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Bergmann's rule and elevational - size pattern in millipede species along elevational gradient

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Abstract

Along altitudinal gradients, body size in animals often exhibits a pattern where species at higher elevations tend to be either smaller or larger with elevation. Herein, we studied altitudinal variation in body size by measuring body length (mm) in eleven most frequent millipede species belonged to seven families (Spirostreptidae, Chelodesmidae, Cryptodesmidae, Oxydesmidae, Pyrgodesmidae, Gomphodesmidae, and Odontopygidae) along elevational gradient. We have also recorded temperature (°c) at each zonation. As result, mean body length in all measured millipedes were negatively correlated with temperature. Within each species, the smallest-sized individuals were recorded at higher temperatures, medium-sized at mid-temperatures, while the largest-sized individuals occurred at lower temperatures. Mean body length was positively associated with elevation. In the largest millipede species, *Telodeinopus caniculatus* (Spirotreptidae), size increased from lower to mid-elevations (14.75 cm to 15.20 cm) and reached a maximum size at higher elevations (16.22 cm). The same pattern was observed in the smallest species *Tymbodesmus falcatus* (Gomphodesmidae), with 0.1 cm found at lower elevations, 0.15 cm at mid-elevations and 0.2 cm at higher elevations. This geographic variation pattern found in eleven different millipede species belonging to seven families, support ecogeographic rule of Bergmann of increasing body size with increasing elevation. It also aligns with increasing body size and decreasing in temperature at higher elevations.

Keywords: Elevational gradient, millipede species, body length, bergmann's rule

Introduction

Altitudinal gradients can be used as a model for future impacts of increasing temperatures on biodiversity (Botes *et al*. 2006 [9]; Korner 2007). Many patterns of biodiversity dependent on altitude, with the gradual decreasing and the hump-shaped relationships being the most commonly described (Rahbek 1995 [42]; Hodkinson 2005 [22]; Sanders & Rahbek 2012) [43].

Montane regions are model systems (Garten *et al*.1999) [17] in which to conduct ecological research (Korner &Paulsen 2004). Multiple studies have documented species distribution along elevational and latitudinal gradients in a variety of habitats and taxa, and many mechanisms have been suggested to explain spatial variation in species richness (Hawkins *et al*. 2003 [20, 21]; McCain & Grytnes 2010 [32]; Rahbek 2005) [41].

Because of their global distribution, recurrent broadscale ecological patterns can be detected with reasonable power, and contrasts between tropical and temperate or humid and arid contexts are possible (Grytnes & McCain 2007 [18]; McCain & Grytnes 2010) [32]. Bergmann's rule (Bergmann 1847) [5] proposed that homeothermic animals display size clines; species within a genus are larger in cooler climates and smaller in warmer climates because of selection on the ability to thermoregulate (Blackburn *et al*. 1999 [7], Ashton *et al*. 2000) [2]. Species with ample latitudinal and/or altitudinal geographic ranges are useful models for the analysis of body-size distribution at the intraspecific level (Cigliano & Otte 2003 [12]; Bidau & Martí 2007) [6]. Large distributions expose species to very different climatic conditions. The importance of climate studied through its main features, temperature, precipitation, evapotranspiration, etc. or their combinations, has been indicated in different vegetation or plant geography surveys (Prentice *et al*. 1992 [40]; Blasi *et al*. 1999) [8].

There is increasing knowledge about the effect of climate change on different species groups over latitudinal (Chen *et al*. 2011 [10]; Devictor *et al*. 2012) [14], as well as altitudinal gradients (Chen *et al*. 2009 [11]; Pizzolotto *et al*. 2014 [39]; McGrann &Furnas 2016) [33]. A general negative metabolic response to temperature shifts was observed for high elevation specialists across vertebrate and invertebrate ectotherm taxa (Žagar *et al*. 2018) [44]. However, only a few abiotic parameters change gradually with altitude: atmospheric pressure, temperature and clear sky turbidity (Korner 2007).

This study investigated in eleven millipede species belonging to seven families, the influence of environmental factors including elevation and temperature on morphological variation in millipede body size along elevational gradient.

Materials and Methods

Study sites

This study was carried out from November 2022 to march 2024 in the southern Cameroon rainforest (03°48'N, 11°21'E). An elevation gradient was set up from the coastal region (Edea: 3°48'N, 10°08'E; altitude 88 m asl), mid-elevation region (Libel-Lingoï: 3°54'N, 10°55'E; altitude :455 m asl) to Kala mount ((3°50'N and 11°21'E; altitude 954 m asl) (Figure 1): The southern Cameroon experiences two type of seasons: four distinct seasons with two wet seasons and two dry seasons in the center region, and the rainfall pattern with two seasons (one long rainy season and one short dry season) in Littoral region. The vegetation is dominated by the Atlantic evergreen rainforest with an average temperature of 27°C in littoral region, while in center region, the vegetation is dominated by the semi-deciduous, hygromesophilic and montane forests.

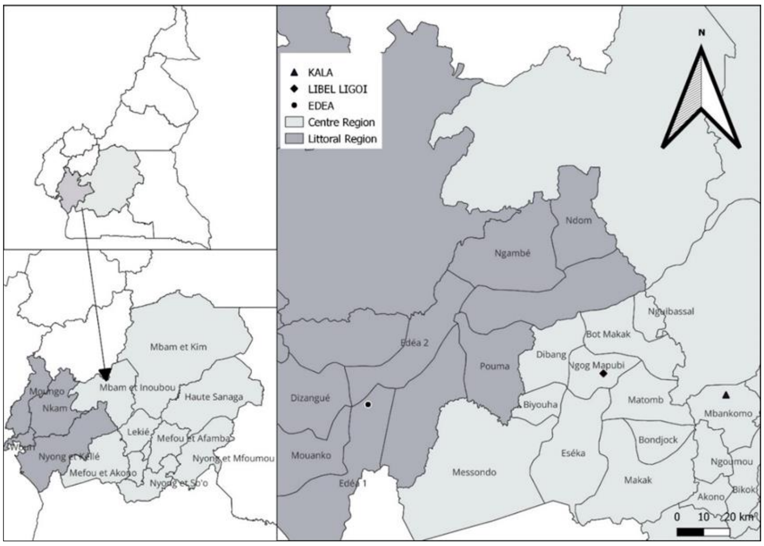


Fig 1: map showing the location of the eleven-millipede species along altitudinal gradient in southern Cameroon.

Protocol design

Diplopoda were surveyed using hand collection, pitfall trapping and Winkler extraction (Domingo-Quero, 2010) [15] in three altitudinal bands. These sampling methods were implemented along the three parallel transects (110 m length and 2 m width each) spaced 10 m apart. Fifteen sampling events were conducted at each altitudinal level, yielding a total of 450 samples per elevation (1 site× 10 samples × 3 methods × 15 replicates). Measurements were conducted on a minimum of 10 aldults from each species collected across elevation bands. Body length (in millimeters), which was taken from the tip of the head to the distal end of the body, was measured using calipers. Abiotic factor (temperature) was also recorded using a temperature logger (Data logger). All millipedes were collected with forceps or by hands and preserved in labelled vials containing 70% ethanol. Each specimen was then photographed, dissected (only diplopod species) and identified at the family, genus and species levels or assigned to morphospecies with the help of relevant dichotomous keys available in the literature (Kraus, 1960 [29]; 1966 [30]; Krabbe, 1982 [28]; Hoffman, 2005 [23]; Hamer 1999 [19]; Minelli, 2011 [34]; 2015) [35]. Voucher specimens were deposited in the reference collections of the Laboratory of Zoology at the University of Yaounde.

Statistical analysis

Data matrixes of body size and temperature values were constructed and saved in an excel spreadsheet version 2016. To identify the relationship between different parameters (temperature and altitude, altitude and body length), we used least-squares multiple regression. Spearman's correlation was used and regression curves were plotted to explore associations among different parameters. All statistical tests were carried out using SPSS software version 16.0 for Windows. All probabilities were two-tailed, and the significance level was set at $P < 0.05$.

Results

Variation in body length and temperature

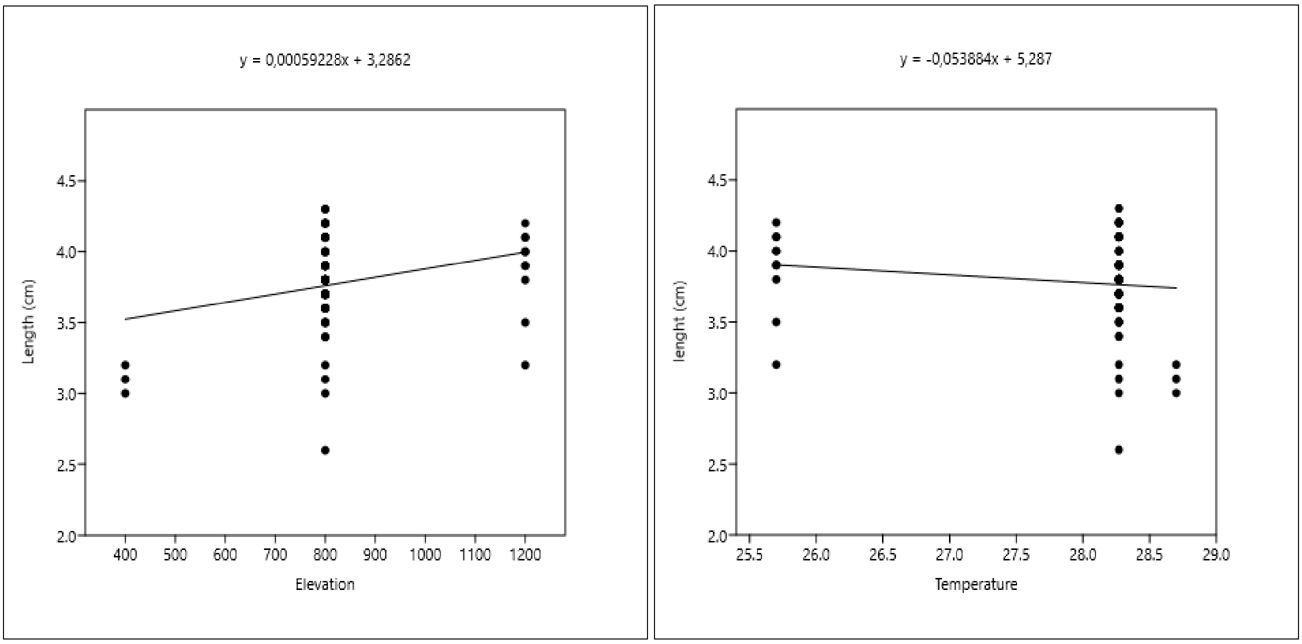
The mean body length of the eleven millipede species were indicated in Table 1. The body length ranged from 0.1 cm to 16.22 across different elevations, and temperature from 22.8 cm to 28.8 cm. The body size of most of the millipede species increased with elevation. Controversily, the temperature decreased with elevation. A significant vriation in body length across elevation bands occurred in Spitotreptidae family. This family was represented by the biggest-sized millipede species such as *Telodeinopus canliculatus, Kartinikus colonus,* and *Kartinikus laevis.* The smallest-sized species were found in Pyrgodesmidae (*Urodesmus cornutus*) and Gomphodesmidae (*Tymbodesmus falcatus*) families.

Table 1: Mean body length (mm) and mean temperature (°c) of eleven millipedes' species across three elevation bands in southern cameroon rainforest.

Family	Species	Body length/altitudes			Temperature (°c)/altitudes		
		88 m	**445 m**	**945 m**	**88 m**	**445 m**	**945 m**
Spirostreptidae	*Kartinikus colonus*	5.7	6.3	5.8	27.3	28.8	24.3
	Telodeinopus canliculatus	14.8	15.2	16.2	26.4	26	23.6
	Kartinikus laevis	5.9	6.8	7.1	25.8	23	26.6
Chelodesmidae	*Diaphorodesmus dorsicornis*	3	3.8	3.9	28.7	28.3	25.7
	Paracordyloporus porati	3.5	3.8	4	26.3	27.7	22.8
Cryptodesmidae	*Aporodesmus falcatus*	3.4	3.6	3.6	27	26	24.1
	Aporodesmus gabonicus	3.7	4.3	4.4	26.7	26.2	24.1
Oxydesmidae	*Coromus* sp.2	4.8	5.2	6	27.2	26	24
Pyrgodesmidae	*Urodesmus cornutus*	0.1	0.15	0.2	28	27.8	23.8
Gomphodesmidae	*Tymbodesmus falcatus*	2.9	3	3.2	26.8	24.2	23.8
Odontopygidae	*Coenobothrus bipartitus*	4.7	5.2	5.4	27	25.9	23.9

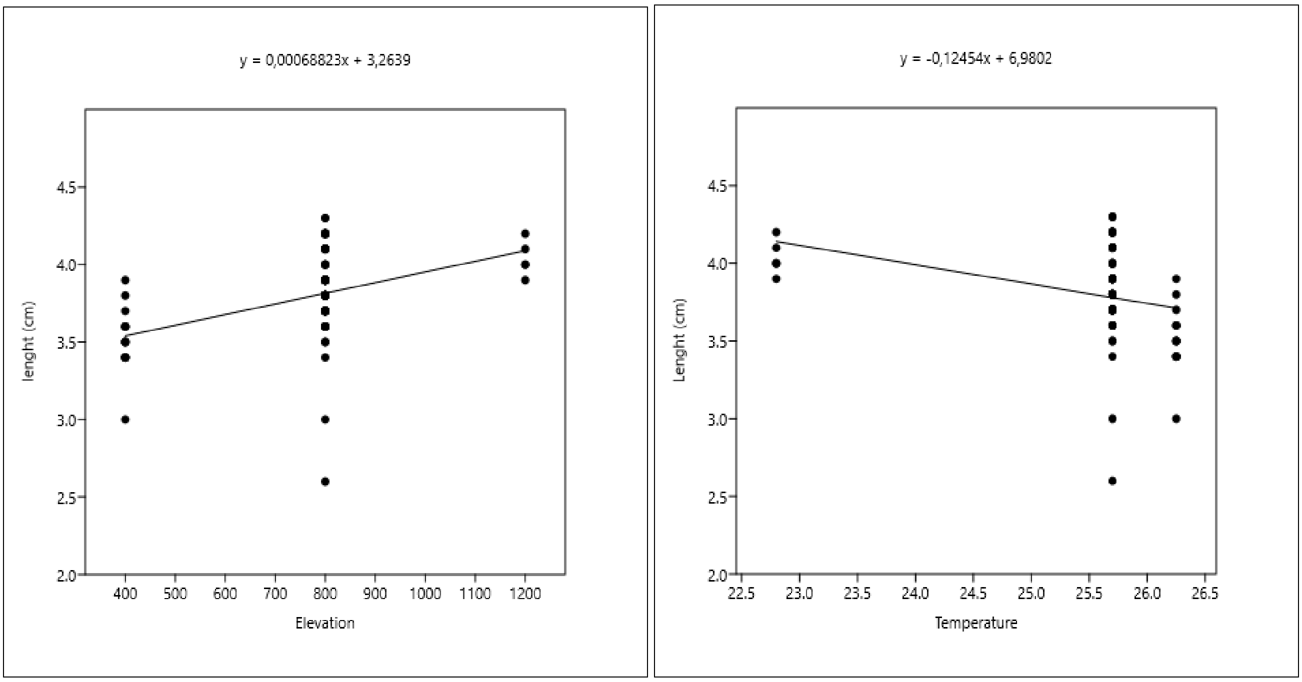
Correlation between body length and environmental factors

Overall, mean body length positively correlated with elevation, and negatively correlated with temperature in eleven measured millipede species. In *Diaphorodesmus dorsicornis*, body length correlated with elevation (Spearman's correlation $r= 0.283$, $p=0.005$) and the negative association was found with temperature ($r = -0.141$, $p = 0.173$) (Figure 2). The same trend was observed in *Paracordyloporus porati* (elevation, $r = 0.435$, $p <0.05$; temperature, $r = -0.313$, $p <0.05$) (Figure 3), in *Aporodesmus falcatus* (elevation, $r = 0.197$, $p =0.04$; temperature, $r = -0.187$, $p =0.05$) (Figure 4),), in Aporodesmus gabonicus(elevation, $r = 0.587$, $p <0.05$; temperature, $r = -0.544$, $p <0.05$) (Figure 5), in Tymbodesmus falcatus (elevation, $r = 0.582$, $p <0.05$; temperature, $r = -0.564$, $p <0.05$) (Figure 6), in Coenobothrus bipartitus (elevation, $r = 0.588$, $p <0.05$; temperature, $r = -0.568$, $p <0.05$) (Figure 7), in Coromus sp.2 (elevation, $r = 0.906$, $p <0.05$; temperature, $r = -0.921$, $p <0.05$) (Figure 8), in Urodesmus cornutus (elevation, $r = 0.436$, $p =0.118$; temperature, $r = -0.471$, $p = 0.08$) (Figure 9), in Kartinikus colonus (elevation, $r = 0.01$, $p =0.841$; temperature, $r = 0.107$, $p = 0.159$) (Figure 10), in Kartinikus laevis (elevation, $r = 0.919$, $p <0.05$; temperature, $r = -0.411$, $p = 0.417$) (Figure 11), and in Kartinikus laevis (elevation, $r = 0.180$, $p = 0.502$; temperature, $r = -0.09$, $p = 0.715$) (Figure 12).



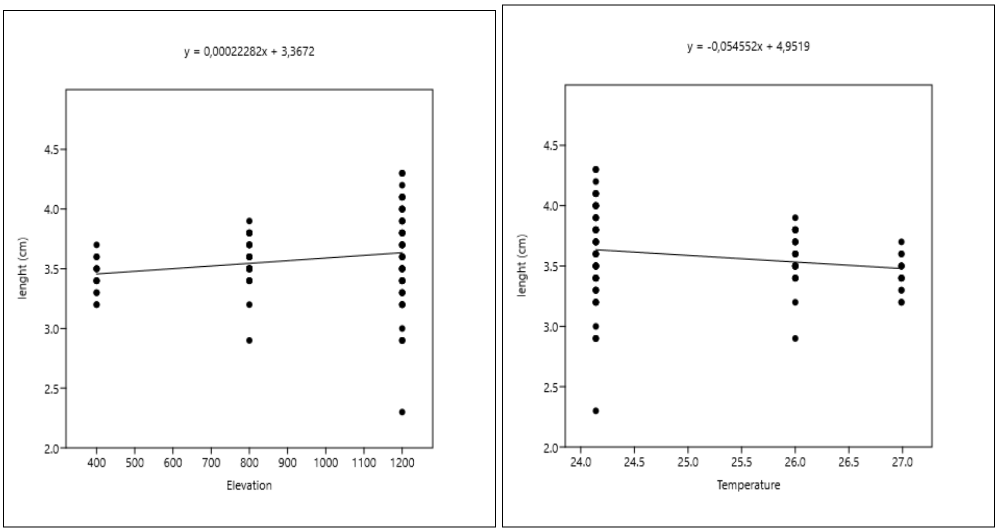
(a) **(b)**

Fig 2: Correlation between mean body length and (a) altitude, and (b)temperature in *Diaphorodesmus porati*



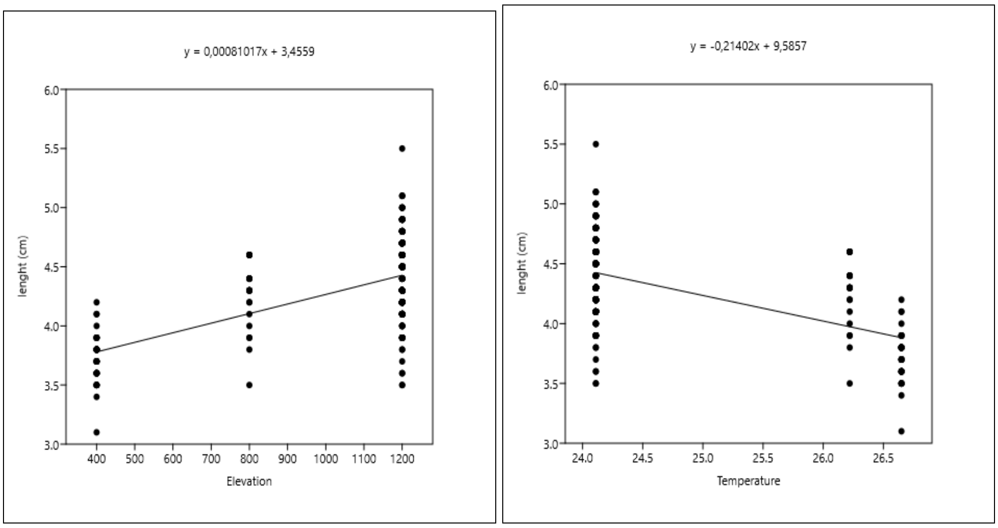
(a) **(b)**

Fig 3: Correlation between mean body length and (a) altitude, and (b)temperature in *Paracordyloporus porati*



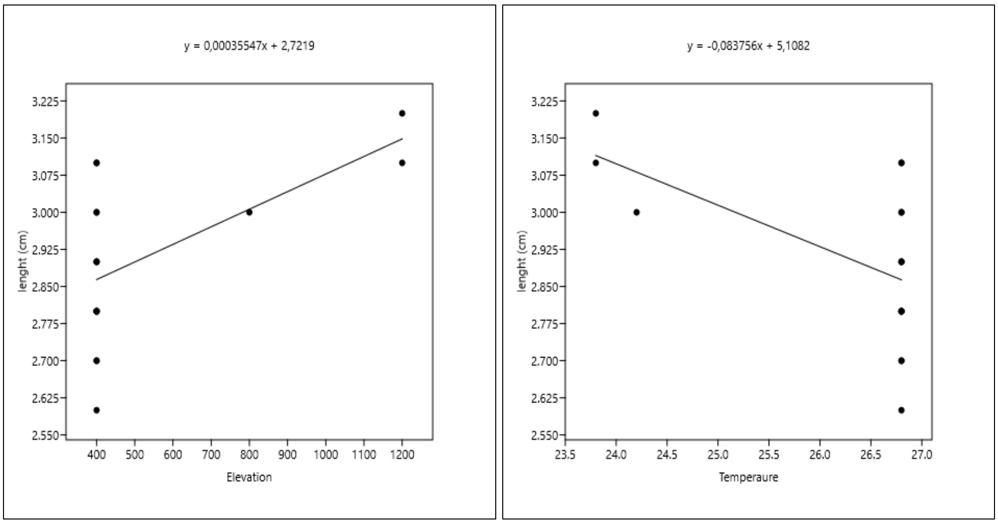
(a) **(b)**

Fig 4: Correlation between mean body length and (a) altitude, and (b)temperature in *Aporodesmus falcatus*



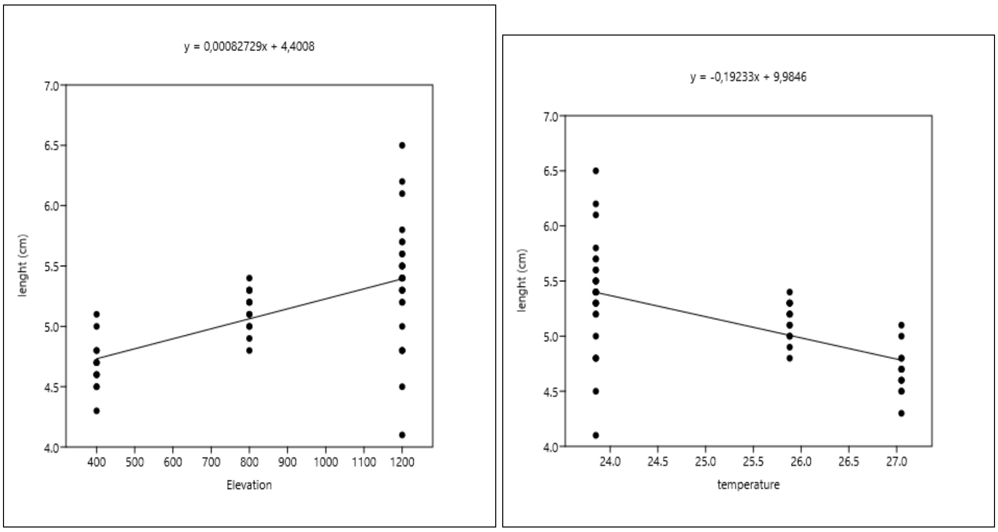
(a) **(b)**

Fig 5: Correlation between mean body length and (a) altitude, and (b)temperature in *Aporodesmus gabonicu*



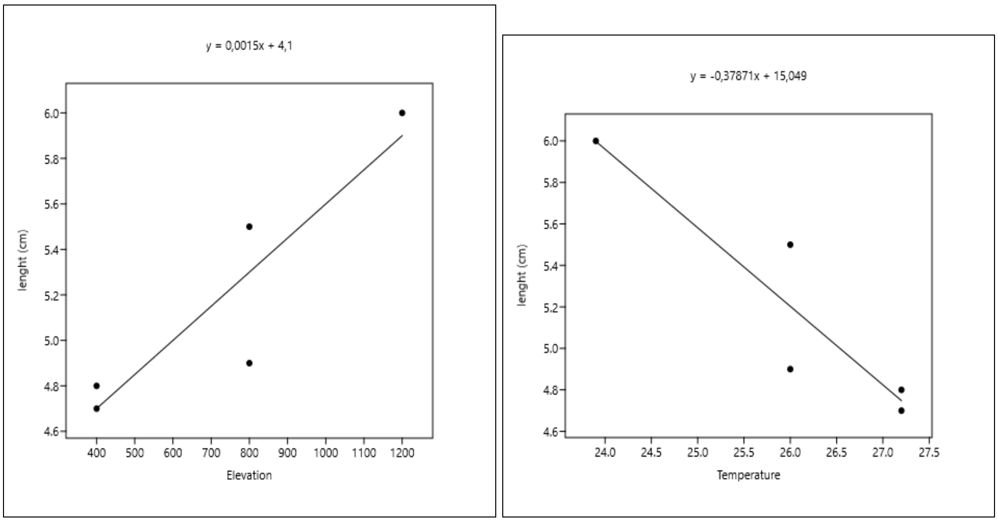
(a) **b)**

Fig 6: Correlation between mean body length and (a) altitude, and (b)temperature in *Tymbodesmus falcatus*



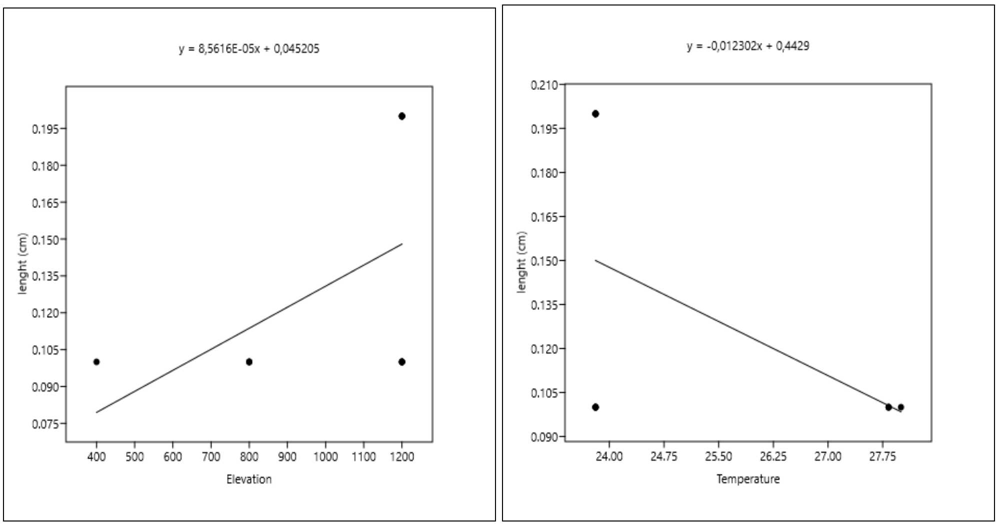
(a) **(b)**

Fig 7: Correlation between mean body length and (a) altitude, and (b)temperature in *Coenobothrus bipartitus*



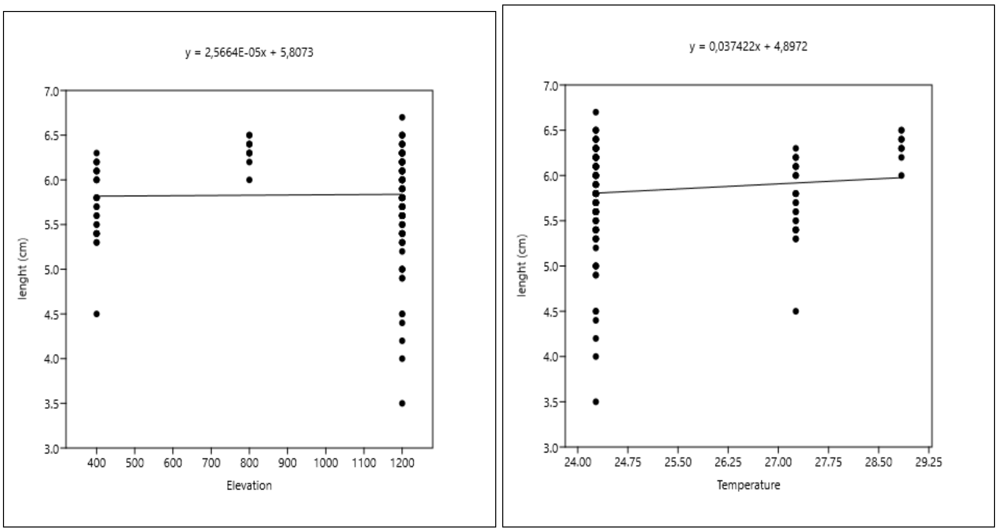
(a) **(b)**

Fig 8: Correlation between mean body length and (a) altitude, and (b)temperature in *Coromus* sp.2



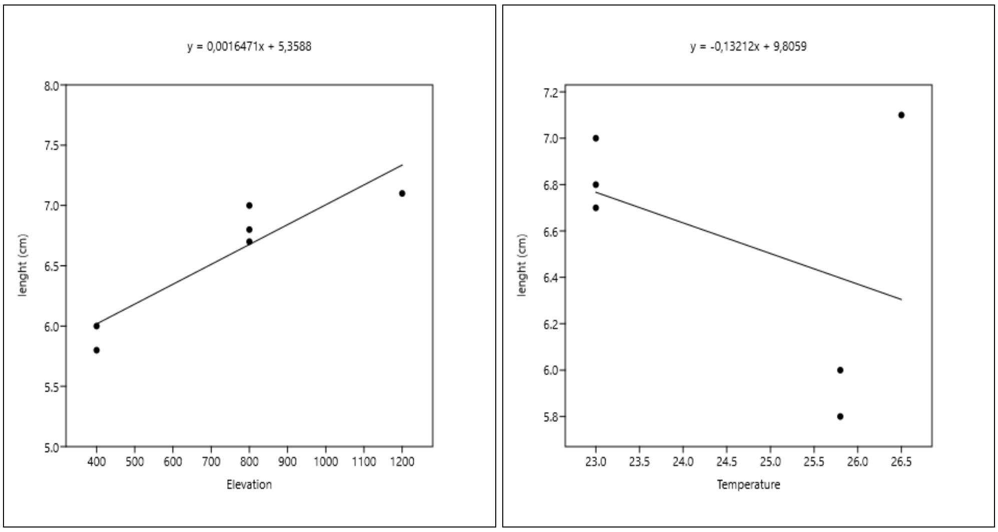
(a) **(b)**

Fig 9: Correlation between mean body length and (a) altitude, and (b)temperature in *Urodesmus cornutus*



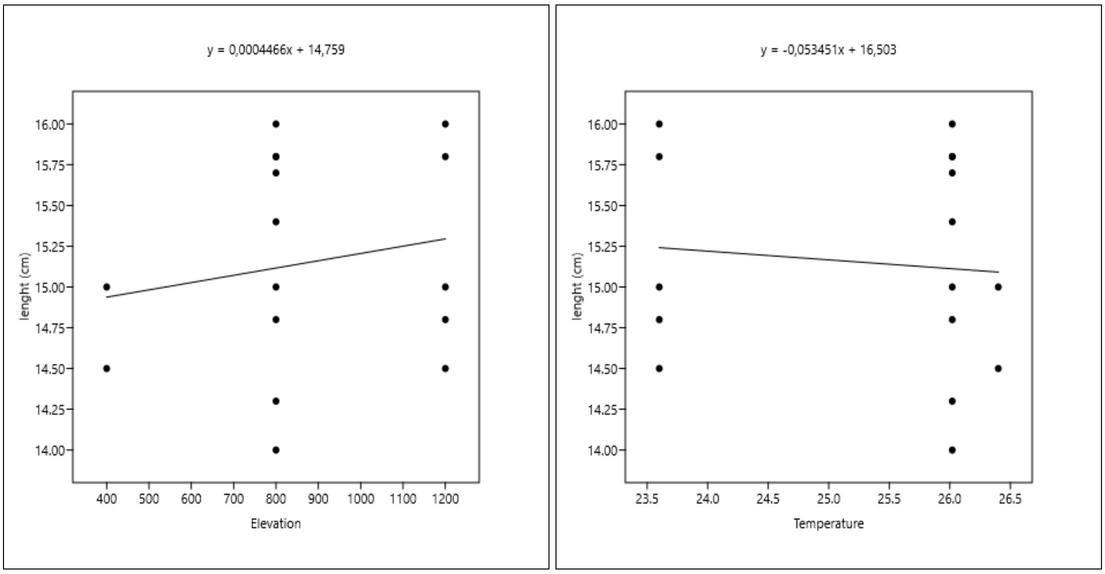
(a) **(b)**

Fig 10: Correlation between mean body length and (a) altitude, and (b)temperature in *Kartinikus colonus*



(a) **(b)**

Fig 11: Correlation between mean body length and (a) altitude, and (b)temperature in *Kartinikus laevis*



(a) **(b)**

Fig 12: Correlation between mean body length and (a) altitude, and (b)temperature in *Kartinikus laevi*

Discussion

Along altitudinal gradients, body size often exhibits a pattern where species at higher elevations tend to be smaller at cooler climates. In contrast, this study shows increasing in millipede body size with increasing elevation. This is consistent with Bergmann's rule and that found in endothermic animal such as birds and mammals (Ashton 2002 [3], Nwaogu *et al*. 2018) [37]. In other ectothermic animals, such as reptiles, fish, amphibians, and arthropods, a reverse Bergmann's rule, has been reported (Ashton & Feldman 2003 [1]; Fisher *et al*. 2010 [16]; Liu *et al*. 2025) [31]. This phenomenon is partly explained by the physiological constraints imposed by lower temperatures and reduced oxygen availability at higher altitudes. Smaller body sizes can enhance thermoregulation and reduce metabolic costs in these challenging environments (Hawkins *et al*. 2003) [20, 21]. Millepedes like insect are ectotherms and are dependent on the environmental temperature for development (Bale *et al*. 2002) [4]. They have a strong preference for wetlands. This means that some species are adapted to colder, higher elevation areas offered this climatic area (Zagar *et al*. 2018).

The significant change of abiotic and biotic environmental variables along elevational gradients strongly affects patterns of body size in animals. morphological and physiological traits are known to vary among species populations and are correlated with latitudinal and altitudinal gradients, as well as temperature gradients (Munch & Salinas 2009) [36]. In this study, we observed a negative correlation between temperature and body length in millipede, as temperature decreased, body length increased. This study supports temperature as a predictor of body size variation in millipede species in studied site. Indeed, many millipede species found in this study from seven families including Spirostreptidae, Chelodesmidae, Cryptodesmidae, Oxydesmidae, Pyrgodesmidae, Gomphodesmidae, and Odontopygidae exhibit larger-sized body at higher elevations, medium-sized body at mid-elevations, and small-sized body at lower elevations. The same trend was found in eleven millipede species measured such as Diaphorodesmus dorsicornis, Paracordyloporus porati, Aporodesmus falcatus, Aporodesmus gabonicus, Tymbodesmus falcatus, Coenobothrus bipartitus, Coromus sp.2, Urodesmus cornutus, Kartinikus colonus, Kartinikus laevis, and Kartinikus laevis. This funding inconsistent with those found in temperate climates in millipede genus Centrobolus (Pachybolida, Pachybolidae) (Cooper 2022) [13]. This clade is largely distributed along the eastern coast of southern Africa characterized by temperate and tropical climates (Pitz and Sierwald, 2010) [38]. This genus follows different rules for size variation depending on temperature and fitness, but also present a reverse Bergmann's rule, with positive relationships between body size variation and temperature along latitudinal gradient (Kingsolver and Pfenning 2004 [24]; Kingsolver and Huey, 2008) [25].

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