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MODELLING OF GLOBAL VEGETATION DIVERSITY PATTERN

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Summary

Here we present an analytical model of species richness for vascular plants, based on limitations in the form of available latent heat and landscape structure (altitudinal difference).

The resulting species-energy relationship is scale independent; is applicable over six orders of magnitude and reproduces both global and regional patterns of vegetation diversity.

The study is based on a recent allocation and growth theory for plants, suggested by Enquist and co-authors.

Introduction

Broad-scale patterns of species diversity

Species are distributed heterogeneously across the Earth. Some regions show a high concentration of species (for example, tropics), others are almost lifeless (for example, polar or arid deserts) and most are between these two extremes. An explanation for these striking regional differences has long been a core task of community ecology and biogeography. The past decade has seen numerous studies exploring broad-scale species diversity patterns and their possible mechanisms of them (see review of Gaston (2000)). There are two reasons for contemporary development of broad-scale studies dealing with species diversity. First, it reflects a raising concern about the future of species diversity in conditions of rapid global environmental and socio-economic changes and corresponding efforts of science to solve theoretical and practical questions of nature conservation worldwide. Second, in the last decade an explosion in the number of broad-scale studies in environmental sciences has been facilitated by appearance of new good quality global data sets, including remote sensing, and new powerful computer technologies for support and analysis of these information sources (GIS and spatial analysis software).

The term 'species diversity' intuitively seems to be rather simple. However, there are a variety of competitive indexes (nearly 100) suggested for their measurement (Magurran 1992). Most combine two factors of species diversity, namely species richness, i.e. the number of species observed or estimated for certain area, and evenness of species by individual distribution, i.e. the more even distribution associated with larger species diversity. We consider further in this work a spatial variation of 'species diversity' in its most popular definition, i.e. as a spatial variation of species richness for an area.

The analysis of broad-scale spatial variation of species diversity was so far branched into four theoretical mainstreams: latitudinal dependence in species richness, species-energy relationships, scaling up and down of species richness and historical factors of species spatial distribution.

The main conclusion drawn from these theoretical and experimental considerations is that no universal mechanism can adequately explain all features of existing diversity patterns for different taxons. The variation in balance of casual mechanisms results in a spectrum of exceptions to any given theoretical spatial patterns of species diversity.

Latitudinal dependence of species diversity

Numbers of terrestrial and fresh-water species within a sampling area of a certain size decreases from the Tropics to the Poles in both Hemispheres. This has been documented for morphologically different taxonomic groups (micro-organisms, trees, insects, primates) (Stevens 1989). Some important features of the latitudinal gradient of species richness were identified for these groups. A decrease in richness with latitude seems to be faster in the Northern than in the Southern Hemisphere and richness peaks are not found at the Equator, rather in some distance in both Northern or Southern directions. Two main hypotheses were suggested to describe such latitudinal gradients in species diversity, both based on the physical structure of the Earth. First, mathematical models that assume no environmental gradients, but only a random latitudinal association between the size and placement (midpoint) of the geographical ranges of species predict a high concentration of species in tropics (Colwell et al. 1994). Indeed, the entire latitudinal range of certain taxa is bounded to the north or south, by area constraints or/and climate thresholds. Therefore, the random placement of a single species in the centre of the zone may result in a large or a small extent by latitude, while extent of species located near the bounds will be always small due to truncation. Such models, however, can be applied only to regions with specific configurations (e.g. large islands stretching mainly in latitudinal directions), because including of longitudinal direction is problematic for these models. The second hypothesis is based on the role of surface area structure of latitudinal bands (Terborgh 1973). The surface area of the tropics comprises the largest homogeneous ecoclimatic zone. The reasons are 1) the land area of latitudinal bands decreases towards the poles; 2) the means and dispersions in temperatures are relatively constant between the Tropic of Cancer and Capricorn; 3) outside of the tropical latitudinal band climate may vary considerably. Changes of homogeneous ecoclimatic area, however, cannot be the only mechanism of Earth latitudinal dependence in species richness, because at high latitudes this area is also large. Additional mechanisms are needed to explain the spatial variation in the balance of specification and migration of species, resulting in the observed latitudinal gradient in species diversity. Around 20 phenomenological and mechanistic explanations have been suggested to describe the existing latitudinal distribution of species (Brown et al. 1998).

The core of the discussion on latitudinal gradients in species richness is the hypothesis that if a spatial pattern is common for many taxa it must result from a single or combination of similar mechanisms. However, there is little evidence for such simplicity in real nature. Any latitudinal patterns for different taxa are disrupted significantly by the influence of other factors like high elevation or lack of precipitation. This indicates that the latitudinal dependence of species richness should be investigated mainly as a correlate of other environmental factors. One of the central points in debates on latitudinal gradients of species richness is the role of scale dependence (Rosenzweig 1995). Indeed, casual mechanisms put forward to explanation of the gradients may appear as a by-product of scale dependency. Recent studies of bats and marsupials diversity in South and North America demonstrate that there is no scale dependence in latitudinal gradients in the range of study areas from 1000 km^2 to 25000 km^2 (Lyons et al. 1999). However, the applicability of the finding at smaller or larger scales and for other taxonomic groups is still questionable. For instance, the analogous study for vegetation species of the relationship between the richness, productivity and the area of the study site (from one to the several square meters) showed interaction between these variables.

Species-energy theory

The most important factor for determining latitudinal gradients of global species richness seems to be some form of transformed solar energy, mostly because incoming short-wave radiation is distributed by latitude over the Earth's surface and drives major climatic and biological processes. The type of available environmental energy and the form of the relationship between this energy and the number of species in an area are some of the major hot topics in the recent biodiversity debates (Whittaker 1999, Gaston 2000). From polar to temperate regions there is evidence, based on observations, for a positive monotonic dependence of species richness by environmental energy (Gaston 2000). The type of energy which correlates might differ between different taxonomic groups. Actual evapotranspiration, i.e. a measure of latent heat flux, was found to describe well tree species diversity of North America and Great Britain (Currie et al. 1987) mean seasonal temperatures i.e. measures of sensible heat, were best correlates with birds and butterfly species richness in the UK (Turner, Gatehouse et al. 1987, Turner, Lennon et al. 1988). The accumulative measures of environmental energy like net primary production can also provide a good description of species richness for certain taxa (for instance for tree species richness in temperate Europe, eastern North America and East Asia (Adams et al. 1989)). The dependence of species richness with energy in tropics and subtropics is not strong, but it is believed to remain positive and monotonic as elsewhere (Gaston 2000). The range of possible temporal variability in available energy appears to be a candidate for correlation with species abundance here. In addition, the type of environmental energy or/and energy variation in species-energy relationship for tropics and subtropics depends critically as well on the taxon concerned (Gaston 2000).

However, despite recent findings on the species-energy relationship there is a lot of unresolved issues in latitudinal gradients of species richness. Indeed, the well- known positive relationship between the numbers of species in the area and the area size may depend on scale resolution (Francis et al. 1998). Therefore, consideration of global patterns on species richness for different scales can provide insights into their physical and biological determinants. A systematic reconciliation of species-energy relationship for different scales has so far not been carried out. Different scientists interpreted this fact as the weak feature of the entire theory (a lack of spatial matching of processes and species samples in many causes) (Lathman et al. 1993) or the strong feature (suggested scale independence of the relationship from a scale) (Francis et al. 1998) with the general conclusion that further analysis is needed.

The most popular explanation of the positive monotonic relationship between species richness and energy on the coarse spatial resolution is an increase in biomass with larger levels of available environmental energy. The increase in biomass promotes coexistence of more individuals, a larger number of viable populations and, thus, more species. Such an argument assumes equivalence in energy requirements for species within different levels of the available energy, which is not obvious.

The species-energy theory has conceptual similarities with the area theory, described above. Indeed, the area theory is based on ecoclimatic zoning, i.e. on climate fields which are to a greater extent determined by solar energy. The species-energy theory assumes the influence of energy to species richness through population size, while the area theory assumes that the available area affects diversity through a range of sizes for species. An observed positive interspecific relationship between the size range and population density (Gaston et al. 1997) makes both assumptions similar. Most likely, available biomass, determined by environmental energy per area unit, is redistributed by the natural processes of extinction and specification which both are affected by available area and its geometry. Species richness within this hypothesis will be assessed as a functional combination (e.g. product) of the environmental energy per area unit and the area.

An application of species-energy theory may provide an important connection to theories of the functional role of biodiversity for terrestrial ecosystems. Indeed, the vegetation physical parameters (like roughness, albedo etc.) can significantly control regional climate (Claussen et al. 1998) making it more humid or arid with further influence on availability of energy and, thus, species composition.

Species-energy models in their recent state have some shortcomings and difficulties in casual explanations of some phenomena:

All of them relate species richness by non-linear regressions with climate variables (like temperature or precipitation) but not energy itself.

Many taxonomic groups use so small amounts of the total solar energy that detection of their species-energy relationships using contemporary measurement techniques is unlikely.

The likely effects of temporal variation in the available total energy are poorly represented in the recent species-energy models.

The processes of extinction and specification operate on millennium time scales. Therefore, recent environmental conditions or their geographical pattern should be a good proxy for the past which is not proven.

Scaling of species diversity

The question how diversity at one scale can relate to other scale is key in understanding global patterns of species richness. Local species richness can be either proportional (but less) than regional richness, or local richness can reach a limit above which it does not rise, despite of increase on regional richness (Cornell et al. 1992). The predominance of direct proportionality between regional and local richness is supported by field observations for a wide variety of taxa(Cornell and Lawton 1992, Lawton 1999, Huston 1999). The observation of proportionality for spatial gradients in species richness at localities and regions was also documented. The century-old classic species-area relationship, which states a power dependence of the species richness with area, is in line with these observations.

There are, however, indications that there is no saturation of local limits of species richness, which one could expect from known ecological interactions (like parasitism, competition etc.). This fact is in contradiction with the simple proportionality between local and regional richness (Cornell 1999). It is unlikely that regional species diversity is important for comprising local species assemblages. Indeed, the size and structure of the available species pool are affected by regional geography (climate, geology etc.) and by broad-scale regional evolutionary processes (like migration and extinction). However, the extent to which local species assemblages can be presented just as a random sample from the regional species pool is unknown (Gotelli et al. 1996). It seems that regional species pools can be seen as mainly contributors rather than determinants of local assemblages and local ecological processes are still important for shaping local species diversity.

Historical factors of species diversity

Historical factors had a substantial role in shaping contemporary patterns of species diversity. For instance, fossil analysis shows that west-central Europe had more tree species during the Upper Tertiary (25-2 Myr BP) with genera, which are now only present in North America and Asia. Elimination of these genera has happened during the Pleistocene glacial periods with the consequent failure of recolonization. (Adams et al. 1989) analysed the relationship between climate factors and tree richness in the northern temperate forests in Europe, eastern North America and eastern Asia using the productivity prediction model. They found by regression analysis that tree species richness in the three regions can be mainly explained by present day climate factors. However, much higher levels of richness are reached at corresponding levels for eastern Asia in comparison with the other two regions. The authors argue that this may indicate that parts of eastern Asia served as a refugia and had lower extinction rates during glacial periods. The recent debate on respective roles of energy (in form of observed actual annual evaporation) and long-term geographical processes for tree species richness in the moist tropical forest has highlighted difficulties in distinguishing the two factors (Lathman and Ricklefs 1993, Francis and Currie 1998, Ricklefs, Latham et al. 1999). Only developing accurate methods in molecular phylogenesis, with estimation of diversification events, can provide data for testing different hypotheses about influence of history on patterns of global species diversity patterns.

Objectives

Recent efforts in climate and vegetation modelling as well as in global species diversity analysis can be combined. First of all, spatial and temporal variations in vascular plants species richness should be analysed, because these species are major primary producers of biomass in trophic chains in almost all terrestrial ecosystems and a major component of human living space.

The following objectives can be identified (see Introduction) for the study of global patterns in vascular plants diversity

Analysis of biotic and abiotic factors of vegetation diversity

Investigation of species-energy relationships for vascular plants

Analysis of spatial scaling rules for vegetation communities

The complete logically (even if rather simplistic) view on these identified problems would allow us to design a dynamic model for the variation of species richness of high plants based on the recent Dynamic Global Vegetation Models (DGVM) and to make projections in the future.

Additional investigation of latitudinal gradients and historical factors in contemporary plant species ranges are needed to conduct a study of paleo-vegetation and covariance of plant richness with the other taxa.

Data

Species numbers of vascular plants: maps and surveys

Rich data on total species numbers of vascular plants (SNVP) for different regions have been collected by many authors. The range of areas with described vegetation diversity varies from small plots (0.1 m^2-1 m^2) to large countries and continents (several million km^2).

Spatial extrapolation of richness observed for local floras provides data about regional or global species abundance. Correlation and logarithmic or linear regression analysis are used as methods for calculating the expected numbers of species for variable areas. Exponential equations (Arrehenius 1920, Evans, Clark et al. 1955) are widely applied for these purposes. The theoretical basis for usage of exponential equations is the existence of so-named local or (“elementary”) floras. A local flora is the elementary unit of a flora (Tolmachev 1986). It is comparatively homogeneous as a whole, but may include several types of vegetation communities. Appropriate size of local flora in the Arctic was estimated as 100 km^2 (Yurtsev 1987), while it enlarges southward, reaching 1000 km^2 in the Tropics (Malyshev 1991). Down scaling or up scaling of data for the local floras by exponential equations allows calculation the expected numbers of species in areas of a standard size (sampling areas). The 10-fold deviation of the initial area size in the exponential equation provides still acceptable possible error for the expected species numbers in the sampling area (less then 15% see (Malyshev et al. 1994b)).

The published global maps of SNVP were assembled per sampling area of 10000 km^2 (Barthlott, et al. 1999) and per sampling area 100 000 km^2 (Malyshev 1991).

Malyshev (1991) has chosen 10^5 km² as the sampling area size for the comparative evaluation of floristic richness on a global scale because the observed data were recorded mostly from area of similar size. Thus it was possible to calculate data for 459 vascular plant floras with the areas ranging from 10^4 to 10^6 km². Especially abundant data exists for Europe, Africa and the USA.

The Arrhenius equation was used for all calculation. Averaged for the globe mean deviation of computed species numbers by extrapolation of possible actual values is estimated to be only 2,6% (Malyshev 1991).

However, in the compilations authors had endeavored to use published data mainly for native and naturalized adventives, excluding species introduced in culture and excluding microspecies. The completeness of the checklists in some cases could not be ascertained and authors of floras most likely have somewhat different concepts of species abundance. This fact also affects the reliability of comparisons based on such data (Malyshev 1991).

For example, flora of British Isles, West Germany and East Europe were used as initial data for modeling of spatial floristic diversity in Europe. For the British Isles, the manual ‘Atlas of the British Flora’ (Perring et al. 1968) was adopted as a data basis. The area is divided into squares of 100 km²; these small squares are joined into major ones, measuring 10^5 km². The numbers of plant species in small squares are directly given in the ‘Atlas’, for areas 10^4 km², as well as for those of $2*10^4$, $3*10^4$, and $4*10^4$ km²; they were calculated from distribution maps.

The flora of West Germany is suitable for a comparative analysis due to the publication of the ‘Atlas der Farn- ind Blutenpflanzen der Bundesrepublik Deutschland’ (Haeupler et al. 1989). The territory is divided into squares, whose sides correspond to one degree of latitude and one degree of longitude, each square being subdivided into 60 small quadrangles reporting the occurrence of plant species. Their size depends on the northward convergence of meridians, decreasing from 140 km² on the south till 120 km². These, grid based, species abundance data were used for extrapolation for the sampling areas in West Germany (Malyshev 1991).

The model of spatial floristic diversity in eastern Europe is based on a transect extending between 20ºE and 34ºE, from northern Scandinavia to the steppe region near the Black Sea. This latitudinal profile, about 2,900 km. long comprises different biomes: forest-tundra, northern, middle and southern taiga, subtaiga, nemoral forest, forest-steppe and true steppe. These data enable to calculate the expected species abundance in the sampling areas of standard size in the region.

Mosaics of extrapolated species richness, either grid based, or transect based, were smoothed and combined onto the global map of SNVP per 100 000 km^2.

A cartographic depiction of global map of SNVP per sampling area 10 000 km^2 (Barthlott, et al. 1999) is based upon data from about 1400 floristic surveys on both continental and regional scales. Species numbers were calculated using the Evans, et al. (1955) equation and were divided into ten Diversity Zones which have a variable span (hundreds of species in the lower categories and thousands in the higher categories due to enlarged species diversity, mainly in the tropics).

Additionally the inventory based approach (Barthlott, et al. 1999) was applied to design the world map of the species numbers of vascular plants per 10 000 km^2. Not only data for species or family numbers in a region, but also taxon numbers of selected groups are used by the inventory based approach. These numbers may be estimated relatively reliably by specialists long before all involved taxa are exactly and systematically assessed. The general centers of diversity can be depicted using these expert estimates and then species numbers of vascular plants can be mapped in a region.

The recent map of diversity zones for numbers of species per 10000 km² (Barthlott, et al. 1999) was digitised and transformed into the 0.5°x0.5° longitude/latitude map of SNVP per 10000 km² The digitalisation and transformation of this map is described in Appendix 1. The computerised map of SNVP per 100000 km² with the same resolution (0.5° grid cell) was obtained from the map of (Malyshev 1991) by digitalisation of contour lines and their further interpolation. These two maps were used to investigate abiotic factors of vegetation diversity on the global scale.

The four maps of SNVP per 100 km², 1000 km², 10000 km² and 100000 km² for the Former Soviet Union (Malyshev 1994c)were put into the GIS in the same manner as the global map of SNVP per 100000 km² and were used for the continental scale analysis. The initial maps, illustrating the levels of species abundance of vascular plants in the sampling areas of 10^2, 10^3, 10^4, 10^5 km² of former Soviet Union, were designed by (Malyshev 1994c) from 409 sites, using extra/interpolation not exceeding 10-fold size of initial area and expert evaluation of the spatial floristic diversity.

Literature surveys from various authors were used to study vascular plant species richness in Europe (see Table 2 below). These observations were conducted for different vegetation zones (from arctic tundra to southern steppe) and for areas with different sizes from 100km² to 4500 km². The survey of (Malyshev 1975) for SNVP per 100 km² sampling area was used for other continents (see Table 3 below).

The species numbers of vascular plants for large geographical areas were collected from different literature sources (see Table 4 below)

Abiotic factors of vegetation diversity

For the analysis of climate effects on vegetation species diversity we used the CRU05 (1901-98) 0.5°x0.5° longitude/latitude monthly climate data, provided by the Climate Research Unit, University of East Anglia, U.K. These data include monthly fields of mean temperature, precipitation and cloud cover.

The soil texture dataset was constructed based on the textural information digitised by Zobler (1986) from the FAO soils map (FAO/UNESCO 1974) . The data set distinguishes fine, medium and coarse textured soils and combinations of these classes, with a separate category for organic soils. In addition, extra category for vertisols was added.

The elevation data with resolution 0.5°x0.5° was prepared from the Digital Elevation Model of the World, developed through a collaborative effort led by staff at the U.S. Geological Survey's EROS Data Centre (http://edcwww.cr.usgs.gov/landdaac/gtopo30/gtopo30.html).

The altitudinal gradients for the sampling areas of 10^2, 10^3, 10^4, 10^5 km² were calculated from these elevation data using standard ARC-INFO procedure.

The Boolean cropland data set, in which each 0.5° grid cell is represented as either natural or cropland at the present day (Ramankutty et al. 1998), was used for investigation of the influence of land use on vegetation diversity.

Method

Hypothesis of energy equivalence across vascular plants species

The main hypothesis of our model lies within a new approach in biology, suggested by Geoffrey West, James Brown and Brian Enquist (West, et al. 1997, Whitfield 2001). This biological theory states that the growth of an individual and community structure are both based on fractal geometry and the size of organism. The background to this theory is the general model of transportation of essential materials (blood, water) through a fractal network of branching tubes within an individual (West, et al. 1997). It was demonstrated that the metabolic rate is equal to the body mass to the power ¾ when the energy, dissipated during transportation, is minimized and the terminal tubes of space-filling network do not vary with the body size. This and other allometric scaling relationships can be drawn for different types of distribution networks, like cardiovascular systems of animals, plant vascular systems, insects tracheoids etc. The ¾ law of body mass to metabolic rate has been known for a long time in animal ecology as Kleiber’s law (Kleiber 1932). However, it was applied successfully for the first time in plant ecology by (Enquist, et al. 1999a, Enquist, et al. 1999b, Enquist, et al. 1998, Enquist and Niklas 2001) where previous considerations of body mass to metabolic rate relations and the other allometric relationships were based on simple principles of Euclidian geometry. The geometric model predicts that the metabolic rate scales as the 2/3 power of the body mass (relation of surface area, where the heat is lost, to the mass proportional to the volume). Appling the resource distribution model through fractal networks for xylem transport of water and nutrients in vascular plants, Enquist and co-authors suggested a general model of plant vascular systems with the ¾ law analogous to animal systems (Enquist, et al. 1999b). They provided a justification for this model with the twenty years time series, measured from 2283 trees of 45 species found in Costa Rica (Enquist, et al. 1999a). The data fits the ¾ power law realtive the rate of gross primary production to body mass remarkably well, when variation in wood density is taken into account. Using the new, energy and fractal geometry based model of plant individual growth, (Enquist, et al. 1998) predicted a –4/3 exponent for the intraspecific thinning law. The traditional geometric model of thinning assumes that stand volume is proportional to –3/2 power of population density, because the number of individual plants in an area is reciprocal to projection coverage area calculated as a function of the average stem diameter (Yoda, et al. 1963) Unfortunately, adjustment of the theoretical thinning exponents to real-life tree species by design of more sophisticated geometric models have had only limited success (Lonsdale 1990). Meanwhile, the new (fractal geometry based) thinning model fitted well the observed data for 251 population of plants ranging from *Lemma* to *Sequoia*, i.e. 12 orders of magnitude in plant size (Enquist, et al. 1998).

There are two important implications of the new allocation and thinning theory for plant diversity studies. First, the rate of whole-plant xylem transport or transpiration are an appropriate indices of plant metabolism, while the allometric exponents for gross photosynthesis, water and nutrient use must be equivalent due to stoichiometric constraints. Second, total energy use of plants for a given area is invariant with respect to body size. Indeed, the rate of energy resource use (transpiration or gross photosynthesis) for a given area Q_{tot} is the product of the rate of energy use per individual Q_{ind} and the population density N, therefore:

$$Q_{tot} = N \cdot Q_{ind} \propto M^{-3/4} M^{3/4} \propto M^{0}, \qquad (1)$$

where M is the above-ground plant biomass of the individual (Enquist, et al. 1998, Enquist and Niklas 2001).

This strongly supports the hypothesis of energy equivalence across vascular plant species on a given spatial scale: despite the fact that energy is implemented in variety of growth-form and life-history strategies, all plant vascular species attain the same optimal use of energy. Certainly, there are interspecific differences in resource allocation over the lifespan, which are seen in varying volume increments, reproductive strategies (Magnani 1999). However, energetics seems to be crucial to plant species diversity due to the consistent scaling relationship for intraspecific energy use within a plant community.

Energy-diversity relationship for plants

Indeed, the transpiration balance equation in energy units for the area A can be written in this case as:

$$\gamma * E * A = Q * A_h \qquad (2)$$

where γ is the spatially averaged ratio of transpiration to the total evapotranspiration, E is the rate of available for evaporation latent heat per area unit, A_h is the projection of total amount of transpiring area for vascular plants, Q is the constant rate of transpiration in energy units per unit transpiring area, according to the hypothesis of energy equivalence across vascular plant species (see equation 1). The equation represents the balance between available for transpiration energy and actual transpiration in the area A.

When $\overline{N}_A(1)$ is the average number of species in the one area unit, we get:

$$\gamma * E * A = Q * \frac{1}{\overline{N}_A(1)} * \sum_{i=1}^{N_{sp}(A)} A_h^i , \tag{3}$$

where $N_{sp}(A)$ is the number of terrestrial vascular plant species in area A and A_h^i is the projection of total amount of transpiring area for the species *i*.

The projection of transpiring area for the species *i* can be estimated using the Korcak empirical relation for area distribution within an archipelago of ‘self-similar’ transpiring islands (vegetation patches). The number of irregularly shaped islands $N^i{}_{patch}(a)$ smaller than area *a* will be given by the cumulative hypergeometric size-frequency distribution (Burrough 1986):

$$N^i{}_{patch}(a) = k_i * \frac{1}{h_i} * a^{\frac{D_i}{2}} , \tag{4}$$

where k_i is the constant (maximum number of patches in the area unit), $\frac{1}{h_i}$ is the unit less factor describing reciprocal to relative local lacunarity of landscape (less or equal to one) (Milne 1992), D_i is the fractal dimension of landscape for the species *i*.

Assuming the relative local lacunarity and the fractal dimension of landscape constant across the plant species, , i.e. $\frac{1}{h_i} = \frac{1}{h}$ and $D_i = D$ for the entire set of species, we obtain the sum of projections for the total transpiring area as:

$$\sum_{i=1}^{N_{sp}(A)} A_h^i = \overline{A_{isl}} * \sum_{i=1}^{N_{sp}(A)} N^i{}_{patch}(A) = \frac{1}{h} * A^{\frac{D}{2}} * \overline{A_{isl}} * \sum_{i=1}^{N_{sp}(A)} k_i = \frac{1}{h} * A^{\frac{D}{2}} * \overline{A_{isl}} * \overline{k} * N_{sp}(A) = \frac{1}{h} * A^{\frac{D}{2}} * N_{sp}(A) \tag{5}$$

where $\overline{A_{isl}}$ is the averaged by all species area of a vegetation patch, $\overline{k}$ is the averaged by all species averaged maximum number of patches in the area unit, so their multiple is equal to one.

Combining equations (5) and (3) provides an estimate of the species numbers of vascular plants for an area *A*:

$$N_{sp}(A) = \left(\frac{\gamma}{Q_{tot}^{sp}}\right) * E * h * A^{\frac{2-D}{2}} , \tag{6}$$

where $Q_{tot}^{sp} = Q * \frac{1}{\overline{N}_A(1)}$ is the averaged rate of transpiration for one species per area unit, constant for a certain landscape.

Indeed, maximum annual available energy for evaporation *E* per square meter can be obtained as a long term averaged value:

$$\overline{E} = \sum_{1}^{N_{year}} \sum_{T_j > 0} \min(LH_j ; L_j) / N_{year} , \tag{7}$$

where LH_j is available part of the radiation balance for evaporation in the month j in MJ/sq.m, L_j is energy for evaporation of available monthly precipitation in month *j* in MJ/m², N_{year} is the averaging period in number of years.

The fraction of the radiation balance available for evaporation part can be calculated from the monthly temperature as:

$$LH_j = \beta * R_j * t_{month} , \tag{8}$$

where R_j is the radiation balance in Wt/m² , $t_{month} = 2.592*10^6$ sec is the number of seconds in a month time, β is equal to the global value 2/3 (Baumgartner et al. 1975). Applying the dependence of surface temperature on the radiation balance as used in the energy-balance climate models (Ramanathan and Coakley 1978, Ramanathan, Lian et al. 1979, Balobaev 1991) one can approximate LH_j as :

$$LH_j = \beta * (F + K * T_j) * t_{month} \ , \tag{9}$$

where T_j is the mean monthly temperature (°C), F = 46.9 Wt/m^2 and K= 2.2 Wt/(m^2 *°C) are constants.

The total energy needed for evaporation of the monthly precipitation is equal to:

$$L_j = L * P_j \tag{10}$$

where L=2.45 MJ/kg is the latent heat of evaporation, P_j is the monthly precipitation in mm (equivalent to kg/m^2).

The constant γ can be estimated as the averaged for the total land surface ratio of transpiration to the total evapotranspiration. Indeed, when A is equal to area unit (e.g. A=1 m^2) and h is being set to 1., the equation (6) can be rewritten as:

$$\overline{T}_{land} = \gamma * \overline{P}_{land} \tag{11}$$

where $\overline{T}_{land} = \dfrac{\overline{N}_{Earth}(1) * Q^{sp}_{tot}}{L}$ is the average over the land surface annual transpiration per area unit (e.g in kg/m^2 or mm), $\overline{P}_{land} = \dfrac{E}{L}$ is the average over the land surface annual latent heat for evapotranspiration per area unit (e.g in kg/m^2 or mm).

The model values of the global ratio between transpiration and global evapotranspiration (i.e including interception and evaporation from bare soil) γ are in the range 0.67-0.69 (Gerten, personal communication). (Baumgartner et al. 1975) estimated the total annual land evapotranspiration as 0.71 * 10^5 km^3, which is equivalent to 507 mm year^{-1} m^{-2} (1242 MJ/m^2 of latent heat). Applying equation 11, we obtain an average transpiration in a square meter of 342 mm (837 MJ/m^2 of latent heat).

A rough global estimate of the annual averaged rate of transpiration for one species per square meter Q^{sp}_{tot} can be calculated from the annual global transpiration and the average number of species per m^2 for the natural vegetation across the globe $\overline{N}_{Earth}(1)$:

$$Q^{sp}_{tot} = \frac{\overline{T}_{land}}{\overline{N}_{Earth}(1)} * L \ , \tag{12}$$

set to 4.5 sp./m^2, which coincides with the average value for the temperate broadleaved forest (4.38-4.8 sp./m^2 see Gleason, 1925), i.e. for the zone with average for the globe climatic conditions.

Therefore, $Q^{sp}_{tot} \approx 186$ MJ/(m^2 * species) which is equivalent to the 76 mm a year.

Taking into consideration equations 6 to 12 we can calculate the number of species of vascular plant as:

$$N_{sp}(A) = \nu * \sum_{1}^{N_{year}} \sum_{T_j > 0} \min(\beta * (F + K * T_J) * t_{month} ; L * P_j) / N_{year} * h * A^{\frac{2-D}{2}} \ , \tag{13}$$

where $N_{sp}(A)$ is the number of vascular plant species in the area A, T_j is the mean monthly temperature (°C), P_j is the monthly precipitation in mm, N_{year} is the averaging period in number of years, D is the fractal dimension of landscape fragmentation, ν = 0.0036 species/MJ, β =2/3, F = 46.9 Wt/m^2, K= 2.2 Wt/(m^2*°C), t_{month}=2.592*10^6 sec and L=2.45 MJ/kg are constants.

This physically based model uses water-energy dynamics to estimate number of vascular plants species as the regression based Interim General Model (O'Brien 1993). The potential minimum evaporation and annual precipitation are the major determinants in IGM for estimating of species numbers of vascular plants (SNVP) around the world.

This approach allows considering seasonal distribution of available heat and water for plants, which is important for regions with summer (winter) dry climates, like India or continental Brazil.

Scaling of vegetation diversity

Energy theory allows us to estimate SNVP for different scales from the climate variables (see 13) as long as values of fractal dimension of landscape fragmentation *D* and lacunarity of landscape *h* are known. The lacunarity of the landscape depends on abiotic geographical features making climatic or physical barriers for plant species migration, like altitudinal differences, presence of water bodies, rock outcrops etc.

Let us take into account only the influence of altitudinal difference upon contagion within area *A* and make it in a linear form:

$$h = 1 + R * \Delta H(A), \qquad (14)$$

where *R* is the constant and $\Delta H(A)$ is the mean altitudinal difference (in meters) within area *A*.. One can argue that *R* should be small, but slightly greater than 10^{-3} (1/m) based on radiation balance considerations. Indeed, higher elevations receive more insolation than lower elevations. This results both because higher elevations have more open viewsheds and because the solar beam travels through less air mass. The effect is negligible for a change of 10 m, but a rise from sea level to 5,000 m can result in an increase of 52% in global radiation for the latitude 39° N, (Fu et al. 1999). The effect of elevation upon insolation can be described approximately by formula 14 with $R=10^{-4}$ (1/m) (see Table 3 in the above paper) and we take this *R* as an initial value for description of lacunarity changes with the mean altitudinal difference.

The fractal dimension of patches (or landscape fragmentation) *D* is related to the persistence parameter of the fractional Brownian motion model *H* (Hastings, et al. 1982). Under certain limiting assumptions (Sugihara et al. 1990) the relationship between *H* and *D* is $H = 2 - D$. According to this model of habitat occupation, increased persistence (more memory in the process) should correspond to smoother boundaries and patches with larger and more uniform areas; whereas reduced persistence (less memory in the process) will correspond to more complex and highly fragmented landscapes dominated by many small areas.

Persistence refers to the degree of autocorrelation of adjacencies: for $H < 0.5$, a fractional Brownian motion trace is negatively correlated, whereas values are positively correlated for $H > 0.5$ and $H=0.5$ is a classical Brownian motion model without correlation of adjacencies. Generally, there are only few objective tests on the validity for ecological systems of theoretical persistence-patchiness relationships (Johnson et al. 1995). For example, Hastings et al. (Hastings, et al. 1982) used this method successfully to compare early successional and late successional patches in Okefenokee Swamp. They found that the earlier successional vegetation (cypress patches) shows a higher fractal dimension (i.e. greater patchiness) and decreased persistence than broadleaf evergreen patches with vegetation in the late stage of succession.

As a global average value of fractal dimension of landscape fragmentation we took $D=1.5$ ($H=0.5$), which corresponds to classic fractional Brownian movement, i.e. stochastic habitat occupation by plant species. Similar values were obtained during an assessment of vegetation heterogeneity in New Zealand. (Nikora, et al. 1999). On the North Island, vegetation patches covering the areas from 1 to 10000 km² have $D=1.42$ whereas the South Island have a corresponding fractal dimension equal to 1.4.

After these considerations, energy theory logically leads us to the species-area relationship (SAR) with the coefficients, which can be directly estimated by long-term climate variables and heterogeneity of landscape (see 13):

$$N_{sp}(A) = C * (1 + R * \Delta H(A)) * A^{z}, \qquad (15)$$

where

$$C = \nu * \sum_{1}^{N_{year}} \sum_{T_j > 0} \min(\beta * (F + K * T_J); L * P_j) / N_{year} \qquad (16)$$

is the average for area A potential number of vascular plants per m² and

$$z = \frac{2 - D}{2} \qquad (17)$$

is the floristic diversity index (Malyshev 1975)

Setting $\Delta H(A)$ to zero in (15), results in the oldest and best-documented relationship between number of species and area in community ecology. It is known in the plant ecology as the Arrhenius equation (Arrehenius 1920,. Crawley and Harral 2001) has shown that z varies at small (0.1-10 m²) and intermediate (10-1000000 m²) scales from 0.2 to 0.5 and then drops back at larger scales (10^{8} to 10^{12}) to 0.2-0.3. Malyshev (1975) suggested that z ranges from 0.07 (deserts and tundra) to 0.36 (tropics). Widely represented field data for animal and plant species (Preston 1962) and several theoretical models (island biogeography of (MacArthur and Wilson, 1967) models of resource by species distribution (Sugihara 1980, Pielou 1975) suggest that z is a constant approximately equal to 0.25.

According to the energy theory z is determined by the fractal dimension of patches (or landscape fragmentation) with a global average value 0.25. Landscapes with high vegetation fragmentation, caused for example by climate extremes like deserts or tundra, will have lower values of z (see equation 17), while landscapes with uniform areas, like tropical evergreen forests, will have values exceeding 0.25.

With the suggested average values of constants it is possible to estimate the species numbers of vascular plants for area A (in m²) when climate variables and altitudinal difference are known:

$$N_{sp}(A) = 3.6 * 10^{-3} * \sum_{1}^{N_{year}} \sum_{T_j > 0} \min((81. + 3.8 * T_J); 2.45 * P_j) / N_{year} * (1 + 10^{-4} * \Delta H(A)) * A^{0.25} \qquad (18)$$

Results

Statistical analysis of species numbers of vascular plants against abiotic and biotic factors

A correlation analysis for the global map of SNVP per 10000 km² at a 0.5°x0.5° degree resolution was carried out for abiotic factors using ARC-INFO (GRID) statistic tools.

It was found that the following abiotic variables are positively correlated to species richness (on global scale):

The annual sum of positive temperatures with r=0.45, annual sum of precipitation (r=0.64) and elevation gradient (r=0.1).

Cloudiness, soil texture and recent land use had insignificant correlation (coefficient less than 0.1).

The maximum annual available energy averaged over 98 years for evaporation *E* per square meter was calculated from the CRU05 climate dataset (see formula 7).

The global species numbers of vascular plants were obtained using the equation 18 with 10000 km² and 100000 km² sampling areas. The correlation between the theoretical and observed SNVP is high in both cases, for 10000 km² sampling area r =0.77, and for 100000 km² the correlation coefficient is 0.76 (see scaterrograms Figure 1, 2).

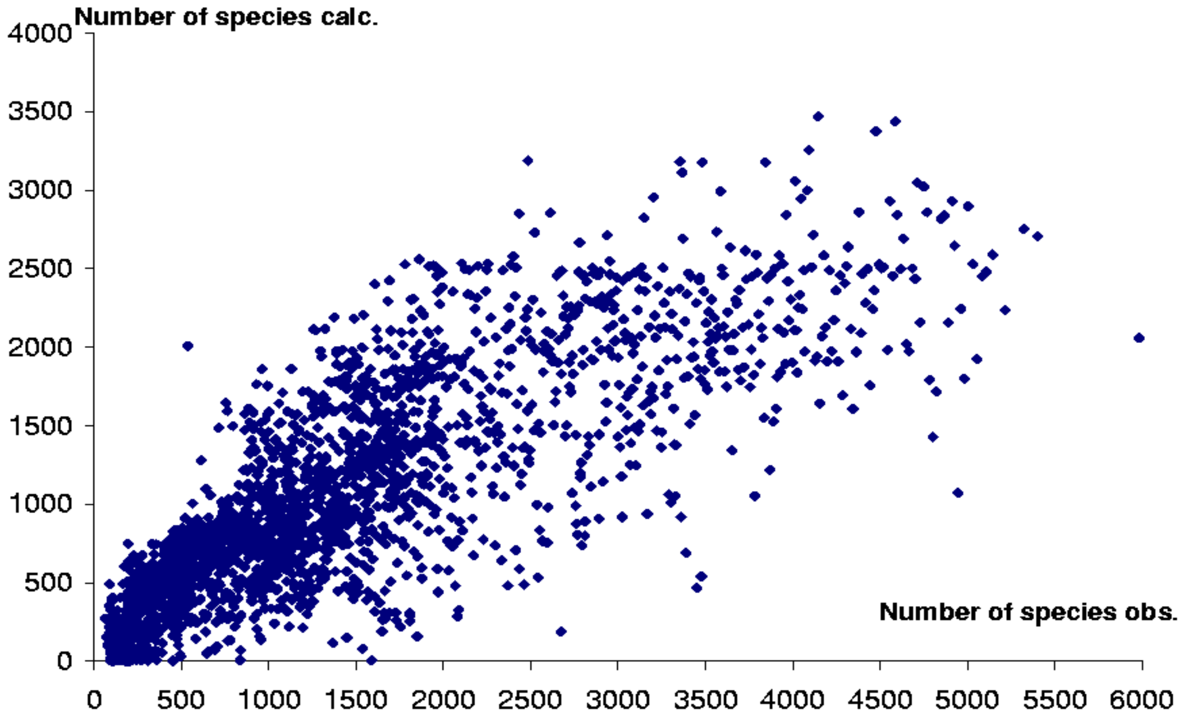

Figure 1. Species number of vascular plants per 10000 km² for the globe, observed against calculated from the theoretical species-energy relationship.

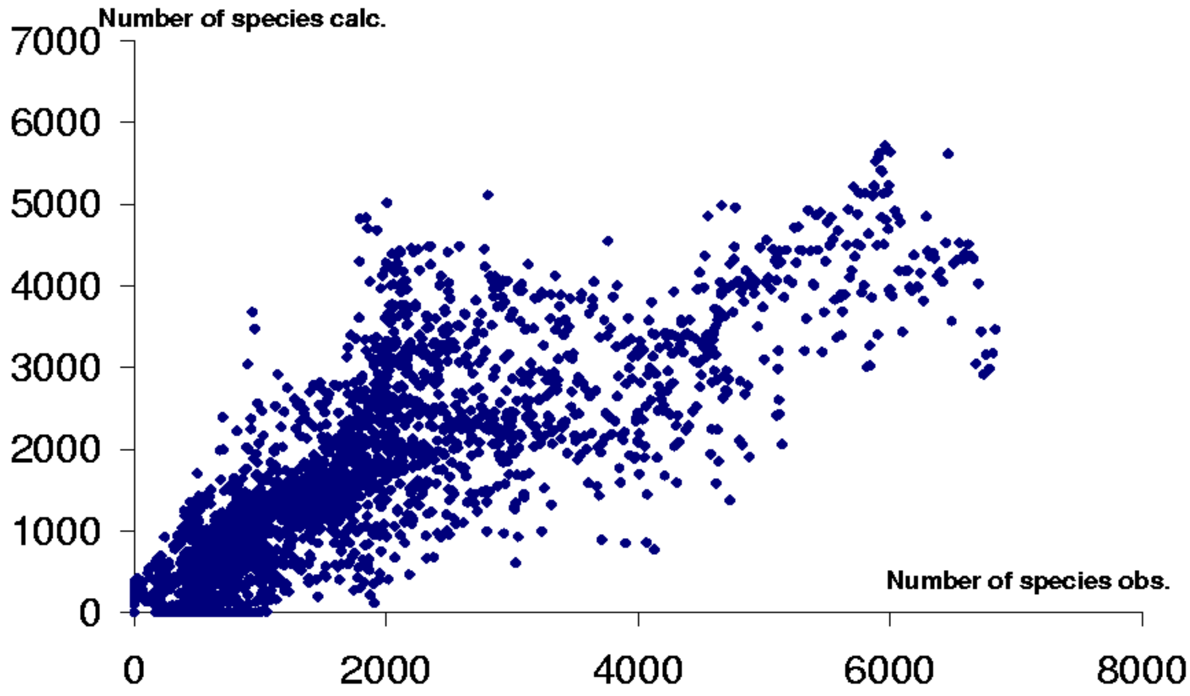

Figure 2. Species number of vascular plants per 100000 km² for the globe, observed against calculated from the theoretical species-energy relationship.

A step regression optimisation for theoretical coefficients ν, R and D in equations (16-17) was carried out using the global map of SNVP per 10000 km² (i.e. with lowest sampling area) and the global pattern of maximum annual available energy for evaporation E. The correlation coefficient improved modestly (r=0.78). The coefficients obtained with the regression are practically the same as theoretical, except of R: ν =0.0037 sp./MJ against the theoretical value 0.0036 sp./MJ; averaged fractal dimension of vegetation patches D = 1.52 , i.e. almost equal to theoretical Brownian stochastic occupation of habitat by vegetation; R= 3.0 * 10^{-4} 1/m against 1.0 * 10^{-4} 1/m, which probably indicates that the altitudinal gradient affects lacunarity of landscape by additional factors and not only to insolation changes. These optimised coefficients were used in further calculations.

Global vegetation diversity per 10000 km^2 and per 100000 km^2

The simulated species number of vascular plants per 10000 km² is shown in Figure 3. The comparison with the map of (Barthlott, et al. 1999) based on observations, (see Figure 4) demonstrates a successful reproduction of the global vegetation diversity pattern.

Both absolute numbers of species and their relative spatial distribution are very well reproduced. The 'hot spot' areas are obtained in the Central America and the Andean, at the Brazilan Coast and in Venezuela, in the western part of Amazon basin, in the Central and Southern Africa, in Madagascar, in the Southern India, China, Indonesia and Eastern coast of Australia. Desert and tundra areas have lowest species numbers. However, in some regions with extremely sparse vegetation (Central Australia, Arctic tundra), the numbers of species are slightly overestimated. Most likely this is the consequence of significant deviation from the global average value of landscape patchiness D in these areas.

The computed species numbers of vascular plants per 100000 km² (see Figure 5) are also reasonable in comparison with the expert estimates of Malyshev (1975) (see Figure 6). The predicted values are generally slightly overestimated, i.e. scaling up by an order of magnitude the sampling area to small extent decreases the performance of the model. The absolute values differ by 30% at maximum (e.g. in the South-Eastern US and in the Central Africa) and the geographical pattern of simulated SNVP per 100000 km² fits well with observation.

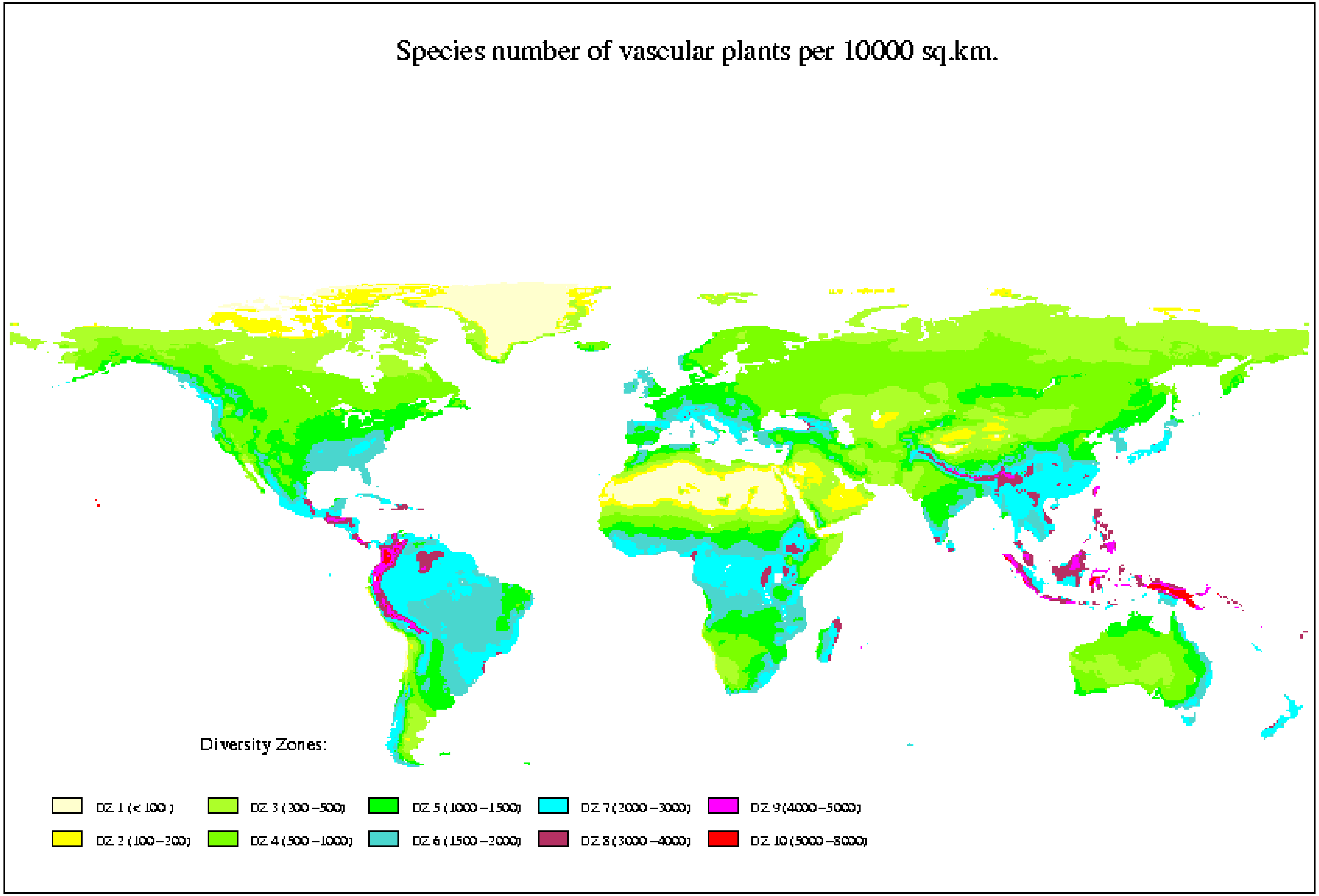

Figure 3. Species numbers of vascular plants per 10000 km², predicted by the species-energy relationship.

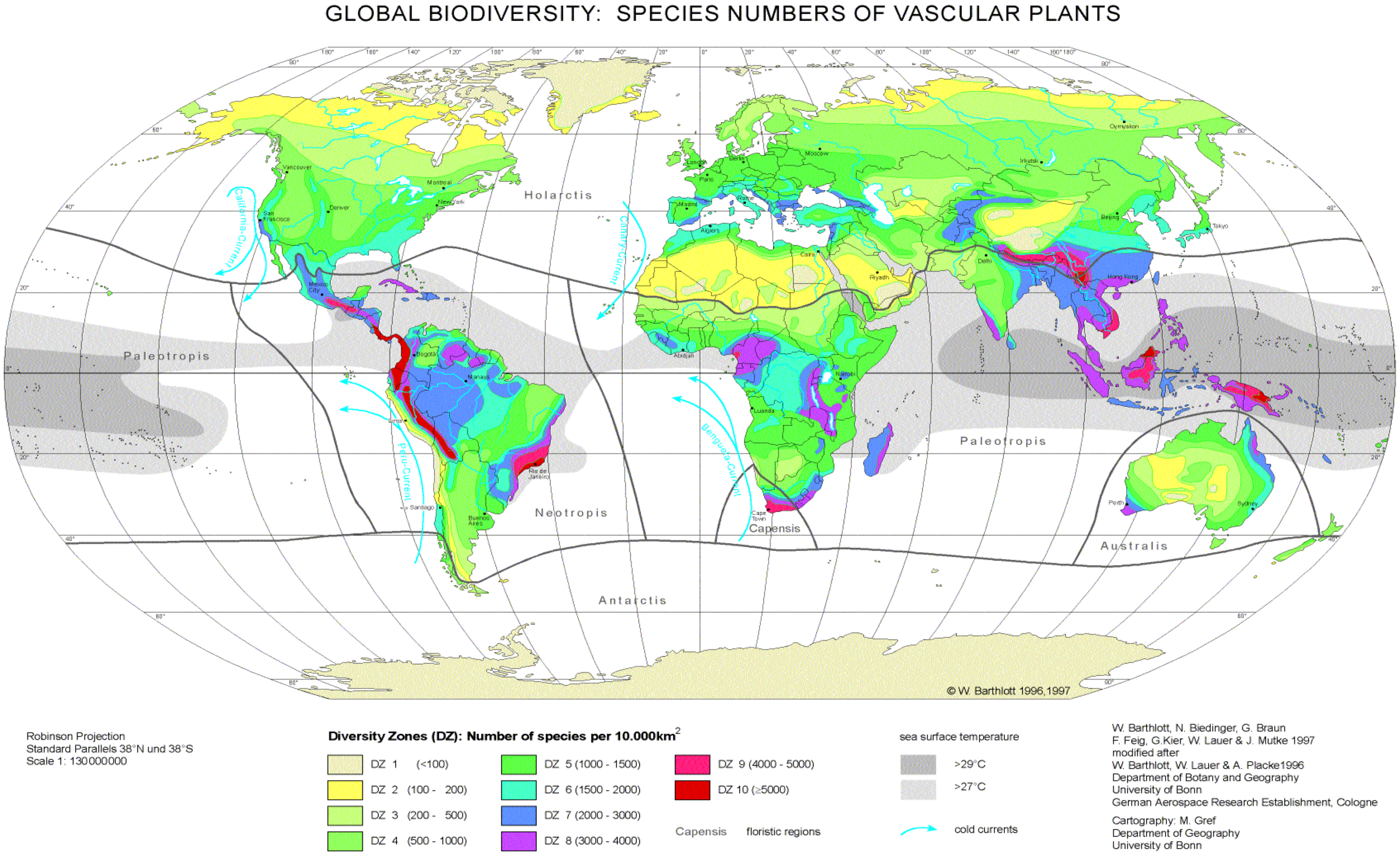

Figure 4. Observed species numbers of vascular plants per 10000 km² (available on the internet at http://www.botanik.uni-bonn.de/system/biomaps.htm)

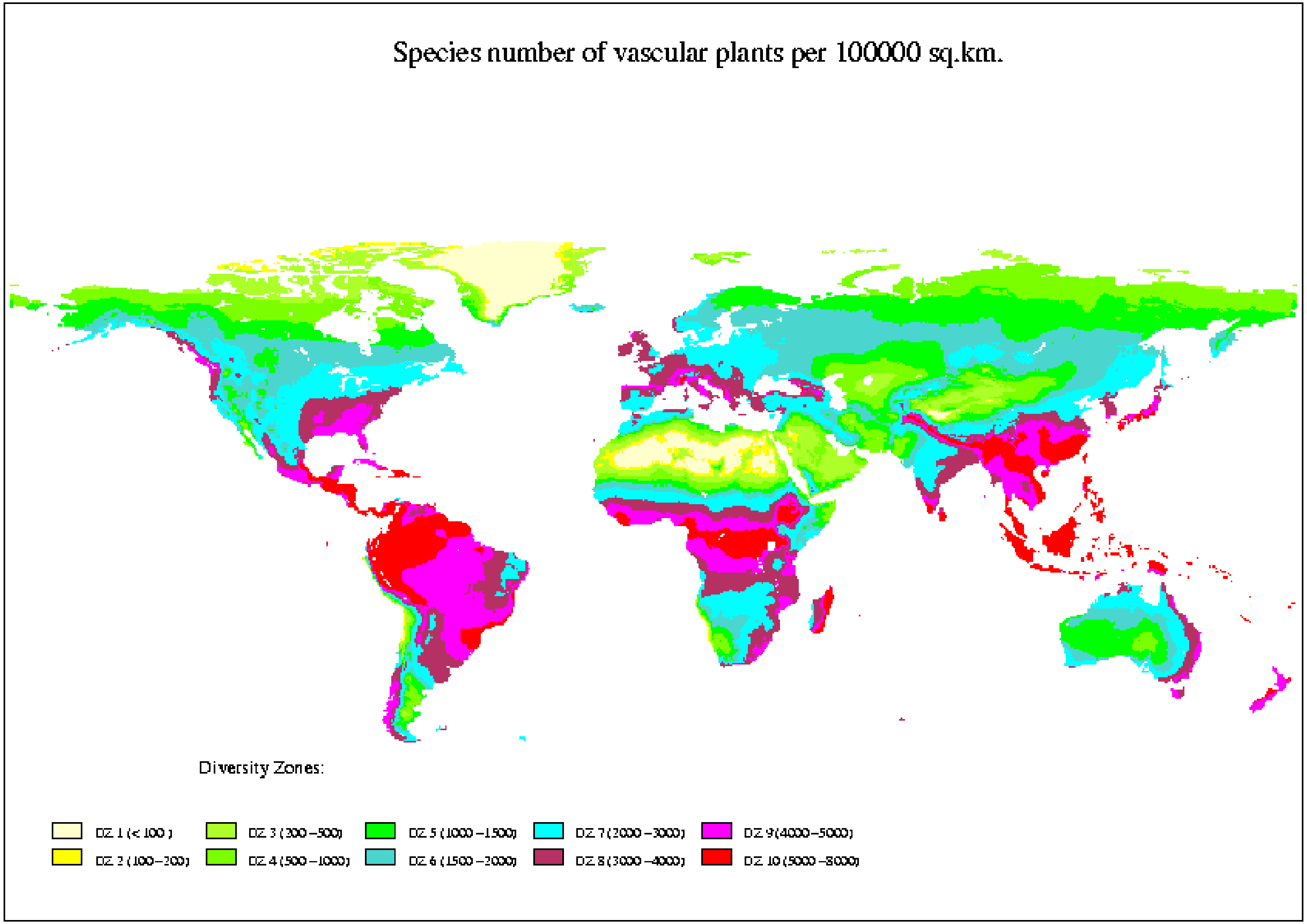

Figure 5. Species numbers of vascular plants per 100000 km², predicted by the species-energy relationship

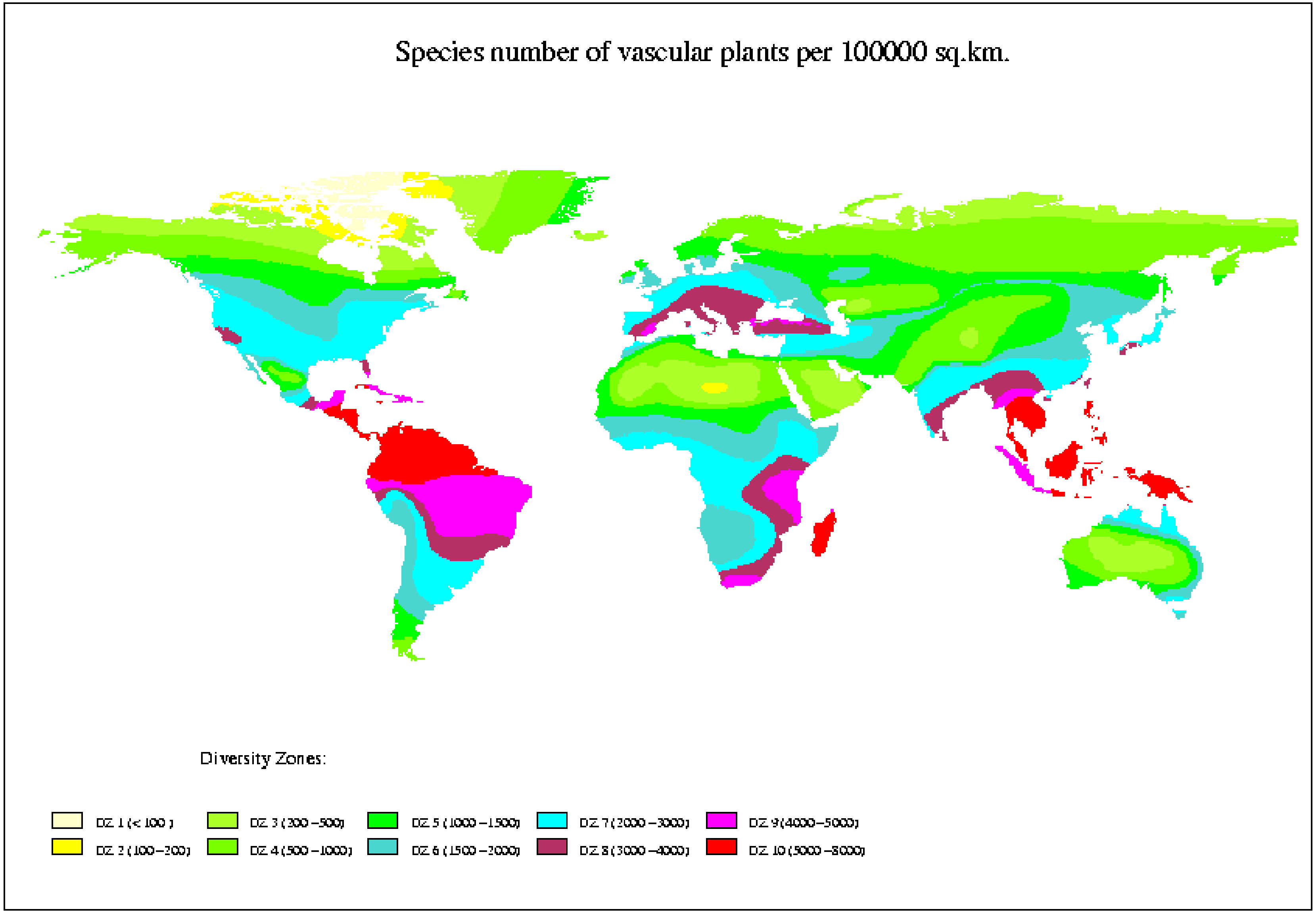

Figure 6. Observed species numbers of vascular plants per 100000 km² (Malyshev 1975)

Vegetation diversity of the Former Soviet Union for different scales

The influence of scaling on model performance was estimated using the observed values of SNVP in the Former Soviet Union (FSU) (see Malyshev (1994c)) for the four different sampling areas (100 km^2, 1000 km^2, 10000 km^2 and 100000 km^2). The correlation between observed and simulated values of SNVP is high in all four cases with the lowest for the largest sampling area, i.e. 100000 km^2 (see Table 1)

Sampling area (km^2)	Correlation coefficient SNVPobs/SNVPcalc
100	0.77
1000	0.77
10000	0.76
100000	0.6

Table 1. Correlation between observed and calculated values of species numbers of vascular plants in the FSU for four different sampling areas.

The absolute values for number of species are computed very well for the scales from 100 to 10000 km^2 and reasonably for the sampling area 100000 km^2 (see Figures 7 – 10)

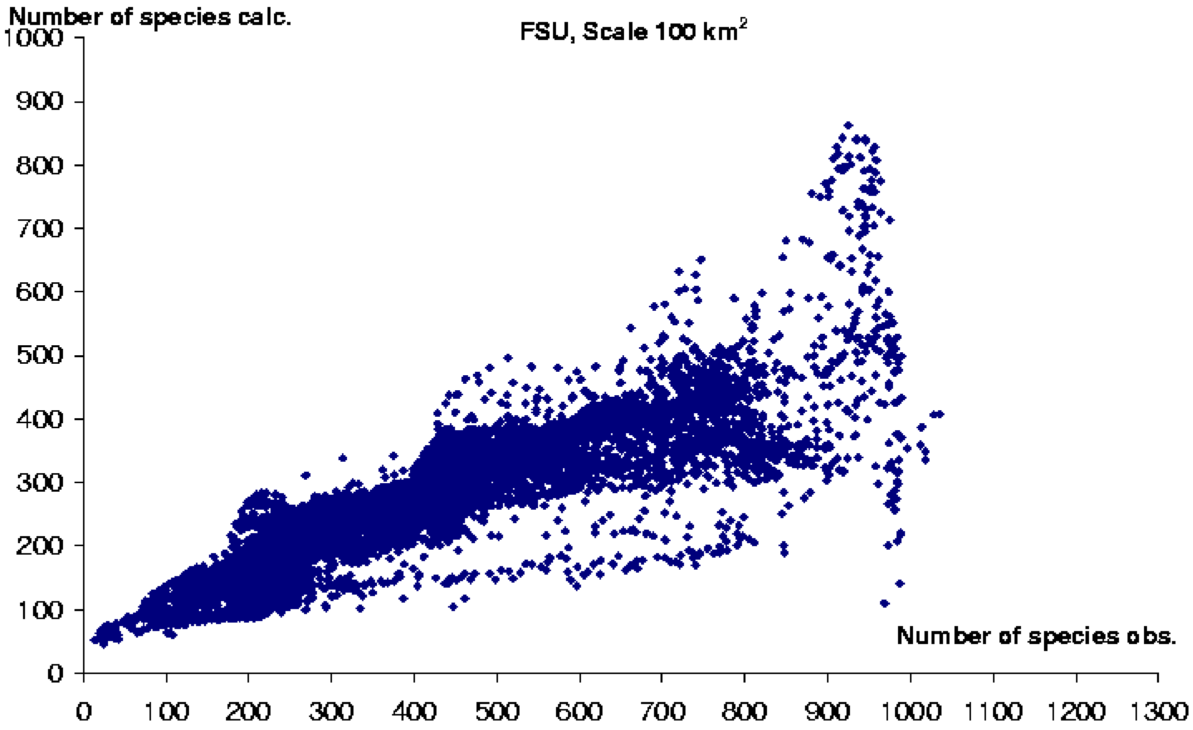

Figure 7. Observed against calculated number of species in the Former Soviet Union, sampling area 100 km^2

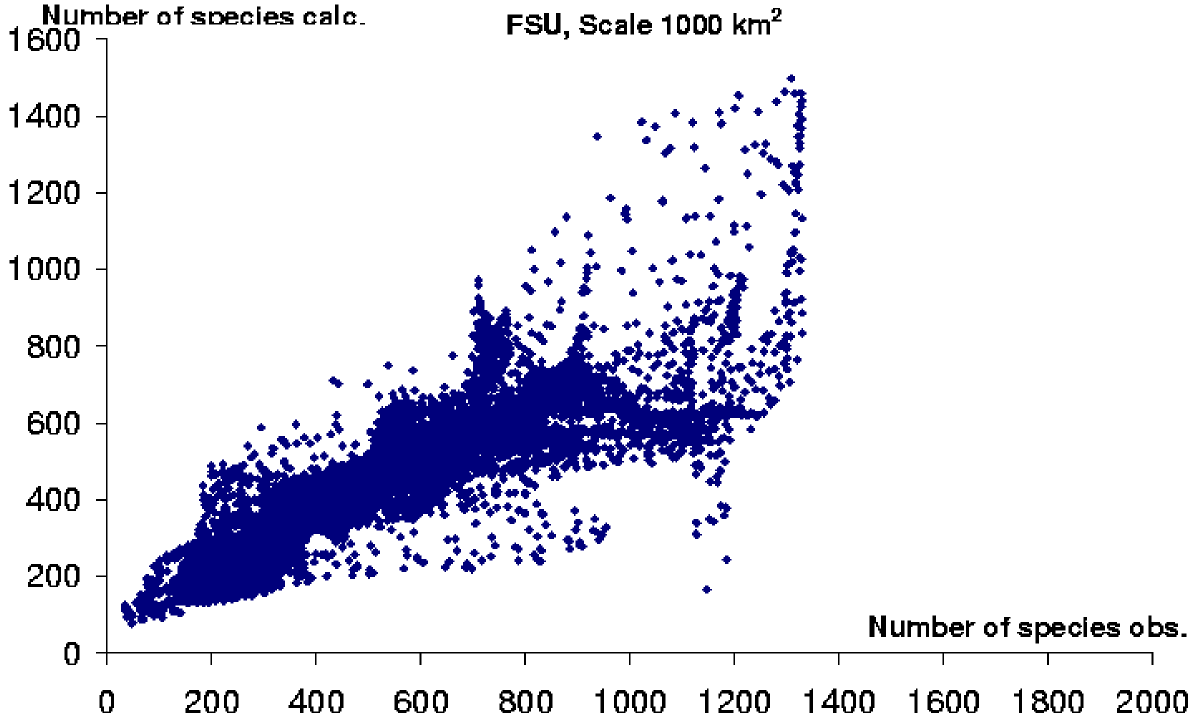

Figure 8. Observed against calculated number of species in the Former Soviet Union, sampling area 1000 km²

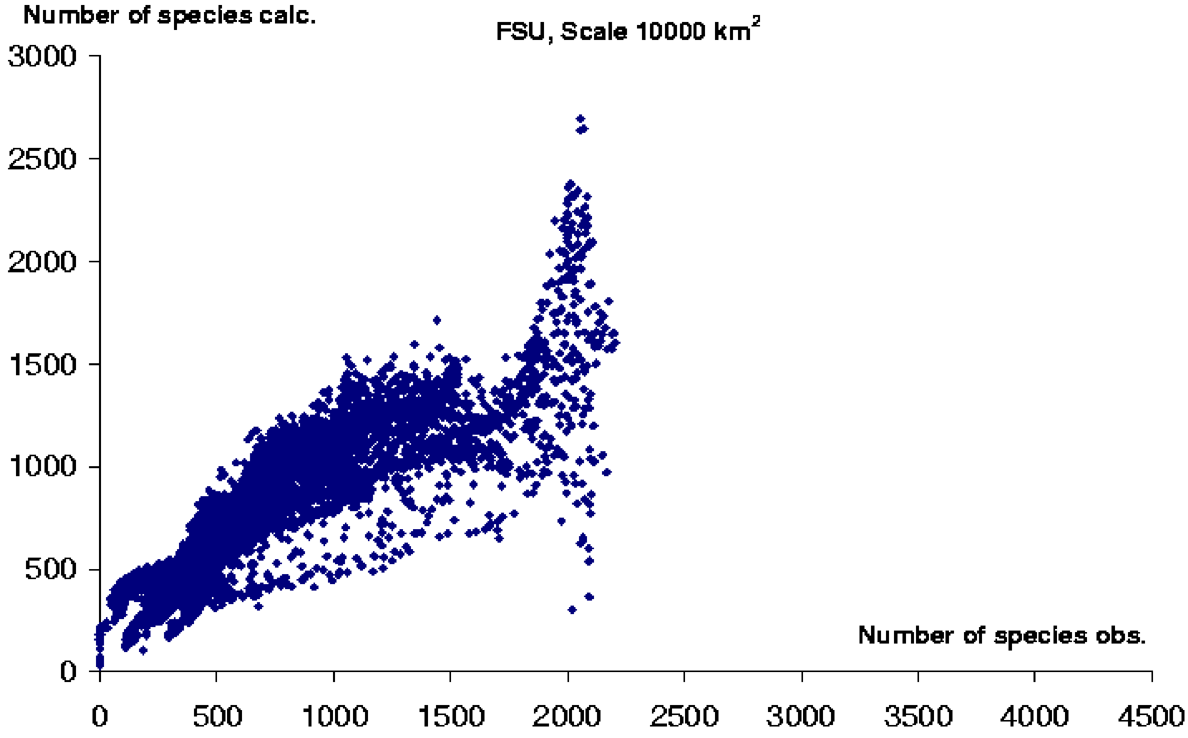

Figure 9. Observed against calculated number of species in the Former Soviet Union, sampling area 10000 km²

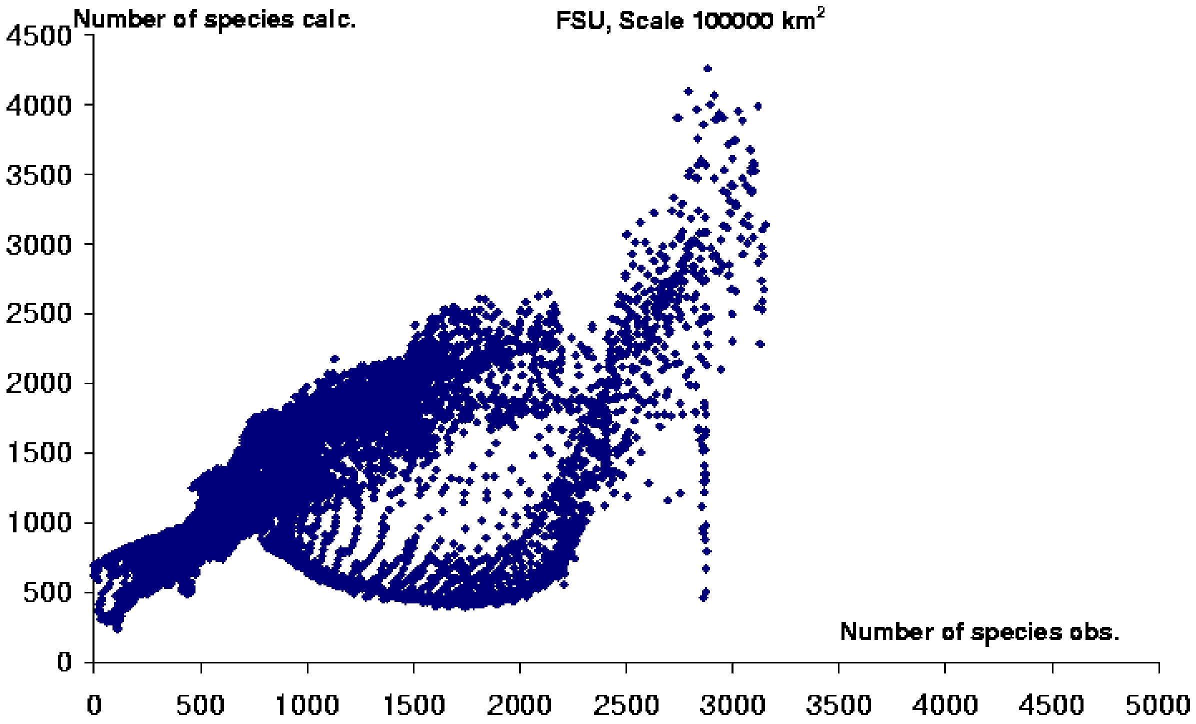

Figure 10. Observed against calculated number of species in the Former Soviet Union, sampling area 100000 km²

Regional vegetation diversity for different scales

The data for the FSU may have shortcomings for the analysis of the scaling problem, because of the similarity in data processing for the four different sampling resolutions. Hence, we analysed the coincidence of computed values of SNVP with the observed data for different area sizes in Europe, ranging from 100km² to 4000 km² (see Table 2).

No.	Locality	Long	Lat	Area(km^2)	SNVPobs	SNVPcalc	Reference
Forest-tundra subzone	1 Nord Fugloy I. Norway	20	69	248	290	306	(Engelskjön 1970)
	2 Rastigassa, Lapland	26.2	69.8	265	292	322	(Ryvarden 1969)
	3 West Utsjoki,Finland	27.3	69.5	1075	310	409	[Laine, 1955)
Northern taiga subzone	4 Lapland Reserve,Russia	32.3	67.8	2784	523	682	(Ablaeva 1981)
	5 Khibin Mts, Kola Pen.	33.7	67.7	1800	429	564	(Andreev et al. 1988)
Middle taiga subzone	6 Oulanka Nat. Park	29.2	66.4	107	429	291	(Soyrinki et al. 1980)
Southern taiga subzone	7 Korpilahti, Finland	25.6	62	804	530	554	(Rousi 1958)
	8 Karku, Finland	22.1	61.3	190	503	394	(Suominen 1961)
	9 Sakyla, Finland	22.2	61	156	454	385	(Saltin 1955)
	10 Nizhne-Svirsk Reserve	33.2	60.6	410	477	474	(Baranova et al. 1985)
Subtaiga subzone	11 Novgorod Prov.:Liubytino	33.4	58.8	700	538	598	(Schmidt 1979)]
	12 Latvia: mean of 4 areas	33.4	57.4	630	718	606	(Tabaka et al. 1987)
	13 Pskov Prov:mean of 10 areas	29	57.3	707	700	640	(Baranova 1973)
	14 Novgorod Prov.: Kholm	31.2	57.2	750	587	611	(Schmidt et al. 1973)
	15 Pskov Prov.: Pushkinsky	28.9	57	750	604	622	(Schmidt 1972)
	16 Latvia:mean of 6 areas	28.9	56.6	630	762	596	(Tabaka et al. 1987)
	17 Centralnolesnoy Reserve	32.9	56.5	213	546	458	(Minyaev et al. 1976)
	18 Pskov Prov.:Zhizhiza	31.4	56.3	750	607	623	(Schmidt 1972)
	19 Lithuanian Nat.Park	26.2	55.5	308	743	526	(Yankiavichene et al. 1988)
	20 Kurshskaya Kossa	21	55.1	160	630	502	(Kucheneva 1989)
	21 Beresinsky Reserve	28.4	54.7	760	768	663	(Parfenov et al. 1983)
	22 Naliboki, Belorussia	26.5	53.7	2400	820	909	(Bibikov et al. 1980)
Nemoral subzone	23 Belovezhs. Pucha	24	52.8	876	889	729	(Nikolaeva et al. 1971)
	24 Pripiatsky Reserve	28	52	603	740	665	(Parfenov 1980)
	25 Shatskye Osera	23.8	51.6	710	825	702	(Yashchenko 1983)
	26 Polessky Reserve	28	51.5	201	602	499	(Andrienko et al. 1986)
	27 Kolbuszowa, Poland	21.8	50.2	2000	1001	952	(Dubiel et al. 1979)
	28 Strzyzow, Poland	21.6	49.8	1125	916	885	(Towpasz 1987)
	29 Bieszezady Niskie	21.5	49.4	800	850	891	(Zemanek 1989)
	30 Opolye Ukraine	24.5	49.3	4170	1298	1170	(Shelyag-Sosonko et al. 1982)
Forest-steppe subzone	31 Cherkasskiy Bor, Ukraine	31.3	49.4	417	796	593	(Temchenko 1988)
	32 Olt Gorge, Romania	24.3	45.2	500	958	949	(Popescu et al. 1970)
	33 Bucharest-Danube Plain	26.3	44.2	1597	1180	915	(Borza 1968)
Genuine steppe subzone	34 Babadag Plateau,Romania	28.3	44.8	600	994	652	(Dihoru et al. 1970)

Table 2. Observed and calculated species numbers of vascular plants for Europe

Despite the variety of vegetation zones and area sizes the values of SNVP are computed very well (r^2=0.79, F=114, P<10 $^{-9}$). The slope of calculated against observed SNVP is 1.03 (see Figure 11), so one can say that for Europe the model works very successful for different scales.

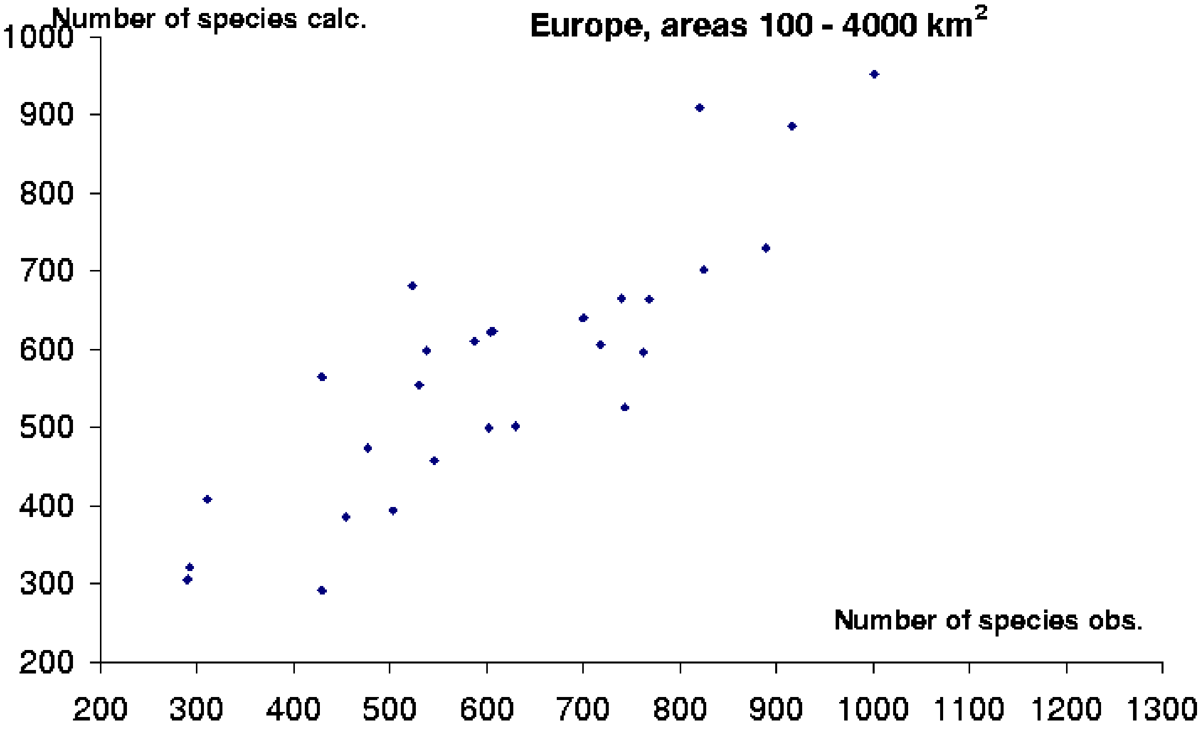

Figure 11. Observed against calculated SNVP for different scales in Europe.

Generalised by Malyshev (1975) the observed data for SNVP per 100 km² in other continents (see Table 3) were also reproduced very well by the theoretical model (parameters of observed SNVP against calculated SNVP regression are: r^2=0.79, F=90, P<1.4*10 $^{-9}$, slope =1.06).

No.	Locality	Long	Lat	SNVPobs	SNVPcalc
Asia/Oceania 1	Putoran plateu	95	68	262	210
2	Chukotka	-175	65	267	194
3	Igarka	86.24	67.29	304	195
4	Novosibirsk	83.03	56.03	463	305
5	Low Amur river	135	49	500	391
6	Mountains of S. Siberia	90	50	663	395
7	Maritime south	131.56	43.07	473	442
8	S.steppe Kazachstan	72	41	413	497
9	Repetek	63.13	38.34	151	147
10	Borzhomi	43.23	41.51	1263	917
11	Japan Islands	140	39	544	454
12	Mount Jamizo	138	35	920	990
13	Savanna N. India	85	25	720	567
14	Deccan penninsula	75	17	635	600
15	Aden	44.5	13	232	202
Australia/New Zealand 16	New Zeland	168	-47	452	690
17	South East Australia	150	-36	512	670
Africa 18	Sahara	0	18	156	132
19	Bassin of the river Kongo	15	-16	596	457
20	S. Africa	28	-30	1217	824
21	Rodezhia	28	-20	664	480
North America 22	Devon island	-90	75	102	70
23	East Greenland	-45	61	152	221
24	USA mainland	-100	40	500	466
25	South-Eastern States	-80	35	750	742
26	Alaska(Ogot.-Creek)	-150	66	297	231

Table 3. Observed and calculated species numbers of vascular plants for the sampling area 100 km^2

The ability of the model to correctly represent species numbers of vascular plants over large spatial scales can be proven by using of surveys over countries or geographical provinces. We collected data on species numbers for 16 regions (see Table 4), ranging from 0.8 to 16 million km^2 and analysed the applicability of the model, based on species-energy theory, for these areas. The regions differ significantly in numbers of vascular plant species, from 390 species in Greenland to 18000 in Sub-Saharian Africa. Therefore, we compared the theoretical and (derived from the observed data) averages for the numbers of species in 1 m^2 in the regions. The 0.5°x0.5° degree resolution map of theoretical numbers of vascular plant species per 1 m^2 was calculated from climate data using equation 16 and the values for the 16 regions were obtained by spatial averaging (see Table 4). The observed values for numbers of vascular plant species per 1 m^2 were derived from formula 15 with D=1.52 and R= 3.0 * 10^{-4} 1/m, i.e. with optimised values of the model coefficients (see Table 4).

Region	Area (Mio km^2)	SNVP	obs SNVP/m^2	theor SNVP/m^2
Central America and Mexico	2.36	12000	8.16	6.23
Venezuela	0.94	12000	11.86	10.24
Africa South of Sahara	16.84	18000	9.74	6.9
Australia, Queensland	1.74	4700	4.74	4.59
Australia, extra tropical	1.3	1935	2.14	3.69
Australia and Tasmania	7.77	4200	3.01	4.06
USA, south eastern states	1.63	6321	6.62	7.9
China and Korea	3.89	8200	5.05	4.07
New South Wales	0.8	3105	3.66	5.09
Mediterranean	1.42	7000	5.73	4.6
Central and North Eastern US	2.59	3300	3.09	4.11
Europe	9.25	11500	6.79	5.14
Canada	9.58	3209	1.94	2.1
Skandinavia and Denmark	0.82	1677	1.81	3.5
Alaska	1.52	684	0.57	2.1
Greenland	0.83	390	0.42	0.36

Table 4. Species numbers of vascular plants over large geographical regions and the spatially averaged observed versus theoretical SNVP per 1 m^2.

Despite both significant values and variance in the regional areas, the model correctly estimates averaged SNVP per 1 km^2 (see Figure 12).

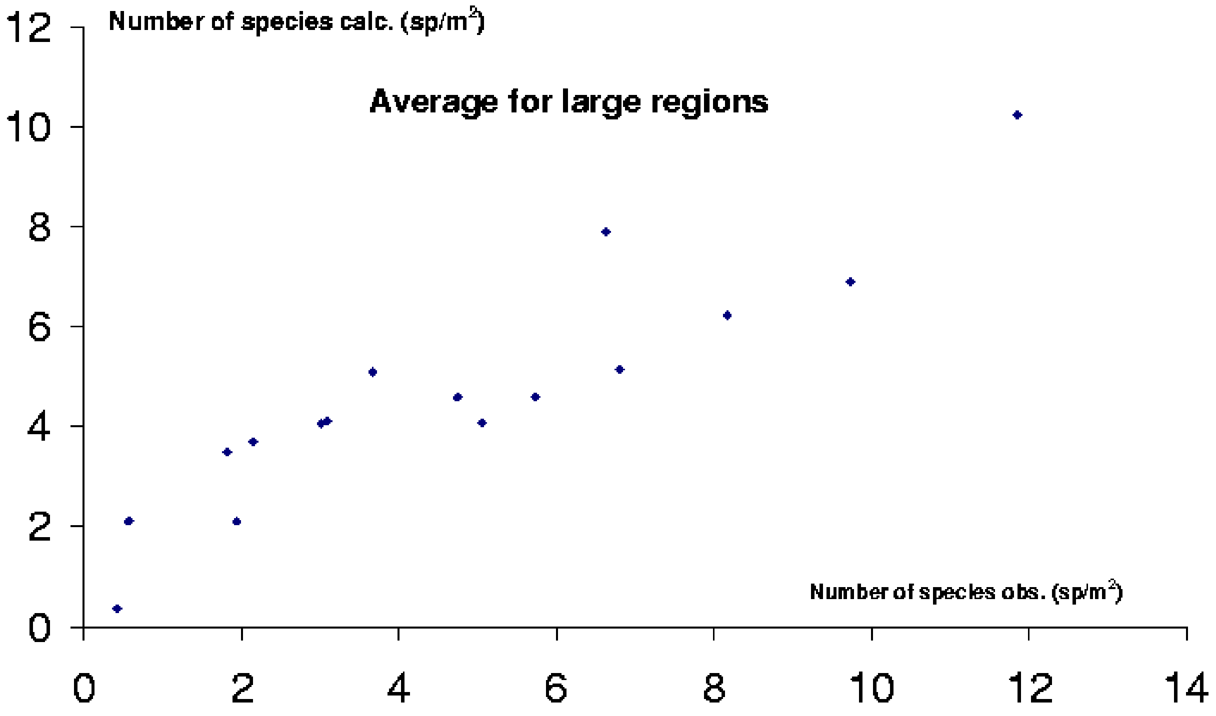

Figure 12. Observed against theoretical SNVP per 1 m^2 for large regions with variable areas.

The high correlation between observed and theoretical SNVP per 1 m^2 (r^2=0.83, F=70, P<7.6*10^{-7}) for the 16 regions proves that the model can be applied for the scales up to several million kilometres. One can see, however, an over prediction in the regions with sparse vegetation (like Alaska) and an underestimate in regions with dense vegetation (like Venezuela). The structural differences in landscapes for the contrasting biomes, described by fractal dimension D, are more clearly seen for large scales (see formula 15), making estimates of the SNVP more approximate.

Conclusions and discussion

The application of fractal geometry principles for energy optimisation of vertical structure in vascular plants allows to accept the hypothesis of energy equivalence across vascular plant species. The principle of energy equivalence between the species and use of fractal theory for the description of habitat occupation by vegetation in the horizontal direction makes it possible to suggest a physically-based model of vegetation diversity. The model describes the species-energy relationship in direct form and not via non-linear regressions. It takes into account seasonality and inter-annual variability. Despite its simple form in comparison with recent models of biodiversity (Kleidon et al. 2000) the model reproduces very successfully global patterns of vegetation diversity for scales 10000 and 100000 km².

It works well across scales from 100 to 10000000 km², i.e. has a range of applicability equal to six orders. The simple form makes possible immediate application of the model in practical fieldwork.

One can see, that the model (see 2) can easily be further developed for dynamic applications, using different simple hypothesis about development of landscape diversity and changes in probabilities of species appearance.

Investigation of spatial variation of ν can identify a role of historical factors in the development of vegetation, via changes in efficiency of energy use by species.

The model allows analysing latitude dependence of vegetation diversity and taxonomic covariance of vascular plants with other kingdoms (like animals, fungi etc.)

Acknowledgments

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Appendix

Elaboration of the 0.5°x0.5° longitude/latitude map of SNVP per 10000 sq.km

The basic data for the map of SNVP per 10000 km² were patterns of diversity zones, or classes, from 1 to 8.

1 class (0-100 SNVP by 10^4 km^2)
2 class (100-200 SNVP by 10^4 km^2)
3 class (200-500 SNVP by 10^4 km^2)
4 class (500-1000 SNVP by 10^4 km^2)
5 class (1000-1500 SNVP by 10^4 km^2)
7 class (2000-4000 SNVP by 10^4 km^2)
8 class (more than 4000 SNVP by 10^4 km^2)

These data were published by Barthlott, 1999 in a graphic format (http://www.botanik.uni-bonn.de/system/biomaps.htm). The map was converted to ASCII numerical format for ARC-INFO conversion.

The following hypothesis were taken for a design of the SNVP map:

Continuity of SNVP distribution along climatic/altitude gradients

Monotonous increase or decrease of SNVP from a point to the nearest isoline (hypothesis of trend existence).

The ASCII map of SNVP classes was converted into the GRID (ARC-INFO) format and then subdivided into 17 windows in the GRID format in order to avoid the influence of the ocean during interpolation:

Region	Xmin	Ymin	Xmax	Ymax
South Africa	8	-35	60	4
South America	-82	-56	-35	13
Caribbean	-120	12	-64	33
Australia and New Zealand	112	-47	179	-10
Indonesia	95	-11	170	8
Central Asia	72	40	165	60
China	72	7	165	41
North Africa	-20	3	73	26
Europe	-20	25	73	60
Canada and USA	-140	32	-52	60
Aleutian	-170	53	-148	60
Panama	-88	7	-81	13
North Canada	-180	59	-13	85
Scandinavia	4	59	52	71
Northern islands	5	77	115	82
West Russia	51	59	115	78
East Russia	114	59	180	75

The 17 grids were converted into point vector format and trend interpolation by polynomials of order 7 to 10 order for classes was conducted for the each grid. The ocean grid cells were assigned NODATA by masking.
It was assumed, that within a certain class the SNVP linearly rise from the lower border of the class to the upper border of the class (see Figure 12).

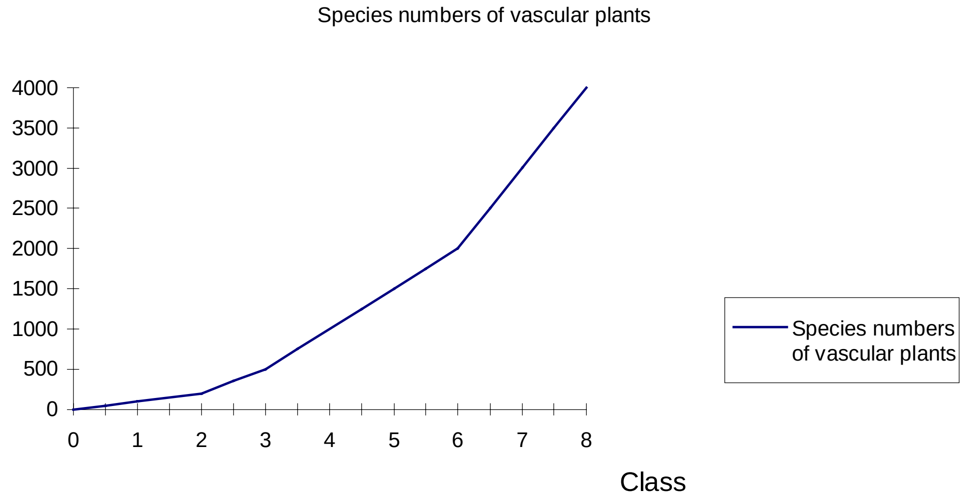

Figure 13. Approximation of SNVP from the diversity classes

The SNVP for the 17 windows was calculated using this assumption and then the final global map of SNVP by 10^4 km^2 in the GRID format was elaborated by combining the 17 windows.

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