helicid</i> sp. A *	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0			
<i>Vicariibelix gregorii</i> (E.A. Smith)	9	21	22	14	0	1	12	19	0	0	7	0	0	0	0	0	0	0			
<i>Helicid</i> sp. C *	0	2	1	0	0	0	1	1	0	2	2	1	4	0	7	0	0	0			
<i>Halolimnobelix</i> cf. <i>iredalei</i> Connolly	1	0	0	0	1	0	0	2	25	6	9	3	0	0	0	0	0	0			
<i>Vicariibelix</i> cf. <i>mukulensis</i> (Pilsbry)	0	0	6	11	1	0	0	0	0	0	0	0	1	6	5	9					
<i>Halolimnobelix planulata</i> (Preston)	5	1	22	9	0	0	1	0	0	1	0	0	0	2	0	0	0	0			
Streptaxidae																					
<i>Gulella ugandensis</i> <i>ugandensis</i> (E.A.Smith)	5	0	0	15	0	3	1	1	4	0	0	0	0	0	4	1	0	0			
<i>Gulella columella</i> (E.A.Smith)	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	7	6				
<i>Gulella princei</i> (Preston)	2	2	0	1	4	0	1	0	0	0	10	0	3	0	24	1					
<i>Gulella insolita</i> (E.A.Smith)	3	1	3	0	2	0	0	8	1	5	0	6	7	16	15						
<i>Gulella pervitrea</i> (Preston)	0	0	0	0	0	0	14	19	0	0	0	0	0	0	0	0	0	0			
<i>Gulella pilula</i> (Preston)	0	0	0	6	0	0	1	2	0	0	0	0	0	0	0	0	0	0			
<i>Gulella pretiosa pretiosa</i> (Preston)	0	0	0	20	0	0	0	6	0	0	0	0	0	0	0	0	0	0			
<i>Gulella simplicima</i> (Preston)	0	2	0	1	1	0	0	68	10	9	0	0	0	18	20	1					
<i>Gonaxis</i> cf. <i>imocens</i> (Preston)	0	0	1	1	4	6	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Ptychotrema uniliratum</i> (E.A.Smith)	5	0	1	2	16	0	0	0	0	0	0	0	0	0	13	39	7				
<i>Streptostele</i> cf. <i>crassiremulata</i> Connolly	11	3	5	8	3	0	0	3	42	11	0	0	14	3	19	2					
<i>Streptostele</i> cf. <i>exasperata</i> Preston	2	0	0	2	0	0	0	3	57	48	45	0	10	3	63						
<i>Streptostele</i> sp. C	0	3	0	0	0	0	4	35	0	0	0	25	0	0	0	0	0				
<i>Tayloria</i> near <i>marsabitensis</i> (Preston)	0	0	0	0	0	6	7	1	0	0	0	0	0	0	0	0	0	0			
Unidentified spp.	5	1	0	9	3	1	1	3	2	0	1	0	5	6	8	21					

Data are number of specimens (dead plus living).

Nomenclature for species and morphospecies follows Warui *et al.* (2001), except species marked as *.

Families follow Verdcourt (1983).