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Mark Cooper
School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Johannesburg 2050, South Africa

Corresponding Author:
Mark Cooper
School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Johannesburg 2050, South Africa

The inverse latitudinal gradient in species richness of forest millipedes: Pachybolidae Cook, 1897

Mark Cooper

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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 Spirobolida family Pachybolidae to distinguish between the two hypotheses. There was a significant correlation between the number of species and latitudinal degrees away from the equator (r=-0.82, r^2=0.68, n=38, p<0.01). An evolutionary preference for temperate environments appearing to have led to climatic constraints on dispersal based on precipitation seasonality gradients and predation was suggested.

Keywords: diversity, gradient, latitude, richness, species

1. Introduction
Species richness is the number of different species represented in an ecological community, landscape, or region [2-5]. 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) [11, 22]. Inverse LDG in invertebrates is hypothesized and explained as the result of predation, which plays an important "keystone" role in structuring the community [23]. Wisdom predicts as the abundance of the top predator, decreases, a greater number of taxa in lower trophic levels can persist.
The forest family of diplopods belonging to the Order Spirobolida found along the eastern coast of southern Africa was the subject of this study [17]. The family Pachybolidae consists of the four genera *Centrobolus*, *Epibolus*, *Hadrobolus* and *Microbolus*. The (multi-specific] genus *Chersastus* (=*Centrobolus*) is confined to the temperate South African subregion, its northern limits on the east coast of southern Africa being about -17° latitude S. It occurs in all the forests of the coastal belt from the Cape Peninsula to Beira in Mocambique. While the coastal forests of the South-West and Eastern Cape are mist belt temperate forests, those of the Transkei, Natal, Zululand and Mocambique are somewhat different, being better described as East Coast Bush. They are developed almost entirely in a narrow strip of the litoral on a dune sand substratum, are more tropical in aspect and composition than those to the west of them; there is a summer rainfall of 30-40 inches, a uniform temperature, and an absence of frost; the component trees of the coastal bush with their abundant creepers and lianes, while not usually reaching a height of more than 35 feet, provide a dense covering with abundant shade and humidity at ground level. As essentially shade-loving Diplopoda, the members of the genus are especially well represented in these litoral forests of the eastern half of the subcontinent [17].
The LDG is measured and tested in the Spirobolida family Pachybolidae Cook, 1897. 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 [20]. 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 [24]. I tested for interactions with latitude in the detritivores by measuring and comparing their LDGs. 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
42 valid species were identified as belonging to the suborder Spiroboloidea [10].

Type localities were obtained from Hamer [10]. These were tabulated and known type localities also listed in Microsoft Word online (https://office.live.com/start/Word.aspx) (Table 1). GPS coordinates were obtained from internet sources for known type localities using google (https://www.google.co.za/maps/place). The Easy Histogram Maker (https://www.socscistatistics.com/descriptive/histograms/default.aspx) was used to plot latitudinal localities across the genus. The number of species and latitude were checked for a correlation using the Pearson Correlation Coefficient Calculator (https://www.socscistatistics.com/tests/pearson/default.aspx).

3. Results

15 species were found between –33 and 35 degrees South, 9 species between -29 and –32 degrees South, 6 species between –26 degrees South and –29 degrees South, 3 species between –23 and –26 degrees South, and 5 species between –17 and –20 degrees South (Figure 1). There was a significant negative correlation between the number of species and latitudinal degrees away from the equator (Figure 2: r=-0.8219, r^2=0.6755, n=38, p=0.00001).

Table 1: Species in the family Pachybolidae, with type or collected localities and GPS latitude points.

Species	Location	Latitude
Centrobolus albitarsis	Lochiel	-26.1501744
Centrobolus angelicus	Makhanda	-33.3181344
Centrobolus anulatus	Umhlanga Rocks	-29.7461905
Centrobolus atrophus	Signal Hill	-33.9172739
Centrobolus bifidus	Nkhandla	-28.7280194
Centrolbolus coriaceus	caffraria	-
Centrobolus decoratus	Ngome Forest	-27.8402581
Centrobolus digrammus	Hout bay	-34.0476859
Centrobolus dubius	Gans bay	-34.5848950
Centrobolus formosus	caffraria	-
Centrobolus fulgidus	Richards Bay	-28.7784170
Centrobolus immaculuatus	Gorongosa	-18.6865976
Centrobolus inscriptus	Scottburgh	-30.2804608
Centrobolus inyanganus	Inyanga village	-29.7079641
Centrobolus lawrencei	Pietermaritzburg	-29.6301178
Centrobolus litoralis	Algoa Bay	-33.9671353
Centrobolus luctuosus	Inhambambane	-23.9000711
Centrobolus lugubris	Glenconnor	-33.9322149
Centrobolus miniatomaculatus	Tsitsikamma	-32.2209179
Centrobolus pococki	Cape Peninsula	-34.2442951
Centrobolus promontorius	Little Lions Head	-34.0163703
Centrobolus pusillus	Qolora River mouth	-32.5716889
Centrobolus richardii	Richards Bay	-28.7784170
Centrobolus ruber	Port Shepstone	-30.7157402
Centrobolus rubricollis	Karkloof waterfall	-29.3998690
Centrobolus rugulosus	Hluhluwe	-28.0246218
Centrobolus sagatinus	Between Uitenhage and Addo	-33.6367095
Centrobolus sanguineomarginatus	Bain's Kloof	-33.6131794
Centrobolus sanguinipes	Qolora River mouth	-32.5716889
Centrobolus saussurii	caffraria	-
Centrobolus silvanus	Kentani	-32.5063981
Centrobolus splendidus	Masiene near Chai Chai	-25.6155273
Centrobolus strigosus	caffraria	-
Centrobolus striolatus	Port St Johns	-31.6333718
Centrobolus titanophilus	DeHoop vlei	-34.4141792
Centrobolus transvaalicus	Mariepskop	-24.5391465
Centrobolus tricolor	Champaigne Castle	-29.0938694
Centrobolus validus	Haroni River	-19.8176444
Centrobolus vastus	Port St Johns	-31.6333718
Epibolus mossambicense	Xiluvo	-19.2438018
Hadrobolus crassicollis	Island of Mozambique	-19.3022330
Microbolus broadleyi	Bandula, Manica	-19.0274662

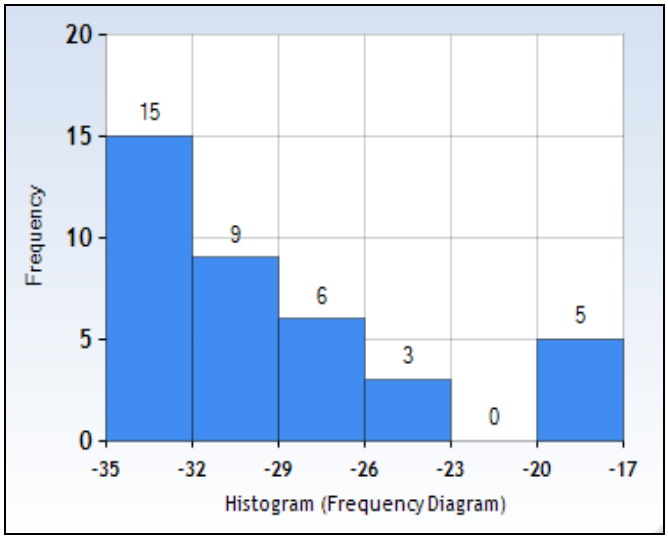

Fig 1: Histogram showing the number of species (Frequency) across latitudes in Pachybolidae.

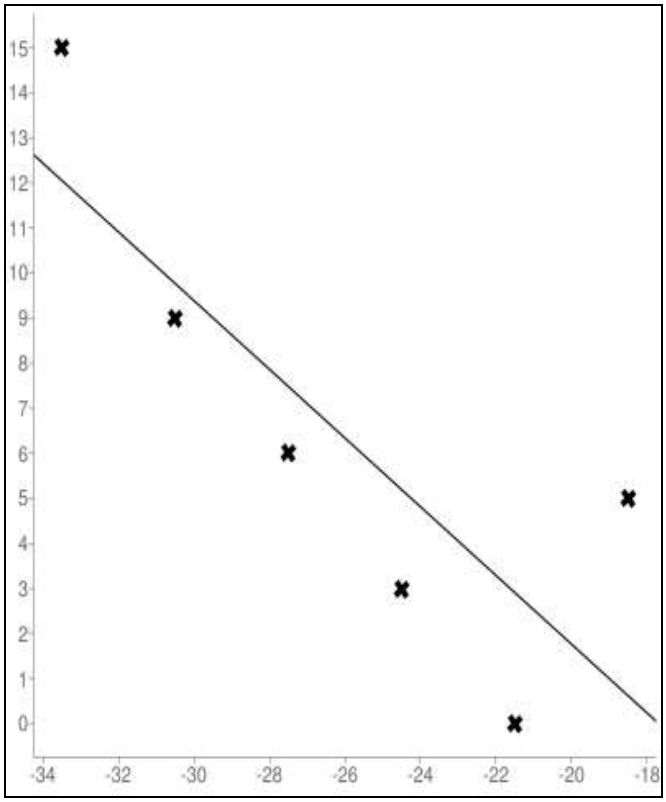

Fig 2: Linear regression of species number (Y) on latitude S (X) in Pachybolidae.

4. Discussion

Southern Africa's Pachybolidae range in latitudinal distribution from *Centrobolus immaculatus* at Gorongosa (-18.6865976°S) to *C. dubius* at Gans Bay (-34.584895°S). There was a significant negative correlation between the number of species and latitudinal degrees away from the equator, indicating an inverse LDG in Spiroboloidea, supporting the Biogeographical Conservativism Hypothesis [24]. 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 [14-16, 18, 19, 21, 24, 25, 27-29].

Two general explanations for the inverse trends in LDG include precipitation and predation, which may be pertinent to Pachybolidae [8]. Predation affects Pachybolidae as many species have some form and degree of conglobation [7]. This behavior is also an adaptive response to conserve moisture [8]. Because these millipedes are shade-loving, I rejected the moisture conservation hypothesis in favor of predation. There is a higher predation risk for insect prey at lower latitudes [26]. Density-dependent mortality in the millipedes is supported by differences in relative abundance, mating frequencies, and sex ratios of sympatric species.

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 [13, 24]. LDG depends on proximate factors affecting processes of speciation, extinction, immigration, and emigration, and in Pachybolidae these factors are dependent on size, which were investigated in *Centrobolus* is based on temperature, precipitation, and latitude. LDG relates to body size in Pachybolidae, which does not agree with the trends in other taxa such as birds and fishes [30]. The trend of a small body size associated with the inverse LDG is similar to the weak tendency found in mammals however there was no significant association between body mass and species-richness [9]. In Pachybolidae size is significantly related to latitude.

5. Conclusion

There was a significant negative correlation between the number of species and latitudinal degrees away from the equator indicating an inverse LDG in Spiroboloidea supporting the Biogeographical Conservativism Hypothesis. An evolutionary preference for temperate environments appearing to have led to climatic constraints on dispersal based on precipitation seasonality gradients and predation were suggested.

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