RESILIENT FOREST FAUNAL COMMUNITIES IN SOUTH AFRICA: A LEGACY OF PALEOCLIMATIC CHANGE AND EXTINCTION FILTERING?

M. J. Lawes, H. A.C. Eeley, N. J. Findlay and D. Forbes
Forest Biodiversity Research Unit, School of Biological and Conservation Sciences,
University of KwaZulu-Natal, Pietermaritzburg

In press: Journal of Biogeography

Abstract

Spatial patterns in the distribution of vertebrate taxa (birds, mammals and frogs) in the indigenous forests of South Africa were examined to investigate the large-scale, historical processes that have shaped contemporary assemblage composition, patterns of species richness and regional endemism. Climatic extinction filtering during and immediately after the Last Glacial Maximum (LGM, approximately 18,000 years BP) and the subsequent re-radiation of forest faunas have had a major influence on forest faunas in the region. Three broad forest types are identified: Afrotemperate, scarp and Indian Ocean coastal belt forests, with different evolutionary histories. The major pattern in Afrotemperate forest is one dominated by climatic extinction filtering and the infiltration of communities by generalist species from matrix habitats, supplemented in the northern and central regions by re-colonisation from refugia located principally along the scarp forest belt in KwaZulu-Natal and the Eastern Cape, and in frogs by autochthanous speciation in localised, minor refugia, particularly in the southern and western Cape. Afrotemperate forest communities are largely unsaturated, they have a lower overall species richness and contain fewer forest dependent species than do coastal or scarp forest assemblages, but they are relatively robust and resilient to further perturbation. The scarp forests of KwaZulu-Natal and the Eastern Cape mark a belt along which Afrotemperate forest refugia occurred during the LGM and which today represents a contact zone between Afrotemperate and coastal belt forest. Species richness in all three taxa reached a peak in northern KwaZulu-Natal, where central Afrotemperate (mistbelt), scarp and coastal forests lie in close proximity, and decreased to the north, west and south of this region. Contemporary faunal communities in Indian Ocean coastal belt forests are primarily due to the post LGM radiation of faunas down the eastern seaboard from tropical East African refugia. The response of different vertebrate taxa to large-scale, historical processes is largely dependent on their relative mobility: more mobile taxa being better able to respond to unfavourable conditions and to recover through re-colonisation following climatic perturbation. Thus, in South Africa, forest birds best illustrate patterns resulting from post-glacial faunal radiation, while among mammals and frogs the legacy of climatic extinction filtering remains stronger.

1. Introduction

Large-scale regional and historical processes (e.g., speciation, extinction, geographical dispersal and paleoclimatic change) have dominated local ecological processes in determining the composition of forest faunal assemblages in South Africa (Lawes, 1990; Lawes *et al.*, 2000). Here we examine two regional processes believed to have most influenced the distribution and assemblage structure of forest fauna in southern Africa: climatic extinction filtering (*sensu* Balmford, 1996) and the radiation of forest faunas following the last glacial maximum (LGM, approximately 18,000 yr BP). We argue that prior exposure to environmental challenges, such as climatic fluctuation, has purged communities of their less robust taxa, leaving a core set of species that are relatively resilient to further pressure (Coope, 1995; Jackson, 1995; Balmford, 1996; Danielsen, 1997).

South African forests are broadly divided into three main types: inland Afrotemperate forests, subtropical Indian Ocean coastal belt forests and, between the two, a band of scarp forests that comprise a mix of Afrotemperate and coastal flora and fauna, along with paleoendemic species and relict tropical elements (White, 1983; Cooper, 1985; Low & Rebelo, 1996; Midgley *et al*., 1997; von Maltitz *et al.*, 2003) (Figure 1).

We test three main hypotheses:

(1) Afrotemperate forest faunas are the outcome of extinction filtering events during the LGM and the subsequent re-radiation of species from scarp forest refugia.

(2) Coastal and scarp forest faunas are primarily due to post LGM radiation events, as opposed to filtering or extirpation events.

(3) Scarp forests mark a belt along which Afrotemperate forest refugia occurred during the LGM and today represent the remnants of a contact zone between Afrotemperate and coastal belt forest.

2. Methods

Twenty one forest sub-regions were identified and assigned to one of the three major forest types; Afrotemperate, scarp and Indian Ocean coastal belt.

Data comprised species presence-absence by quarter-degree grid cell (total 288 grid cells) for forest-dependent and forest-associated birds, non-volant mammals and frogs. Data were collated from the Southern African Bird Atlas Project (SABAP: Harrison *et al.*, 1997), Southern African Frog Atlas Project (SAFAP: Minter *et al.*, 2004), University of Pretoria (Keith, 2004) and Ezemvelo KZN Wildlife, and augmented outside South Africa with descriptions and distribution maps from the literature. In total 174 bird, 99 mammal and 42 frog species were identified, of which 58, 25 and 20 species were forest dependent, respectively.

Single grid cells were treated as representative of individual forests or forest complexes, an assumption which was validated prior to analysis. Analyses focused on forest dependent bird species, but as most grid cells held <5 forest dependent mammal or frog species both forest dependent and forest associated species were included for these taxa.

Differences among forest types were examined though patterns and gradients of species richness and endemism, assemblage similarity, species turnover (β diversity indices) and coefficients of species dispersal direction. Alternative biogeographic hypotheses for the radiation of forest faunas in Southern Africa were tested.

3. Results

3.1 General biogeographical patterns

Across selected forests, mean total richness and mean number of forest dependent species were significantly lower in Afrotemperate forests than in scarp or coastal forests supporting the hypothesis that Afrotemperate assemblages are less species rich as a result of past extinction filtering events (Table 1). Mean total richness and mean number of forest dependent species were highest either in scarp forests, supporting the hypothesis that these were paleorefugia in which specialist species persisted through the LGM and now represent a species rich contact zone, or in coastal forest, which is also plausible in this younger, more dynamic forest type (Table 1).

There was considerable overlap in species between forest types, particularly for birds. Among forest dependent bird species similarity was highest between scarp and coastal forests (Table 2). In contrast, among forest dependent mammal species similarity was highest between scarp and Afrotemperate forests (Table 2). This suggests that for birds scarp forests have experienced relatively recent species enrichment from coastal forest, while the historical link between Afrotemperate and scarp forest is better demonstrated among mammals. The low similarity between Afrotemperate and scarp or coastal forest frog assemblages (Table 2) is due to several localised Afrotemperate endemics.

Despite these broad similarities there were significant differences in the assemblage composition across all forest types, suggesting the faunal assemblages have independent evolutionary histories (MRPP Birds: T = -29.607, P < 0.001, A = 0.190; Mammals, T = -9.577, P < 0.001, A = 0.036; Frogs T = -19.068, P < 0.001, A = 0.113).

Although scarp forest occurs over a shorter latitudinal gradient than Afrotemperate forest, the turnover (β_{sim}, Lennon *et al.*, 2001) of species in scarp forest was higher than in either Afrotemperate or coastal forest (Table 3). This change in assemblage composition along the scarp forest belt is a reflection of its complex evolutionary history, the location of paleorefugia along this belt, and the infiltration of coastal forest elements in the north. When the length of the latitudinal gradient was accounted for (β_{H1}, Harrison *et al.*, 1992), species turnover of birds and mammals was lowest in Afrotemperate forest (Table 3), providing further support for the hypothesis that the regional pool of Afrotemperate forest species has been reduced to a common suite of relatively robust or resilient species as a result of past climatic extinction filtering.

3.2 Patterns of faunal radiation

A series of biogeographic hypotheses for the radiation of forest faunas in South Africa were examined.

3.2.1 Coastal forest

Hypothesis: *Following the LGM, Indian Ocean coastal belt forest expanded from tropical East African refugia down the Mozambican coast and into northern KwaZulu-Natal, accompanied by a radiation of Afrotropical faunas into the region*.

Support:
(1) The similarity between faunas of adjacent coastal sub-regions was generally high (birds: 61.8-86.7%; mammals: 57.1-67.7%; frogs: 38.9-70.0%).
(2) There was a southward decrease in the species richness along the coastal plain from central to southern Mozambique (Figure 2).
(3) Two species were endemic to the coastal sub-regions.
(4) The central and south Mozambique coast clustered with the KwaZulu-Natal sand forest sub-region (and were linked to the geographically proximate but Afrotemperate eastern highlands of Zimbabwe) (Figure 3).

Faunal interchange between the KwaZulu-Natal scarp and KwaZulu-Natal coast sub-regions explains their high similarity (Figure 3), the increase in species richness in the KZN coast and KZN sand sub-regions (Figure 2), and the dominant south to north direction of species dispersal from the KZN coast to the southern Mozambique.

3.2.2 Scarp forest

Hypothesis: *Afrotemperate faunas survived the LGM in refugia located along the scarp forest belt in KwaZulu-Natal and the Eastern Cape, from which they have subsequently re-radiated, and with the expansion of coastal forest into northern KwaZulu-Natal from Mozambique, Afrotropical elements entered scarp forest along its north-eastern edge*.

Support:
(1) Species richness was generally higher in scarp forest sub-regions than in adjacent Afrotemperate or coastal sub-regions (Figure 2).
(2) Two species were endemic to the scarp forest sub-regions.
(3) The dominant direction of species dispersal was from scarp to neighbouring Afrotemperate forest sub-regions.
(4) Assemblage similarity was high between scarp and adjacent coastal and Afrotemperate sub-regions, particularly among birds (birds: 75.0-90.2%; mammals: 38.5-84.6%; frogs: 66.7-86.7%).
(5) Ten forest dependent species were restricted to the scarp and coastal forest sub-regions, and the Zimbabwe highlands, providing evidence for a radiation route for forest faunas extending along the Mozambique coast into South Africa and penetrating the scarp forest belt.
(6) There was a southward decline in species richness along the scarp forest belt (Figure 2).

3.2.3 Afrotemperate forest

Because Afrotemperate forest covers a larger geographical area and has a more complex evolutionary history than coastal or scarp forest, we examined potential radiation routes in three broad areas: (1) northern (Mpumalanga and Limpopo Province) (2) central (KwaZulu-Natal and the Eastern Cape), and (3) southern (Western Cape Province)

Two hypotheses are common to all three areas: (1) *despite adverse conditions forest faunas persisted through the LGM in situ in local refugia*, and (2) *following the LGM, barriers to dispersal remained effective and faunal assemblages largely comprise matrix species that have invaded the forest biome*.

Support:
(1) Three endemic forest dependent mammal species, one in the northern area, and two in the southern area, provide some evidence for the persistence of local Afrotemperate forest refugia. Greater support was found among frogs, with eight endemic forest dependent species: one in the northern area, one in the central area, and six in the southern area.
(2) Habitat generalists made up a high proportion of Afrotemperate sub-regional assemblages in all three areas examined (northern: 74.0-76.9%, 89.6-94.1%, 80.0-90.9%; central: 71.3-79.6%, 90.0-96.9%,

66.7-90.0%; southern: 73.8-76.9%, 90.6-96.0%, 64.3-87.5%, for birds, mammals and frogs, respectively), supporting the hypothesis that empty niches in these climatically filtered Afrotemperate forests have been filled by matrix species, particularly in taxa with a poorer dispersal ability (mammals and frogs).

A third hypothesis was examined in each of the three broad areas: *contemporary Afrotemperate faunas are a result of re-colonisation from scarp forests following the LGM*.

3.2.3.1 In the northern area:

(1) There was little evidence to suggest re-colonisation of these forests from the Zimbabwe highlands to the north. Assemblage similarity between northern Afrotemperate sub-regions and the Zimbabwe highlands was low for all taxa (birds: 41.5-49.0%; mammals: 52.3-61.3%; frogs: 20.0-25.0%), and they did not cluster (Figure 3). This confirms the Limpopo River valley as a significant barrier to post LGM faunal dispersal (Clancey, 1994; Poynton & Boycott, 1996).
(2) There was also little evidence to support re-colonisation of these forests directly from the Mozambique coastal plain. The similarity between northern Afrotemperate assemblages and the Afrotropical assemblages of the central and south Mozambique coast was generally low (birds: 30.2-58.3%; mammals: 44.8-65.5%; frogs: 12.5-38.5%), and they did not cluster (Figure 3).
(3) Northern Afrotemperate assemblages were more similar to those of the scarp forest sub-regions to the immediate south (Swaziland and KZN scarp) than to those of either the Mozambique coast or Zimbabwe highlands (compare birds: 60.0-81.8%; mammals: 60.3-71.4%; frogs: 38.9-83.3% with values above), and this similarity decreased from south to north across the sub-regions of the northern area. Species richness also decreased south to north across the northern Afrotemperate sub-regions (Figure 2). Together this suggests that the primary radiation route into the area has been from the south via Swaziland and along the Mpumalanga Escarpment. Cluster analyses supported these results, particularly for mammals, with northern Afrotemperate sub-regions clustered with Swaziland, the KZN scarp and KZN coast, although for birds and frogs somewhat broader associations were indicated that included additional scarp and central Afrotemperate sub-regions (Figure 3). Five forest dependent species were found in various combinations of scarp, northern Afrotemperate, coastal and/or central Afrotemperate forests providing further support for this southerly dispersal route into the northern Afrotemperate forests and highlighting the central Afrotemperate/scarp/coastal area as one of faunal interchange.

3.2.3.2 In the central area:

There was a decrease in species richness and a dominant direction of species dispersal from scarp forest sub-regions to adjacent Afrotemperate sub-regions (Figure 2), and a close similarity in their assemblage composition. The primary re-colonisation route for higher altitude Afrotemperate forests was via the KZN mistbelt sub-region. This was clearly seen among birds, in which the KZN mistbelt was more similar to adjoining scarp sub-regions than were higher altitude sub-regions (75.6-79.0% vs. 46.3-64.7%), which in turn were more similar to the KZN mistbelt (61.3-77.4%). Only two forest dependent species were restricted to the central Afrotemperate and scarp forests, which is unsurprising given the complex history of radiation and species dispersal in the region. This complexity of inter-relationships between these central Afrotemperate forests, the scarp forests and northern and southern Afrotemperate forests was also illustrated by the cluster analyses (Figure 3).

3.2.3.3 In the southern area:

Among birds and mammals species richness declined from the scarp and Afrotemperate sub-regions of the Eastern Cape, through the Southern Cape and into the Western Cape (Figure 2). There was also a decline in the similarity of bird and mammal assemblages along this path: with Southern Cape faunas more similar to those of Amatole and Transkei Scarp sub-regions than to Western Cape faunas (birds: 68.8-71.0% vs. 46.9-48.4%; mammals: 35.0-60.0% vs. 30.6-50.0%), which in turn were more similar to the Southern Cape (birds: 68.2%, mammals: 58.3% and frogs: 37.5%). Three bird species and four mammal species were found only in southern Afrotemperate, central Afrotemperate and scarp forest sub-regions. Thus, there may have been some limited augmentation of southern Afrotemperate forest faunas by species dispersing into the region following the LGM from refugia located to the northeast, in the Eastern Cape. This was supported by the cluster analyses of these taxa (Figure 3).

No such southerly dispersal route was apparent for frogs, among which the pattern was dominated by a large increase in species richness in the Western Cape (Figure 2). Overall patterns of similarity for frogs were lower than among birds and mammals, although the Southern Cape fauna was again more similar to the Amatole and Transkei Scarp sub-regions than was the Western Cape fauna (46.0-54.5% vs. 25.0-27.8%). The southern Afrotemperate forest frog faunas are dominated by matrix (forest associated) species and an array of local, endemic species, particularly in the Western Cape sub-region.

4. Discussion

Afrotemperate, scarp and Indian Ocean coastal belt forests have different evolutionary histories. Afrotemperate faunas were dominated by climatic extinction filtering events during the LGM; they are relatively unsaturated and infiltrated by generalist species (Lawes *et al.*, 2000). In the northern and central regions this has been supplemented by re-colonisation from scarp forest refugia (Figure 4), and among frogs by autochthanous speciation in localised refugia, particularly in the south (Poynton & Boycott, 1996; Minter *et al.*, 2004). Scarp forests were Afrotemperate refugia during the LGM and are a contemporary overlap zone between Afrotemperate and coastal forest (Lawes, 1990; Eeley *et al.*, 1999; Lawes *et al.*, 2000). Coastal faunas derive mainly from post LGM radiation along the eastern seaboard from tropical East African refugia (Lawes, 1990; Clancey, 1994; Poynton & Boycott, 1996; Figure 4). The greatest diversity is achieved in scarp and coastal forest faunas in northern KwaZulu-Natal province. The response of different vertebrate taxa to large-scale, historical processes is largely dependent on their relative mobility (Williams, 1997): forest birds best illustrate patterns resulting from post-glacial faunal radiation, while among mammals and frogs the legacy of climatic extinction filtering remains stronger.

The confirmation that large-scale, historical processes have been important in shaping contemporary patterns of forest faunas has a number of implications for forest management and conservation. Most importantly, variation in past history has implications for the vulnerability of these faunas to modern pressures (Balmford, 1996). As a result of climatic extinction filtering in the past, Afrotemperate forest today supports relatively simple but robust communities, dominated by generalist species, which are likely to be highly resistant and very resilient to future challenges (Danielsen, 1997; Lawes *et al.*, 2000). Coastal and scarp forests, which have not experienced paleoclimatic extinction filters and are particularly species rich, are likely to be less resilient to future change and perturbation, and experience comparatively high rates of species loss. Second, while species may have responded to past challenges by movement across the landscape, human induced changes (habitat fragmentation, matrix habitat conversion) have limited their ability to do so in the future. Seeking landscape level connectivity between forest complexes along the radiation routes described in this study, may be one way of ensuring at least some level of natural response among forest faunas to future environmental challenges. Finally, the current emphasis on ‘fire-fighting’ in areas where threats are already extensive should be reviewed and efforts should be partly redirected towards potentially more rewarding pre-emptive conservation in relatively untouched and therefore vulnerable areas. In this regard, the most proactive approach is to identify biologically rich assemblages that have been exposed to only moderate levels of habitat loss or other threats, such as the scarp and Indian Ocean coastal belt forests of northern KwaZulu-Natal, and to develop conservation plans that incorporate the role of historical and large-scale processes in maintaining species richness in these areas.

Acknowledgements

Our thanks to Craig Morris, David Ward, Johan Kotze and Megan Griffiths for their advice and comments on an earlier draft of this work. This research was supported by the SA National Research Foundation (NRF), Focus Area Programme: Conservation and Management of Ecosystems and Biodiversity (Gun 2069339). We are also grateful to the Mazda Wildlife Fund, which has provided us with transport over the years.

References

BALMFORD, A. (1996). Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution* 11: 193-196.

CLANCEY, P.A. (1994). Combined biogeographic role of river valleys and aridity in Southern African bird distribution. *Durban Museum Novitates* 19: 13-29.

COOPE, G.R. (1995) Insect faunas in ice age environments: why so little extinction? In: J.H. LAWTON & R.M. MAY (eds.) *Extinction Rates.* Oxford University Press, Oxford. pp. 55-74.

COOPER, K.H. (1985). *The Conservation Status of Indigenous Forests in Transvaal, Natal and O.F.S., South Africa*. Wildlife Society of South Africa, Durban.

DANIELSEN, F. (1997). Stable environments and fragile communities: does history determine the resilience of avian rain-forest communities to habitat degradation? *Biodiversity and Conservation* 6: 423-433.

EELEY, H.A.C., LAWES, M.J. & PIPER, S.E. (1999). The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. *Journal of Biogeography* 26: 595-617.

HARRISON, J.A., ALLAN, D.G., UNDERHILL, L.G., HERREMANS, M., TREE, A.J., PARKER, V. & BROWN, C.J. (1997). *The Atlas of Southern African Birds*. Birdlife South Africa, Johannesburg.

HARRISON, S.H., ROSS, S.J. & LAWTON, J.H. (1992). Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61: 151-158.

JACKSON, J.B.C. (1995). Constancy and change of life in the sea. In: J.H. Lawton & R.M. May (eds.). *Extinction Rates*. Oxford University Press, Oxford. pp. 45-54.

KEITH, M. (Technical Editor) (2004). *Geographic Information System (GIS) data of South African mammal taxa*. Department of Zoology and Entomology, University of Pretoria, South Africa. Accessed online: http://zoology.up.ac.za/samammals/

LAWES, M.J. (1990). The distribution of the samango monkey (*Cercopithecus mitis erythrarchus* Peters, 1852 and *Cercopithecus mitis labiatus* I. Geoffroy, 1843) and forest history in southern Africa. *Journal of Biogeography* 17: 669-680.

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.

LENNON, J.J., KOLEFF, P., GREENWOOD, J.J.D. & GASTON, K.J. (2001). The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70: 966-979.

LOW, A.B. & REBELO, A.G. (eds.) (1996). *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria.

MIDGLEY, J.J., COWLING, R.M., SEYDACK, A.H.W. & VAN WYK, G.F. (1997). Forest. In: R.M. COWLING, D.M. RICHARDSON & S.M. PIERCE (eds.). *Vegetation of Southern Africa*. Cambridge University Press, Cambridge. pp. 278-299.

MINTER, L.R, BURGER, M., HARRISON, J.A., BRAACK, H.H., BISHOP, P.J. & KLOEPFER, D. (eds.) (2004). *Atlas and Red Data Book of the Frogs of South Africa, Lesotho and Swaziland*. SI/MAB Series #9, Smithsonian Institution, Washington DC.

POYNTON, J.C. (1961). Contribution to the zoogeography of southern Africa. *South African Journal of Science* 57: 75-80.

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.

VON MALTITZ, G., MUCINA, L., GELDENHUYS, C., LAWES, M.J., EELEY, H.A.C., ADIE, H., VINK, D., FLEMING, G & BAILEY, C. (2003). *Classification System for South African Indigenous Forests: An objective Classification for the Department of Water Affairs and Forestry*. Environmentek Report ENV-P-C 2003-017, CSIR, Pretoria.

WHITE, F. (1983). *The Vegetation of Africa*. United Nations, Paris.

WILLIAMS, S.E. (1997). Patterns of mammalian species richness in the Australian tropical rainforests: are extinctions during historical contractions of the rainforest the primary determinants of current regional patterns in biodiversity? *Wildlife Research* 24**:** 513-530.

Addendum

Table 1. **Total species richness and number of forest dependent species of birds, mammals and frogs occurring in selected Afrotemperate, scarp and coastal forests in South Africa. Highest values highlighted in bold**

	No. forests (grid cells)	Mean ± 1SE total richness[1]	Mean ± 1SE forest dependents[1]
Birds			
Afrotemperate	50	79.5 ± 2.8	19.3 ± 1.0 (50)
Scarp	16	100.8 ± 3.3 ***	**28.0 ± 1.3 (16)** ***
Coastal	13	**106.6 ± 3.1** ***	26.3 ± 1.2 (13) ***
Mammals			
Afrotemperate	47	18.6 ± 1.5	1.2 ± 0.2 (47)
Scarp	12	22.0 ± 2.3 *	**3.5 ± 0.4 (12)** ***
Coastal	13	**24.5 ± 2.8** ***	3.2 ± 0.4 (13) ***
Frogs			
Afrotemperate	50	7.3 ± 0.3	1.1 ± 0.1 (50)
Scarp	15	**10.1 ± 0.6** ***	**2.7 ± 0.4 (15)** ***
Coastal	13	8.4 ± 0.8 NS	1.7 ± 0.4 (13) NS

[1] Difference between Afrotemperate and scarp and coastal forest types tested using Generalised Linear Models (GLM) with response variables modelled following a Poisson error distribution and a log link function. Probability: NS = not significant; * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

Table 2. **Jaccard's coefficients of assemblage similarity for forest dependent species of birds, mammals and frogs occurring in Afrotemperate, scarp and coastal forest in South Africa**

Jaccard similarity	Birds	Mammals	Frogs
Afrotemperate & scarp	0.81	0.62	0.36
Afrotemperate & coastal	0.74	0.33	0.36
scarp & coastal	0.88	0.46	1.00

Table 3. **Species turnover across the latitudinal gradient within different forest types (Afrotemperate: 23°S, 29.75°E to 34°S, 18.25°E; scarp: 27.25°S, 32°E to 32.5°S, 28.25°E; coastal: 26.75°S, 32.25°E to 29.75°S, 30.75°E)**

	N	β_{sim}	β_{H1}
Birds			
Afrotemperate	27	0.04	2.9
Scarp	13	0.06	4.4
Coastal	9	0.03	4.5
Mammals[1]			
Afrotemperate	23	0.28	10.1
Scarp	10	0.32	18.2
Coastal	9	0.27	16.6
Frogs[1]			
Afrotemperate	30	0.13	8.8
Scarp	12	0.46	5.6
Coastal	9	0.11	11.3

[1] includes both forest dependent and forest associated species.

Figure 1. **The distribution of indigenous forest in South Africa. Afrotemperate forest occurs between the two dashed lines, scarp forest between the solid and dashed lines and Indian Ocean coastal belt forest to the east of the solid line. Provinces mentioned in the text are labeled.**

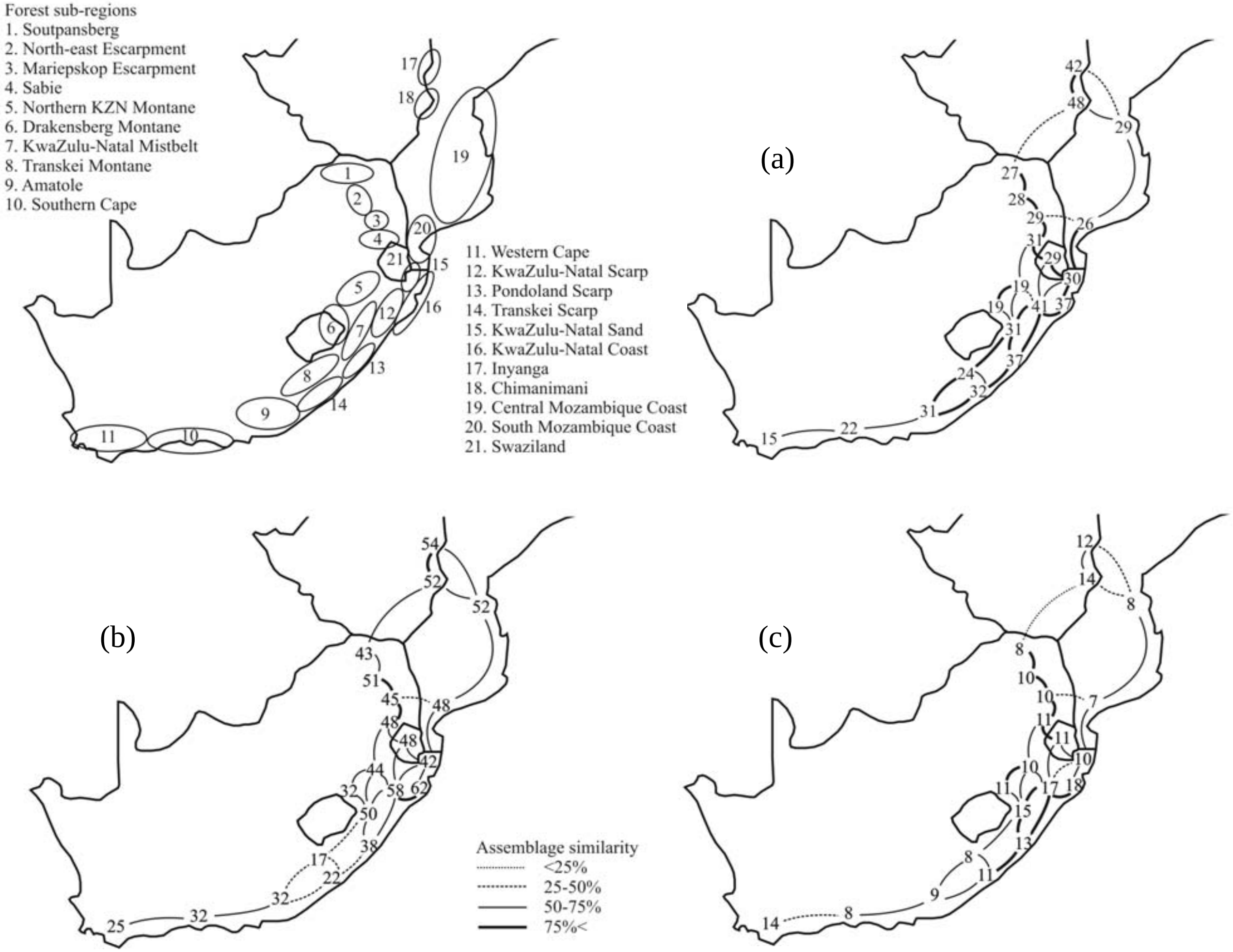

Figure 2. **Patterns of species richness and assemblage similarity across forest sub-regions among (a) birds (forest dependent species only), (b) mammals (forest dependent and associated species) and (c) frogs (forest dependent and associated species).**

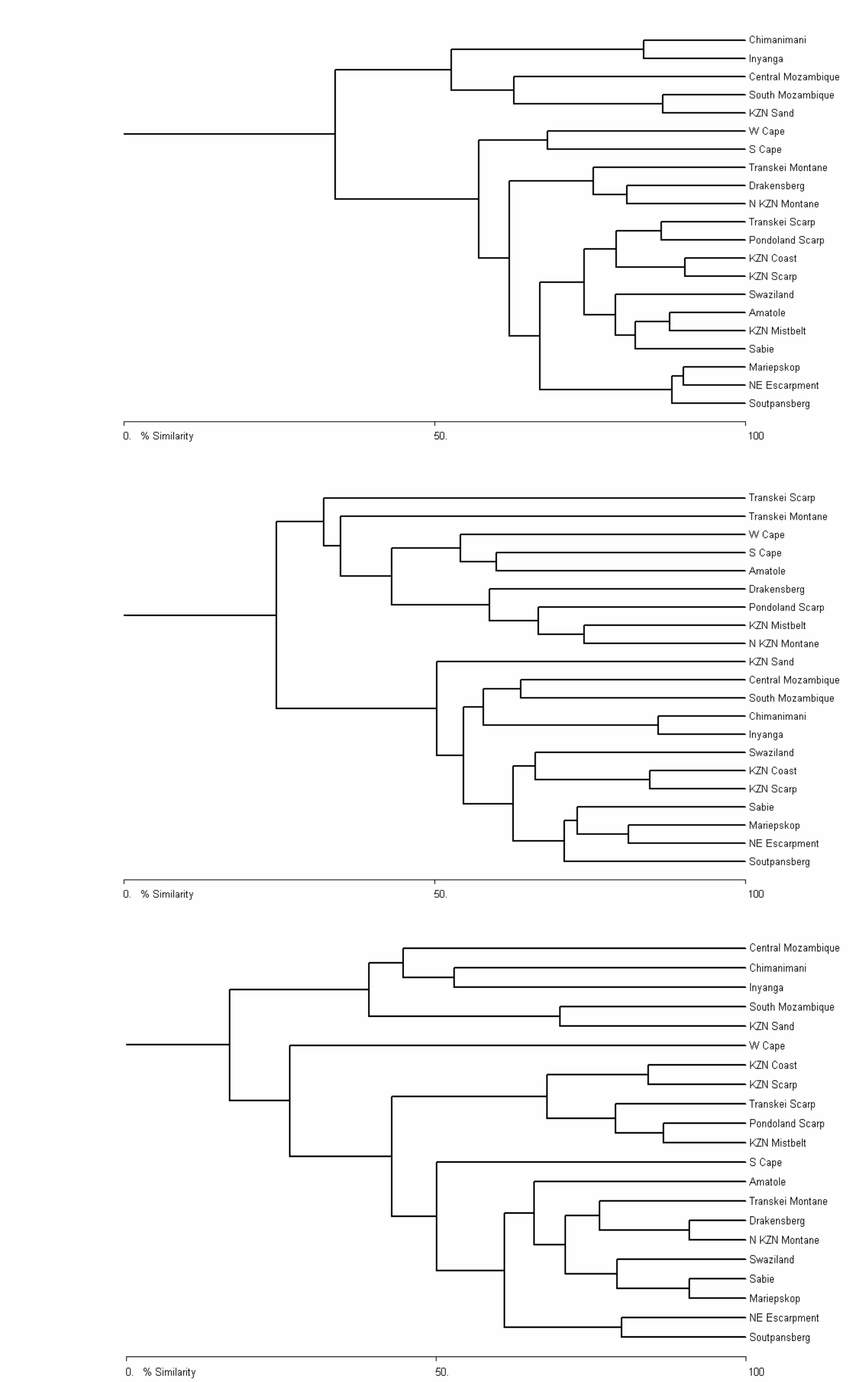

Figure 3. Cluster analyses (Jaccard's similarity coefficient, simple average link) showing the relationships between sub-regional forest faunas for (a) birds (forest dependent species only), (b) mammals (forest dependent and associated species) and (c) frogs (forest dependent and associated species).

Figure 4. **Summary illustration of the post LGM radiation of forest faunas in southern Africa. Arrows indicate the direction of radiation of Afrotemperate (solid) and Afrotropical (dashed) faunas. Arrow weights indicate the relative importance of radiation routes from major (black) and minor (grey) refugia.**