Article

Latitudinal gradient in species richness of *Sphaerotherium*

Mark Cooper [1,2]
[1]University of Johannesburg, Johannesburg, South Africa
[2]School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Johannesburg 2050, South Africa
E-mail: cm.i@aol.com

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Abstract
The Tropical Conservativism Hypothesis and Biogeographical Conservativism Hypothesis were tested in forest millipedes. Latitudinal diversity gradient (LDG) was measured in the genus *Sphaerotherium* in order to distinguish between the two hypotheses. There was a significant correlation between the number of species and latitudinal degrees away from the equator (r=−0.8701, r^2=0.7571, n=46, p<0.00001). An evolutionary preference for temperate environments appearing to have led to climatic constraints on dispersal based primarily on precipitation seasonality gradients was suggested.

Keywords diversity; gradient; latitude; richness; species.

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1 Introduction

Species richness is the number of different species represented in an ecological community, landscape or region (Colwell and Hurrt, 1994; Colwell and Lees, 2000; Colwell et al., 2004; Colwell, 2009). Species richness and biodiversity increase from the poles to the tropics for a wide variety of terrestrial and marine organisms and is referred to as a latitudinal diversity gradient (LDG) (Pianka, 1989; Hillebrand, 2004). Inverse LDG includes aphids, Chinese litter-dwelling thrips, diving beetle subfamily Colymbetinae, European bryophytes, freshwater zooplankton, Holarctic tree frogs, ichneumonids, marine benthic algae, marine bivalves Anomalodesmata, New World snake tribe Lampropeltini, North American breeding birds, penguins, peracarid crustaceans, pitcher plant mosquito, pond turtles, Shallow-water molluscs, shorebirds, southeastern United States trees, subarctic forests and tropical leaf-litter ant communities (Kindlmann et al., 2007; Krug et al., 2007; Kwon et al., 2019; Marshall and Baltzer, 2015; Mateo et al., 2016; Morinière et al., 2016; Pyron and Burbrink, 2009; Rivadeneira et al., 2011; Silva and Brandão, 2014; Sime and Brower, 1998; Wang et al., 2014).

The LDG is measured and tested in the Oniscomorph forest millipede genus *Sphaerotherium* Brandt, 1833. This forest clade belonging to the Order Sphaerotheriida is distributed along the eastern coast of southern

Africa consisting of species with concentrations around coastal bush and forests (Silvestri, 1910, 1917; Attems, 1926, 1928; Jeekel, 1951; Schubart, 1958; Lawrence, 1966; Hamer, 1998; Van den Spiegel et al., 2002; Golovatch et al., 2012; Wesener, 2016; Cooper, 2018). The null hypothesis is the Tropical Conservativism Hypothesis which suggests processes of speciation, extinction and dispersal result in higher species richness at the tropics and decline away from the equator (Mittelbach et al., 2007). The alternative is the Biogeographical Conservativism Hypothesis which suggests the processes invoked are not intrinsic to the tropics but are dependent on historical biogeography to determine the distribution of species richness (Pyron and Burbrink, 2009).

2 Materials and Methods

49 valid species were identified as belonging to the genus *Sphaeotherium* Brandt, 1833 (Hamer, 1998). These were tabulated and known localities also listed (Table 1). Localities were obtained from Hamer (1998). GPS coordinates were obtained from internet sources for known localities using the locality followed with the keyword “GPS”. Latitude and longitude coordinates were obtained. When co-ordinates were not in decimal degrees, they were subsequently converted to decimals in dividing the seconds in 60 and adding these to the minutes which were together divided through 60 to get the decimal behind or following the degree. Species accepted were in accordance with MilliBase (http://www.millibase.org).

3 Results

25 *Sphaerotherium* species were found between -31- and -35-degrees latitude, 9 species between -27- and -31-degrees latitude, 7 species between -23- and -27-degrees latitude, 3 species between -19- and -23-degrees latitude, 1 species between -15- and -19-degrees latitude and 1 species between -11- and -15-degrees latitude South. There was a significant correlation between the number of species and latitudinal degrees away from the equator (Fig. 2: r=-0.8701, r^2=0.7571, n=46, p<0.00001). Species with the locality "Caput Bonae Spei" on MilliBase (Sierwald and Spelda, 2020; http://www.millibase.org) were not included. One taxonomic change from Hamer (1998) to Sierwald and Spelda (2020) included accepting *Sphaerotherium ancillare* Attems, 1928 as *Sphaerotherium compressum* Brandt, 1833.

Table 1 Species in the genus *Sphaerotherium* with type or collected localities and GPS points.

Species	Locality	GPS latitude	GPS longitude
S. alticola	Mount Morosi	-30.2786	27.8721
S. apicale	Maputo	-25.9537	32.5887
S. boerium	Pretoria	-25.7313	28.2184
S. capense	Blinkwater Ravine	-33.9573	18.4031
S. cinctellum	Knysna	-34.0490	23.0479
S. civicum	Burgersdorp	-30.9906	26.3354
S. commune	Houw Hoek	-34.2051	19.1510
S. compressum	Klaastenbosch	-33.9923	18.4309
S. coniferum	Maputo	-25.9537	32.5887
S. convexitarsum	Port Elizabeth	-33.9820	25.6590
S. dicrothrix	Acornhoek	-24.5930	31.0970
S. dingonum	Knysna	-34.0490	23.0479
S. dorsale	Caffraria	-	-

S. dorsaloide	Knysna	-34.0490	23.0479
S. eremita	Table mountain	-33.9481	18.4030
S. eucalyptophylum	Soutpansberg	-23.0423	29.5483
S. fulvum	Zuurburg pass	-33.3515	25.7438
S. giganteum	Caffraria	-	-
S. granulatum	Port Elizabeth	-33.9820	25.6590
S. hanstömi	Pietermaritzburg	-29.6180	25.6590
S. intermedium	Peninsula	-34.2708	18.4598
S. kitharistes	Macequece	-18.9707	32.6709
S. krugeri	Gomondwane	-25.3584	31.8923
S. mahaium	Mahai River	-28.6883	28.9475
S. millipunctatum	Chai Chai	-11.8525	40.0250
S. modestum	Pafuri	-22.4491	31.3157
S. narcissei	Melsetter	-19.8000	32.8667
S. nigritarse	Hermanus	-34.4187	19.2345
S. perbrincki	Gudu falls	-28.6773	28.9276
S. permodestum	Transvaal	-	-
S. pinnatum	Van Stadens pass	-33.9091	25.1970
S. plagiarium	Knysna	-34.0490	23.0479
S. punctulatum	Amanzimtoti	-30.0500	30.8830
S. rotundatum	Hogsback	-32.5667	26.9500
S. rudebecki	Quthing	-30.4000	28.0000
S. selindum	Mount Selinda	-20.4333	32.7000
S. similare	Tsitsikamma	-33.9738	23.8866
S. solitarium	Crocodile Bridge	-25.3583	31.2583
S. spinatum	Keoga	-33.7667	25.6667
S. steppense	Middleton, EC	-32.9500	25.8167
S. subdorsale	East London	-32.1000	29.0833
S. submite	Knysna	-34.0490	23.0479
S. tenuitarse	Knysna	-34.0490	23.0479
S. tomentosum	Gudu falls	-28.6773	28.9276
S. trichopygum	Millars point	-34.2467	18.4746
S. tuberosum	Camps bay	-33.9640	18.3830
S. tzitzikamum	Tsitsikamma	-33.9738	23.8866
S. weberii	Table mountain	-33.9481	18.4030
S. zuluense	Hluluwe	-28.0070	31.6860

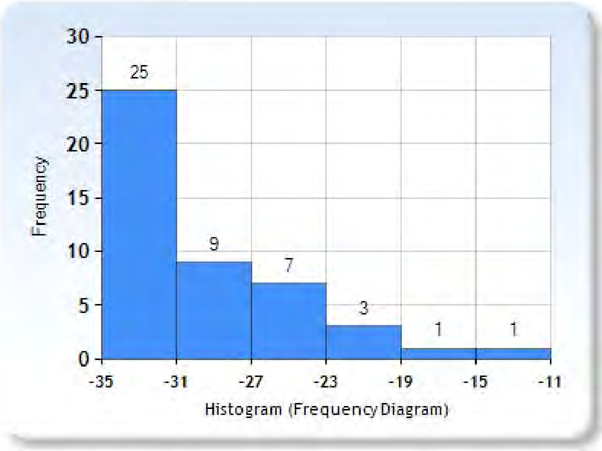

Fig. 1 Histogram showing the number of species (Frequency) across latitudes in *Sphaerotherium*.

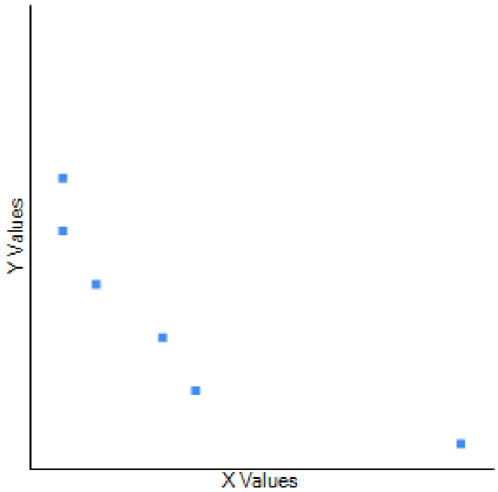

Fig. 2 Correlation between species number (Y Values) and latitude S (X Values) in *Sphaerotherium*.

4 Discussion

Sphaerotherium are a Gondwanan relict (Hopkin and Read, 1992). *Sphaerotherium* are more temperate and show a general decline in LDG (Colwell and Hurrt, 1994; Colwell and Lees, 2000; Colwell et al., 2004; Pielou, 1977; Willig and Lyons, 1998; Zapata et al., 2003). Other groups showing an inverse LDG includes aphids, Chinese litter-dwelling thrips, diving beetle subfamily Colymbetinae, European bryophytes, freshwater zooplankton, Holarctic tree frogs, ichneumonids, marine benthic algae, marine bivalves Anomalodesmata, New World snake tribe Lampropeltini, North American breeding birds, penguins, peracarid crustaceans, pitcher plant mosquito, pond turtles, Shallow-water molluscs, shorebirds, southeastern United States trees, subarctic forests and tropical leaf-litter ant communities (Kindlmann et al., 2007; Krug et al., 2007; Kwon et al., 2019; Marshall and Baltzer, 2015; Mateo et al., 2016; Morinière et al., 2016; Pyron and Burbrink, 2009; Rivadeneira et al., 2011; Silva and Brandão, 2014; Sime and Brower, 1998; Wang et al., 2014).

Two general explanations for the inverse trends in LDG include precipitation and predation which may be pertinent to *Sphaerotherium* (Ferguson 2004; Smigel and Gibbs, 2008; Tuf et al., 2016). Predation affects *Sphaerotherium* as all species have some form and degree of conglobation (Wesener et al., 2011; Tuf et al., 2016). This behaviour is also an adaptive response to conserve moisture (Ferguson, 2004; Smigel and Gibbs, 2008). Rapoport's rule, which states there is a decrease in the latitudinal extent of ranges at lower latitudes may exist independently of biodiversity gradients so it cannot be used as an explanation in *Sphaerotherium* (Stevens, 1989).

There may be an evolutionary preference for temperate environments appearing to have led to climatic constraints on dispersal based primarily on precipitation or temperature seasonality gradients (Kadamannaya et al. 2009; Pyron and Burbrink, 2009). LDG depends on proximate factors affecting processes of speciation, extinction, immigration, and emigration and in *Sphaerotherium* these factors are dependent on size which need investigating in *Sphaerotherium* based on temperature, precipitation and latitude. LDG may relate to body size in *Sphaerotherium* probably which does not agree with the trends in other taxa such as birds and fishes (Yen et al. 2018). The trend of a small body size associated with the inverse LDG is expected to be similar to the weak tendency found in mammals (Gittleman and Purvis, 1998).

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