

Article

Latitudinal gradient in *Gnomeskelus* species richness

Mark Cooper

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 Conservatism Hypothesis suggests processes of speciation, extinction and dispersal resulted in higher species richness at the tropics and declined away from the equator. Biogeographical Conservatism Hypothesis suggests that the processes invoked are not intrinsic to the tropics but were dependent on historical biogeography to determine the distribution of species richness. 77 valid species were identified as belonging to the genus *Gnomeskelus* in order to test between the two hypotheses. There was a significant correlation between the number of species and latitudinal degrees away from the equator ($r=-0.7145$, $r^2=0.5105$, $n=77$, $p<0.00001$). Alternatively, there may be an evolutionary preference for temperate environments appearing to have led to climatic constraints on dispersal based primarily on temperature seasonality gradients.

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, 2009; Colwell and Hurtt, 1994; Colwell and Lees, 2000; Colwell et al., 2004). 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) (Colwell, 2009). Inverse LDG include include aphids, Chinese litter-dwelling thrips, European bryophytes, freshwater zooplankton, Holarctic tree frogs, ichneumonids, New World snake tribe Lampropeltini, marine benthic algae, 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; Kwon et al., 2019; Marshall and Baltzer, 2015; Mateo et al., 2016; Pyron and Burbrink, 2009; Rivadeneira et al., 2011; Silva and Brandão, 2014; Sime and Brower, 1998; Wang et al., 2014).

Here the LDG is tested in the millipede genus *Gnomeskelus* (Hamer, 1998). This clade of millipedes belonging to the Order Polydesmida is distributed throughout southern Africa (Hamer, 1998; Theron, 2001).

The null hypothesis was the Tropical Conservatism 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 was the Biogeographical Conservatism Hypothesis which suggest that 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

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

3 Results

19 *Gnomeskelus* species were found between -31 and -35 degrees latitude, 44 species between -27 and -31 degrees latitude, 10 species between -23 and -27 degrees latitude, 2 species between -19 and -23 degrees latitude, and 2 species between -11 and -15 degrees latitude (Fig. 1). There was a significant correlation between the number of species and latitudinal degrees away from the equator (Fig. 2: $R=-0.7145$, $R^2=0.5105$, $n=77$, $p<0.00001$).

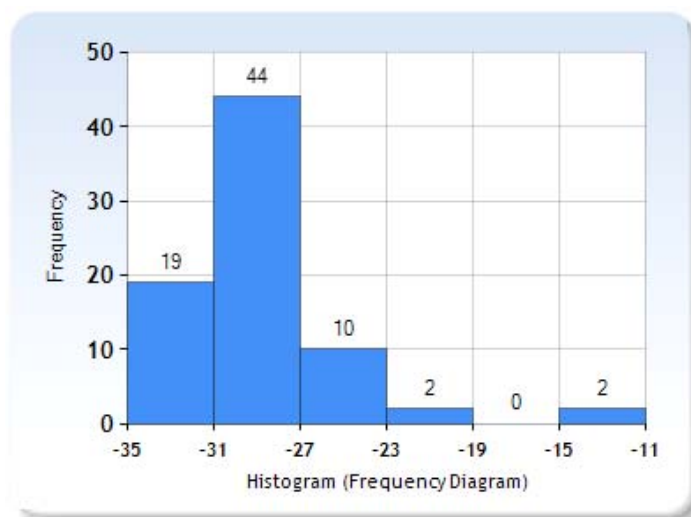


Fig. 1 Histogram showing the number of species (Frequency) across latitudes in *Gnomeskelus*.

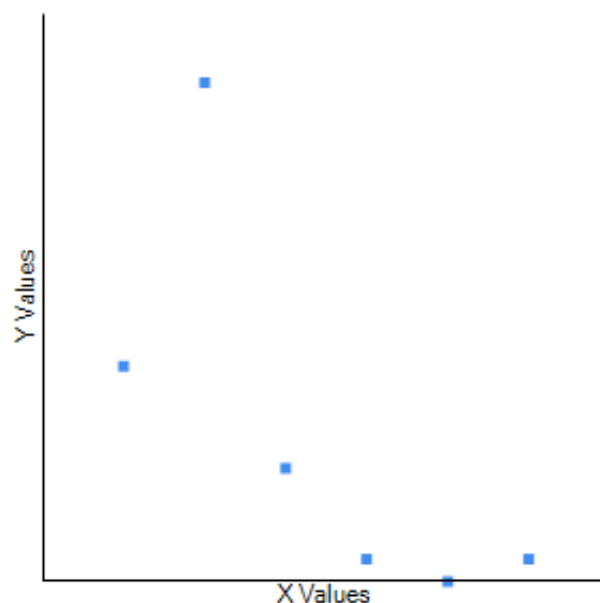


Fig. 2 Correlation between species number (Y Values) and latitude S (X Values) in *Gnomeskelus*.

4 Discussion

Gnomeskelus are more temperate and show a general decline in LDG (Colwell and Hurtt, 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 include aphids, European bryophytes, freshwater zooplankton, Holarctic tree frogs, ichneumonids, New World snake tribe Lampropeltini, marine benthic algae, North American breeding birds, penguins, peracarid crustaceans, pitcher plant mosquito, pond turtles, Shallow-water molluscs and shorebirds (Kindlmann, 2007; Mateo, 2016; Pyron and Burbrink, 2009; Rivadeneira et al., 2011). Two general explanations for the inverse trends in LDG include precipitation and predation which may be pertinent to *Gnomeskelus*. 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 *Gnomeskelus* (Yen et al., 2018).

There may be an evolutionary preference for temperate environments appearing to have led to climatic constraints on dispersal based primarily on temperature seasonality gradients (Schubart, 1966). LDG depends on proximate factors affecting processes of speciation, extinction, immigration, and emigration and in *Gnomeskelus* these factors are dependent on size which need investigating in *Gnomeskelus* based on temperature, precipitation and latitude. LDG may relate to body size in *Gnomeskelus* probably which does not agree with the trends in other taxa such as birds and fishes (Yen et al., 2018). The trend of small body size associated with the inverse LDG is expected to be similar to the weak tendency found in mammals (Zapata et al., 2003). Size-reductions makes sense for diplopods because the class has reduced in size over evolutionary time (Cooper, 2014, 2016-2020).

Appendix 1 Species in the genus *Gnomeskelus* with type or collected localities and GPS points.

Species	Locality	GPS latitude	GPS longitude
<i>G. arator</i>	Magoebaskloof	-23.8812	29.9833
<i>G. arcuatus</i>	Umgeni Poort	-29.8689	31.0617
<i>G. armiger</i>	Bainskloof	-23.4667	28.5667
<i>G. attemsii</i>	Champaigne Castle	-29.0030	29.4645
<i>G. auriculatus</i>	Rosetta	-29.3233	29.7153
<i>G. bacillifer</i>	Barkley East	-30.9694	27.5908
<i>G. basuticus</i>	Maseru	-29.3151	27.4871
<i>G. bicornis</i>	Van Stadens Pass	-33.9091	25.1970
<i>G. bifurcates</i>	Kranskop	-23.0500	29.5500
<i>G. breviceps</i>	Bulwer	-29.8034	29.7637
<i>G. brincki</i>	Gudu falls	-28.6773	28.9276
<i>G. burius</i>	Pietermaritzburg	-29.6180	25.6590
<i>G. ceresinus</i>	Swellendam	-34.0034	20.3333
<i>G. circulipes</i>	Karkloof	-29.3000	30.0670
<i>G. clavatus</i>	Mossel bay	-34.1811	22.1058
<i>G. cyclocanthus</i>	Kranskop	-23.0500	29.5500
<i>G. cygniceps</i>	Entabeni	-22.9833	30.2500
<i>G. dentipes</i>	Chai Chai	-11.8525	40.0250
<i>G. edentulous</i>	Giant's Castle	-29.2705	29.5203
<i>G. elizabethae</i>	Port Elizabeth	-33.9820	25.6590
<i>G. fitsimonsi</i>	George	-33.9680	22.4499
<i>G. fluvialis</i>	Bulwer	-29.8034	29.7637
<i>G. forcipifer</i>	New Hanover	-29.355	30.5264
<i>G. furculatus</i>	Port Shepstone	-30.667	30.5130
<i>G. glaber</i>	Kloof	-29.7723	30.8302
<i>G. globifer</i>	Uitenhage	-33.7746	25.3788
<i>G. globulatus</i>	Makhanda	-33.3100	26.5270
<i>G. gonoarthrodus</i>	Cathedral Peak	-28.9441	29.2307
<i>G. graemi</i>	Makhanda	-33.3100	26.5270
<i>G. hamuliger</i>	Nkhandla forest	-28.7167	31.1333
<i>G. harpagonifer</i>	Nkhandla forest	-28.7167	31.1333
<i>G. hewitti</i>	Makhanda	-33.3100	26.5270
<i>G. inermis</i>	Redhouse	-33.8166	25.5500
<i>G. jaculator</i>	Pietermaritzburg	-29.6180	25.6590
<i>G. kambianus</i>	Kambi forest, Umtata	-31.4667	28.6000
<i>G. krausi</i>	Ngomi forest	-27.8667	31.4000
<i>G. krugeri</i>	Punda Maria	-22.6954	31.0161
<i>G. laevigatus</i>	Champaigne Castle	-29.0030	29.4645

<i>G. larvatus</i>	Pietermaritzburg	-29.6180	25.6590
<i>G. latzeli</i>	Van Reenen	-29.0002	29.4691
<i>G. lawrencei</i>	Nkhlandla forest	-28.7167	31.1333
<i>G. maritimus</i>	Umhlali	-29.4500	31.2667
<i>G. medius</i>	Bluff Durban	-29.7723	30.8302
<i>G. montifelis</i>	Winterberg	-32.5167	26.4500
<i>G. montivagus</i>	Cathkin Peak	-29.0538	29.3955
<i>G. multidentatus</i>	Ingwavuma	-27.1343	31.9965
<i>G. natalicus</i>	Empangeni	-28.7549	31.9015
<i>G. origensis</i>	Drakensberg	-29.0030	29.4645
<i>G. outeniqua</i>	Nature's Valley	-33.9797	23.5567
<i>G. pencillatus</i>	Mossel bay	-34.1832	22.1536
<i>G. petersii</i>	Ingwavuma	-27.1343	31.9965
<i>G. processiger</i>	Kokstad	-30.5475	29.4244
<i>G. pugnifer</i>	Champaign Castle	-29.0030	29.4645
<i>G. puteinus</i>	Matjesfontein	-33.2319	20.5803
<i>G. retrusus</i>	Pietermaritzburg	-29.6180	25.6590
<i>G. rhodobates</i>	Humansdorp	-34.0299	24.7707
<i>G. rudebecki</i>	Entabeni	-30.5485	28.2590
<i>G. serratus</i>	Karkloof	-29.4064	30.2805
<i>G. setosus</i>	Champaign Castle	-29.0030	29.4645
<i>G. silvaticus</i>	Knysna	-34.0357	23.0485
<i>G. skukuzae</i>	Skukuza	-24.9613	31.5900
<i>G. spectabilis</i>	Umhlali	-29.4773	31.2181
<i>G. spiculifer</i>	Port St Johns	-31.6205	29.5453
<i>G. spinifer</i>	Chai Chai	-11.8525	40.0250
<i>G. stuckenbergi</i>	Pilgrim's Rest	-24.9044	30.7536
<i>G. subterraneus</i>	Elandskop	-29.7242	30.0700
<i>G. swazianus</i>	Mbabane	-26.3257	31.1447
<i>G. swazius</i>	Swaziland	-26.5625	31.3991
<i>G. tembulicus</i>	Qolora River Mouth	-32.6345	28.4273
<i>G. tenuipes</i>	Kosi Bay	-27.2593	32.7522
<i>G. tereticornis</i>	Ngome forest	-27.8667	31.4000
<i>G. transvaalicus</i>	Barberton	-25.7822	31.0475
<i>G. trichardti</i>	Makhado	-23.0383	29.9067
<i>G. trifurcatus</i>	Kranskop	-30.9892	23.7709
<i>G. tristriatus</i>	Albert falls	-30.9892	23.7709
<i>G. tuberosus</i>	Drakensberg	-29.0474	29.4178
<i>G. tugelanus</i>	Cathkin Peak	-29.0538	29.3955

References

- Colwell RK. 2009. Biodiversity: Concepts, Patterns and Measurement. In: The Princeton Guide to Ecology (Levin SA, ed). 257-263, Princeton University Press, Princeton, USA
- Colwell RK, Hurtt GC. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist*, 144: 570-595
- Colwell RK, Lees DC. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution*, 15: 70-76
- Colwell RK, Rahbek C, Gotelli NJ. 2004. The mid-domain effect and species richness patterns: what have we learned so far? *American Naturalist*, 163: E1-E23
- Cooper MI. 2014. Sexual size dimorphism and corroboration of Rensch's rule in *Chersastus* millipedes (Diplopoda: Trigonulidae). *Journal of Entomology and Zoology Studies*, 2(6): 264-266
- Cooper MI. 2016. Heavier-shorter-wider females in the millipede *Centrobolus inscriptus* (Attems). *Journal of Entomology and Zoology Studies*, 4(2): 509-510
- Cooper MI. 2016. The relative sexual size dimorphism of *Centrobolus inscriptus* compared to 18 congenics. *Journal of Entomology and Zoology Studies*, 4(6): 504-505
- Cooper M. 2017. Re-assessment of Rensch's rule in *Centrobolus*. *Journal of Entomology and Zoology Studies*, 5(6): 2408-2410
- Cooper MI. 2017. Relative sexual size dimorphism *Centrobolus ruber* (Attems) compared to 18 congenics. *Journal of Entomology and Zoology Studies*, 5(3): 180-182
- Cooper MI. 2017. Allometry of copulation in worm-like millipedes. *Journal of Entomology and Zoology Studies*, 5(3): 1720-1722
- Cooper MI. 2018. Allometry for sexual dimorphism in millipedes (Diplopoda). *Journal of Entomology and Zoology Studies*, 6(1): 91-96
- Cooper MI. 2018. Sexual dimorphism in pill millipedes (Diplopoda). *Journal of Entomology and Zoology Studies*, 6(1): 613-616
- Cooper MI. 2018. Volumes of *Centrobolus albitarsus* (Lawrence, 1967). *International Journal of Entomology Research*, 3(4): 20-21
- Cooper M. 2018. Allometry in *Centrobolus*. *Journal of Entomology and Zoology Studies*, 6(6): 284-286
- Cooper M. 2018. *Centrobolus anulatus* reversed sexual size dimorphism. *Journal of Entomology and Zoology Studies*, 6(4): 1569-1572
- Cooper M. 2018. *Centrobolus lawrencei* (Schubart, 1966) monomorphism. *Arthropods*, 7(4): 82-86
- Cooper M. 2018. *Centrobolus sagatinus* sexual size dimorphism based on differences in horizontal tergite width. *Journal of Entomology and Zoology Studies*, 6(6): 275-277
- Cooper M. 2018. *Centrobolus silvanus* dimorphism based on tergite width. *Global Journal of Zoology*, 3(1): 003-005
- Cooper M. 2018. *Centrobolus* size dimorphism breaks Rensch's rule. *Arthropods*, 7(3): 48-52
- Cooper M. 2019. *Centrobolus titanophilus* size dimorphism shows width-based variability. *Arthropods*, 8(2): 80-86
- Cooper M. 2019. Non-significant intersexual differences in millipede mass. *Journal of Entomology and Zoology Studies*, 7(3): 763-765
- Cooper M. 2019. Size dimorphism and directional selection in forest millipedes. *Arthropods*, 8(3): 102-109
- Cooper M. 2019. Xylophagous millipede surface area to volume ratios are size-dependent in forests. *Arthropods*, 8(4): 127-136
- Cooper M. 2019. Size dimorphism in six juliform millipedes. *Arthropods*, 8(4): 137-142

- Cooper MI. 2019. Lawrence's red millipede *Centrobolus lawrencei* shows length-based variability and size dimorphism. *Journal of Entomology and Zoology Studies*, 7(2): 1037-1039
- Cooper M. 2020. Year-round correlation between mass and copulation duration in forest millipedes. *Arthropods*, 9(1): 15-20
- Cooper M. 2020. Kurtosis and skew show longer males in *Centrobolus*. *Arthropods*, 9(1): 21-26.
- Gittleman JL, Purvis A. 1998. Body size and species-richness in carnivores and primates. *Proceedings of the Royal Society B: Biological Sciences*, 265(1391): 113-119
- Hamer ML. 1998. Checklist of Southern African millipedes. *Annals of the Natal Museum*, 39(1): 39-43
- Hillebrand H. 2004. On the Generality of the Latitudinal Diversity Gradient. *The American Naturalist*, 163(2): 192-211
- Hopkin SP, Read HJ. 1992. Taxonomy, evolution, and zoogeography. *The Biology of Millipedes*. 8-23, Oxford University Press, UK
- Kindlmann P, Dixon AFG, Traxmandlová-Schödelbauerová I. 2007. Inverse latitudinal gradients in species diversity. In: Storch D, Marquet PA. (ed.). *Scaling Biodiversity*. Cambridge University Press, Cambridge, UK
- Kwon Y, Lee T, Lang A, Burnette D. 2019. Assessment on latitudinal tree species richness using environmental factors in the southeastern United States. *PeerJ*, 7: e6781
- Lawrence RF. 1967. The Spiroboloidea (Diplopoda) of the eastern half of Southern Africa. *Annals of the Natal Museum*, 18(3): 607-646
- Marshall KE, Baltzer JL. 2015. Decreased competitive interactions drive a reverse species richness latitudinal gradient in subarctic forests. *Ecology*, 96(2): 461-470
- Mateo RG, Broennimann O, Normand S, Petitpierre B, AraOyújo MB, Svenning J-C, Baselga A, Fernández-Gozález F, Rubio VG, Muñoz J. 2016. The mossy north: An inverse latitudinal diversity gradient in European bryophytes. *Scientific Reports*, 6: 25546
- Mittelbach GG, Schemske GW, Cornell HV, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10: 315-331
- Pianka ER. 1989. Latitudinal Gradients in Species Diversity. *Trends in Ecology and Evolution*, 4(6): 223
- Pielou EC. 1977. The latitudinal spans of seaweed species and their patterns of overlap. *Journal of Biogeography*, 4: 299-311
- Pitz KM, Sierwald P. 2010. Phylogeny of the millipede Order Spirobolida (Arthropoda: Diplopoda: Helminthomorpha). *Cladistics*, 26: 497-525
- Pyron RA, Burbrink FT. 2009. Can the Tropical Conservatism Hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lampropeltini. *Global Ecology and Biogeography*, 18: 406-415
- Rivadeneira MM, Thiel M, Gonzalez ER, Haye PA. 2011. An inverse latitudinal gradient of diversity of peracarid crustaceans along the Pacific Coast of South America: Out of the deep south. *Global Ecology and Biogeography*, 20(3): 437-448
- Schubart O. 1966. Diplopoda III. In: *South African Animal Life*, 12: 33-72
- Silva RR, Brandão CRF. 2014. Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. *PLoS ONE*, 9(3): e93049
- Sime KR, Brower AVZ. 1998. Explaining the latitudinal gradient anomaly in ichneumonid species richness: evidence from butterflies. *Journal of Animal Ecology*, 67: 387-399
- Stevens GC. 1989. The latitudinal gradients in geographical range: how so many species co-exist in the tropics. *The American Naturalist*, 133: 240-256

- Theron LJ. 2001. Distribution And Abundance of Rodents, Millipedes and Trees In Coastal Dune Forests In Northern Kwa Zulu-Natal. University of Pretoria, South Africa
- Wang J, Tong X, Donghui W. 2014. The effect of latitudinal gradient on the species diversity of Chinese litter-dwelling thrips. *Zookeys*, 417: 9-20
- Willig MR, Lyons SK. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos*, 81: 93-98
- Yen JDL, Thomson JR, Keith J, Paganin DM, Fleishman E, Bennett AF, Dobkin DS, Mac Nally R. 2018. Linking species richness and size diversity in birds and fishes. *Ecography*, 41(12): 1979-1991
- Zapata FA, Gaston KJ, Chown SL. 2003. Mid-domain models of species richness gradients: assumptions, methods and evidence. *Journal of Animal Ecology*, 72: 677-690