

Species Richness and the Analytic Geometry of Latitudinal and Altitudinal Gradients

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Received: 15 February 2007 / Accepted: 5 March 2008 / Published online: 18 March 2008
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Abstract Extensive empirical work has shown that species richness decreases roughly exponentially or quadratically with latitude. What appears to be a latitudinal gradient in fact may simply be a negative correlation of latitude with area at that latitude, due to convergence of lines of meridian at the poles. There is simply less area at high latitudes, which means fewer niches and fewer opportunities for speciation, hence diminished biodiversity at high latitudes. Similarly, analytic geometry of a cone shows that species number should decrease linearly with altitude on a conical mountain. Here, I provide an explicit mathematical model of the area hypothesis of species richness along latitude and altitude gradients. I re-analyze a previously published latitudinal gradient dataset and show that species number is a linear function of the predicted area and that species number is more fully explained by predicted area than by a quadratic function of latitude. However, analytic geometry is not needed if precise measures of area are known.

Keywords Latitude gradient · Species richness

Gradients of decreasing species richness have been extensively documented with increasing latitude from the equator to either pole. This empirical pattern has been demonstrated for a wide variety of plant and animal taxa (reviewed in Rosenzweig 1995). Many hypotheses have also been proposed for these latitudinal patterns of species richness, such as productivity gradients, Rapoport's rule (latitudinal ranges of species are proportional to latitude), and increased speciation in the tropics (Rosenzweig 1995; Jetz and Rahbek 2001; Martin and McKay 2004). Testing of each of these hypotheses requires extensive data that is often very difficult or nigh

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impossible to collect. For example, productivity is non-trivial to measure and geometric boundaries are often highly irregular and even fuzzy in nature (Colwell and Hurtt 1994). I provide a parsimonious and spatially lowest order model for latitudinal gradients of species richness that is based on the spherical geometry of the earth's surface. This simple analytic geometric model has the potential to explain most of the variation in species richness without invoking more cumbersome empirical methods or higher order geometric models. Such a model has been suggested by Terborgh (1973) and Rosenzweig (1995), but only as a verbal model and that has never been formalized.

Perusal of data on latitudinal versus altitudinal gradients of species richness shows one striking difference: the decrease in species richness with latitude is often portrayed as a non-linear decrease, whereas the decrease in species richness with altitude is often portrayed as distinctly linear (Stevens 1992; Rahbek 1995; Rosenzweig 1995; Grytnes and Vetaas 2002; Witman et al. 2004, Fig. 1). Any model of species richness gradients should account for this difference.

In their classic paper on geometric constraints, Colwell and Hurtt (1994, p. 581) stated, "Our models may be justly criticized for being one dimensional—for not taking into account the complications and compensations possible when the shape of geographic ranges is considered instead of simply their breadth along a geographic transect." I partially rectify this deficiency by explicitly accounting for reduced area on a spherical three-dimensional globe, as lines of meridian converge towards the poles. Latitude and area at a given latitude are negatively correlated, and therefore latitudinal gradients in species richness are merely a reflection of such correlation. What we perceive as variation in species richness in response to latitude is really a response to variation in area, not latitude. A similar argument applies to altitudinal gradients. Terborgh (1973) and Rosenzweig (1995) suggested such notions, albeit without a mathematical model. Less area at higher latitudes or

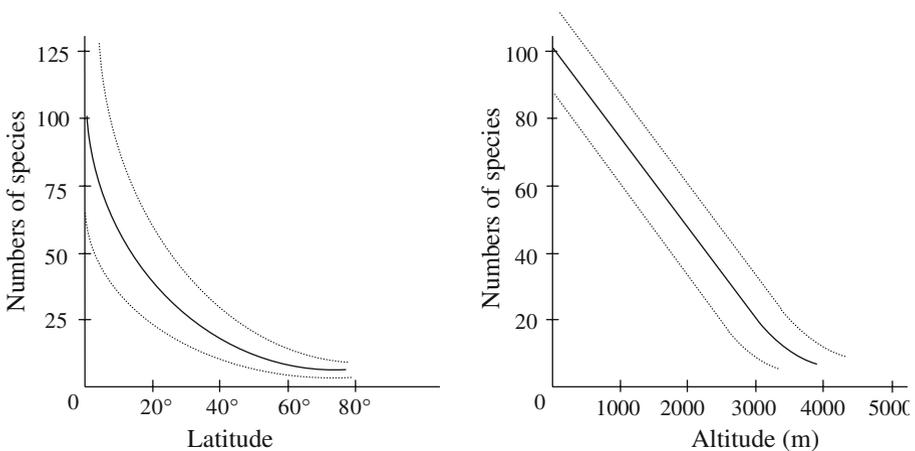


Fig. 1 Species richness versus spatial gradients. Solid lines are best-fit curves; dashed lines are one-sigma error bounds. Latitude gradient is based on Rosenzweig (1995) and Begon et al. (1996). Altitude gradient is based on Stevens (1992)

altitudes results in a smaller number of possible niches or fewer opportunities for allopatric speciation (Pianka 1966; Rohde 1992; Martin and McKay 2004).

Consider the earth to be a perfectly smooth sphere, i.e. disregard such details as the spatial distribution of continental plates and oceanic abyssal plains. Using elementary calculus, we can compute the surface area of sphere at a given latitude. Similarly, consider mountains to either be isolated cones or mountain ridges to be triangular in transverse section and compute the surface area of the mountain at a given altitude. Although clearly disregarding important topographic features, these are the fundamental first-order approximations to what the earth and mountains, respectively, look like. Disregarding these effects is like ignoring the lowest-order terms in a power series approximation, the first component in a principle component analysis, or the lowest-order harmonics in geodesy.

For a sphere, the surface area at a given latitude is readily computed as a surface of revolution. At a given latitude L of a sphere, Surface Area = $2\pi r(L)dz$, where $r = R \cos(L)$ and $z = R \sin(L)$ and R is the radius of the sphere, i.e. the radius of the earth (Fig. 2). Therefore, $dz = R \cos(L)dL$ and Surface Area = $2\pi R^2 \cos^2(L)dL$, i.e. Surface Area is proportional to $\cos^2(L)$. There are two alternative ways in which to see that surface area of a sphere decreases at a faster than linear rate as latitude increases. First, invoke de Moivre's formula that $e^{i^n L} = (\cos(L) + i\sin(L))^n$, where $i^2 = -1$, i.e. the cosine function is merely the real part of the exponential function. Second, compute a second order Taylor series expansion to obtain $\cos^2(L) \approx 1 - L^2$, which is the basis for invoking quadratic regressions when analyzing latitude gradients. Note that $\cos^2(L) \approx 1 - L^2$ decreases at a faster than linear rate for all latitudes greater than or equal to $\frac{1}{\pi}90^\circ \approx 28.65^\circ$.

For a cone, the surface area at a given altitude z is Surface Area = $2\pi r(z)dz$, where $r(z) = (h - z) \cdot (r(0)/h)$ in which the second factor is a constant because h is the height and $2 r(0)$ is the diameter of the base of the cone (Fig. 3). The surface area of the cone at a given altitude is directly proportional to $(h - z)$. Thus, we expect a linear decrease in surface area and consequently a linear decrease in

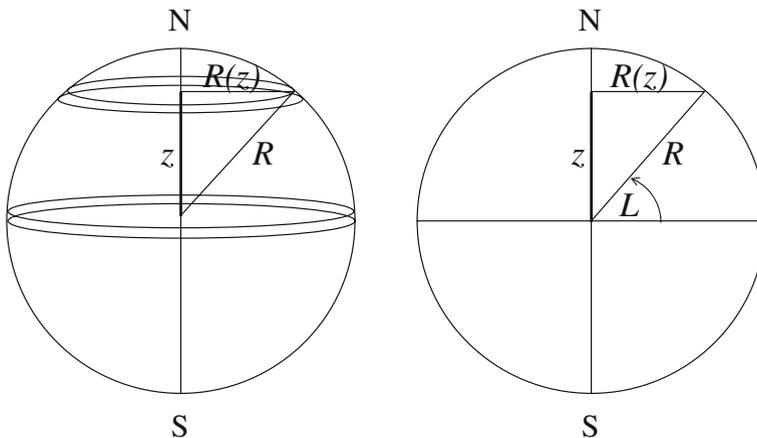


Fig. 3 Surface of area of a conical mountain

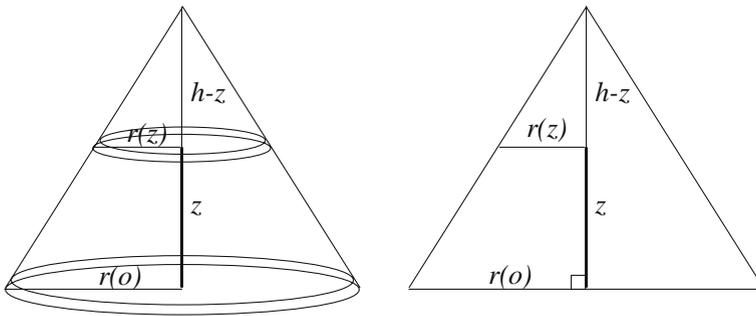


Fig. 2 Surface area of a sphere

species diversity as altitude increases up a conical mountain. Anyone who has played with a toddler's stack of plastic rings of decreasing size placed on a vertical pole will recognize this effect. Identical computations apply to a mountain ridge, so long as the transverse section through the ridge is a triangle. Similarly, Körner (2000) illustrates more complex solids of revolution in place of conical mountains. With convex or concave sides, non-conical mountains will show deviations from linearity in their relationship between altitude and species numbers.

As an illustrative example, I re-analyzed marine species data in Witman et al. (2004), who had examined a dozen regions from 62°S to 63°N (Table 1). I first calculated a quadratic regression of species number versus latitude and obtained the same values of $p = 0.03$ as they had for the independent variable of interest, the square of latitude. In other words, their data shows a relatively pronounced latitudinal gradient. Next, I calculated a linear regression of species number versus $\cos^2(L)$ and found $p = 0.02$. Therefore, using $\cos^2(L)$ as a proxy for area at a given latitude yields a better predictor of number of species than does L^2 . Because Witman et al. (2004) only examined marine species, I calculated percentage of the earth at each latitude that is marine and then computed actual area at each latitude as $\text{Area} = \cos^2(L) \cdot (\% \text{ marine at } L)$. The linear regression of species number versus Area yielded $p = .01$. The fit to their data improves as we go from the traditional quadratic model ($R^2 = 0.35$), to the model using analytic geometry of the sphere ($R^2 = 0.38$), to the model using actual measured area ($R^2 = 0.45$). The analytical geometry approach advocated herein yields a better fit than the traditional model of latitudinal gradients, albeit not as good as using actual area.

Table 1 Regression models of latitude gradients

Model	Independent variable(s)	p -values (t -test)	Overall F -test	R^2_{adj}
Traditional	L and L^2	0.355 and 0.031	0.059	0.35
Analytic geometry	$\cos^2(L)$	0.020	0.020	0.38
Actual area	$\cos^2(L) \cdot (\% \text{ marine at } L)$	0.010	0.010	0.45

Dependent variable is number of species. Input data from Witman et al. (2004)

Given that area on a sphere is proportional to $\cos^2(L)$ and assuming that species–area curves follow power laws (i.e. species number are proportional to area raised to some power, x), the number of species at a given latitude is therefore proportional to $\cos^{2x}(L)$, where empirically x is usually between 0.1 and 1.0 (Rosenzweig 1995; Collins et al. 2002). It should come as no surprise that latitudinal gradients in species numbers are non-linear (despite the warnings that Collins et al. 2002 provide regarding applying species–area curves to global scales).

What is perhaps more surprising is that altitudinal gradients in species numbers are generally presented as linear, even though a combination of simple analytical geometry of cones or triangles with power laws of species–area curves indicates that the number of species should be proportional to $(h - z)^x$, where $(h - z)$ is how far down from the top of the mountain you are and x is the exponent derived from species–area curves. At least the Taylor series expansion $\cos^2(L) \approx 1 - L^2$ shows that latitudinal gradients should be even more non-linear than are altitudinal gradients.

According to the review by Colwell and Lees (2000), there have only been two analytic models of latitudinal gradients for species richness. Willig and Lyons (1998) came close to an analytic geometry approach, but considered the earth to be a two-dimensional circle rather than a three-dimensional sphere. Lees et al. (1999) provided a one-dimensional analytic model that does not even account for the circular or spherical geometry of the earth. Unfortunately, neither model is particularly relevant here. The closest thing to the analytic geometry arguments that I have proposed here for latitudinal gradients were alluded to by Rosenzweig (1995, p. 284) and Lyons and Willig (1999), but they did not attempt an analytic solution. Instead, they relied upon maps with equal-area projections of the continents, without delving into the mathematics. Rosenzweig (1995) also credits Terborgh (1973) for these ideas, but he did not proffer any such analytical solution either.

The analytic geometry approach I proffer here is very broad and global, therefore it should work best with global datasets and less well where specific local micro-climatic and edaphic conditions are responsible for species compositions. This simple analytic geometry approach should work best with latitudinal gradients over large geographic scale and less well with altitudinal gradients over small geographic scales (cf. Hillebrand 2004). Nonetheless, these latitude and altitude models help unify conceptually biogeography in that they both say that species numbers should be directly and linearly proportional to estimated surface area.

This analytic geometry approach is of lower spatial order than any other hypothesis to explain species richness gradients with latitude and therefore should provide the model that is tried before any others. However, this proposed model does not appear to have ever been previously explicated mathematically. I am not advocating discarding other hypotheses. Instead, I am suggesting that we first apply this coarsest resolution hypothesis and evaluate how much variation it explains. A key principle in geodesy or any form of spatial analysis is to include all lower order terms before attempting to estimate higher order ones. Then, if needed, layer on other hypothesis (i.e. higher order terms), such as Rapoport's rule and geometric constraints to explain the remaining variation, as well as micro-climatic and local edaphic data. This can be done by using $A = \cos^2(L)$ as the input to this model or by

including lower order terms along with higher order terms. For example, to incorporate elevation (z) of a conical mountain of height (h), distance from midpoint of range (m), and length of geometric constraints (l) in a single regression model to explain species number (S), use $S = \beta_1(h - z) + \beta_2m + \beta_3l + \varepsilon$, where the β 's are regression coefficients and ε is the residual. My prediction is that β_1 will explain most of the variation, especially compared with β_2 and β_3 .

The purpose of this paper was to introduce spherical (and conical) geometry as a proxy for measured areas and to use this in estimating species numbers with latitudinal and altitudinal gradients. I do not pretend that area of terrestrial or marine ecosystems are completely determined by latitude. As the re-analysis of Witman et al. (2004) shows, spherical geometry yields a better estimate of species number than do traditional models of latitudinal gradient, but neither method is as good as having an estimate of actual area. However, it is often too difficult or expensive to precisely estimate such areas (although things are changing with the advent of geographical information systems), and the method outlined herein simply provide an estimate for area in classical species–area relationships. If precise area data are available, then the analytic geometry arguments proffered here should be ignored and area data that are closest to the truth should be used.

Acknowledgements Thanks to three anonymous reviewers for greatly improving this manuscript.

References

- Begon M, Harper J, Townsend C (1996). *Ecology: individuals, populations, and communities*, 3rd edn. Blackwell, Oxford
- Collins M, Vázquez D, Saunders N (2002) Species–area curves homogenization and loss of global diversity. *Evol Ecol Res* 4:457–464
- Colwell R, Hurtt G (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *Am Nat* 144:570–595
- Colwell R, Lees D (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol Evol* 15:70–76
- Grytnes J, Vetaas O (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *Am Nat* 159:294–304
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163:192–211
- Jetz W, Rahbek C (2001) Geometric constraints explain much of the species richness pattern in African birds. *Proc Natl Acad Sci USA* 98:5661–5666
- Lees D, Kremen C, Andriamampianina L (1999) A null model for species richness gradients: bounded range overlap of butterflies and other rainforest endemics in Madagascar. *Biol J Linnean Soc* 67:529–584
- Lyons S, Willig M (1999) A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology* 80:2483–2491
- Körner C (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends Ecol Evol* 15:513–514
- Martin P, McKay J (2004) Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution* 58:938–945
- Pianka E (1966) Latitudinal gradients in species diversity: a review of concepts. *Am Nat* 100:33–46
- Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? *Ecography* 18:200–205
- Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514–527
- Rosenzweig M (1995). *Species diversity in space and time*. Cambridge Univ Press, Cambridge

- Stevens G (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *Am Nat* 140:893–911
- Terborgh J (1973) Notion of favorableness in plant ecology. *Am Nat* 107:481–501
- Willig M, Lyons S (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
- Witman J, Etter R, Smith F (2004) The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proc Natl Acad Sci USA* 101:15664–15669