SOIL ORGANISMS Volume 81 (3) 2009 pp. 701–717

ISSN: 1864 - 6417

A comparison and conservation assessment of the high-altitude grassland and forest-millipede (Diplopoda) fauna of the South African Drakensberg

Michelle Hamer[1, 2 *] & Rob Slotow[1]

[1] *School of Biological & Conservation Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, 3209, KwaZulu-Natal, South Africa*

[2] *Biosystematics Division, South African National Biodiversity Institute, Private Bag X101, Pretoria, Gauteng, South Africa, 0001; e-mail: M.Hamer@sanbi.org.za; slotow@ukzn.ac.za*

[*] *Corresponding author*

Abstract

The Drakensberg mountains, classified as part of the Afromontane region, form the division between the more low lying coastal plain and the high-lying interior of South Africa, and comprise a relatively homogenous and continuous grassland matrix, with small, isolated forest patches. The millipede fauna of the region, particularly in grassland, was previously neglected, and existing data provided no basis for making conservation decisions in this global hotspot of biodiversity. We carried out a quantified survey of the region in order to identify the millipede fauna and its distribution in forest and grassland. We measured levels of endemism and beta diversity, and then made recommendations for conservation. We collected 1184 specimens representing 51 species. The 28 species recorded in the forest were predominantly Polydesmida, mainly Dalodesmidae, and also from two orders unique to forest, the Siphonophorida and Nematozoniida. The 23 grassland species were dominated by Spirostreptida, but some Polydesmida were also recorded. No orders, families or genera were unique to grassland. The Sphaerotheriidae were represented in both habitats, but by different species. Only four species were recorded from both biomes. Each biome was characterised by a distinct fauna, of almost equal richness, but with a different composition (β_{sim} value for grassland and forest = 0.8). Overall, 85 % of species sampled have only been recorded from the Drakensberg region, with a similar level of endemism in both grassland (78 %) and forest (79 %), although the forests had more site endemics (64 %), i.e. restricted to one region. This high level of narrow endemism resulted in high levels of beta diversity especially in grassland (β_{sim} for most pairs of regions = 1) but also in forest (β_{sim} between 0 and 0.7). Adjacent forest regions were not always the most similar. These trends may be attributed to past climate change and the distribution of forest, but the data must be accepted as being incomplete. The conservation implications of the study are that the millipede fauna has high conservation value, and that a large proportion of the Drakensberg area, for both grassland and forest, will need to be protected in order to conserve the millipede fauna.

Keywords: Afromontane, species richness, endemism, turnover, planning

1. Introduction

High-altitude, mountainous areas are currently receiving attention because of their importance in the context of global climate-change impacts on biodiversity (Hofer 2005). Many high-altitude animal species are affected by global warming (Parmesan & Yohe 2003), and the vegetation of these areas is also predicted to undergo large changes (Doran et al. 2003), which will have an indirect impact on animals, most likely those that are less mobile and with specific habitat requirements, such as millipedes. Many high-altitude areas are hotspots of endemism (Hofer 2005), and they are threatened by a range of disturbances, including uncontrolled fires (Hemp 2009) even in protected and less accessible areas. An understanding of high altitude faunas, species' distributions and habitat specificity is therefore important for understanding potential impacts of climate change (Parmesan & Yohe 2003), but also for protecting species which may have limited distribution and be threatened in the shorter term by habitat alteration or destruction.

The Drakensberg forms part of the Afromontane region (White 1978) and is a mountain range in South Africa which forms a sharp boundary between the eastern coastal plain and the high-altitude inland region. The Drakensberg has been included as a Global Biodiversity Hotspot as part of the Maputaland-Pondoland-Albany Hotspot (Steenkamp et al. 2004)). Part of the study area has been declared a World Heritage Site, based on both biological as well as cultural attributes (http://whc.unesco.org)). Further, the World Bank (GEF) funded a major project to promote integrated conservation planning and implementation in the region (Zunkel 2003).

Afromontane vegetation in the Drakensberg region is characterised by a grassland matrix, with scattered patches of evergreen forest (Hill 1996). These forests, classified as Afrotemperate (Mucina & Rutherford 2005), are generally small patches (< 10 ha) and are naturally fragmented such that forest-dependent taxa are geographically isolated (Eeley et al. 1999). It is likely that the forest and grassland distributions have undergone major changes in terms of extent in Africa over the last 100 000 years, with cyclic changes in temperature and aridity causing expansion of forests during warmer and wetter periods, and reduction during drier and colder periods (Lawes et al. 2007). These repeated changes in distribution of forest and grassland would be expected to have resulted in radiations of taxa, and in high levels of endemism at least in forest, as has occurred in the Afromontane forests in Tanzania (Rodgers & Homewood 1982).

The South African millipede fauna comprises 458 species in seven orders (Hamer et al. 2006), and there is a very high level of endemism within the South African fauna (Hamer & Slotow 2002). Many species are known only from a single locality, and they may be site endemics (Hamer & Slotow 2002). In terms of South African biomes or bioregions, 52 % of species occur in forest (Hamer et al. 2006), even though forest covers less than 0.5 % of the surface area of South Africa. An additional 16.6 % of species occur in savanna (Hamer et al. 2006), which covers about a third of the country's surface. The grassland biome covers 28 % of South Africa's surface (Mucina & Rutherford 2005), but its millipede fauna has not previously been investigated in any detail.

Grassland is perceived as being relatively homogenous in terms of vegetation and, in the Drakensberg, forms a continuous matrix habitat, while forest comprises isolated, small patches. In terms of millipede diversity, the following patterns of diversity and distribution could be expected: low diversity, low turnover and low levels of endemism in the grassland, and high diversity, turnover and levels of endemism in the forests. This would suggest that forests would have high priority for conservation while grassland would not be prioritised. The aim of this study was to assess the grassland and forest millipede faunas of the Drakensberg, in order to contribute to knowledge and understanding of their conservation value. The specific objectives of this study were (i) to document the millipede fauna of the Drakensberg, (ii) to compare the millipede fauna of the forest and grassland biomes in terms of diversity at different taxonomic levels, levels of endemism, and species turnover, and (iii) comment on the conservation implications of the findings.

2. Materials & methods

2.1. Study site

The study was carried out in the main region of the Maloti-Drakensberg region from Golden Gate in the north (28.50ºS), to the Prentjiesberg region of the Eastern Cape in the south (31.14ºS), and between 28.19º–29. 67ºE (Fig. 1). This area covers 28 174 km^2, and an altitudinal gradient of 1200 to 3200 m.a.s.l. Most forest occurs between 1400 and 1900 m. The Drakensberg experiences summer rainfall, with summer (November to March) accounting for 70 % of the annual precipitation (Schulze 1997). Average annual precipitation is between 1000 and 1800 mm. Mean annual temperature in the Drakensberg is 16 °C, with daily maximum temperatures ranging from 26.7 °C in summer to 15.6 °C in winter (Schulze 1997). Temperatures may drop to below zero in winter.

2.2. Survey of millipedes

The grassland study was carried out in the summer months, between 22 October and 23 December 2005. Seven grassland regions (Golden Gate, Cathedral Peak, Kamberg, Garden Castle, Qachas Nek, Ongeluksnek and Prentjiesberg) were selected for sampling, and these were positioned from the northern to the southern-most extent of the Drakensberg (Fig. 1). Within each region eight sampling sites were surveyed (except for Garden Castle, where six were sampled), with each site representing similar habitat in terms of vegetation and altitude, but representing the range of local aspects, slope and rockiness. Latitudinal effects were controlled for by sampling at declining altitude from north (2000 m.a.s.l.) to south (1600 m.a.s.l.). Grassland sites measured approximately 1.5 ha (estimated 100 x 150 m) but this area was not strictly delimited. Sampling for millipedes involved active searching of suitable habitat, such as under rocks or at the base of grass tussocks for a total of 90 min per site. This searching was carried out by three or four people, but the total time searching was kept constant.

Between four and six individual forest patches were sampled across six regions (Royal Natal, Cathedral Peak, Monks Cowl, Highmoor/Kamberg, Lotheni and Prentjiesberg) (Fig. 1) between 10 January and 15 April 2006. The regions were selected based on the presence of sufficient forest patches (forest patches decline in the south of the Drakensberg (Hilliard & Burtt 1987)), and individual forest patches were selected to represent a range of sizes, altitudes, and vegetation structure. Forest area ranged from 1.8 to 36 ha. Within each forest, millipedes were sampled by active searching of suitable microhabitats in: (1) 20 x 20 m plots for one hour, with three people each searching for 20 min (total search time = 1 h), with two plots per forest. (2) A 10 x 2 m quadrant, divided into contiguous 2 x 2 m blocks, with one person searching a single block thoroughly, with no time limit (each block required 30 – 45 min to search all microhabitats). In addition, passive sampling included ten pitfall traps made up of 125 ml plastic bottles (4 cm diameter) half filled with 70 % ethanol set up in each forest in two rows, with a 10 m distance between each trap and row. These traps were left open for five days before being collected.

Millipedes were frozen and stored in 70 % ethanol, and were identified by the first author. Specimens will be deposited in the Natal Museum, Pietermaritzburg, South Africa. At some sites large numbers of the same millipede species were collected, and where there was certainty about the identity of the specimens (all confirmed by the first author), only a representative sample was collected, and once recorded, the other specimens were released.

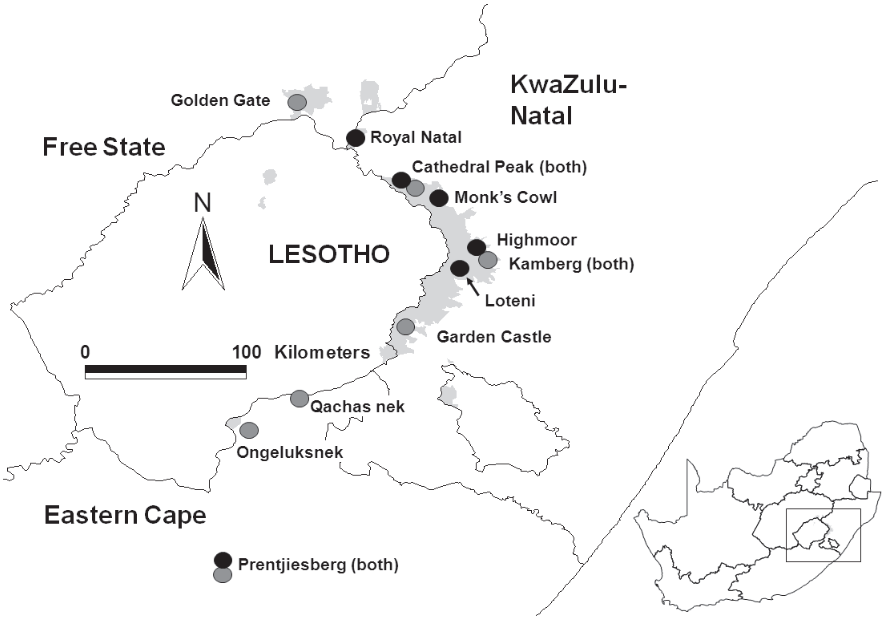

Fig. 1 Map of South Africa showing the location of the Drakensberg mountains (right), with detail of the regions surveyed in this study (left). The grey area represents existing protected areas. Black circles = forest regions, grey circles = grassland regions. Names are presented for South African provinces, and the land-bound country, Lesotho. Note that Highmoor and Kamberg were considered a single region for forests. The co-ordinates for the regions were Golden Gate: 28.52ºS/28.60ºE; Royal Natal: 28.71ºS/28.93ºE; Cathedral Peak: 29.98ºS/29.25ºE; Monks Cowl: 29.03ºS/29.39ºE; Highmoor: 29.31ºS/29.66ºE; Kamberg: 29.37ºS/29.66ºE; Lotheni: 29.42ºS/29.52ºE; Garden Castle: 29.74ºS/29.20ºE; Qachas Nek: 30.16ºS/28.60ºE; Ongeluksnek: 30.33ºS/28.34ºE, Prentjiesberg: 31.05ºS/28.18ºE.

2.3. Analyses

Sampling completeness was assessed using the species-area relationship generated using Primer 5, with 999 iterations (Clarke & Warwick 2001).

Species turnover was calculated using the beta diversity equation of Koleff et al. (2003):

$ß_{sim}$ = min (b, c) divided by min (b, c) + a

where *a* = the total number of species common to both sites, *b* = the number of species present in the neighbouring site but not in the focal site, i.e. species gain and *c* = the number of species present in the focal site but not in the neighbouring site, i.e. species loss. A value of 1 for β_{sim} would indicate maximum species turnover, with no shared species, while a value of 0 indicates low species turnover, with most species being shared. β_{sim} was calculated between all pairs of regions for forest and for grassland, and for grassland and forest in general. A further measure of turnover among regions was by contrasting community composition within the grassland and within the forest biomes. We did a Bray-Curtis similarity analysis (presence/absence transformation), performed in Primer 5, and we illustrate the results using the CLUSTER procedure (Clarke & Warwick 2001).

For the assessment of level of endemism, our database including all known records of millipedes of South Africa was used to identify additional localities for species recorded. The categories and associated criteria for different levels of endemism were taken from Hamer & Slotow (2002), where a site endemic is known only from a single locality, or if from more than one locality, these have a maximum of 10 km separating the furthest localities and a local endemic has a maximum distance of 11 to 70 km separating localities.

3. Results

3.1. The Diplopoda fauna

A total of 1184 specimens were collected representing 51 millipede species. A further four species, listed in the Appendix I, but excluded from analyses, were collected outside the normal sampling areas. Twenty-six species (50 %) could not be matched to existing descriptions, i.e. they are probably undescribed. We sampled between zero and three millipede species at each grassland site, and one to nine species in each region. In forest, a minimum of one and maximum of nine species were collected per forest patch, and the range for regions was five to 12 species. In total, 23 species (45 % of the total) were collected in grassland, of which 13 (57 %) are undescribed. Twenty-eight species (55 % of the total) were collected from the forests, and 14 (50 %) of these are undescribed. Only four species (9 % of the total), belonging to the Spirostreptidae and Sphaerotheriidae, were collected in both grassland and forest. A list of the species and their abundance in the different regions is provided in Appendix 1.

Not all millipede species likely to be present in the area were collected in either grassland or forest, and the total species richness for both vegetation types is likely to be higher than actually recorded. This is illustrated by species accumulation curves which show that with each additional forest or grassland site sampled, previously unrecorded species were added (Fig. 4). The implication of this pattern is that a large proportion of both grassland and forest in the region needs to be conserved in order to capture the entire millipede fauna.

In terms of the composition of the fauna, Polydesmida, specifically Dalodesmidae, dominated the forest fauna with 18 species, while Spirostreptidae, with 11 species dominated the grassland (Fig. 2). Forest was inhabited by three families known only from forest. The Gomphodesmidae, although only recorded from forest in the present study is well represented in grassland and savanna in other areas (pers. obs.; Hamer et al. 2006). Similarly, the Vaalogonopidae was the only family unique to grassland in this study, but elsewhere the family has been sampled from forest (Hamer, 1998). Four genera were unique to forest (*Drakensius*, *Rhyncomecogaster*, *Nematozonium* and *Julomorpha*), and while *Phygoxerotes* was only sampled in the grassland, this genus was previously only known from forest. The faunal composition therefore suggests that the forest is richer at both higher and species taxonomic levels, but that each biome has a distinct fauna. The forests also had far greater abundances of millipedes than grassland (Appendix 1).

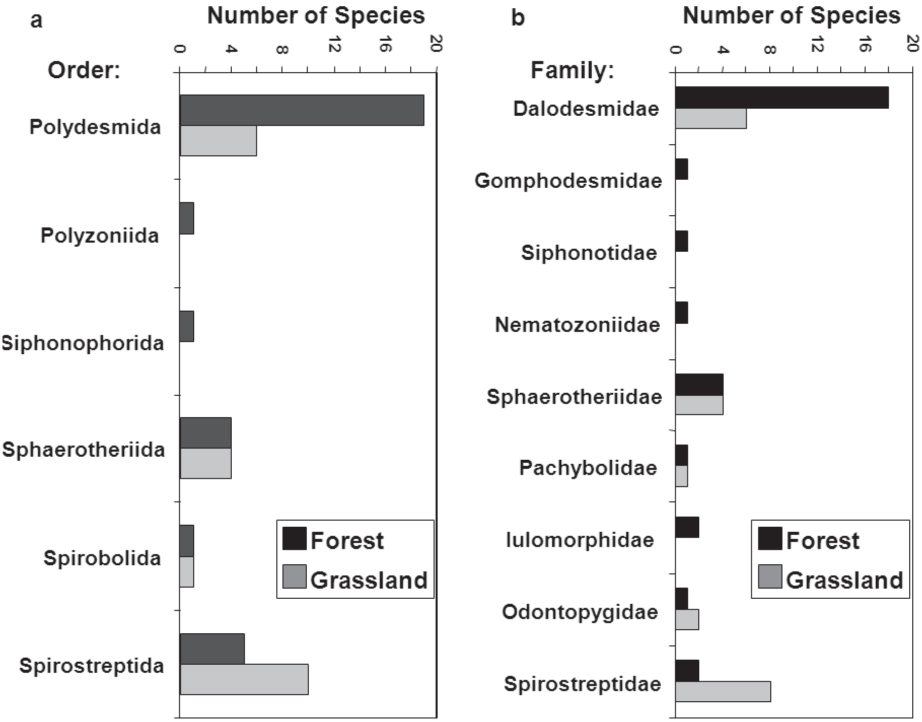

Fig. 2 Comparison of the millipede species richness of the Drakensberg forest and grassland at the level of (a) Order and (b) Family.

3.2. Comparison of endemism in the Drakensberg forests and grassland

Over half of the described millipede species represented in the area surveyed have not been recorded outside of the Drakensberg area (Tab. 1). If it is assumed that those undescribed species collected are also endemic to the Drakensberg region, then this proportion increases to 84 %, with 18 of these being grassland species (78 %) and 23 forest species (82 %) (Tab. 1).

Tab. 1 Levels of endemism in Drakensberg millipedes.

Level of Endemism	Number of species (%)		
	Total	Grassland	Forest
Endemic to Drakensberg (described species only)	14 (56 %)		
Endemic to Drakensberg (all species)	43 (84 %)	18 (78 %)	23 (82 %)
Site Endemics (from 1 region only)		13 (57 %)	18 (64 %)
Local Endemics (from 2 regions only)		4 (17 %)	0

Possible site endemics, i.e. occurring at a single location (Hamer & Slotow 2002) included over 64 % of species in forest, and 57 % in grassland (Tab. 1). In the case of the four species in grassland that were collected from two regions (Tab. 1), these regions were positioned adjacent to each other, i.e., they would be considered local endemics (10–70 km separating the furthest localities) according to Hamer & Slotow's (2002) categorization. The forest species either qualified as site endemics, or were relatively widespread within the Drakensberg, with no species recorded from two regions. None of the grassland species occurred in more than two regions (Fig. 3).

In terms of the higher taxonomy of the endemic species, there were generally similar patterns in the orders that were present in both grassland and forest. Few species were widely distributed, the exception being the wider distribution of the forest sphaerotheriids which were all found in three or more regions (Fig. 3). Four *Doratogonus* species (Spirostreptida) were sampled from a single region during the survey.

3.3. Comparison of species turnover in grassland and forest

The β_{sim} value between grassland and forest in general was 0.8, indicating low levels of similarity between the two habitats. For grassland there was complete turnover of species across most regions ($\beta_{sim} = 1$), with evidence of shared species between Cathedral Peak and Kamberg ($\beta_{sim} = 0.5$), and between Qachas Nek and Ongeluksnek ($\beta_{sim} = 0.3$). In both cases these are adjacent pairs of sites (Figs 1, 5). This trend of virtually no shared species may be a sampling artifact as a result of very low abundances for most species in grassland, and the low number of species sampled (Appendix 1).

The beta diversity indices for forest indicated more shared species. Royal Natal and Cathedral Peak and Cathedral Peak and Monks Cowl shared most species ($\beta_{sim} = 0$). Highmoor/Kamberg and Lotheni, Highmoor/Kamberg and Prentjiesberg and Lotheni and Prentjiesberg showed the highest amount of species turnover ($\beta_{sim} = 0.7$), and the other pairs of sites had intermediate values (β_{sim} between 0.4 and 0.6), suggesting some turnover. The relationship between the forests in different regions based on similarity in their millipede fauna is illustrated in Fig. 5, where the three northern regions showed some similarity in their millipede community, but the southern regions showed very little similarity.

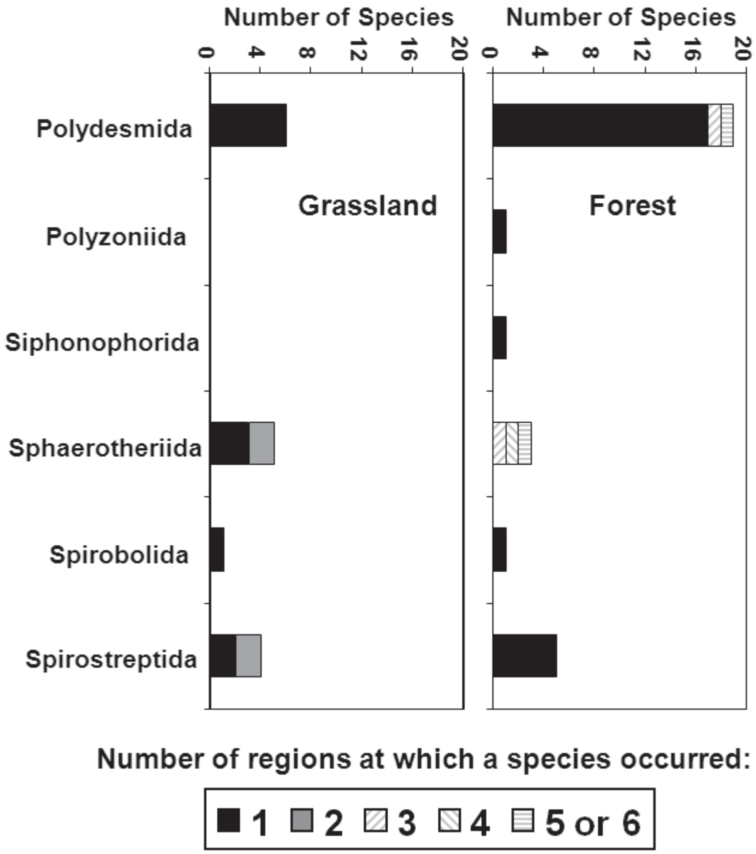

Fig. 3 Comparison of level of endemism (number of sites at which species occurred) for millipede orders in grassland and forest across the six forest and seven grassland regions. Species at one region would be site endemics, and at two regions would be local endemics (see text).

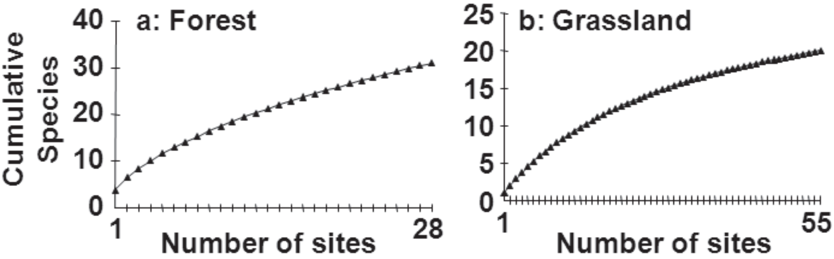

Fig. 4 Species-area relationship for (a) forest, and (b) grassland millipedes. Data are based on 28 sites for forest, and 55 sites for grassland, and are iterated curves based on 999 permutations.

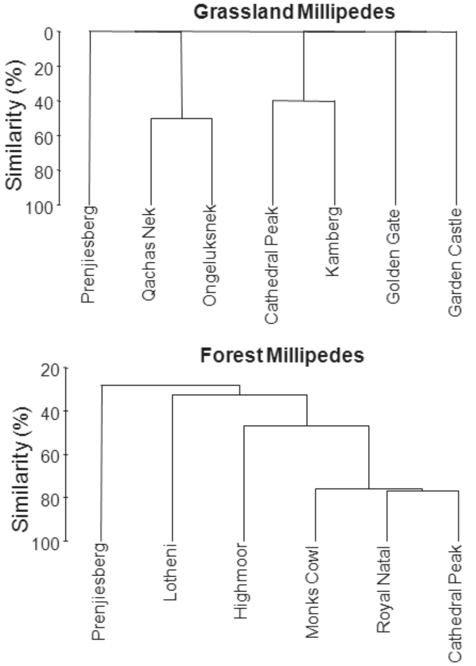

Fig. 5 Relationships between grassland and forest regions based on extent of similarity in the community of Diplopoda (Bray-Curtis similarity analyis).

4. Discussion

If only the described species are considered, then the Drakensberg millipede fauna represents 5.7 % of the total known South African species richness and considering the large area and latitudinal gradient within the study area, this is not especially high. However, the number of species recorded is likely to be an underestimate because not all forest patches or the full altitudinal range of the grasslands were surveyed. The high proportion of undescribed species collected emphasises the poor state of millipede survey and knowledge of the region, and more widely, since a similar proportion of undescribed species was also been recorded from savanna (Hamer et al. 2006).

The measured richness of the grassland fauna was almost as high as that of forests, which is surprising given that the grassland habitat sampled included no woody vegetation or obvious shading, and little leaf litter. Many of the grassland species were collected from under rocks or large mammal dung, which they probably use for protection from desiccation, and, for the latter, as a source of moisture and food. Millipedes are traditionally considered a 'forest' group, requiring moist, shaded habitats with much litter (Kime & Golovatch 2000). However, we have previously shown the South African savanna millipede fauna to be surprisingly rich (Hamer et al. 2006), and here we present further data indicating high diversity in grassland, despite limiting our sample to one altitudinal band across all regions. Grassland appears to be a relatively homogenous vegetation type, both in terms of dominant plant species and physiognomy, but there was almost equal diversity (richness and endemism) relative to the more complex forest habitats.

We do highlight, however, that several orders and families typically considered as being limited to forest were absent from the grassland (Polyzoniida and Siphonophorida, Siphonotidae, Nematozoniidae, Iulomorphidae). Further, no unique higher taxa are known from the high-altitude grasslands of the Drakensberg. This supports the hypothesis that the forest floor is the original habitat for millipedes (Kime & Golovatch 2000). The fact that the genera *Sphaerotherium*, *Platytarrus* and *Gnomeskelus* are represented by different species in grassland and forest suggests that divergence within these genera between the two habitats may have been relatively recent. The *Bradypodion* dwarf chameleon diversity in the region has been ascribed to major recent (2.5 mya) changes in climate, with the oldest *Bradypodion* lineages in forests, and the phenotypically distinct open-habitat species showing relatively little molecular divergence from the forest species (Tolley et al. 2008). Grassland endemics may have evolved if forest species that were tolerant of more open habitats, or able to avoid exposure through burrowing, moved from forest, as has been the case with dwarf chameleons (Tolley et al. 2008). The plants of the Drakensberg grasslands have high levels of endemism and they are species rich (Bredenkamp et al. 2002). The explanation for this is the great age of this vegetation type in the Drakensberg (40 to 50 million years) (Bredenkamp et al. 2002). During this period, and related to climate change, forest would have expanded, possibly fragmenting grassland. During glacial maxima forest retreated and grassland expanded. How these changes in forest and grassland dominance and distribution impacted on isolation and speciation and may be linked to endemism and radiations is unclear from the literature. Molecular phylogenetic investigations of those millipede taxa that are represented in both forest and grassland in the Drakensberg, and particularly those that have radiated, such as *Gnomeskelus*, will be useful for investigating biogeographical trends in millipedes. We also recommend molecular work on *Platytarrus*, *Spinotarsus* and *Sphaerotherium,* which occur in both biomes, in order to understand the evolution of the fauna in the Drakensberg.

The extremely high levels of narrow endemism in the Drakensberg forest millipedes is not unusual, with 87.5 % of sphaerotheriids recorded from a single collection site in Madagascar (Wesener 2005), and even higher levels of millipede endemism (95 %) in the Usambara Mountain forests of Tanzania in East Africa (Rodgers & Homewood 1982). The authors attributed the richness and endemism of Usambara millipedes to long periods of isolation and geologic stability, together with periods of species immigration during times when forest re-established and was continuous. This explanation for these high levels of endemism may also apply for the Drakensberg forest millipedes. The impacts of historical climate variation on the distribution of forest and grassland may also have contributed to the radiation of some genera, such as *Gnomeskelus*, *Drakensius* and *Julomorpha*, but the timing of these radiations is unknown. The lower levels of beta diversity between the forest regions in the northern section of the Drakensberg (Royal Natal, Cathedral Peak and Monks Cowl) may suggest stronger and possibly more recent connectivity between the forests of these regions. These forests, facing north-west and therefore directed towards the sun, were probably exposed to less extreme temperatures during glacial maxima than the forests in the southern part of the Drakensberg (Lawes et al. 2007). They were therefore less fragmented at those times, which may explain the lower species turnover and levels of endemism in these regions. The forests positioned in the southern half of the Drakensberg on the other hand, experienced (and still experience) much colder winds and temperatures, and forest is likely to have been far more reduced during glacial maxima (Lawes et al. 2007). The effect of this isolation may have been the evolution of species confined to small areas.

The beta diversity values show very high levels of turnover in the grassland regions, but comparative data for this habitat are not available. An intensive survey of forests in the northern Drakensberg showed that between individual forests within the same valley β_{sim} values were 0.2–0.3, and for forests in different valleys the indices ranged between 0.2 and 0.5 (Uys et al. 2009). There was a distinct distance effect with, predictably, those forests that were closest showing least species turnover (Uys et al. 2009). In this study the distances between the regions were much greater, and this, to some extent, may explain the higher levels of species turnover. However, the relationship is not a simple spatial one since the highest $ß_{sim}$ value for forest, indicating high species turnover, included the pairs of Highmoor/Kamberg and Loteni, and Monks Cowl and Highmoor/Kamberg which are adjacent to each other (Fig. 1). The forests at Highmoor/Kamberg had three *Gnomeskelus* species which were site endemics. The positioning of this region at the intersection of the north-west and the south-east facing regions of the Drakensberg, and its millipede fauna and the relevance of this for understanding biogeographic patterns, warrants further investigation.

It is possible that the high levels of endemism in the Drakensberg Diplopoda may be as a result of incomplete sampling, i.e. other distribution records could be found if additional locations were sampled. The small number of specimens and the high number of 'singletons', where a single specimen of a species was sampled in the grassland (Appendix 1), suggests that some species may be rare and easily missed in a survey. Evidence for sampling difficulties is provided by the *Doratogonus* species which are large and conspicuous species and are known to be distributed more widely in the Drakensberg than we recorded during this survey (Hamer 2000, Hamer & Slotow 2000). Our previous experience has indicated that the sampling methods do tend to undersample this genus (Druce et al. 2004). Undersampling therefore accounts for eight of the 11 spirostreptid species being recorded from a single region in the grassland, which is therefore somewhat misleading, and should be interpreted with caution. However, *Spinotarsus* does appear to have undergone massive radiations in southern Africa, with a total of 96 described species (Hamer 1998), and many more undescribed, and the majority of these species are known from a single locality even in areas that have been well sampled (unpublished data). A similar trend is known for the diverse genus *Gnomeskelus* (unpublished data).

It should be noted that we have conducted additional intensive work in both the forests (Uys et al. 2009) and grassland (Uys et al. 2006, Uys & Hamer 2006, Arnott 2007), including at different times of the year, and the distribution of those species categorised as site or local endemics was not expanded through these studies. Furthermore, while sampling millipedes we sampled a range of other taxa including Gastropoda, Asilidae, Tabanidae, Apidae, and Ciccindellidae, and none of those taxa showed similar patterns of local endemism (unpublished data). We therefore believe that while our data may overestimate endemism levels, these will probably remain relatively high, even with additional, extensive surveys.

The implication of the number of potentially narrow endemics is that the millipede fauna of the Drakensberg has high conservation value. Species with restricted distributions are prone to extinction through stochastic events, and loss of habitat through human activities is always a real threat to local or site endemics. Furthermore, global climate change and its consequences are likely to be most evident at high altitudes (Parmesan & Yohe 2003). In addition to high-localised endemism, there was also high species turnover in grassland and forest. The same problems with undersampling, especially in the grassland may account for the extremely high beta diversity values in grassland, but while these values may decrease with additional sampling, the trend measured is unlikely to be completely invalid.

For the process of systematic conservation planning (Magules & Pressey 2000), an explicit target must be set for a particular biodiversity feature, which is often a surrogate such as vegetation type (Noss 2004). In addition, representivity of species is also required (Margules & Pressey 2000, Noss 2004). Therefore, in terms of conservation planning for the Drakensberg region, in order to have all the species surveyed in this study included in a conservation area, all the grassland and all the forest sites and regions would have to be included (i.e. a 100 % target). This is not unique to the Drakensberg and high levels of turnover have also been recorded in other studies, even within uniform vegetation types (e.g. Hamer et al. 2006). As more invertebrate taxa are included, conservation planners will have to develop approaches that can deal with such high turnover that is not necessarily associated with traditional surrogates such as vegetation or environmental factors.

5. Acknowledgements

Funding for the study was provided through a World Bank grant to the Maloti Drakensberg Transfrontier Project, as well as by Earthwatch Institute and the South African National Research Foundation. Collecting permits were provided by SANParks, and KZN Wildlife. Earthwatch volunteers, including a team of BirdLife guides assisted with the collecting, as did various research assistants who also contributed to processing of material in the laboratory. We thank the organisers of the 14th CIM congress for providing the opportunity to present this work and to interact with fellow myriapodologists, and two anonymous reviewers who provided constructive comments on the manuscript.

6. References

Arnott, W. (2007): The effect of burning on invertebrate and indigenous flowering forb diversity in a Drakensberg grassland ecosystem. – M.Sc. Thesis, University of KwaZulu-Natal, Pietermaritzburg: 160 pp.

Bredenkamp, G., J., F. Spada & E. Kazmierczak (2002) On the origin of northern and southern hemisphere grasslands. – Plant Ecology **163**: 209–229.

Clarke, K. R. & R. M. Warwick (2001): Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. – PRIMER-E, Plymouth: 172 pp.

Doran, N. E., J. Balmer, M. Driessen, R. Bashford, S. Grove, A. M. M. Richardson, J. Griggs & D. Ziegeler (2003): Moving with the times: baseline data to gauge future shifts in vegetation and invertebrate altitudinal assemblages due to environmental changes. – Organisms, Diversity, Evolution **3**: 127 – 149.

Druce, D., M. Hamer & R. Slotow (2004): Sampling strategies for millipedes (Diplopoda), centipedes (Chilopoda) and scorpions (Scorpionida) in savanna habitats. – African Zoology **39**: 293–304.

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

Hamer, M. L. (1998): Checklist of Southern African millipedes. – Annals of the Natal Museum **39**: 11–82.

Hamer, M. L. (2000): Review of the millipede genus *Doratogonus*, with descriptions of fifteen new species from Southern Africa (Diplopoda, Spirostreptida, Spirostreptidae). – Annals of the Natal Museum **41**: 1–76.

Hamer, M. & R. Slotow (2000). Patterns of speciation and distribution in the southern African *Doratogonus* (Diplopoda, Spirostreptidae). – In: Wytwer, J. & S. Golovatch (eds): Progress in Studies on Myriapoda and Onychophora. – Fragmenta Faunistica **43** (Suppl.): 295–311.

Hamer, M. & R. Slotow (2002): Conservation application of existing data for South African millipedes (Diplopoda). – African Entomology **10**: 29–42.

Hamer, M. L., R. H. Slotow & S. Lovell (2006): The South African savanna millipede (Diplopoda) fauna: taxonomic diversity, endemism and spatial and temporal effects on conservation assessments. – Norwegian Journal of Entomology **53**: 321–324.

Hemp, A (2009): Climate change and its impact on the forests of Kilimanjaro. – African Journal of Ecology **47**: 3–10.

Hilliard, O. M. & B. L. Burtt (1987): The Botany of the Southern Natal Drakensberg. – National Botanical Gardens, Cape Town: 253 pp.

Hill, T. R. (1996): Description, classification and ordination of the dominant vegetation communities, Cathedral Peak, KwaZulu-Natal Drakensberg. – South African Journal of Botany **62**: 263–269.

Hofer, T. (2005): Introduction: The International Year of Mountains: challenges and opportunity for mountain research. – In: Huber, U. M., H. K. M. Bugmann & M. A. Reasoner (eds): Global Change and Mountain Regions. An Overview of Current Knowledge. – Springer, Netherlands: 1–8.

Kime, R. D. & S. I. Golovatch (2000): Trends in the ecological strategies and evolution of millipedes (Diplopoda). – Biological Journal of the Linnean Society **69**: 333–349.

Koleff, P., K. J. Gaston & J. J. Lennon (2003): Measuring beta diversity for presence / absence data. – Journal of Animal Ecology **72**: 367–382.

Lawes, M. J., H. A. C. Eeley, N. J. Findlay & D. Forbes (2007): Resilient forest faunal communities in South Africa: a legacy of palaeoclimatic change and extinction filtering? – Journal of Biogeography **34**: 1246–1264.

Margules, C. R. & R. L. Pressey (2000): Systematic conservation planning. – Nature **405**: 243–253.

Mucina, L. & M. C. Rutherford (eds) (2006): The Vegetation of South Africa, Lesotho and Swaziland. – South African National Biodiversity Institute, Pretoria: 804 pp.

Noss, R (2004): Conservation targets and information needs for regional conservation planning. – Natural Areas Journal **24**: 223–231.

Parmesan, C. & G. Yohe (2003): A globally coherent fingerprint of climate change impacts across natural systems. – Nature **421**: 37–42.

Rodgers, W. A. & K. M. Homewood (1982): Species richness and endemism in the Usambara mountain forests, Tanzania. – Biological Journal of the Linnean Society **18**: 197–242.

Schulze, R. E. (1997): South African Atlas of Agrohydrology and Climatology. – Water Research Commission, Pretoria, Report TT82/96: 276 pp.

Steenkamp, Y., B. van Wyk, J. Victor, D. Hoare, G. Smith, T. Dold & R. Cowling (2004): Maputaland-

Pondoland-Albany. – [www. biodiversityscience. org/publications/hotspots /Maputaland PondolandAlbany.html] (accessed 19 December 2008).

Tolley, K. A., B. M. Chase & F. Forest (2008): Speciation and radiations track climate transitions since the Miocene Climatic Optimum: a case study of southern African chameleons. – Journal of Biogeography **35**: 1402–1414.

Uys, C. & M. Hamer (2007): The effect of long-term fire treatments on invertebrates results from experimental plots at Cathedral Peak, South Africa. – African Journal of Range and Forage Science **24**: 1–7.

Uys, C., M. Hamer & R. Slotow (2006): The effect of burn area on invertebrate recolonisation in grasslands in the Drakensberg, South Africa. – African Zoology **41**: 51–65.

Uys, C., M. Hamer, & R. Slotow (2009): Turnover in invertebrate species composition over different spatial scales in Afrotemperate forest in the Drakensberg, South Africa. – African Journal of Ecology **47**: 341–351.

Wesener, T. (2005): Giant pill-millipede diversity on Madagascar (Diplopoda: Sphaerotheriida). – Peckiana **4:** 189–194.

White, F. (1978): The Afromontane Region. – In: Werger, M. J. A. (ed): Biogeography and Ecology of Southern Africa. – Junk, The Hague: 463–513.

Zunkel, K. (2003): Managing and conserving South African grasslands with high endemism. The Maloti-Drakensberg Transfrontier Conservation and Development Program. – Mountain Research and Development **23**: 113–118.

Accepted 11 September 2009

Appendix 1 List of millipede species sampled in the Maloti-Drakensberg survey 2005–2006, with the number of individuals sampled for each species for each region (sites totaled) and level of endemism. NE= not endemic to the Drakensberg region. G denotes grassland sites, and F forest sites. The numbers refer to the following regions: G1=Golden Gate; G2=Cathedral Peak; G3=Kamberg; G4=Garden Castle; G5=Qachas Nek; G6=Ongeluksnek; G7=Prentjiesberg; F1=Royal Natal; F2=Cathedral Peak (forest); F3=Monks Cowl; F4=Highmoor/Kamberg; F5=Lotheni; F6=Prenjiesberg (forest). Species marked * were only collected outside quantified samples and were excluded from analyses.

ORDER	**FAMILY**	**SPECIES**	**grassland sites**							**forest sites**						**LEVEL OF ENDEMISM**
			G1	**G2**	**G3**	**G4**	**G5**	**G6**	**G7**	**F1**	**F2**	**F3**	**F4**	**F5**	**F6**	
Polydesmida	Dalodesmidae	*Drakensius minor* Schubart, 1956								10						Site
Polydesmida	Dalodesmidae	*Drakensius minor*? Schubart, 1956								1						Site
Polydesmida	Dalodesmidae	*Drakensius* sp. 1													13	Site
Polydesmida	Dalodesmidae	*Drakensius* sp. 2												13		Site
Polydesmida	Dalodesmidae	*Drakensius* sp. 3												3		Site
Polydesmida	Dalodesmidae	*Gnomeskelus arcuatus* Verhoeff, 1939												1		NE
Polydesmida	Dalodesmidae	*Gnomeskelus attemsii* Verhoeff, 1939								37	1	2	5			Drakensberg
Polydesmida	Dalodesmidae	*Gnomeskelus laevigatus* Lawrence, 1953										8				Drakensberg
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 1											7			Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 2	3													Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 3		2												Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 4											1			Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 5							1							Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 6													21	Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 7													13	Site
Polydesmida	Dalodesmidae	*Gnomeskelus* cf. sp. 7													2	Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 8												38		Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 9												26		Site
Polydesmida	Dalodesmidae	*Gnomeskelus* sp. 10											7			Site

Appendix 1 cont.

ORDER	FAMILY	SPECIES	grassland sites							forest sites						LEVEL OF ENDEMISM
			G1	G2	G3	G4	G5	G6	G7	F1	F2	F3	F4	F5	F6	
Polydesmida	Vaalogonopidae	*Phygoxerotes* sp. 1	1													Site
Polydesmida	Dalodesmidae	*Platytarrus cryptodesmoides* Attems, 1928													3	Site
Polydesmida	Dalodesmidae	*Platytarrus polydesmoides* Verhoeff, 1939												11		Drakensberg
Polydesmida	Dalodesmidae	*Platytarrus* n. sp.	3													Site
Polydesmida	Dalodesmidae	*Rhopaloskelus*? n. sp.	1													Site
Polydesmida	Gomphodesmidae	*Ulodesmus simplex* Lawrence, 1953								8		47		66		Drakensberg
Polyzoniida	Siphonotidae	*Rhyncomecogaster lawrencei*? Verhoeff, 1939												7		Site
Siphonophorida	Nematozoniidae	*Nematozonium filum* Verhoeff, 1939										2				NE
Sphaerotheriida	Sphaerotheriidae	*Sphaerotherium alticola* Schubart, 1958					8	19								Local
Sphaerotheriida	Sphaerotheriidae	*Sphaerotherium dorsaloides* Silvestri, 1910		6						2	11	17	10	11	11	NE
Sphaerotheriida	Sphaerotheriidae	*Sphaerotherium mahaium* Schubart, 1958				1				67	25	3		22	41	Drakensberg
Sphaerotheriida	Sphaerotheriidae	*Sphaerotherium perbrincki* Schubart, 1958								39	1	123	164	165	2	Drakensberg
Sphaerotheriida	Sphaerotheriidae	*Sphaerotherium rudebecki* Schubart, 1958							9							Site
Sphaerotheriida	Sphaerotheriidae	*Sphaerotherium tomentosum* Schubart, 1958								11	2	1				NE
Sphaerotheriida	Sphaerotheriidae	*Sphaerotherium* sp. 1		1												Site
Spirobolida	Pachybolidae	*Centrobolus angelicus* (Jeekel, 1956)							4							NE
Spirobolida	Pachybolidae	*Centrobolus* n.sp. 1												1		Site
Spirostreptida	Harpagophoridae	**Zinophora brevispina* (Lawrence, 1965)					1									NE

Appendix 1 cont.

ORDER	FAMILY	SPECIES	grassland sites							forest sites						LEVEL OF ENDEMISM
			G1	G2	G3	G4	G5	G6	G7	F1	F2	F3	F4	F5	F6	
Spirostreptida	Julomorphidae	*Julomorpha* sp. 1													4	Site
Spirostreptida	Julomorphidae	*Julomorpha* sp. 2													5	Site
Spirostreptida	Odontopygidae	**Spinotarsus* sp. 1	1													Site
Spirostreptida	Odontopygidae	**Spinotarsus* sp. 2	1													Site
Spirostreptida	Odontopygidae	*Spinotarsus* sp. 3					5									Site
Spirostreptida	Odontopygidae	*Spinotarsus* sp. 4							1							Site
Spirostreptida	Odontopygidae	*Spinotarsus* sp. 5													2	Site
Spirostreptida	Spirostreptidae	*Doratogonus annulipes* Carl, 1917					2									NE
Spirostreptida	Spirostreptidae	*Doratogonus krausi* (Lawrence, 1965)	2													NE
Spirostreptida	Spirostreptidae	*Doratogonus meridionalis* Hamer, 2000		1												Drakensberg
Spirostreptida	Spirostreptidae	*Doratogonus montanus* Hamer, 2000			1											Drakensberg
Spirostreptida	Spirostreptidae	*Doratogonus xanthopus* Attems, 1928						6	2						1	NE
Spirostreptida	Spirostreptidae	*Orthoporoides* sp. 1	1													Site
Spirostreptida	Spirostreptidae	*Orthoporoides* sp. 2		4	3											Local
Spirostreptida	Spirostreptidae	*Orthoporoides* sp. 3		1												Site
Spirostreptida	Spirostreptidae	*Orthoporoides* sp. 4					5	1								Local
Spirostreptida	Spirostreptidae	*Orthoporoides* sp. 5							8							Site
TOTAL ABUNDANCE			**13**	**15**	**4**	**1**	**21**	**26**	**25**	**175**	**40**	**202**	**174**	**364**	**118**	
TOTAL SPECIES			**8**	**6**	**2**	**1**	**5**	**3**	**6**	**8**	**5**	**8**	**6**	**12**	**12**	