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THE SPECIES-AREA-ENERGY RELATIONSHIP IN ORCHIDS

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ABSTRACT. Area, energy available and latitude are the main factors influencing species richness: (1) species richness increases with area – the species-area relationship (SAR); (2) according to the species-energy relationship (SER) the energy available to an assemblage (i.e. that which it can turn into biomass) at a particular spatial resolution influences the species richness; (3) there are more species per unit area in the tropics than in the temperate regions. To test the relative importance of area, energy available and latitude on species richness, we have collected data on species richness of orchids for various areas in the world and calculated the mean Normalized Difference Vegetation Index (NDVI) as a measure of energy availability in these areas. We show that area considered is always very important, and that latitude is more important than energy available.

KEY WORDS: orchids, species-energy relationship, NDVI

Introduction

Species–energy theory predicts a positive relationship between species richness and available energy (Brown 1981, Wright 1983, Wright *et al*. 1993). Species richness of a variety of taxa has been shown to increase with various amounts of available energy including net primary productivity (Hutchinson 1959, Brown 1981, Wright 1983, Guegan *et al*. 1998, Kaspari *et al.* 2000), potential and actual evapotranspiration (Rosenzweig 1968, Lieth 1975, Wright 1983, Currie & Paquin 1987, Currie 1991, Francis & Currie 2003) and precipitation (Brown & Davidson 1977). According to the *area hypothesis* (Connor & McCoy 1979, Wright 1983) larger areas contain more resources, which may support larger populations of each species, resulting in lower extinction rates and ultimately in more species. Similarly, the *more individuals hypothesis* (Wright 1983, Srivastava & Lawton 1998, Gaston 2000, Kaspari *et al.* 2003) assumes that there is a direct relationship between energy availability, the overall amount of resources in an area, the total number of individuals that can be maintained, and consequently the number of species. The *energy limitation theory* maintains that primary productivity is higher, because the tropics usually receive higher solar radiation and precipitation. This provides a wider resource base and enables more species to co-occur by increasing population sizes (Connell & Orias 1964, Wright 1983).

To test the relative importance of area, energy available and latitude on species richness, we have collected data on species richness of orchids for various areas in the world and calculated the mean Normalized Difference Vegetation Index (NDVI) as a measure of energy availability in these areas. We show that area considered is always very important, and that latitude is more important than energy available.

Methods

The numbers of orchid species recorded from 116 locations (countries or parts thereof) were obtained from a literature search. The areas of these locations were obtained from The Columbia Gazetteer of the World (Cohen 1998). Mean latitude of each location was calculated as the centroid of the area considered. We considered four regions: Africa, Eurasia, America and whole world.

The Normalized Difference Vegetation Index (NDVI) was used as a measure of energy available to

TABLE 1. Relationship between species richness of orchids from the regions and area and mean NDVI.

Region	Ln area	Ln mean NDVI	R^2	p-level
Africa	$F_{1,10}$ 2.9	$F_{1,10}$ 20.7**	0.676	0.0036
Eurasia	$F_{1,58}$ 0.2	$F_{1,58}$ 9.6**	0.155	0.0077
Whole America	$F_{1,39}$ 3.1	$F_{1,39}$ 0.6	0.108	0.1085
Whole world	$F_{1,113}$ 5.4*	$F_{1,113}$ 0.3	0.053	0.0461

*P < 0.5; **P < 0.01; ***P < 0.001; ****P < 0.0001

TABLE 2. Relationship between species richness of orchids from the regions and area.

Region	Ln area	Ln max NDVI	R^2	p-level
Africa	$F_{1,10}$ 2.6	$F_{1,10}$ 23.6***	0.704	0.0023
Eurasia	$F_{1,58}$ 0.2	$F_{1,58}$ 9.7**	0.155	0.0076
Whole America	$F_{1,39}$ 3.9	$F_{1,39}$ 0.0	0.094	0.1450
Whole world	$F_{1,113}$ 5.7*	$F_{1,113}$ 0.1	0.052	0.0491

*P < 0.5; **P < 0.01; ***P < 0.001; ****P < 0.0001

TABLE 3. Relationship between species richness of orchids from the regions and area and latitude.

Region	Ln area	Latitude	R^2	p-level
Africa	$F_{1,10}$ 0.9	$F_{1,10}$ 9.5*	0.490	0.0344
Eurasia	$F_{1,58}$ 3.8	$F_{1,58}$ 99.5****	0.637	0.0000
Whole America	$F_{1,39}$ 0.9	$F_{1,39}$ 8.5**	0.256	0.0031
Whole world	$F_{1,113}$ 0.5	$F_{1,113}$ 47.2****	0.331	0.0000

*P < 0.5; **P < 0.01; ***P < 0.001; ****P < 0.0001

an assemblage. NDVI is strongly positively correlated with green-leaf biomass, green-leaf area, and absorbed photosynthetically active radiation. This index has been viewed as providing reasonable representations of net primary productivity and vegetative growth of terrestrial ecosystems at the continental and global scale (Ustin *et al.* 1991, Kerr & Ostrovsky 2003), and thus as a suitable measure of the energy available to consumers. NDVI is derived from the visible and near infrared channel reflectances (0.58 to 0.68 ∝m and 0.73 to 1.10 ∝m, respectively). It is a dimensionless number with typical range from –0.200 to 0.730. This data set is produced as part of the NOAA/NASA Pathfinder AVHRR Land program (see http://disc.gsfc.nasa.gov/interdisc/readmes/pal_NDVI.shtml) and month data sets are available from the years 1981-1994. We used mean and maximum NDVI values from the vegetation season in 1994 (mean January – April NDVI for the southern hemisphere and May – August NDVI for the northern hemisphere) for the analyses.

The number of species, area and mean or maximum NDVI for each location were log transformed. We used the Statistica software (vs. 5.5, StatSoft, Inc., Tulsa, USA) for plotting 3D Surface Linear Plots with X-axis: ln(area); Y-axis: ln(mean NDVI), ln(max NDVI) or latitude; Z-axis: ln(number of species).

To determine the influence of area, NDVI or latitude on species richness we used Multiple Regression in General Linear Models (Statistica vs. 5.5, StatSoft, Inc., Tulsa, USA) with the number of species (ln(species richness)) as dependent variable and ln(area) and ln(mean NDVI), ln(max NDVI) or latitude as predictors.

For each region, linear regression was then fitted to the dependence of the logged number of species in location i, ln(species richness$_i$), and

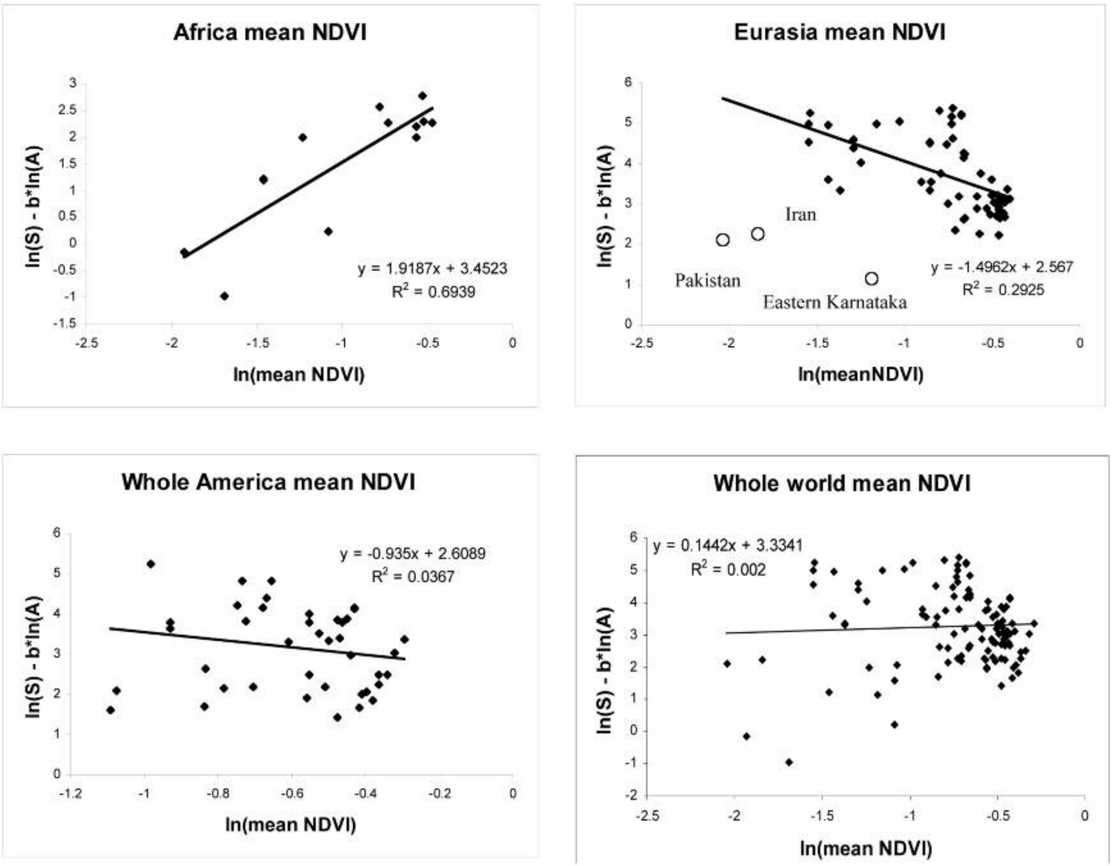

FIGURE 1. Relationship between logarithmically transformed mean NDVI and species richness per unit area.

logged area in location i, ln(area$_i$): ln(species richness$_i$) =a+b*ln(area$_i$). The b-values so obtained were then used to eliminate the influence of area on the number of orchid species at each location: we used the estimated number of species per unit area, ln(species richness$_i$)-b*ln(area$_i$), in each location instead of ln(species richness$_i$) for further analyses.

Results

Multiple regression in GLM with ln(species richness) as dependent factor and ln(area) and ln(mean NDVI) or ln(max NDVI) as predictors has shown a significant influence of ln(mean NDVI) and ln(max NDVI) only in Africa and in Eurasia (Tables 1, 2). Ln(area) significantly affected species richness only in the data set from the whole world (Tables 1, 2).

When the logged number of species per unit area was considered, a positive influence of ln(mean NDVI) or ln(max NDVI) was recorded only in Africa (Figures 1 and 2). A negative influence of ln(mean NDVI) and ln(max NDVI) on the species richness was recorded in Eurasia, where species richness decreases with NDVI (Figures 1, 2). Data sets from America and whole world did not show any significant trend (Figures 1, 2).

A significant influence of latitude was recorded in all regions (Table 3). From Figure 3 it is obvious that species richness decreases with latitude. Somalia and Sudan from Africa, Eastern Karnataka from Eurasia and Somalia, Sudan, Eastern Karnataka, Ethiopia and Morocco from the whole world data set were excluded as outliers in these figures. The reason for the exclusion will be discussed in the Discussion. No difference was found between temperate South and North America. Absolute value of latitude was used

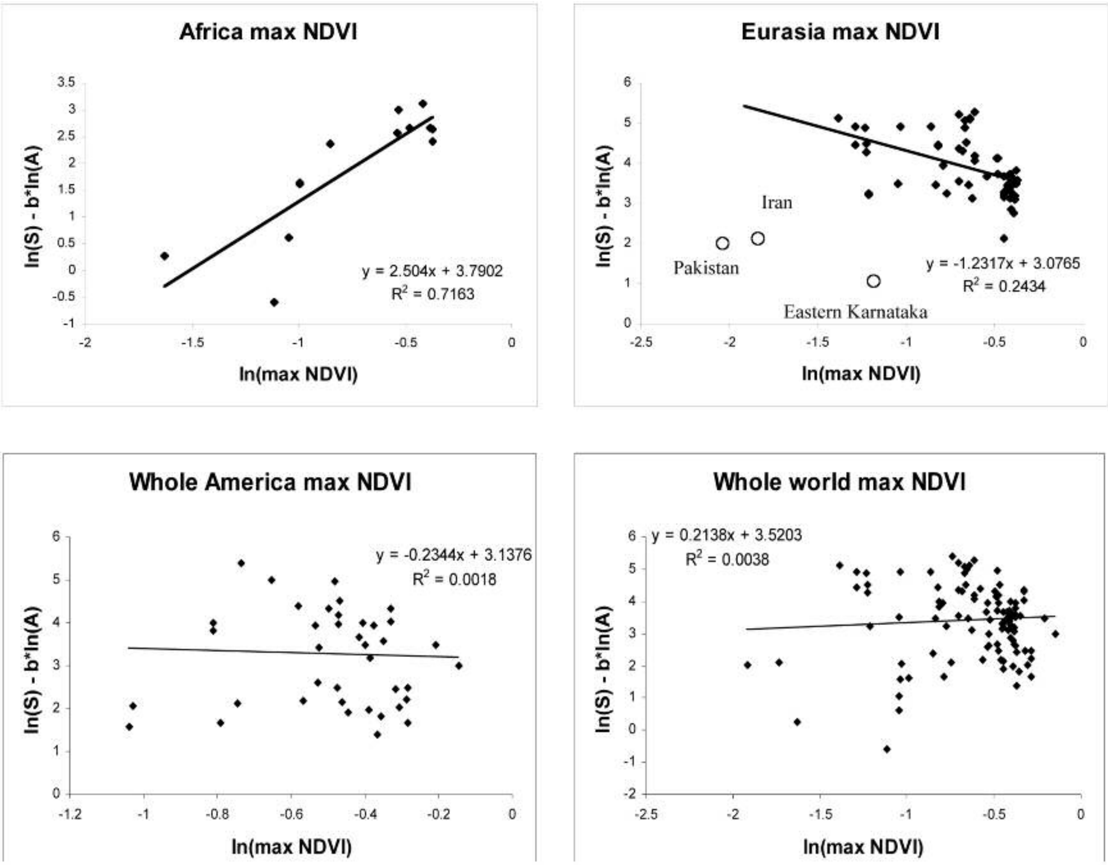

FIGURE 2. Relationship between logarithmically transformed maximum NDVI and species richness per unit area.

in the data set for the whole world to demonstrate the decrease of species richness from the tropics to the poles.

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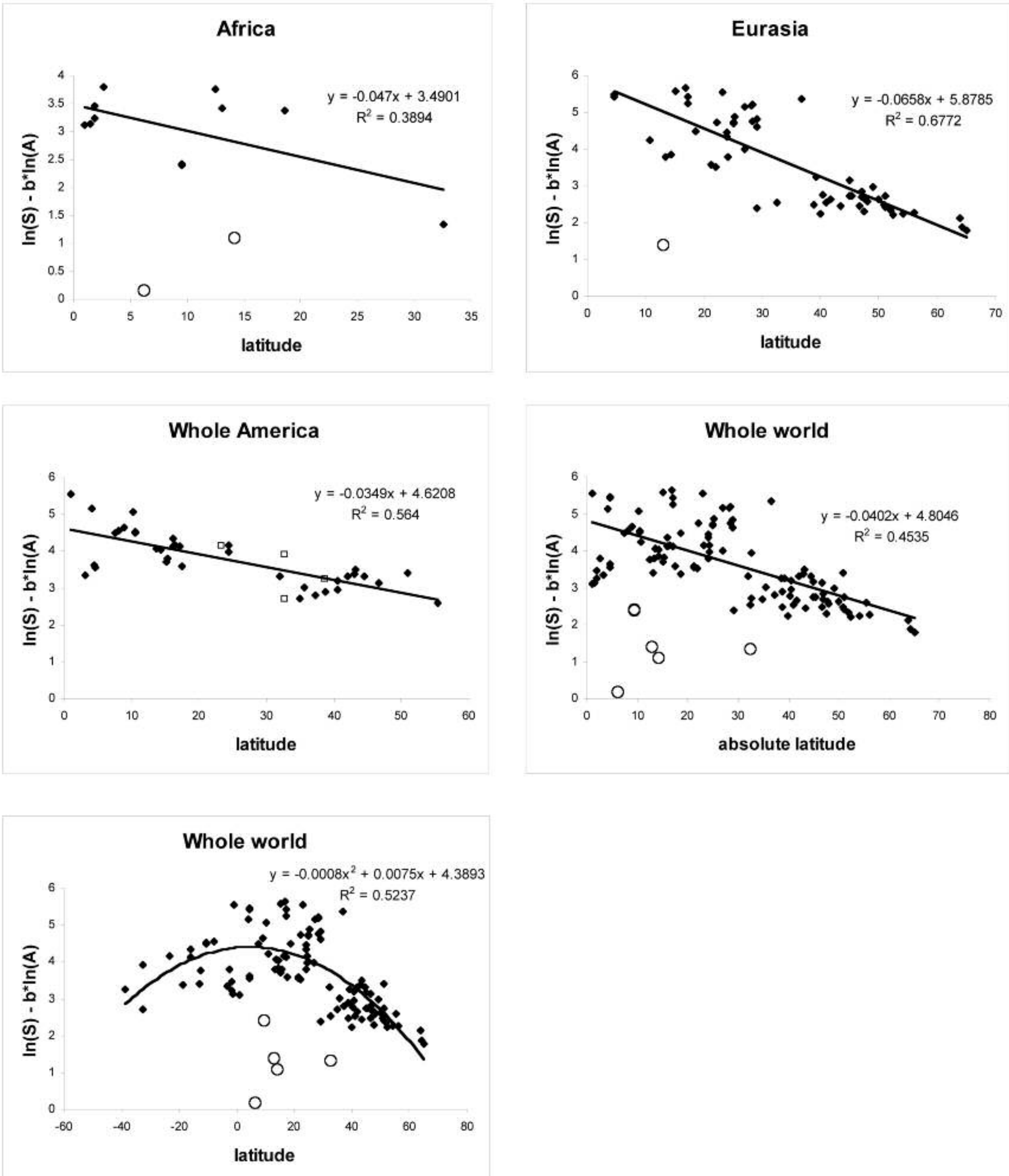

FIGURE 3. Relationship between latitude and logarithmically transformed species richness per unit area.

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