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Centres of moss diversity in southern Africa

JACQUES VAN ROOY[1] & NONKULULO PHEPHU[2]
[1]*National Herbarium, South African National Biodiversity Institute (SANBI), Private Bag X101, Pretoria 0001, South Africa. Corresponding author: j.vanrooy@sanbi.org.za*
[2]*Restoration and Conservation Biology Research Group, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, PO WITS 2050, South Africa.*

Abstract

Moss diversity in southern Africa is greatest in the Cape Fold Mountains of the southwestern Cape, and the Drakensberg mountains along the Great Escarpment of KwaZulu-Natal, Mpumalanga and Limpopo Provinces of South Africa. Five main, and five secondary centres of moss diversity are described, based on the number of moss species per half degree grid square in southern Africa (South Africa, Namibia, Botswana, Lesotho and Swaziland). The main centres are the Southwestern Cape, Outeniqua, Amathole, KwaZulu-Natal and Mpumalanga Centres of Moss Diversity. The KwaZulu-Natal centre is divided into the Drakensberg and Midlands Subcentres of Moss Diversity and the Mpumalanga centre into the Wolkberg and Blyde Subcentres of Moss Diversity. The secondary centres are the Cederberg, Witteberge, Pondoland, Magaliesberg and Soutpansberg Centres of Moss Diversity. Although collecting bias is responsible for concentrations of species records in many areas, moss diversity is strongly influenced by habitat heterogeneity and mean annual rainfall. This is in agreement with existing hypotheses of a broad-scale correlation between environmental heterogeneity and climate on the one side, and vascular plant diversity and distributions on the other.

Keywords: biodiversity, centres of diversity, southern African mosses, environmental factors

Introduction

The *Flora of southern Africa* (FSA) region, which comprises the countries of South Africa, Namibia, Botswana, Lesotho and Swaziland, has a diverse moss flora with strong tropical African affinities (Schofield 1992). According to the latest checklist of southern African mosses (Van Rooy 2003), there are 59 families, 217 genera and 555 species (including infraspecific taxa) in the region. This represents about 5% of the world's mosses and 17% of mosses in Africa.

To determine which areas might be considered for priority conservation action, it is important to identify centres of plant diversity and endemism (Davis *et al.* 1994, Marchese 2015). However, diversity patterns in bryophytes do not always coincide with those of vascular plants and other organisms, and field studies indicate that centres of high bryophyte diversity have different substrate and habitat conditions (Hallingbäck & Tan 2010 and references therein). Bryophyte hot-spots should therefore be determined independently to facilitate the conservation of this important plant group. Tan & Pòcs (2000) listed the 'Drakensberge in Natal-Lesotho' as well as the 'Cape' as centres of high endemism and bryodiversity in Africa. These areas were also among the African centres of high vascular plant species richness identified by Mutke *et al*. (2001).

Goldblatt (1978) attributed the extraordinary diversity of plants in southern Africa to environmental diversity, rainfall seasonality, recurrent climatic fluctuations since the mid-Pliocene and the survival of relicts in favourable habitats along the coasts. Cowling *et al*. (1997) discussed a number of hypotheses commonly invoked to explain patterns of plant diversity at a regional scale. They can be summarised under the following headings: area, environmental heterogeneity, climatic favourableness, energy, seasonality and irregularity, dispersal, speciation history, effect of local processes, and convergence of regional richness. Of these, environmental heterogeneity and climatic variables, in particular rainfall, are widely accepted as the most important factors in determining the diversity and distribution of plants in southern Africa (Linder 1991, 2001; O'Brien 1993; Cowling & Hilton-Taylor 1994; Cowling *et al*. 1997; Mutke *et al*. 2001; Barthlott *et al*. 2005).

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The main aim of this paper is to describe centres of moss diversity in southern Africa and to compare these with known centres of vascular plant diversity. We also hypothesise on the possible determinants of these centres.

Materials and methods

This study is based on the geographical distribution dataset used to determine bryofloristic regions (Van Rooy & Van Wyk 2010, 2012) and bryofloristic elements (Van Rooy & Van Wyk 2011) in southern Africa. Geographical distribution data were recorded directly from specimen labels in PRE (incorporating specimens from NH, SAM, GRA and STE) (Magill 1980, Van Rooy 2013), specimens on loan from other southern African herbaria (BLFU and BOL), type and other collections on loan from overseas herbaria (B, BM, E, FH, G, H, HBG, PC, MANCH, NY, S and Z), as well as literature records based on herbarium specimens. The data matrix contained the presence/absence of 503 species/infraspecific taxa in 1036 half degree grid squares, covering the entire FSA area. The (half) degree reference system employed is described by Edwards & Leistner (1971).

The original dataset was updated with the geographical distributions of new species and records of southern African mosses published up to 2011 (Anderson 1997; Arts 1998; Blockeel *et al*. 2001, 2002, 2003, 2005, 2006; Camara & Magill 2009; Cano 2011; Ellis *et al*. 2011; Frahm 1998; Frahm & Hedderson 2004; Hedderson & Zander 2007, 2007a, 2008, 2008a; Hodgetts e*t al.* 1999; Lara e*t al.* 2009; Matcham & Duckett 2003; Rao 2001; Snider e*t al.* 1999; Sollman 1998, 2006, 2009; Van Rooy 2011; Vanderpoorten & Barker 2004; Zander & Hedderson 2009, 2011, 2011a). Recent moss records from the Tankwa Karoo National Park, a previously under-collected area (Bester *et al*. 2012), have also been incorporated. As a result of the dataset update, four previously empty grid squares now have species records and 57 grids had their species counts increased by between one and 17.

The grid squares were divided into classes according to the number of moss species/infraspecific taxa recorded in each. The distribution at a four class interval (1–49, 50–99, 100–149 & 150+), with the first class further subdivided (1–9, 10–24 & 25–49), is shown in Fig. 1. The distributions of the top three classes, that constitute the centres of moss diversity, are shown in Fig. 2.

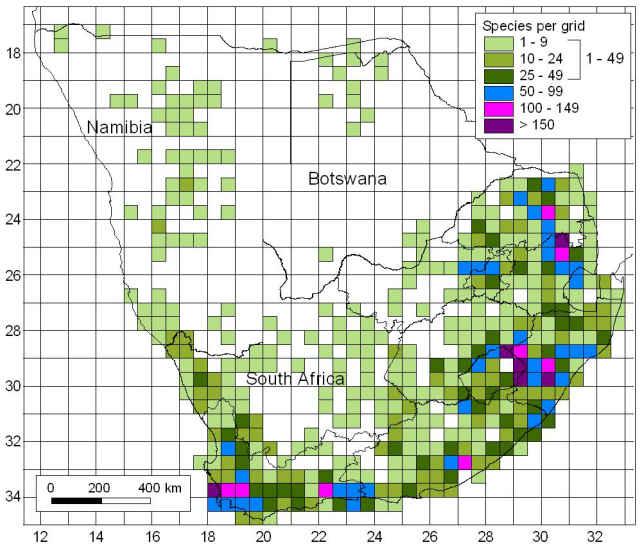

FIGURE 1. The joint geographical distribution of mosses in the Flora of Southern Africa region. The number of moss species/infraspecific taxa per half degree grid square are shown in six intervals.

The centres of moss species diversity were compared with a range of ecological and environmental, mostly climatic, variables (see Cowling *et al*. 1997 and Schulze 1997, 1997a) and found to be strongly related to habitat heterogeneity, rainfall and the moss flora of a particular area. To illustrate these relationships, the centres are superimposed on maps of 1) the topography of southern Africa, as described by altitude, original map based on the GTOPO30 global digital elevation model and obtained from http://edcsnw4.cr.usgs.gov/adds/data.php (accessed 30/05/2003), colours subsequently modified in Global Mapper v. 6.06 (Fig. 1); 2) mean annual precipitation over South Africa, from the electronic version of Schulze (1997a) (Fig. 2); and 3) the bryofloristic regions of southern Africa, after Van Rooy & Van Wyk (2010).

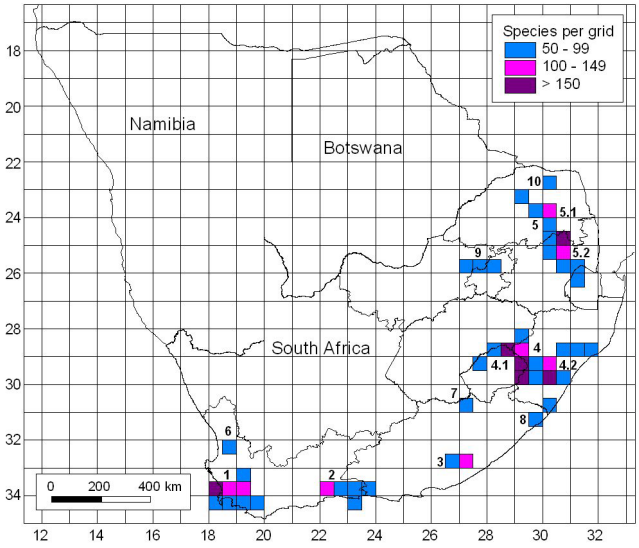

FIGURE 2. Centres (1–10) and subcentres (4.1, 4.2, 5.1 and 5.2) of moss species diversity in southern Africa. 1. Southwestern Cape, 2. Outeniqua, 3. Amathole, 4. KwaZulu-Natal, 4.1. Drakensberg, 4.2. Midlands, 5. Mpumalanga, 5.1. Wolkberg, 5.2. Blyde, 6. Cederberg, 7. Witteberge, 8. Pondoland, 9. Magaliesberg, and 10. Soutpansberg.

Results and discussion

Only 41 percent (431) of half degree grid squares in southern Africa contain records of mosses (Fig. 1). Therefore 59 percent (616) of grid squares are 'empty' while a further eight percent (86) only contain up to nine records. The five areas with the highest concentrations of moss species (100 + species recorded) are formally described as primary or main centres of moss diversity (Fig. 2). Two of these centres are subdivided into subcentres. Other areas of relatively high species richness (with more than 50, but less than 100 species), are described as secondary centres of moss diversity.

Main centres of moss diversity

1. Southwestern Cape Centre of Moss Diversity

This centre of moss diversity is situated in the southwestern corner of South Africa, at the junction between the two axes of the Cape Fold Mountains (Fig. 2 & 3). The half degree grid square with the highest number of species (194) is the Cape Town or Table Mountain grid (3318 C), also the most species-rich grid in southern Africa (Fig. 1). Other grids with high numbers of species are 3318 D and 3319 C, covering the Cape Fold Mountains between Stellenbosch, Villiersdorp and Worcester. This centre also covers the Cape Peninsula (grid 3418 A), the Hottentots Holland Mountains and Cape Hangklip (grid 3418 B), extending east to Riviersonderend (3419 A&B), and north to the mountains around Ceres and Tulbagh (grid 3319 A).

This centre, also known as the Caledon Centre, has long been recognised as the most species-rich area in the Cape as well as southern Africa (Levyns 1954, Dahlgren 1963, Croizat 1965, Nordenstam 1969). The moss centre of diversity is also more or less congruent with the Southwest Biogeographical Region of Bradshaw *et al*. (2015), which they found to contain the highest levels of endemism and richness in the CFR. Rebelo & Siegfried (1990) identified the Cape Hangklip region and Oliver *et al*. (1983) the Hottentots-Holland Mountains, as the most species-rich areas in the southwestern Cape. The southwestern Cape contains the highest concentration of threatened vascular plants and plants of conservation concern in South Africa (Raimondo & Van Staden 2009).

This centre of moss diversity falls into The Cape Floristic Region (CFR), identified as one of 20 global centres of vascular plant diversity (Barthlott *et al*. 2005) and recognised as a global biodiversity hotspot (Mittermeier *et al*. 2011). The CFR is also one of Linder's (2001) broad-scale centres of plant species richness and endemism in sub-Saharan Africa.

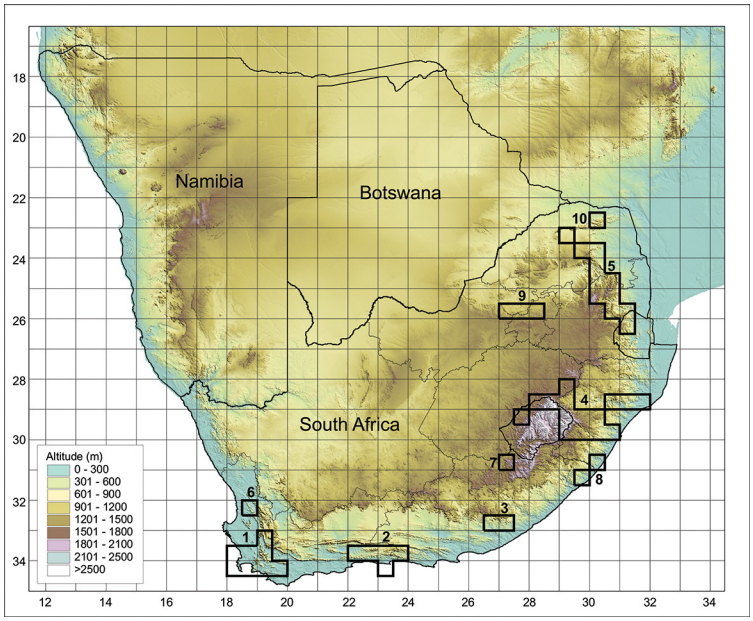

FIGURE 3. Centres of moss diversity in southern Africa, superimposed on a topographic map of the region, based on the GTOPO30 global digital elevation model and obtained from http://edcsnw4.cr.usgs.gov/adds/data.php (accessed 30/05/2003), colours subsequently modified in Global Mapper v. 6.06. 1. Southwestern Cape, 2. Outeniqua, 3. Amathole, 4. KwaZulu-Natal, 5. Mpumalanga, 6. Cederberg, 7. Witteberge, 8. Pondoland, 9. Magaliesberg, and 10. Soutpansberg.

2. Outeniqua Centre of Moss Diversity

This centre covers the Knysna and Tsitsikamma forests of South Africa, roughly between George in the west and Stormsriviermond in the east, and between the Outeniqua Mountains and the Indian Ocean (Fig. 2 & 3). However, high numbers of species are found right up to the Port Elizabeth area. The grid with the highest number of species recorded is the George-Oudtshoorn grid (3322 C) with 111 species. Between 50 and 100 species have been recorded in each of the grid squares to the east (3322 D, 3323 C & D, and 3423 A).

This area was described as the Zitzikamma subcentre of the South-eastern centre of endemism by Weimarck (1941). He remarked on the high number of vascular plant species in this area. The Outeniqua Mountains as well as the Amathole Mountains (that constitutes the next centre) are known as Afromontane 'outliers' (Beentje *et al*. 1994, Van Wyk 1994). Contemporary schemes include this area in the CFR (also Centre or hot-spot) of plant diversity and endemism (Cowling & Hilton-Taylor 1994, 1997; Rebelo 1994; Linder 2001; Van Wyk & Smith 2001).

3. Amathole Centre of Moss Diversity

This comparatively small centre is situated in the high-rainfall Hogsback-Keiskammahoek area of the Eastern Cape Province of South Africa where substantial stands of Afromontane forest survived (Fig. 2). The area is dominated by the Amathole mountain range in the northern part of the centre (Fig. 3). Geologically this centre is associated with mudstones and sandstones (with dolorite intrusions) of the Beaufort Group. A total of 105 species has been recorded from grid 3227 C (Keiskammahoek-King William's Town), most of these from the Pirie Forest, a historical collecting site. Hogsback (3226 D) has also been a popular collecting site and 56 species are known from this grid.

The Amatola Range was recognised as a subcentre of the Eastern Highlands within the geographical distribution area of the palaeogenic element of Stuckenberg (1962). The Amathole centre borders on, but is certainly not part of the low-lying Albany Centre of Van Wyk & Smith (2001). The approximate location of the Amathole Centre is shown on the map of Van Wyk's (1994) Maputaland-Pondoland Region.

4. Kwazulu-Natal Centre of Moss Diversity

This area of high moss species richness covers the Afromontane forests of the KwaZulu-Natal Drakensberg and Midlands (Fig. 2 & 3). Grid squares with more than 150 species are found along the Drakensberg escarpment, from the Mount aux Sources grid in the north (2828 D) to the Champagne Castle (2929 A) and Sani-Sehlabathebe area in the south (2929 C), and at Pietermaritzburg (2930 C) in the Midlands. Although the Drakensberg and Midlands areas are

linked by grids with more than 50 species (Fig. 2), they are provisionally separated as subcentres. Geologically, this centre is associated with rocks of the Karoo Sequence, topped with basalt of the Drakensberg Formation.

This centre of moss diversity falls mainly into the Maputaland-Pondoland Region as defined by Van Wyk (1994), and the Drakensberg Afromontane Regional System as described by Beentje *et al.* (1994), both treated as regional centres of plant diversity in Davis *et al*. (1994). The Maputaland-Pondoland Center is one of 20 global centres of vascular plant diversity recognised by Barthlott *et al*. (2005). Van Wyk (1991) identified this region as a centre of diversity and endemism in the distribution of *Lotononis*.

4.1 Drakensberg Subcentre of Moss Diversity

This centre is located in the Drakensberg and Maloti mountains of KwaZulu-Natal and northern Lesotho (Fig. 2 & 3). It extends from Maseru (2927 B) in the west and Van Reenen (2829 C) in the north, to Sehlabathebe (2929 C) in the south.

The Drakensberg Alpine Region (Killick 1994) is generally recognised (under different names) as one of the southern African centres of vascular plant diversity and endemism (Weimarck 1941; Croizat 1965; Nordenstam 1969; Davis *et al*. 1994; Cowling & Hilton-Taylor 1994, 1997; Van Wyk & Smith 2001). However, the Afromontane forests below c.1800 m, which greatly contribute to the high number of mosses in the Drakensberg subcentre, are generally excluded from the Drakensberg Alpine Region. Weimarck's (1941) Drakensberg Centre included the Drakensberg mountain range north of Lesotho, right up to Limpopo, with the Soutpansberg as outlier.

4.2 Midlands Subcentre of Moss Diversity

This subcentre is separated from the Drakensberg subcentre on the basis of high species numbers in grids 2930 A (Karkloof area) and 2930 C (Pietermaritzburg) (Fig. 2). The centre probably extends right up to the Kranskop area east of Greytown.

Collections from the Afromontane forests of Qudeni, Nkandla, Ngoje, Dlinza, Umgoye and Mtunzini are largely responsible for the high numbers of moss species in the Zululand grids of Kranskop (2830 D), Nkandla-Eshowe (2831 C), and Empangeni (2831 D). The Zululand forests are separated from the Midlands centre by the Tugela River valley and may represent a separate centre or subcentre of moss diversity in South Africa.

The 'Afromontane region of the Natal/Transkei Midlands' is listed as a 'centre' within the Drakensberg Afromontane Regional System (centre of diversity) by Beentje *et al*. (1994).

5. Mpumalanga Centre of Moss Diversity

This centre covers the Drakensberg escarpment of Limpopo and Mpumalanga in South Africa, roughly from the Wolkberg Mountain east of Polokwane, all the way to the mountains of north-western Swaziland (Fig. 2 & 3). Afromontane forests such as Woodbush, De Hoek, Serala, New Agatha, Mariepskop, Uitsoek and Kaapsehoop (Von Breitenbach 1990) are largely responsible for the high degree of moss diversity. The centre is associated with rocks of the Transvaal Sequence (Matthews *et al*. 1993).

Grid squares with more than 100 species recorded are: 2330 C (Tzaneen-Duiwelskloof area), 2430 D (Graskop-Blyderivierspoort), and 2530 B (Nelspruit-Sabie). The Graskop-Blyderivierspoort grid (2430 D) with 184 species is second only to the Cape Town grid (3318 C) in the number of moss species recorded in southern Africa.

This centre coincides with the Barberton Centre of Croizat (1965), Nordenstam (1969) and the Barberton Centre of endemism of Van Wyk & Smith (2001), as well as the Wolkberg Centre (of endemism) of Matthews *et al*. (1993), Cowling & Hilton-Taylor (1994, 1997) and Van Wyk & Smith (2001). The concentration of Eastern Highlands mosses along the Mpumalanga escarpment (see Van Rooy & Van Wyk 2011) overlaps with the Eastern Transvaal Subcentre of Stuckenberg (1962).

5.1 Wolkberg Subcentre of Moss Diversity

The northernmost of the two Mpumalanga subcentres is named after the Wolkberg Mountain situated between Polokwane and Tzaneen in the Limpopo Province of South Africa (Fig. 2). It comprises the Drakensberg escarpment area roughly to the north of the Olifants River gorge. The highest number of species (100) is found in grid 2330 C (Tzaneen) while grids 2329 D (Haenertsburg-Houtboschdorp area) and 2430 A (Wolkberg Wilderness area) have more than 50 species recorded.

The Wolkberg subcentre of moss diversity is synonymous with the Serala Subcentre of Matthews *et al*. (1993).

5.2 Blyde Subcentre of Moss Diversity

The main area of this subcentre is situated along the Drakensberg escarpment of Mpumalanga, between Blyderivierspoort (grid 2430 D with 184 species) and Nelspruit (grid 2530 B with 120 species). However, grid squares to the east (2430 C & 2530 A) and to the south (2530 D, 2531 C & 2631 A) of the main area are also species-rich with between 50 and 100 records. This subcentre extends as far south as the mountains at Barberton and the Malolotja-Mbabane area in north-western Swaziland.

This subcentre is named after the Blyde Subcentre of Matthews *et al*. (1993). The Barberton/north-western Swaziland area is recognised as a separate centre, the Barberton Centre (of endemism) by Beentje *et al*. (1994), Van Wyk (1994), and Van Wyk & Smith (2001).

Secondary centres of moss diversity

6. Cederberg Centre of Moss Diversity

This area is probably an outlier of the Southwestern Cape centre, but presently grid 3218 B, with 63 species recorded, stands out as a separate centre of moss diversity (Fig. 1, 2 & 3). This grid square covers the town of Clanwilliam and the Pakhuis Pass, leading into the northernmost part of the Cederberg Mountains. It is linked to the Southwestern Cape centre by grids 3219 A & C (38 and 39 species respectively), situated in the Cederberg and Kouebokkeveldberge. It also extends northward along the Bokkeveldberge between Vanrhynsdorp (3118 D) and Nieuwoudtville (3119 A). The Cederberg Centre of Diversity is largely restricted to quartzitic sandstones of the Table Mountain Group.

This centre of moss diversity overlaps with, and is named after, the Cederberg Centre of Weimarck (1941). It borders on the Vanrhynsdorp or Knersvlakte Centre of vascular plant diversity and endemism (Nordenstam 1969; Hilton-Taylor 1994, 1996; Cowling *et al*. 1999; Van Wyk & Smith 2001).

7. Witteberge Centre of Moss Diversity

With 51 species recorded, grid 3027 C in the Witteberge at Lady Grey in the Eastern Cape is by far the most species-rich grid in the area (Fig. 1, 2 & 3). The grid squares between this centre and the KwaZulu-Natal centre are under-collected and may link the two in future. Indeed, the 'southern Drakensberg mountains of Natal and north-eastern Cape' have been listed as one of the 'centres' within the Drakensberg Afromontane Regional System by Beentje *et al*. (1994).

8. Pondoland Centre of Moss Diversity

The Pondoland centre runs roughly from Port Shepstone on the KwaZulu-Natal South Coast in the north, to Port St. Johns on the Wild Coast in the south (Fig. 2). The grids with the highest number of species recorded are 3030 C (Port Shepstone) and 3129 B (Lusikisiki).

The Table Mountain Sandstone areas along the southern KwaZulu-Natal/Pondoland coast are known to be rich in vascular plant endemics (Van Wyk 1990). The moss centre is therefore named after the Pondoland Centre (of plant endemism) or hot-spot recognised by Van Wyk (1994, 1996), Cowling & Hilton-Taylor (1994), Cowling *et al*. (1997) and Van Wyk & Smith (2001). The Pondoland centre falls into the Maputaland-Pondoland Region of vascular plant diversity (Van Wyk 1994).

9. Magaliesberg Centre of Moss Diversity

This centre of moss diversity runs along the Magaliesberg mountains between Pretoria in Gauteng and Rustenburg in the North-West Province (Fig. 2 & 3). Afromontane forest elements are found in sheltered kloofs or ravines on the northern side of this mountain range. More than 50 species of moss have been recorded from grids 2528 C (Pretoria), 2527 D (Brits) and 2527 C (Rustenburg). Like the Mpumalanga centre of moss diversity, the Magaliesberg centre is situated on rocks of the Transvaal Sequence (Carruthers 1990).

10. Soutpansberg Centre of Moss Diversity

Relatively high numbers of moss species are known from the Entabeni (2230 C) and Blouberg (2329 A) areas of Limpopo (Fig. 2 & 3). However, high numbers of mosses are likely to be found all along the Soutpansberg mountain range. Afromontane forests, e.g. the Entabeni Forest, contribute greatly to the recognition of this area as a centre of moss species diversity. This centre is situated on sandstones and conglomerates of the Soutpansberg Group.

Beentje *et al*. (1994) list the Soutpansberg Centre as one of the centres (of endemism) recognised within the Drakensberg Afromontane Regional System. It is also recognised as a principal centre of plant endemism (Van Wyk & Smith 2001) and a centre of biological diversity (Mostert *et al.* 2008).

Other species-rich areas

Concentrations of less than 50 species per half degree grid square, which stand out from the surrounding areas, may also represent centres of diversity, but as a result of insufficient sampling, they are not formally described.

Relatively high species numbers in the Springbok (2917 D) and adjacent grid squares (Fig. 1) may warrant the recognition of a Kamiesberg centre of moss diversity. This area is known as a local centre of vascular plant diversity and endemism within the Succulent Karoo Region (Hilton-Taylor 1994, 1996) or an outlier centre of endemism of the Cape Floristic Region (Weimarck 1941, Van Wyk & Smith 2001).

Grid squares in the Richtersveld of the Northern Cape Province (2816 B & D, 2817 A & C) are relatively species-rich (Fig. 1). This area falls into the Gariep Centre of vascular plant diversity and endemism (Croizat 1965; Nordenstam 1969; Hilton-Taylor 1994, 1996; Cowling *et al*. 1999; Van Wyk & Smith 2001).

Although the Drakensberg escarpment in the Wakkerstroom-Vryheid area (grids 2730 A, B & D and 2731 C) is relatively species-rich (between 25 and 49 species) (Fig. 1) it may prove to be another subcentre of the Kwazulu-Natal centre of moss diversity.

Grids 2427 B (Kransberg) and 2428 C (Nylstroom) in the Waterberg mountains of Limpopo, with between 25 and 49 species recorded in each (Fig. 1), may represent another centre of moss diversity. This centre is situated on sandstone and conglomerate of the Waterberg Group.

Another relatively species-rich centre of moss diversity is located in the Sneeuberg mountain complex on the Great escarpment of the Eastern Cape. Thirty species are known from the Graaff-Reinet grid (3224 B) while grids to the west (3224 A) and north (3124 B & D) have between 10 and 24 species recorded (Fig. 1). This area was recently described as the Sneeuberg Centre of Endemism by Clark *et al.* (2009).

Determinants of moss species richness in southern Africa

Robertson & Barker (2006) demonstrated that insufficient sampling contributes to low plant species richness in large areas of southern Africa (up to 77% of quarter degree grid squares), especially in Botswana, Namibia and the semi-arid to arid central region of South Africa. Bryophytes are no exception and moss records are absent or very low in most of the central, western and northern parts of the region. Areas of high documented moss species richness in southern Africa can be explaining at the hand of collecting bias as well as environmental factors.

Collecting bias

Plant species richness is known to increase with human population size and density, especially around towns and cities where universities and herbaria are present, known as the botanist effect (Rebelo 1994, Moerman & Estabrook 2006, Pautasso & Mckinney 2007). Historically, Cape Town, situated at the foot of Table Mountain (grid 3318 C), the most species-rich area in southern Africa, was the first port of call and plant collecting site for travellers from Europe (Sim 1926, Glen & Germishuizen 2010). The high species diversity in the Pietermaritzburg area of the KwaZulu-Natal Midlands (grid 2930 C) can be explained by the collecting efforts of T.R. Sim, the 'father' of southern African Bryology, who resided there from 1903 to shortly before his death in 1937 (Bayer 1971, Glen & Germishuizen 2010). The grid squares at Bloemfontein (2926 A) and Kimberley (2824 D), the two largest cities in the central part of the study area, are also the most species-rich (Fig. 1). Russell & Van Rooy (1988) observed that existing bryophyte records from Namibia show the influence of population centres and roads on collecting frequency. The grid square where Windhoek, the largest town and capital of Namibia is situated (grid 2217 C), is also the most species-rich in that country.

In the late 1800's and early 1900's, the Rydal Mount and Royal Natal National Park localities, both situated in the species-rich grid of Witsieshoek (2828 D), were the only means of access to the Drakensberg of KwaZulu-Natal and the famed Mont aux Sources for most visitors (Pearse 1973). This form of collecting bias, where more accessible areas are sampled preferentially, is known as geographical bias (Robertson & Barker 2006).

The Mariepskop centre of high species diversity (grid 2430 D) is largely the result of intense collecting by P. Vorster for his M.Sc. thesis (Vorster 1990). The Lady Grey area (grid 3027 C) probably stands out as a centre of diversity as a result of a collecting trip by J. van Rooy (PRE) in February 1986. Higher species numbers along the southern KwaZulu-Natal/Pondoland coast (3030 C, 3129 B, 3130 A) are largely the result of collecting by T. Abbott (who resided there) as well as a collecting trip by J. van Rooy and L. Smook (PRE) in February/March 1985.

One can also recognise roads on the moss diversity map. For example, the relatively high species numbers in grids 3224 A & B, 3124 B & D, 3025 C, 2926 A & C (Fig. 1) represent roadside collections along the N9 and N1 roads between Graaff-Reinet in the Eastern Cape and Bloemfontein in the Free State. In the same area, the N6 road between Bloemfontein and Aliwal North (3026 D) is also visible. The N4 from Middelburg (2529 C) in Mpumalanga, all the

way to Zeerust (2526 C) in the North-West Province, and the R27 from there to Vryburg (2624 D), as well as the road north to Gaborone (2425 D) in Botswana, can also be followed on the species per grid map (Fig. 1).

Environmental factors

The centres of moss diversity are situated in the orogenic zone of southern Africa (Fig. 3). This zone is characterised by steep environmental gradients, e.g. topography, moisture and temperature gradients (see maps in Schulze 1997a), that provide for heterogeneous moss habitats. Orogenic factors have also been put forward by Churchill *et al*. (1995) as the most important determinants of moss diversity in the Neotropics.

The centres are located in areas that contain montane forests, classified as the Afromontane (bryofloristic) Region by Van Rooy & Van Wyk (2010) (Fig. 5). Characteristic of the Afromontane moss flora is the abundance of pleurocarpous mosses belonging to the Orders Hookeriales, Hypnobryales, Isobryales and Thuidiales. The Isobryales is the best represented at the family level with five of its 12 families (Fontinalaceae, Cryphaeaceae, Prionodontaceae, Trachypodaceae and Pterobryaceae) diagnostic for the region. Moss genera and species diagnostic for and endemic to the Afromontane region are listed by van Rooy & Van Wyk (2010).

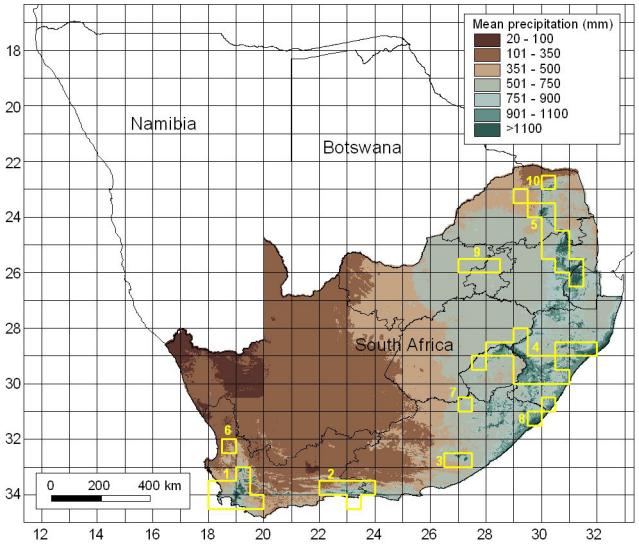

FIGURE 4. Centres of moss diversity in relation to the mean annual precipitation over South Africa, from the electronic version of Schulze (1997a). 1. Southwestern Cape, 2. Outeniqua, 3. Amathole, 4. KwaZulu-Natal, 5. Mpumalanga, 6. Cederberg, 7. Witteberge, 8. Pondoland, 9. Magaliesberg, and 10. Soutpansberg.

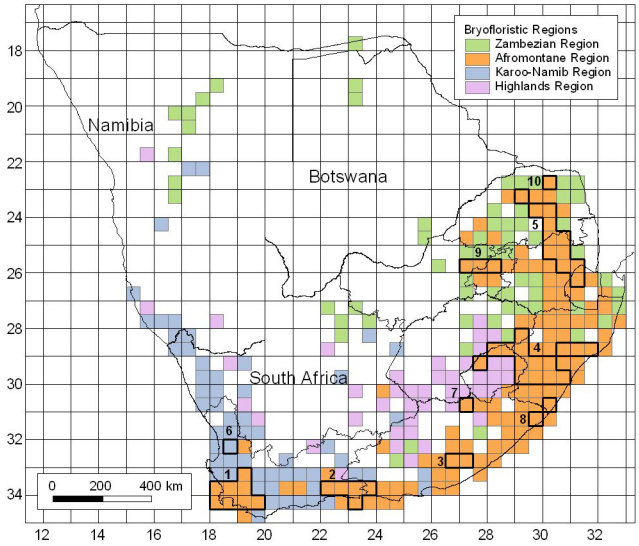

FIGURE 5. Centres of moss diversity in relation to the bryofloristic regions of southern Africa, after Van Rooy & Van Wyk (2010). 1. Southwestern Cape, 2. Outeniqua, 3. Amathole, 4. KwaZulu-Natal, 5. Mpumalanga, 6. Cederberg, 7. Witteberge, 8. Pondoland, 9. Magaliesberg, and 10. Soutpansberg Centres of Moss Diversity.

Although the Cederberg centre of moss diversity appears to fall outside the Afromontane Region, it is only because of the course grain of the two studies. It is generally accepted that climatic factors, especially the higher rainfall and air humidity, lower temperatures, as well as habitat heterogeneity, are responsible for the higher bryophyte (plant) diversity in montane forests (Gradstein & Pòcs 1989, Churchill *et al.* 1995, Gradstein 1995, Webster 1995).

Centres of moss species-richness fall into the highest rainfall areas of southern Africa, measured as mean annual precipitation (Schulze 1997a)(Fig. 4). The three main centres, and most of the secondary centres (the Magaliesberg centre excluded), receive in excess of 1000 mm of rain annually.

All of the centres (except the Magaliesberg centre) are situated along and below the Great Escarpment of South Africa (Fig. 3), a transition zone between the tropical and temperate floras of the subcontinent (the tropical-temperate convergence zone). In this zone, measures of diversity are likely to capture elements of both floras. For example, grid squares covering the species-rich area along the KwaZulu-Natal Drakensberg escarpment include temperate mosses on the Lesotho plateau as well as tropical mosses in the Afromontane forests down below (Van Rooy & Van Wyk 2010) (Fig. 3 & 5).

Conclusions

Moss diversity in southern Africa is greatest in the Cape Fold Mountains of the southwestern Cape, and the Drakensberg of KwaZulu-Natal, Mpumalanga and Limpopo. With increased collecting, and the inclusion of the other bryophyte lineages, liverworts and hornworts, most of the centres will probably link up to form a more or less continuous band of high species diversity all along and below the Great Escarpment of southern Africa. The Cape Town area, including Table Mountain, boasts the highest concentration of moss species in South Africa, followed closely by the Blyderivierspoort/Graskop area of Mpumalanga, and the northern Drakensberg and Pietermaritzburg in the Midlands of KwaZulu-Natal.

Arid conditions and cultivation in the central, northern and western parts of southern Africa make bryologists and other plant collectors turn east and south, rather than west, when looking for bryophytes. As a result, large areas in Botswana, Namibia and the semi-arid to arid central region of South Africa are under-collected and without records of bryophytes.

The Afromontane moss flora, characterised by the abundance of pleurocarpous mosses, is responsible for high moss species diversity in southern Africa. Although collecting bias, including geographical bias and the 'botanist effect', is responsible for concentrations of species in many areas, moss diversity in southern Africa is strongly related to environmental factors. Our results indicate that habitat heterogeneity and mean annual rainfall are good predictors of moss species richness in the region. The more diverse the habitat and the higher the rainfall, the higher the number of moss species present. This is in agreement with existing hypotheses of a broad-scale correlation between environmental heterogeneity and climate on the one side, and vascular plant diversity and distributions on the other.

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