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The inverse latitudinal gradient in species richness of forest millipedes: Pentazonia Brandt, 1833

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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 infraclass Pentazonia to distinguish between the two hypotheses. There was a significant correlation between the number of species and latitudinal degrees away from the equator (r=-0.86, r^2=0.75, n=47, p<0.01). An evolutionary preference for temperate environments appearing to have led to dispersal based on precipitation/temperature gradients and predation was suggested.

Keywords: diversity, gradient, latitude, richness, species

Introduction
Species richness is the number of different species represented in an ecological community, landscape, or region [4-7]. 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) [13, 25]. Inverse LDG in invertebrates is hypothesized and explained as the result of predation, which plays an important "keystone" role in structuring the community [27]. Wisdom predicts as the abundance of the top predator, decreases, a greater number of taxa in lower trophic levels can persist.
The LDG is measured and tested in the Oniscomorph forest millipede infraclass Pentazonia Brandt. This forest clade belonging to the class Pentazonia is partially distributed along the eastern coast of southern Africa, consisting of species with concentrations around coastal bush and forests [1, 2, 8, 11, 15, 20, 31, 36, 37, 40, 42]. The null hypothesis is the Tropical Conservativism Hypothesis which suggests processes of speciation, extinction, and dispersal result in higher species richness in the tropics and decline away from the equator [23]. 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 [28]. The biotic hypothesis claims ecological species interactions, here avian competition on millipede prey, is stronger in the tropics and these interactions promote species coexistence and specialization of species.

2. Materials and Methods
49 valid species were identified as belonging to the genus *Sphaeotherium* [3] and one to *Kylindotherium* [2, 12]. These were tabulated, and known localities were also listed (Table 1). The locality for *Kylindotherium leve* [2] was Wellington (Latitude: -33.643055 degrees South). Localities were obtained from Hamer [12]. GPS coordinates were obtained from https://www.gps-coordinates.net/. Species accepted were in MilliBase (http://www.millibase.org).

3. Results
25 *Sphaerotherium* species and *Kylindotherium leve* 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=-0.8632, r^2=0.74551, n=47, 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 [12] to Sierwald and Spelda [32, 33] 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	25.659
S. hanstömi	Pietermaritzburg	-29.6180	25.659
S. intermedium	Peninsula	-34.2708	18.460
S. kitharistes	Macequece	-18.9707	32.671
S. krugeri	Gomondwane	-25.3584	31.892
S. mahaium	Mahai River	-28.6883	28.948
S. millipunctatum	Chai Chai	-11.8525	40.025
S. modestum	Pafuri	-22.4491	31.316
S. narcissei	Melsetter	-19.8000	32.867
S. nigritarse	Hermanus	-34.4187	19.235
S. perbrincki	Gudu falls	-28.6773	28.928
S. permodestum	Transvaal	-	-
S. pinnatum		-33.9091	25.197
S. plagiarium	Van Stadens pass Knysna	-34.0490	23.048
S. punctulatum	Amanzimtoti	-30.0500	30.883
S. rotundatum	Hogsback	-32.5667	26.950
S. rudebecki	Quthing	-30.4000	28.000
S. selindum	Mount Selinda	-20.4333	32.700
S. similare	Tsitsikamma	-33.9738	23.887
S. solitarium	Crocodile Bridge	-25.3583	31.258
S. spinatum	Keoga	-33.7667	25.667
S. steppense	Middleton, EC	-32.9500	25.817
S. subdorsale	East London	-32.1000	29.083
S. submite	Knysna	-34.0490	23.048
S. tenuitarse	Knysna	-34.0490	23.048
S. tomentosum	Gudu falls	-28.6773	28.928
S. trichopygum	Millars point	-34.2467	18.475
S. tuberosum	Camps bay	-33.9640	18.383
S. tzitzikamum	Tsitsikamma	-33.9738	23.887
S. weberii	Table mountain	-33.9481	18.403
S. zuluense	Hluhluwe		

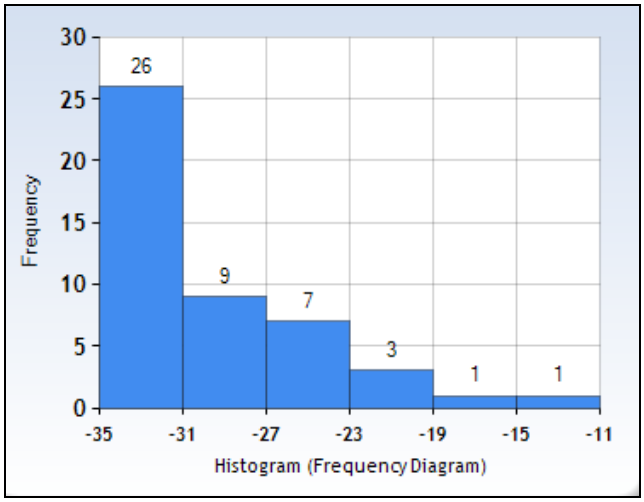

Fig 1: Histogram showing the number of species (Frequency) across latitudes in Pentazonia.

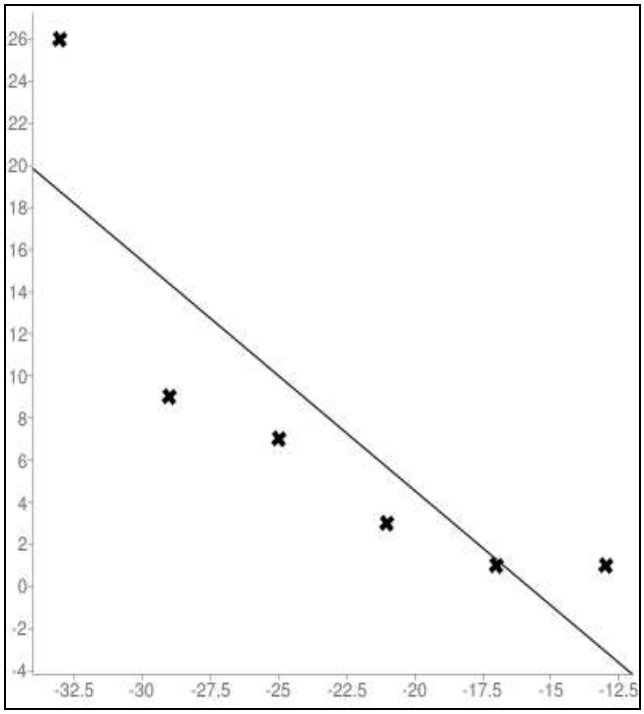

Fig 2: Linear regression of species number (Y Values) on latitude S (X Values) in Pentazonia.

4. Discussion

Sphaerotherium is a Gondwana taxon [14, 44]. *Sphaerotherium* is more temperate and shows a general decline in LDG supporting the Biogeographical Conservativism Hypothesis [28]. *Kylindotherium leve* locality at Wellington, together with the majority (51-54%) of *Sphaerotherium* between -31- and -35 degrees latitude South, support the Biogeographical Conservativism Hypothesis. Other groups showing an inverse LDG include 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 mollusks, shorebirds, southeastern United States trees, subarctic forests, and tropical leaf-litter ant communities [17-19, 21, 22, 24, 28, 29, 34, 35, 41].

Two general explanations for the inverse trends in LDG include precipitation and predation, which may be pertinent to *Sphaerotherium* [9, 38, 39]. Predation affects *Sphaerotherium* as all species have some form and degree of conglobation [39, 43]. This behavior is also an adaptive response to conserve moisture [9, 38]. There is a higher predation risk for insect prey at lower latitudes [30].

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 [16, 28]. LDG depends on proximate factors affecting processes of speciation, extinction, immigration, and emigration, and in Pentazonia these factors are dependent on size, which were investigated in Pentazonia based on temperature, precipitation, and latitude (Cooper, unpublished). LDG may relate to body size in Pentazonia probably, which does not agree with the trends in other taxa such as birds and fishes [45]. The trend of a small body size associated with the inverse LDG is expected to be similar to the weak tendency found in mammals. However, there was no significant association between body mass and species-richness [10]. In pentazonians, size is significantly related to latitude.

5. Conclusion

The inverse LDG in *Sphaerotherium* spp. and *Kylindotherium leve* supports the biogeographical conservativism hypothesis and suggests an effect of predation and precipitation on species richness.

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