

Supporting Online Material for

Plant Species Richness and Ecosystem Multifunctionality in Global Drylands

Fernando T. Maestre,* José L. Quero, Nicholas J. Gotelli, Adrián Escudero, Victoria Ochoa, Manuel Delgado-Baquerizo, Miguel García-Gómez, Matthew A. Bowker, Santiago Soliveres, Cristina Escolar, Pablo García-Palacios, Miguel Berdugo, Enrique Valencia, Beatriz Gozalo, Antonio Gallardo, Lorgio Aguilera, Tulio Arredondo, Julio Blones, Bertrand Boeken, Donaldo Bran, Abel A. Conceição, Omar Cabrera, Mohamed Chaieb, Mchich Derak, David J. Eldridge, Carlos I. Espinosa, Adriana Florentino, Juan Gaitán, M. Gabriel Gatica, Wahida Ghiloufi, Susana Gómez-González, Julio R. Gutiérrez, Rosa M. Hernández, Xuewen Huang, Elisabeth Huber-Sannwald, Mohammad Jankju, Maria Miriti, Jorge Monerris, Rebecca L. Mau, Ernesto Morici, Kamal Naseri, Abelardo Ospina, Vicente Polo, Aníbal Prina, Eduardo Pucheta, David A. Ramírez-Collantes, Roberto Romão, Matthew Tighe, Cristian Torres-Díaz, James Val, José P. Veiga, Deli Wang, Eli Zaady

*To whom correspondence should be addressed. E-mail: fernando.maestre@urjc.es

Published 13 January 2012, *Science* **335**, 214 (2012)
DOI: 10.1126/science.1215442

This PDF file includes:

Materials and Methods
Figs. S1 to S10
Tables S1 to S15
References (35–137)
Caption for Database S1
Caption for Map S1

Other Supporting Online Material for this manuscript includes the following:
(available at www.sciencemag.org/cgi/content/full/335/6065/214/DC1)

Database S1
Map S1

Materials and Methods

Characteristics of the study sites

We restricted our study to arid, semi-arid and dry-subhumid ecosystems (“drylands” hereafter), defined as sites with an aridity index (precipitation/potential evapotranspiration) between 0.05 and 0.65 (35). Original field data were gathered at 224 sites located in 16 countries from all continents except Antarctica (Argentina, Australia, Brazil, Chile, China, Ecuador, Iran, Israel, Kenya, Mexico, Morocco, Peru, Spain, Tunisia, United States of America and Venezuela, map S1). Site selection aimed to capture as much as possible the wide variety of abiotic (climatic, soil type, slope) and biotic (type of vegetation, total cover, species richness) features characterizing dryland ecosystems while keeping the total number of sites at a manageable size (map S1). To obtain data as representative as possible of “real world” ecosystems, we did not limit our survey to pristine or unmanaged ecosystems. The sites surveyed encompass a wide range of human uses, ranging from those with very low human impacts over recent time scales (e.g. National Parks and other protected areas) to those where human activities such as grazing, grass fiber/wood collection and game hunting are currently, or have been recently, carried out. However, we excluded areas devoted to horticulture, occupied by riparian/coastal ecosystems, recently engineered (e.g. planted or recently restored areas) or used for other human activities that have completely removed their vegetation and altered their geomorphologic characteristics (e.g. infrastructure/mining).

To ensure that all the sites surveyed had an index of aridity below 0.65, we used cartography available at the global scale from the United Nations Food and Agriculture Organization (FAO, <http://www.fao.org/geonetwork/srv/en/main.home>). This information was complemented with more precise aridity maps (e.g. http://www.cazalac.org/mapa_zg_gm_2011.html for Central and South America) and with available local climatic data. Standardized climatic data from all the sites were obtained from Worldclim (www.worldclim.org), a high resolution (30 arc seconds or ~ 1km at equator) database based on a high number of climate observations and topographical data (see 36 for details). Mean annual precipitation and annual mean temperature of the study sites span the entire range found in dryland areas (excluding hyper arid areas, which usually have little or no perennial vegetation, 37), and varied from 66 mm to 1219 mm, and from -1.8°C to 27.8°C, respectively (map S1). All the sites included in this study experience high seasonal variability in rainfall and seasonal drought, which varies in intensity and duration depending on location. The range of soil types present at the studied sites is also large, including more than 25 categories from the FAO classification (38) and encompassing all main soil types present in drylands (map S1). Slope values ranged between 0.2° and 28° (Database S1). To minimize the potential effects of different microclimates promoted by slope aspect, which can be very important in drylands (39-44), all sites that had slope values > 2° were located on SE-SW and NE-NW facing slopes in the Northern and the Southern hemispheres, respectively. Elevation varies between 69 m and 4668 m a.s.l. (Database S1). The sites surveyed encompass a wide variety of the representative vegetation physiognomies found in drylands

(grasslands, shrublands, savannas and open woodlands with shrubs, fig. S1). Perennial plant cover also varied widely, and ranged between 3% and 83%.

Field sampling

Data collection took place between February 2006 and December 2010, and all researchers in our global study used a standardized sampling protocol. At each site, we established a 30 m × 30 m plot representative of the vegetation present in that area. In the upper left corner of each plot, we located one 30 m transect oriented downslope for the vegetation survey. Three parallel transects of the same length, spaced 8 m apart across the slope, were added. The cover of perennial vegetation was measured in each transect using the line-intercept method (45). Site estimates were obtained by averaging the values registered in the four transects sampled. We also placed 20 contiguous quadrats (1.5 m × 1.5 m) in each transect and visually estimated the cover of each perennial vascular plant present. We restricted our study to perennial plants because they are instrumental in maintaining ecosystem functioning and preventing desertification in drylands (37, 46). Moreover, annual plant composition in drylands shows a high degree of intra- and inter-annual variability (e.g. 37, 47). Thus, we did not include these annual species in our observational design to avoid confounding effects in the differences on multifunctionality among study sites derived from sampling “incomplete” communities depending on the time of the year and/or year sampled. The total number of perennial species found in the 80 quadrats was used as an effort-standardized estimator of species richness. Strictly speaking, our data give us a measure of “species density” rather than richness (see 48 for a detailed discussion), but we refer to “species richness” throughout the text because this is the term commonly used in the biodiversity-ecosystem functioning literature (e.g. 49). Our surrogate of richness was highly correlated with the total number of species found in the 30 m × 30 m plot, as indicated from detailed surveys carried out at a subset of the sites sampled (fig. S2). From our survey we also obtained other diversity metrics, such as the exponential of the Shannon index and the inverse of the Simpson index (50).

Soils were sampled during the dry season in most of the sites using a stratified random procedure. At each plot, five 50 cm × 50 cm quadrats were randomly placed under the canopy of the dominant perennial vegetation element and in open areas devoid of perennial vegetation. A composite sample consisting of five 145 cm³ soil cores (0-7.5 cm depth) was collected from each quadrat, bulked and homogenized in the field. When more than one dominant plant species was found, samples were also collected under the canopies of five randomly selected individuals of the co-dominant species. Thus, the number of soil samples varied between 10 and 15 per site (over 2600 samples were collected). After field collection, the soil samples were taken to the laboratory, where they were sieved (2 mm mesh), air-dried for one month and stored for laboratory analyses.

Assessment of ecosystem functions: rationale, variables measured and laboratory methods

We obtained data on 14 soil variables related to carbon (C), nitrogen (N) and phosphorus (P) cycling: nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N) availability, organic

C, total N, available inorganic P, aminoacids, proteins, pentoses, hexoses, aromatic compounds, phenols, potential N transformation rate and the activity of two extracellular enzymes, β -glucosidase and phosphatase. These variables measure either “true” ecosystem functions (*sensu* 51, e.g. potential N transformation rate) or are key properties/processes (*sensu* 52, e.g., organic C, total N and soil enzymes), which together constitute a good proxy of nutrient cycling, biological productivity, and buildup of nutrient pools. Variables such as these have been used in previous studies of ecosystem functioning and multifunctionality (e.g. 53-57), and are considered to be critical determinants of ecosystem functioning in drylands (see 37 for a review). For simplicity, all of these variables are hereafter called ecosystem functions (54). Most of these functions are also considered to be supporting ecosystem services, as other types of ecosystem services depend on them (58-60).

All soil samples were analyzed for each of the 14 ecosystem function indicators listed above. These analyses were carried out with dry samples for logistical reasons, as the large number of soil samples gathered made the analysis of fresh soil samples impossible. Previous studies have found that in drylands such as those we studied, air drying and further storage of soils does not appreciably alter the functions of interest in this study (61-62). Indeed, this storage approach is commonly used when analyzing physical and chemical soil properties in dryland environments worldwide (e.g., 57, 63-65). It is also important to note that our sampled soils would have remained dry for a large portion of the year (e.g. 66-69), and that most samples were collected when the soil was in this dry state. Thus, the potential bias induced by our drying treatment is expected to be minimal.

To avoid problems associated with the use of multiple laboratories when analyzing the soils from different sites, and to facilitate the comparison of results between them, dried soil samples from all the countries were shipped to Spain for analyses. All the analyses for organic C, available P and enzymatic activities were carried out at the laboratory of the Biology and Geology Department, Rey Juan Carlos University (Móstoles, Spain). Analyses of total N were carried out at the University of Jaén (Jaén, Spain). The remaining soil analyses were carried out at the laboratory of the Department of Physical, Natural and Natural Systems, Pablo de Olavide University (Seville, Spain).

Organic C was determined by colorimetry after oxidation with a mixture of potassium dichromate and sulfuric acid (70). Total N was obtained using a CN analyzer (Leco CHN628 Series, Leco Corporation, St Joseph, MI, USA). Available P was measured following a 0.5M NaHCO₃ (pH: 8.5) extraction (71). Soil extracts in a ratio of 1:5 were shaken in a reciprocal shaker at 200 rpm for 2 h. An aliquot of the centrifuged extract was used to the colorimetric determination of P inorganic available (PO₄⁻³), based on the reaction with ammonium molybdate and development of the “Molybdenum Blue” color (72); the pH of the extracts was adjusted with 0.1N HCl when necessary. Phosphatase activity was measured by determination of the amount of *p*-nitrophenol (PNF) released from 0.5 g soil after incubation at 37 °C for 1 h with the substrate *p*-nitrophenyl phosphate in MUB buffer (pH 6.5; 73). The activity of β -glucosidase was assayed following the procedure for phosphatase, but using *p*-nitrophenyl- β -D-glucopyranoside as substrate and Trishydroxymethyl aminomethane instead of NaOH when preparing the buffer (74). The remaining soil variables were measured from K₂SO₄ 0.5 M soil extracts in a ratio 1:5. Soil extracts were shaken in an orbital shaker at 200 rpm

for 1 h at 20°C and filtered to pass a 0.45-µm Millipore filter (75). The filtered extract was kept at 2 °C until colorimetric analyses, which were conducted within the 24 h following the extraction. Sub-samples of each extract were taken for measurements of aromatic compounds, phenols, pentoses, hexoses, proteins and aminoacids according to Chantigny *et al.* (76). Ammonium (NH₄⁺-N) and nitrate (NO₃⁻-N) concentrations were also measured for each K₂SO₄ extract subsample. Ammonium concentration was directly estimated by the indophenol blue method using a microplate reader (77). Nitrate was first reduced to NH₄⁺-N with Devarda alloy, and its concentration was determined by the indophenol blue method. Nitrate concentration in the extracts was calculated as the difference between Devarda-incubated and unincubated samples. Potential N transformation rate was measured by determination of total K₂SO₄-extractable N before and after incubation in the laboratory at 80% of field water holding capacity and 30°C for 14 days (78).

Abiotic variables measured: rationale and laboratory/field methods

The coordinates and elevation of each plot were recorded *in situ* with a portable Global Positioning System, and were standardized to the WGS84 ellipsoid for visualization and analyses. The use of elevation as an environmental variable has been criticized because it may confound ecosystem attributes physically linked to altitude in terms of distance (e.g., atmospheric pressure and temperature) and others that are not (e.g. moisture, hours of sunshine, wind, and human activities, 79). However, we included it in our analyses because given the important range found in this variable within our dataset (from 69 m a.s.l. to almost 5000 m a.s.l.), it may encapsulate microclimatic features of the sites that are not properly captured by the global interpolations used. Slope angle was measured *in situ* with a clinometer. This variable is an important driver of the hydrological behavior of drylands, as it strongly influences infiltration, water availability and run-on/run-off processes in these ecosystems (e.g., 80-83).

In addition to the ecosystem functions listed in the preceding section, other soil variables were measured at the laboratory of the Rey Juan Carlos University. Soil pH was measured in all the soil samples with a pH meter, in a 1: 2.5 mass: volume soil and water suspension. Soil texture was measured in two/three composite samples per site, as preliminary analysis revealed that within-site variability was very low. One composite sample each per microsite (open areas or soil under the canopy of the dominant perennial plants) and site were analyzed for sand, clay and silt content according to Kettler *et al.* (84). The three textural variables measured (sand, clay and silt) were highly intercorrelated (Spearman $\rho_{\text{sand-silt}} = -0.966$, $P < 0.001$; Spearman $\rho_{\text{sand-clay}} = -0.562$, $P < 0.001$; Spearman $\rho_{\text{silt-clay}} = 0.365$, $P < 0.001$). Thus, we selected for further analyses the content of sand, which has been found to play key roles in controlling water availability, community structure and biogeochemical processes in drylands (85-88). This variable was also correlated with pH in our database (Spearman $\rho = -0.229$, $P = 0.001$), and thus pH was not used in subsequent analyses.

A total of 21 climatic variables related to different temperature and rainfall characteristics of the study sites were extracted from the Worldclim global database (see www.worldclim.org for details). In addition, we obtained values of the aridity index from another database using the data interpolations provided by Worldclim (89;

<http://www.cgiar-csi.org/data/climate/item/51-global-aridity-and-pet-database>). We first explored the correlations among these climatic descriptors, and excluded 11 variables that were strongly correlated (Pearson's $r > 0.85$) with the remaining variables (table S1). We then conducted a principal component analysis (PCA) using a correlation matrix and a Varimax rotation with the remaining 10 variables (annual mean temperature, mean diurnal temperature range, temperature seasonality, maximum temperature of the warmest month, mean temperature of the wettest quarter, mean temperature of the driest quarter, mean annual precipitation, precipitation seasonality [coefficient of variation of monthly precipitation], precipitation of the driest quarter and precipitation of the coldest quarter). All the components that had eigenvalues > 1 were retained for further analyses (90). Four components of this PCA had eigenvalues greater than one (Component 1 = 3.46, Component 2 = 2.43, Component 3 = 1.34, and Component 4 = 1.14), explaining over 84% of the variance in the data (Component 1 = 34.64%, Component 2 = 24.33%, Component 3 = 13.40%, and Component 4 = 11.42%). Mean annual precipitation ($r = 0.910$), precipitation in the coldest quarter ($r = 0.791$) and temperature seasonality ($r = -0.766$) showed the highest correlations with the first component of this PCA. The second component of this PCA had the highest correlation with the mean temperature of the driest quarter ($r = 0.901$) and the mean diurnal temperature range ($r = -0.726$). The seasonality in precipitation ($r = -0.924$) and the precipitation in the driest quarter ($r = 0.946$) were the climatic features most correlated with the third components, while the fourth component of the PCA was strongly correlated to annual mean temperature ($r = 0.682$) and the mean temperature of the wettest quarter ($r = 0.884$). We consider it preferable to use PCA components over these climatic variables in our analyses (see below) because these components are orthogonal, while variables such as annual temperature and precipitation, and mean temperature and precipitation in the driest quarter show an important degree of correlation among them (see table S1). This approach enables us to distinguish the unique effects of different variables, and is also commonly employed in studies working at regional, continental and global spatial scales and dealing with multiple, highly intercorrelated climatic variables (e.g., 91-94).

Assessment of ecosystem multifunctionality: rationale, approach followed and comparison with alternative approaches

We focused our analyses on ecosystem multifunctionality, i.e. the ability of the ecosystem to maintain multiple functions simultaneously (49, 51, 55, 95). Most of the ecosystem functions evaluated are involved in biochemical pathways leading to the production of proteins and carbon structures, and thus directly linked to the maintenance of primary production, biomass accumulation and nutrient cycling ("ecosystem functioning" *sensu* 52). Organic C, total N and available P are good surrogates of C, N and P availability for plants and microorganisms in dryland ecosystems worldwide, and ultimately control many biogeochemical processes in drylands, as well as plant and microbial performance (e.g., 37, 96-98). Ammonium is considered the preferred source of N for bacteria and fungi (99, 100), and both NH_4^+ -N and NO_3^- -N are the main source of N for vascular plants (101-102). Proteins are an important N input to the soil in terrestrial ecosystems (103-104), while aminoacids provide N sources for both plants and microorganisms (105-109). Phenolic compounds, hexoses, pentoses and aromatic

compounds are an important source of C for heterotrophic organisms in a wide variety of environments (76, 110-112). Similarly, soil enzyme activities catalyze limiting steps in organic matter degradation and are often commonly used as indicators of microbial nutrient demand (113). According to this rationale, and taking into account the size of the plots surveyed and the spatial extent of our study, we assume that the higher the values for the different ecosystem functions measured at a given ecosystem, the higher the overall ecosystem functioning at that site. It should be noted, however, that some studies have reported phenolic inhibition of nitrification (114, 115), albeit contrasting results are also commonly found in many environments (e.g. 108, 116-117). Indeed, positive correlations between the content of phenols and both potential N transformation rate (Spearman $\rho = 0.634$, $n = 224$, $P < 0.001$) and NO_3^- -N content (Spearman $\rho = 0.396$, $n = 224$, $P < 0.001$) have been found at our study sites.

Different approaches have been proposed to quantify ecosystem multifunctionality in the ecological literature. Some authors have used the average of multiple functions (previously standardized) as an index of ecosystem multifunctionality (55, 118). Others have used information criteria to identify the species that affected one or many ecosystem functions (53, 59, 119), or have established minimal thresholds for every function and then evaluated how combinations of different species affected the proportion of replicates/sites capable of maintaining multiple functions above such thresholds (54, 120). The use of a multifunctionality index based on the scaled mean minus the standard deviation of all functions has also been proposed (121). Among these alternatives, we decided to use the average of multiple functions (previously standardized) as an index of ecosystem multifunctionality, as it provided a straightforward and easily interpretable measure of the ability of different communities to sustain multiple functions simultaneously. We acknowledge that the use of such an average may preclude a detailed analysis of how particular species differ in their importance for different functions (e.g., 53, 122), and that by using this average, declines in one function can theoretically be compensated for by increases in one or another function (something that has been criticized in the past; e.g. 54). However, the extent of our global survey and the important differences in composition between the sites makes the identification of particular species that are important for different functions inappropriate, because species composition differs widely among regions and continents. We did not find that particular sites with high values of a single or a few functions had consistently low values for other functions. In our data set, the correlations between most ecosystem function variables were positive or close to 0, and the strongest negative correlation coefficient (r) between any pair of functions among the 224 sites was only -0.168. Moreover, the coefficient of variation among the functions evaluated at each site varied between only 1.24 and 2.36. Finally, the relatively large number of functions employed to calculate our multifunctionality index makes it relatively robust to outliers or atypical values.

To obtain a quantitative multifunctionality index for each site (M), we first calculated the Z scores of the 14 functions evaluated, estimated at the scale of each 30 m \times 30 m plot surveyed. These estimates were obtained by using a weighted average of the mean values observed in bare ground and vegetated areas, weighted by their respective cover at each plot. Raw data were normalized prior to these calculations; a sqrt-transformation normalized most of the variables evaluated. Following this, the Z scores of the 14 variables were averaged to obtain M . This multifunctionality index follows a

normal distribution (Kolmogorov-Smirnov test = 0.058, $df = 224$, $P = 0.068$). We preferred the use of Z scores over other transformations used in the multifunctionality literature (e.g. division by the maximum, 118) because of their good statistical properties: i) average Z scores follow a normal distribution, ii) the means and variances of such averages are poorly correlated ($r = 0.167$ in our dataset), and iii) the Z scores do not constrain the variability found in the raw data, as do other indices that are bounded between 0 and 1.

Variation in cover has been used as proxy for plant biomass and productivity in a wide variety of environments, including grasslands and shrublands (123-126), and as such could be considered as another ecosystem function. However, with the approach we followed, total plant cover is taken into account when estimating ecosystem functions at the plot scale, and thus cannot also be used as an independent variable in subsequent analyses. Nevertheless, we compared the multifunctionality index obtained with our plot-level estimates (M) with an alternative index using average values of the ecosystem functions from bare ground areas plus total plant cover as another function. Both indices were strongly correlated (fig. S3). We therefore preferred to use M obtained with plot-level estimates because these represent ecosystem functioning more realistically at the landscape scale (which includes both bare ground and vegetated areas), and by doing so we avoid overestimating the effect of plant cover.

Prior to further analyses, and to ensure that our results were robust with respect to the method used to calculate ecosystem multifunctionality, we calculated two alternative multifunctionality indices: i) the average of multiple functions, previously standardized by dividing by the maximum (SD index, 118), and ii) this average minus the standard deviation (SDSE index, 121). The comparison between M and these alternative approaches revealed that all the indices were strongly related (fig. S4). Results from M were almost identical to those of the SD index. While highly correlated, results with the SDSE index showed more scatter (fig. S4). Thus, we repeated the different analyses conducted (described below) with both M and the SDSE index to ensure that our results and conclusions are robust to the choice of metric used to estimate multifunctionality.

Statistical analyses

We first evaluated the relationships between the richness of vascular plants and M using ordinary least squares (OLS) regression. In addition, and to account for potential effects caused by the spatial structure of the data, we also fitted the relationship between species richness and M using a simultaneous autorregressive (SAR) method (127), the SAR error model (*sensu* 128). This approach has been highly effective in removing spatial autocorrelation from residuals, while at the time minimizing time coefficient shifts compared to OLS regression (129). Species richness data were sqrt-transformed prior to regression analyses to approximate normality. Regression analyses were conducted using both M and similar indices conducted only with variables from the C (organic C, β -glucosidase, pentoses, hexoses, aromatic compounds and phenols), N (NO_3^- -N, NH_4^+ -N, total N, aminoacids, proteins, and potential N transformation rate) and P (available inorganic P and phosphatase) cycles.

We then explored the relative effects and importance of species richness and different abiotic factors (sand content, slope, elevation and four components derived from

a principal component analysis of climatic data) as drivers of multifunctionality. We focused on species richness for this study because to date it has been the component of biodiversity most widely studied (49), and because other diversity metrics taking into account species abundance, such as the exponential Shannon's index or the Simpson index, were not independent from species richness (fig. S5). Slope, elevation and species richness were sqrt-transformed prior to analyses to approximate normality. Separate analyses were conducted using M and similar indices conducted only with variables from the C, N and P cycles as dependent variables. All the analyses were based on linear regressions.

To examine whether observed effects of species richness were important compared to those of abiotic factors as drivers of multifunctionality, we used a multi-model inference approach based on information theory (130). This approach does not rely on the classical approach to fitting models, based on traditional hypothesis testing, but instead uses information theory to assess the probability that a given model is the most appropriate description of the observed data. Multi-model inference approaches are increasingly being used and recommended when dealing with observational data collected over large spatial scales and environmental gradients, as in this study (e.g., 94, 131, 132). We evaluated all possible linear regression models containing M as the dependent variable and the following independent variables: species richness (sqrt-transformed), elevation (sqrt-transformed), slope angle (sqrt-transformed), sand content and the four components derived from the PCA of climatic data described above. The characteristics of our survey make the presence of spatial autocorrelation likely, since sites within each country are not fully independent from each other. While spatial autocorrelation can be a problem for significance tests, parameter estimates using OLS regressions are not seriously or systematically biased by residual autocorrelation in macroecological analyses (129, 133). However, spatial autocorrelation may still be a problem in multi-model approaches based on information theory, as the metrics chosen to select models are related to unexplained variance of the models, which can be in turn affected by the presence of spatial autocorrelation (134). To control for potential effects of spatial autocorrelation in the data, we also included latitude and longitude as explanatory variables in all the models (129).

We ranked all the 255 models that could be generated with our independent variables according to the second-order Akaike information criterion (AIC_c), calculated as described in Fotheringham *et al.* (135). The AIC_c of each model was then transformed to ΔAIC_c , which is the difference between AIC_c of each model and the minimum AIC_c found for the set of models compared. Values of ΔAIC_c above 7 indicate that a model has a poor fit relative to the "best" model (i.e. that with the lowest AIC_c), whereas values below 2 indicate that models are indistinguishable (130). The ΔAIC_c values were also used to obtain the Akaike weights of each model (w_i), according to Burnham and Anderson (130). This parameter provides evidence that the model is actually the best explanatory model. Akaike's weights were also used to define the relative importance of each predictor across the full set of models evaluated by summing w_i values of all models that include the predictor of interest, taking into account the number of models in which each predictor appears (130).

Exploratory analyses showed that the relationships between ecosystem multifunctionality and some independent variables were explained better with quadratic,

rather than with linear, terms (figs. S6-S9). To ensure that non-linearity was not affecting our conclusions, we conducted an additional model selection analysis that included quadratic terms for elevation, sand content and the four PCA components derived from climatic data. To do this, we selected the best 10 OLS models according to AIC_c , and ran them again, including the quadratic term of the relevant variables. The addition of latitude and longitude effectively removed most of the spatial autocorrelation found in the data, which was virtually nonexistent when quadratic terms were included (fig. S10A). However, the residuals of the best fitted model without these terms still had some evidence of spatial autocorrelation (fig. S10B). To further ensure that spatial autocorrelation was not affecting our conclusions, we conducted an additional model selection based on spatial regression. As with the quadratic terms, we selected the best 10 OLS models according to AIC_c , and ran them again using SAR. The results of the analyses of our multifunctionality index conducted with both OLS, OLS with quadratic terms and SAR analyses were virtually identical (Table 1 in the main text, tables S2 and S3), and thus only the former are presented in the main text.

We also checked for potential biases induced by the covariation between species richness and the different abiotic predictors included in the OLS models. For doing so, we calculated the variance inflation factor (VIF) between the different predictors included in the best and most parsimonious OLS models as an indicator for colinearity between these predictors. The VIF was in all cases below four (table S15), suggesting the absence of colinearity problems (136).

Correlation, PCA and OLS analyses were performed using SPSS 15.0 (SPSS Inc., Chicago, IL, USA). Spatial regression and multi-model analyses were carried out using SAM 4.0 (137).

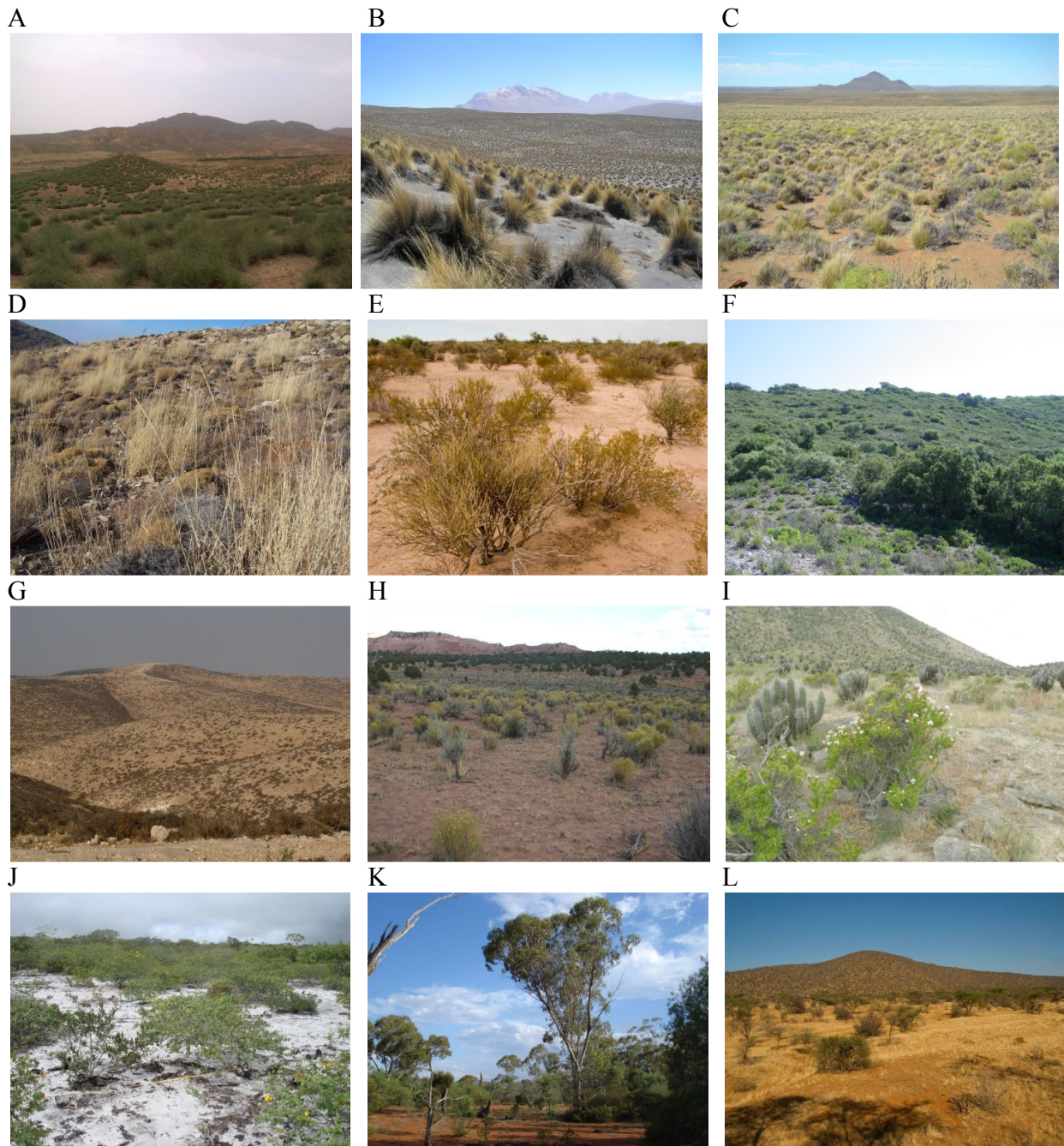


Fig. S1.

Examples of the vegetation types surveyed in this study. A = *Stipa tenacissima* grassland in Morocco (119), B = *Festuca orthophylla* grassland in Peru (128), C = grassland dominated by various *Stipa* and *Festuca* species in Argentina (2), D = Shrubland dominated by cushion shrubs (*Acantholimon evinaceum* and *Acanthophyllum glandulosum*) in Iran (83), E = *Larrea cuneifolia* shrubland in Argentina (18), F = Shrubland dominated by *Quercus coccifera*, *Q. ilex* and *Rosmarinus officinalis* in Spain (163), G = Shrubland dominated by *Coridothymus capitatus* in Israel (86), H = Mixed

shrubland dominated by *Ericameria nauseosum* in Utah, USA (203), I = Shrubland dominated by *Eulychnia acida* in Chile (49), J = Shrubland dominated by *Chamaecrista cytisoides* in Brasil (37), K = Open woodland dominated by *Eucalyptus populnea* and *Acacia aneura* in Australia (32), and L = Savanna of *Acacia totalis* in Kenya (99). The numbers in brackets indicate the number of the study site in Database S1 and map S1.

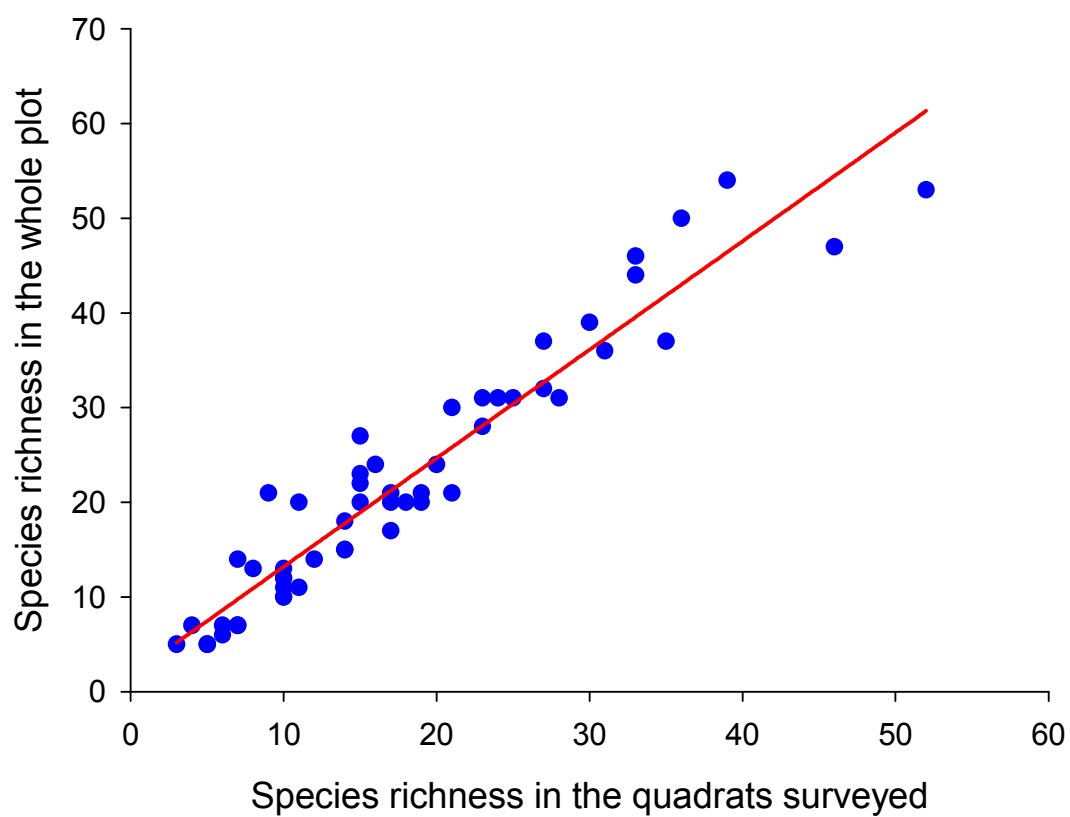


Fig. S2

Relationship between the number of species found within the 80 $1.5 \text{ m} \times 1.5 \text{ m}$ quadrats sampled and the total number of species present within the $30 \text{ m} \times 30 \text{ m}$ plot in a subset of the study sites surveyed. The fitted line indicate results from a linear regression ($R^2 = 0.914$, $P < 0.001$).

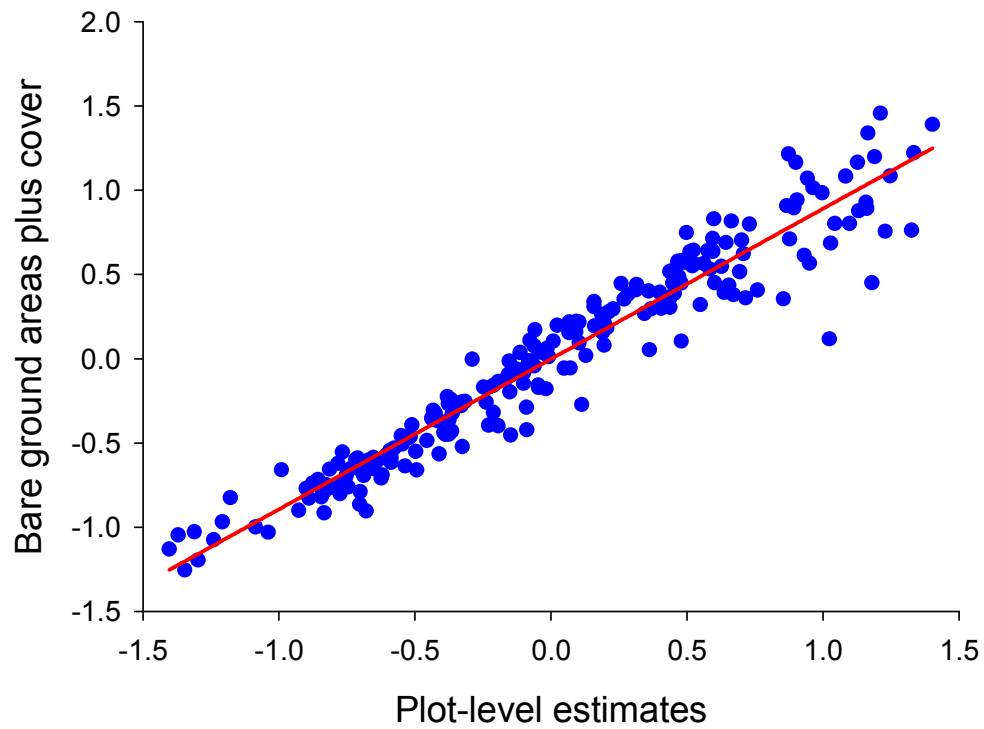


Fig. S3

Relationships between our multifunctionality index (M), based on plot-level estimates of soil functions, and an alternative index made using the values from areas of bare ground for the same functions plus total cover of perennial vascular plants as another function. The fitted line indicate results from a linear regression ($R^2 = 0.932$, $P < 0.001$).

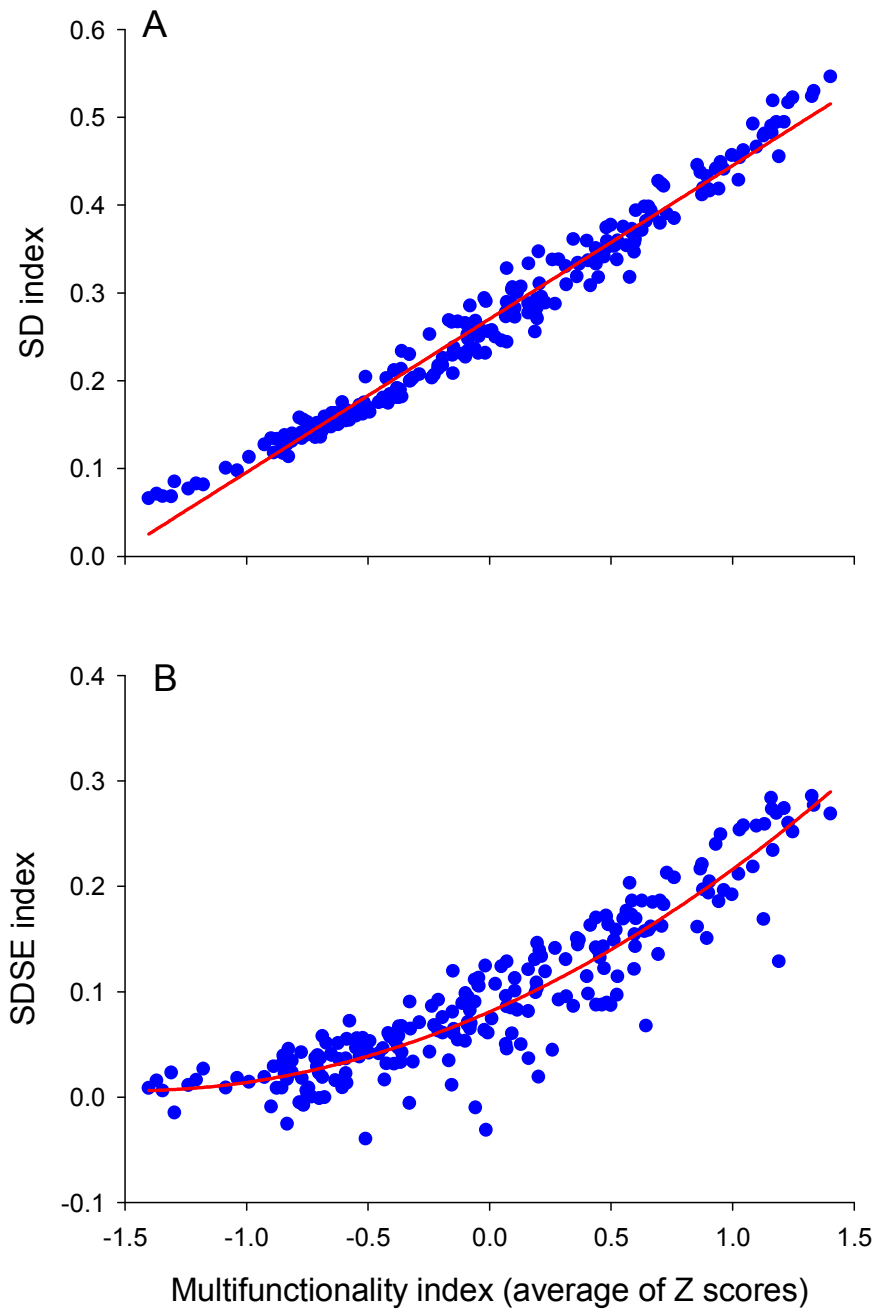


Fig. S4

Relationships between our multifunctionality index, based on the average of Z scores of plot-level estimates of ecosystem functions, and alternative indices based on: A) the average of the functions evaluated previously standardized by dividing by the maximum (SD index), and B) such average minus the standard deviation (SDSE index). The fitted lines indicate results from linear (A, $R^2 = 0.974$, $P < 0.001$) and quadratic (B, $R^2 = 0.854$, $P < 0.001$) regressions.

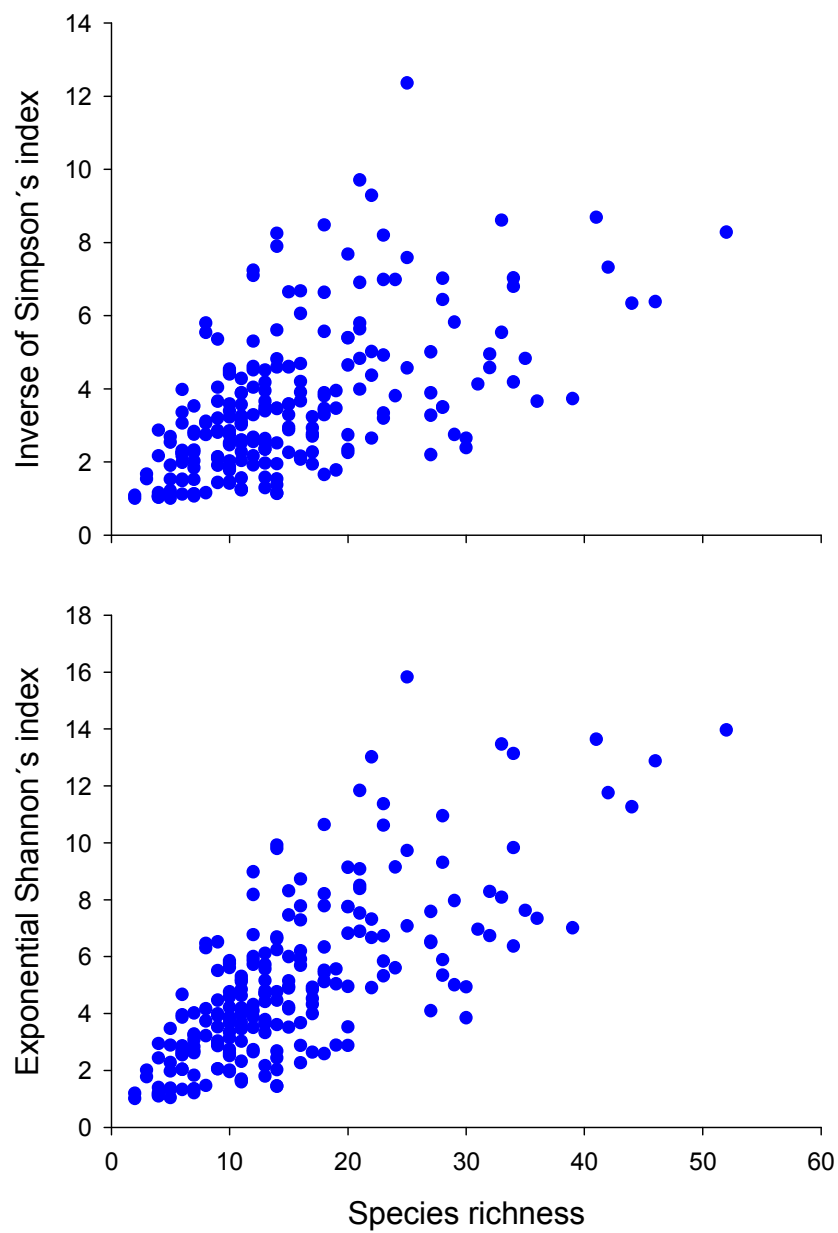


Fig. S5

Scatter plots illustrating the dependence between species richness and two metrics of species diversity: the inverse of the Simpson index (upper panel) and the exponential of Shannon's index (lower panel).

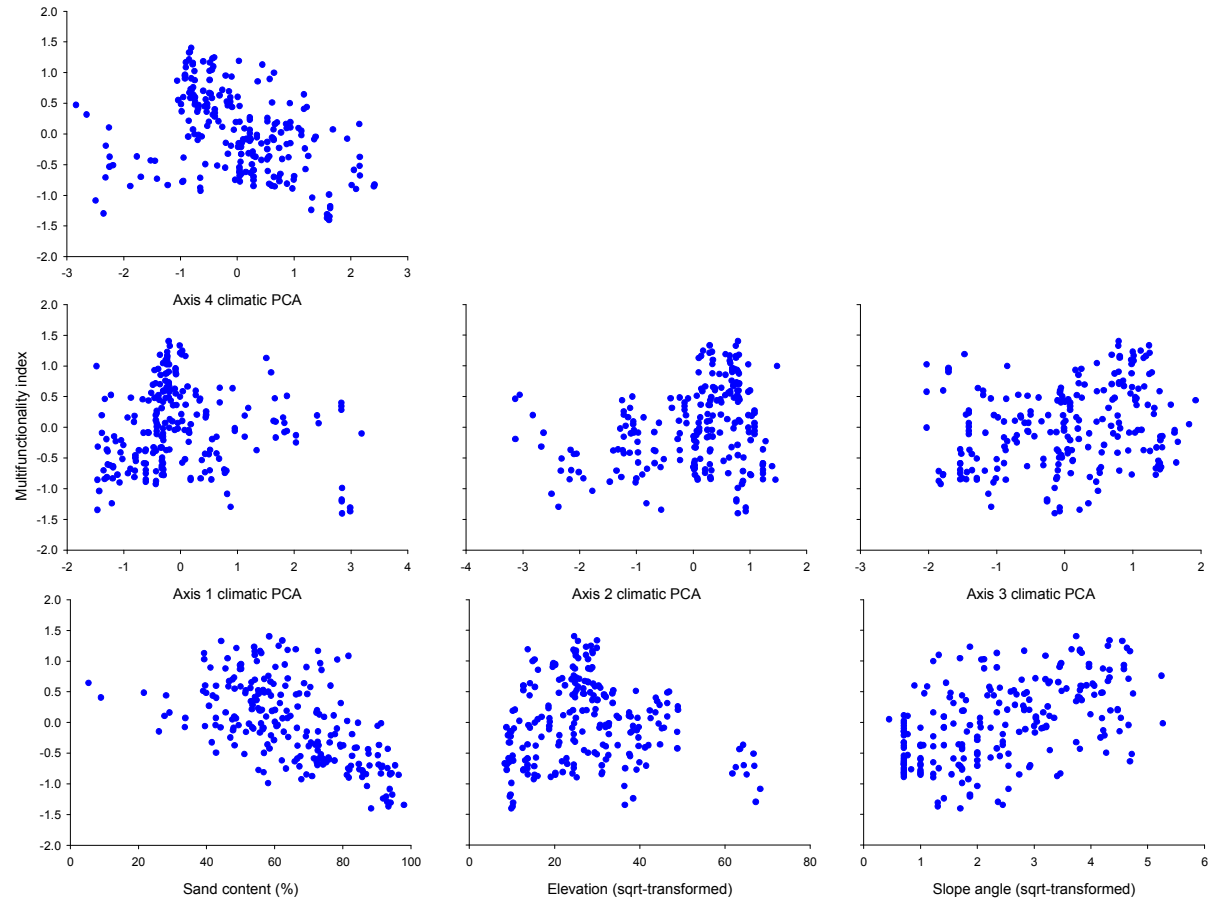


Fig. S6

Scatter plots illustrating the relationships between the abiotic variables included in the models and our multifunctionality index (M). For the same relationship between M and species richness, see fig. 1a in the main text.

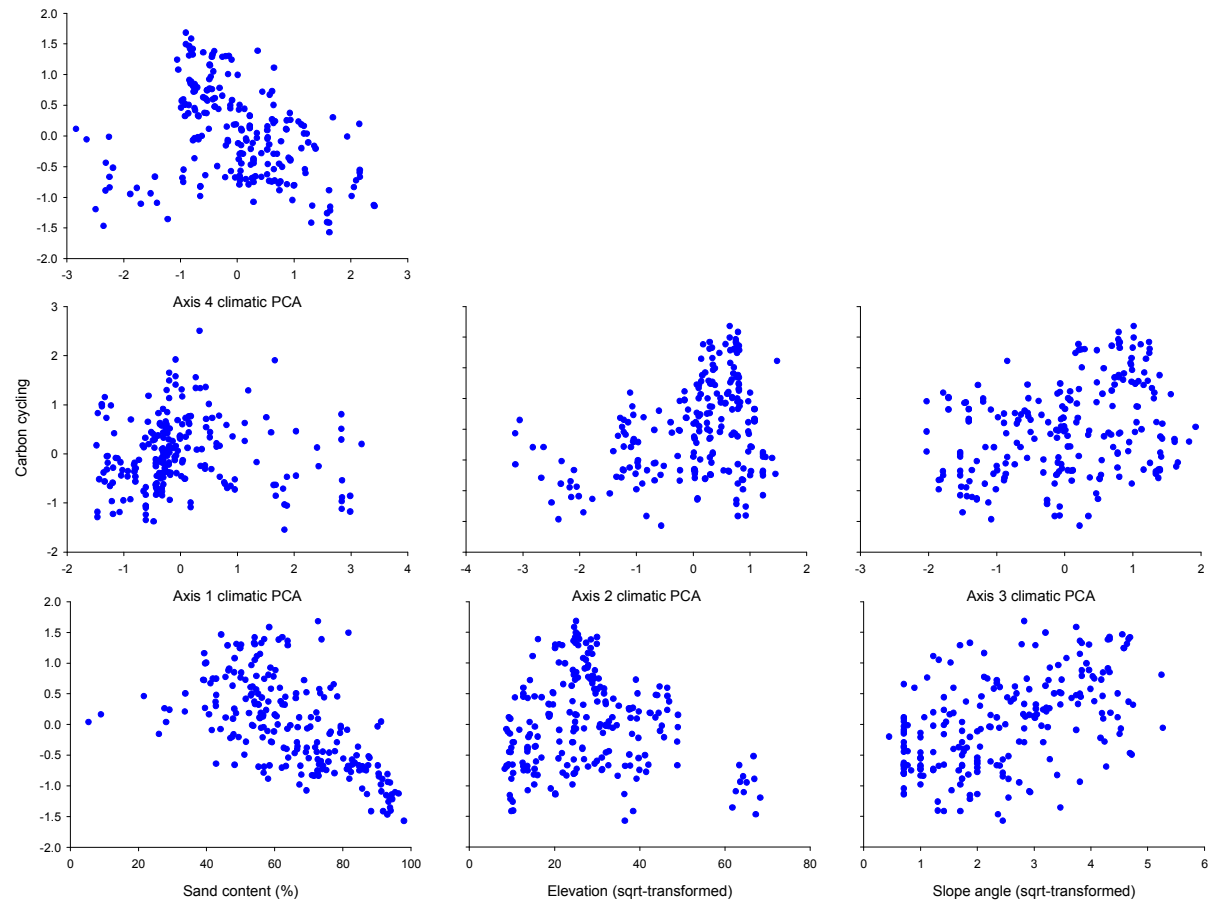


Fig. S7

Scatter plots illustrating the relationships between the abiotic variables included in the models and an index synthesizing multiple functions related to carbon cycling (average of Z scores of organic C, β -glucosidase, pentoses, hexoses, aromatic compounds and phenols). For the same relationship between this index and species richness, see fig. 1b in the main text.

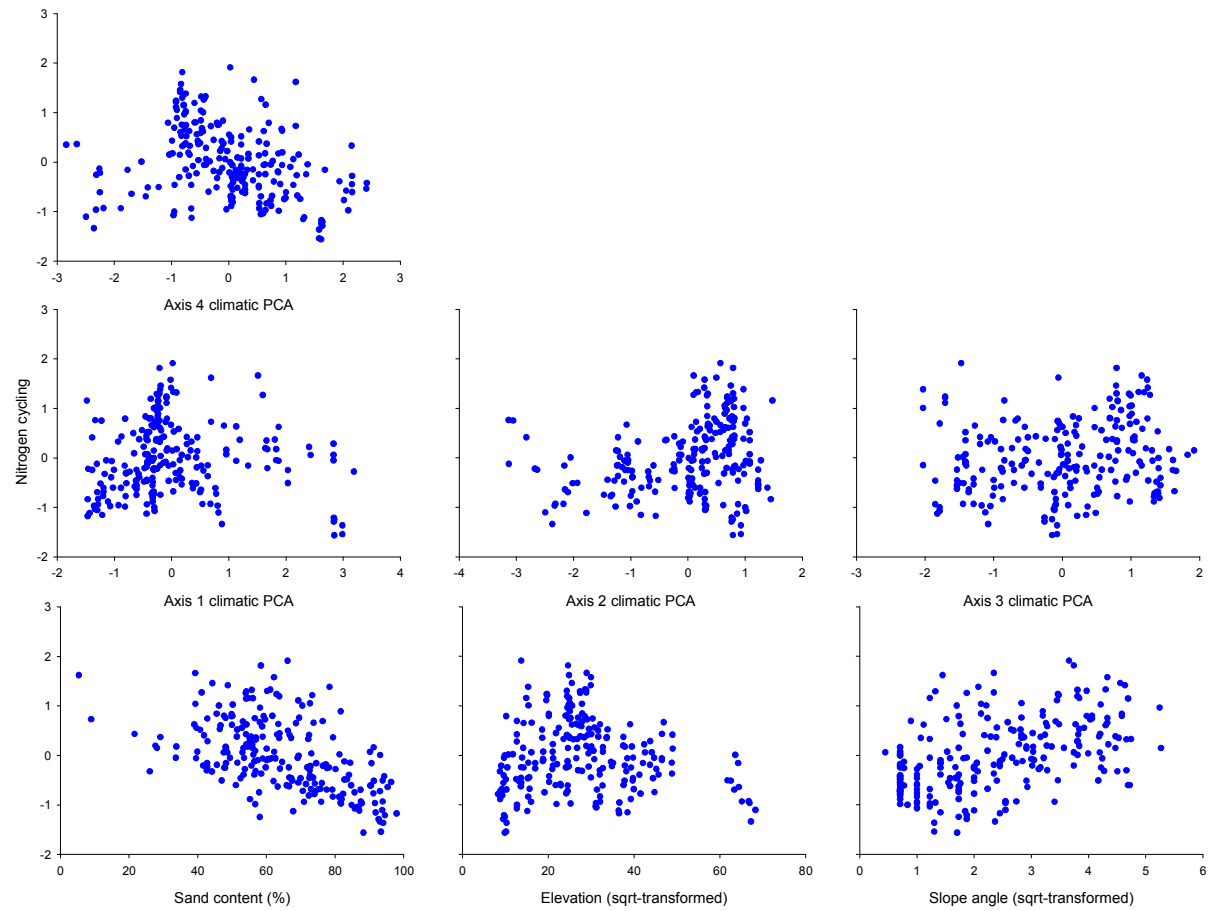


Fig. S8

Scatter plots illustrating the relationships between the abiotic variables included in the models and an index synthesizing multiple functions related to nitrogen cycling (average of Z scores of total nitrogen, NO_3^- -N, NH_4^+ -N, aminoacids, proteins, and potential nitrogen transformation rate). For the same relationship between this index and species richness, see fig. 1c in the main text.

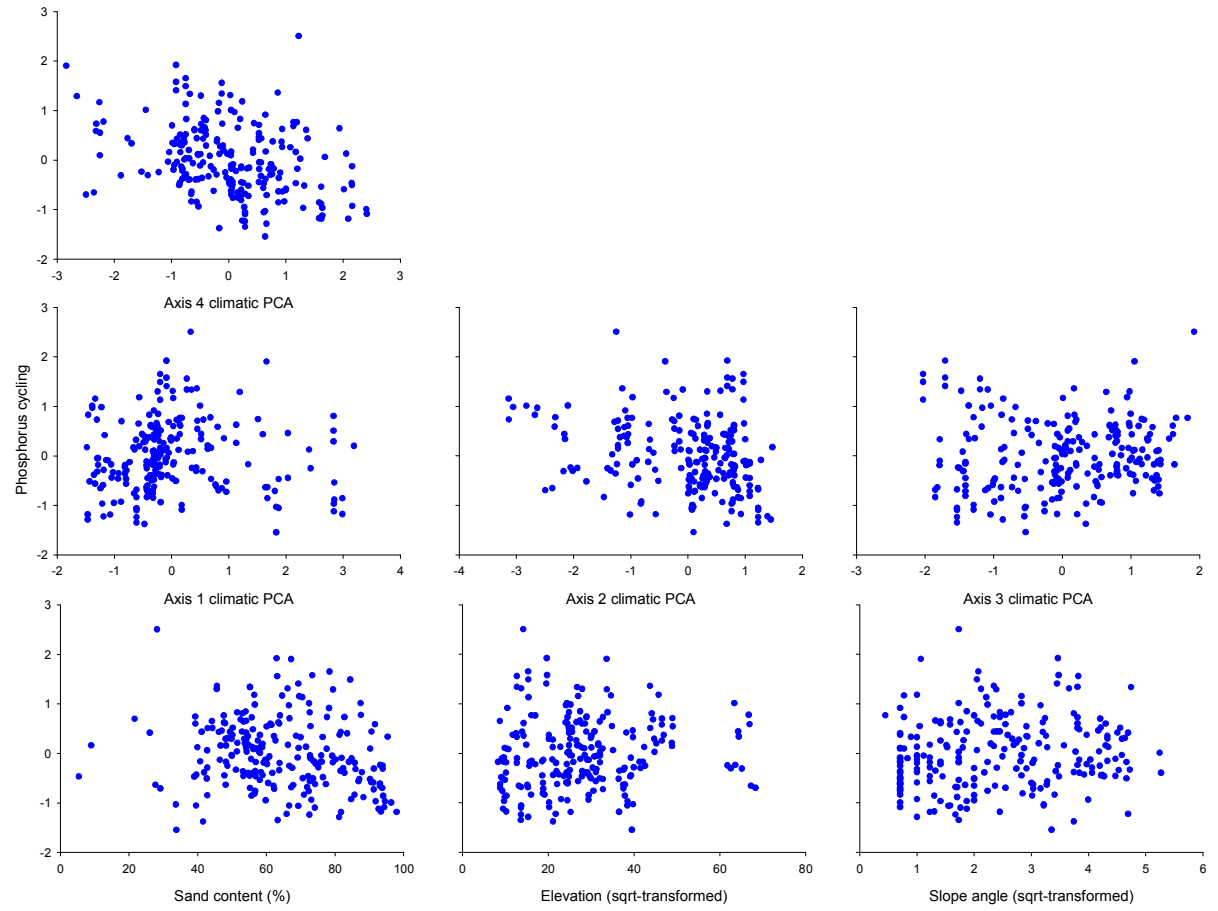


Fig. S9

Scatter plots illustrating the relationships between the abiotic variables included in the models and an index synthesizing multiple functions related to phosphorus cycling (average of Z scores of available inorganic phosphorus and phosphatase). For the same relationship between this index and species richness, see fig. 1d in the main text.

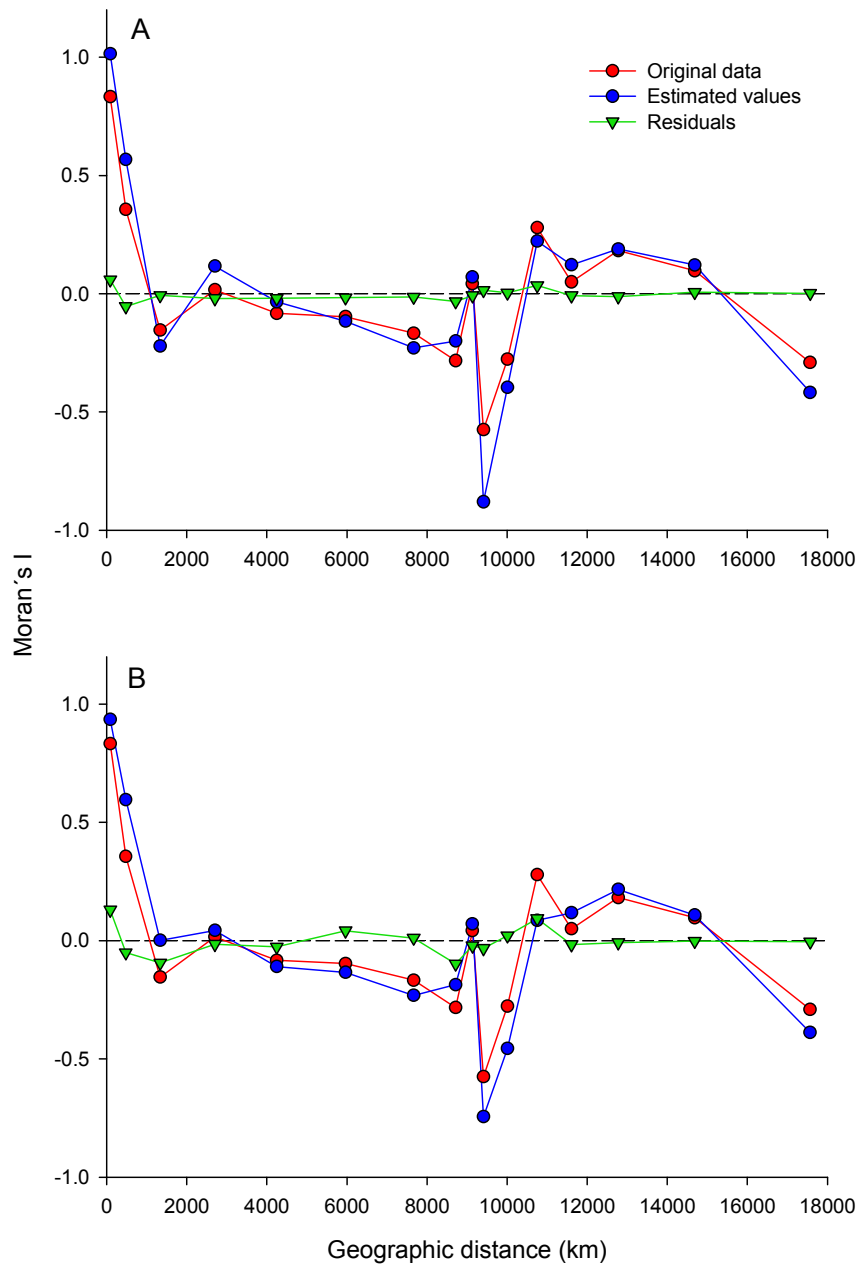


Fig. S10

Moran's correlogram showing the spatial autocorrelation of the original data (red line), the estimated values (blue line) and of the residuals (green line) of the best model fitted to our multifunctionality index with (A) and without (B) quadratic terms in the independent variables. See Table 1 and table S3 for the variables included in the models presented in A and B, respectively.

Table S1.

Pearson correlations among the climatic variables obtained from the Worldclim database (36). Values $> |0.85|$ are in bold.

	AMT	MDR	ISO	TSE	MAWM	MICM	TAR	MTWEQ	MTDQ	MTWAQ	MTCQ
MDR	-0.359										
ISO	0.423	0.082									
TSE	-0.545	0.089	-0.898								
MAWM	0.546	-0.142	-0.421	0.365							
MICM	0.927	-0.435	0.606	-0.776	0.245						
TAR	-0.610	0.349	-0.825	0.962	0.308	-0.847					
MTWEQ	0.576	-0.044	0.371	-0.212	0.345	0.410	-0.213				
MTDQ	0.713	-0.481	0.055	-0.351	0.495	0.731	-0.445	-0.032			
MTWAQ	0.697	-0.360	-0.290	0.218	0.954	0.424	0.108	0.461	0.562		
MTCQ	0.919	-0.290	0.691	-0.830	0.198	0.984	-0.857	0.463	0.658	0.363	
RAI	0.425	-0.181	0.658	-0.538	-0.057	0.520	-0.541	0.415	0.175	0.037	0.535
RAWM	0.289	-0.083	0.745	-0.565	-0.279	0.404	-0.550	0.381	-0.041	-0.161	0.446
RADM	0.148	-0.021	-0.023	0.007	0.228	0.127	0.001	0.221	0.081	0.189	0.101
RASE	-0.157	0.005	0.377	-0.286	-0.592	-0.043	-0.283	-0.030	-0.356	-0.464	0.008
RAWEQ	0.298	-0.074	0.754	-0.588	-0.283	0.420	-0.567	0.362	-0.015	-0.169	0.464
RADQ	0.100	-0.053	-0.142	0.091	0.286	0.078	0.080	0.141	0.152	0.218	0.038
RAWAQ	-0.100	0.404	0.520	-0.290	-0.406	-0.069	-0.155	0.392	-0.512	-0.394	0.050
RACQ	0.449	-0.364	0.509	-0.460	0.020	0.553	-0.531	0.214	0.338	0.140	0.518
MTMAX	0.979	-0.160	0.465	-0.558	0.545	0.885	-0.569	0.599	0.649	0.657	0.908
MTMIN	0.984	-0.519	0.372	-0.517	0.526	0.932	-0.626	0.536	0.745	0.706	0.897
AI	0.076	-0.205	0.440	-0.313	-0.224	0.215	-0.334	0.156	-0.003	-0.170	0.201

Table S1. Continuation.

	RAI	RAWM	RADM	RASE	RAWEQ	RADQ	RAWAQ	RACQ	MTMAX	MTMIN
RAWM	0.902									
RADM	0.284	-0.025								
RASE	-0.004	0.386	-0.724							
RAWEQ	0.915	0.991	-0.023	0.366						
RADQ	0.261	-0.094	0.955	-0.810	-0.090					
RAWAQ	0.437	0.495	0.192	0.212	0.496	0.131				
RACQ	0.798	0.773	0.019	0.112	0.789	-0.021	-0.065			
MTMAX	0.410	0.287	0.152	-0.166	0.299	0.095	-0.017	0.395		
MTMIN	0.424	0.280	0.140	-0.145	0.287	0.102	-0.168	0.481	0.927	
AI	0.908	0.818	0.300	-0.013	0.825	0.321	0.422	0.690	0.036	0.109

AMT = annual mean temperature, MDR = mean diurnal temperature range, ISO = Isothermality, calculated as $100 \times (\text{annual mean temperature} / [\text{maximum temperature of the warmest month} - \text{minimum temperature of the coldest month}])$, TSE = temperature seasonality (standard deviation $\times 100$), MAWM = maximum temperature of the warmest month, MICM = minimum temperature of the coldest month, TAR = temperature annual range (maximum temperature of the warmest month - minimum temperature of the coldest month), MTWEQ = mean temperature of the wettest quarter, MTDQ = mean temperature of the driest quarter, MTWAQ = mean temperature of the warmest quarter, MTCQ = mean temperature of the coldest quarter, RAI = mean annual precipitation, RAWM = precipitation of the wettest month, RADM = precipitation of the driest month, RASE = precipitation seasonality (coefficient of variation of monthly precipitation), RAWEQ = precipitation of the wettest quarter, RADQ = precipitation of the driest quarter, RAWAQ = precipitation of the warmest quarter, RACQ = precipitation of the coldest quarter, MTMAX = mean of maximal temperatures, MTMIN = Mean of minimal temperatures, and AI = aridity index (annual rainfall/annual potential evapotranspiration).

Table S2.

Summary results of the modelling of ecosystem multifunctionality (M index) using ordinary least squares linear regression and quadratic terms in selected independent variables (sand content, elevation and the four components of a principal component conducted with climatic data), to account for potential effects of non-linear relationships between M and these variables (see fig. S6). The same models presented in Table 1 of the main text, ranked according to its second-order Akaike information criterion (AIC_c), are presented. The second model of the table is the most parsimonious model; the same model without species richness had $R^2 = 0.611$, $AIC_c = 261.71$, and $\Delta AIC_c = 8.21$.

Independent variables	R^2	AIC_c	ΔAIC_c
C1, C1 ² , C2, C2 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.637	253.00	0.00
C1, C1 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.629	253.50	0.50
C1, C1 ² , C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.638	257.33	4.33
C1, C1 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.630	257.60	4.60
C1, C1 ² , C2, C2 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.589	276.54	23.54
C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.579	277.47	24.47
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.594	278.34	25.34
C1, C1 ² , C3, C3 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.584	279.21	26.21

ΔAIC_c = difference between the AIC_c of each model and that of the best model, C1 = first component of a principal component analysis conducted with climatic data (PCA_{clim} , mainly related to mean annual precipitation, $r = 0.910$), C2 = second component of PCA_{clim} (mainly related to mean temperature of the driest quarter, $r = 0.901$), C3 = third component of PCA_{clim} (mainly related to precipitation in the driest quarter, $r = 0.946$), C4 = fourth component of PCA_{clim} (mainly related to annual mean temperature [$r = 0.682$] and the mean temperature of the wettest quarter, $r = 0.884$), SA = sand content, SR = species richness (sqrt-transformed), SL = slope (sqrt-transformed), and EL = elevation (sqrt-transformed), LA = latitude, and LO = longitude. Superscripts indicate quadratic terms.

Table S3.

Summary results of the modelling of ecosystem multifunctionality (*M* index) using spatial simultaneous autorregression. The same models presented in Table 1 of the main text, ranked according to its second-order Akaike information criterion (AIC_c), are presented. The first model of the table is the most parsimonious; the same model without species richness had $R^2 = 0.475$, $AIC_c = 316.88$, and $\Delta AIC_c = 7.75$. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c
C4, SA, SR, SL, EL	0.498	309.13	0
C2, C3, C4, SA, SR, SL, EL	0.497	313.81	4.68
C1, C4, SA, SR, SL, EL	0.409	347.86	38.73
C1, C2, C4, SA, SR, SL, EL	0.406	350.98	41.85
C1, C3, C4, SA, SR, SL, EL	0.402	352.57	43.44
C1, C2, C3, C4, SA, SR, SL, EL	0.400	355.32	46.19
C1, C2, SA, SR, SL, EL	0.287	389.75	80.62
C1, C3, SA, SR, SL, EL	0.284	390.52	81.39

Table S4.

Best-fitting regression models of the C cycling index using ordinary least squares regression. Of all 255 possible models, the best ten models are presented, ranked according to the second-order Akaike information criterion (AIC_c). The first model of the table is the most parsimonious; the ΔAIC_c of the same model without species richness is indicated in bold. w_i = Akaike weights. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c	w_i
C3, C4, SA, SR, SL, EL, LA, LO	0.600	320.156	0	0.298
C2, C3, C4, SA, SR, SL, EL, LA, LO	0.603	320.644	0.488	0.234
C1, C2, C3, C4, SA, SR, SL, EL, LA, LO	0.606	321.163	1.007	0.180
C1, C3, C4, SA, SR, SL, EL, LA, LO	0.601	321.607	1.450	0.145
C1, C2, C3, C4, SA, SR, SL, LA, LO	0.598	323.486	3.330	0.056
C2, C3, C4, SA, SR, SL, LA, LO	0.590	325.583	5.427	0.020
C3, C4, SA, SL, EL, LA, LO	0.585	326.134	5.978	0.015
C2, C4, SA, SR, SL, EL, LA, LO	0.588	326.782	6.626	0.011
C4, SA, SR, SL, EL, LA, LO	0.583	326.842	6.685	0.011
C1, C3, C4, SA, SL, EL, LA, LO	0.586	327.907	7.751	0.006

Table S5.

Best-fitting regression models of the N cycling index using ordinary least squares regression. Of all 255 possible models, the best ten models are presented, ranked according to the second-order Akaike information criterion (AIC_c). The first and second models of the table are the best and most parsimonious models, respectively; the same models without species richness had $R^2 = 0.420$, $AIC_c = 387.502$, $\Delta AIC_c = 20.344$, and $R^2 = 0.452$, $AIC_c = 374.698$, $\Delta AIC_c = 7.54$, respectively. w_i = Akaike weights. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c	w_i
C1, C4, SA, SR, SL, EL, LA, LO	0.481	367.158	0	0.270
C4, SA, SR, SL, EL, LA, LO	0.475	367.544	0.386	0.222
C2, C4, SA, SR, SL, EL, LA, LO	0.477	368.965	1.807	0.109
C1, C2, C4, SA, SR, SL, EL, LA, LO	0.481	369.186	2.028	0.098
C1, C3, C4, SA, SR, SL, EL, LA, LO	0.481	369.267	2.110	0.094
C3, C4, SA, SR, SL, EL, LA, LO	0.475	369.728	2.570	0.075
C2, C3, C4, SA, SR, SL, EL, LA, LO	0.477	371.153	3.995	0.037
C1, C2, C3, C4, SA, SR, SL, EL, LA, LO	0.481	371.306	4.149	0.034
C2, C4, SA, SL, EL, LA, LO	0.461	373.464	6.306	0.012
C2, C3, C4, SA, SL, EL, LA, LO	0.464	374.224	7.067	0.008

Table S6.

Best-fitting regression models of the P cycling index using ordinary least squares regression. Of all 255 possible models, the best ten models are presented, ranked according to the second-order Akaike information criterion (AIC_c). w_i = Akaike weights. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c	w_i
C2, C4, SA, EL, LA, LO	0.378	394.669	0	0.211
C2, C4, SA, SR, EL, LA, LO	0.382	395.297	0.629	0.154
C2, C3, C4, SA, EL, LA, LO	0.379	396.405	1.737	0.088
C1, C2, C4, SA, EL, LA, LO	0.379	396.451	1.782	0.087
C1, C2, C4, SA, SR, EL, LA, LO	0.385	396.588	1.919	0.081
C2, C4, SA, SL, EL, LA, LO	0.378	396.785	2.116	0.073
C2, C4, SA, SL, SR, EL, LA, LO	0.382	397.445	2.776	0.053
C2, C3, C4, SA, SR, EL, LA, LO	0.382	397.457	2.788	0.052
C1, C2, C3, C4, SA, EL, LA, LO	0.380	398.045	3.376	0.039
C2, C3, C4, SA, SL, EL, LA, LO	0.379	398.464	3.795	0.032

Table S7.

Summary results of the modelling of the C cycling index using spatial simultaneous autorregression (SAR). The same models presented in table S4, ranked according to its second-order Akaike information criterion (AIC_c), are presented. The first model of the table is the most parsimonious; the same model without species richness had $R^2 = 0.529$, $AIC_c = 355.323$, and $\Delta AIC_c = 7.74$. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c
C2, C3, C4, SA, SR, SL	0.545	347.583	0
C2, C3, C4, SA, SR, SL, EL	0.546	349.047	1.464
C2, C4, SA, SR, SL, EL	0.527	356.483	8.900
C3, C4, SA, SR, SL, EL	0.525	357.217	9.634
C3, C4, SA, SL, EL	0.517	358.910	11.327
C4, SA, SR, SL, EL	0.507	363.191	15.608
C1, C3, C4, SA, SR, SL, EL	0.464	386.489	38.906
C1, C2, C3, C4, SA, SR, SL	0.463	387.022	39.439
C1, C2, C3, C4, SA, SR, SL, EL	0.466	387.808	40.225
C1, C3, C4, SA, SL, EL	0.453	388.822	41.239

Table S8.

Summary results of the modelling of the N cycling index using spatial simultaneous autorregression (SAR). The same models presented in table S5, ranked according to its second-order Akaike information criterion (AIC_c), are presented. The first model of the table is the most parsimonious; the same model without species richness had $R^2 = 0.414$, $AIC_c = 388.788$, and $\Delta AIC_c = 3.054$. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c
C4, SA, SR, SL, EL	0.427	385.734	0
C2, C4, SA, SR, SL, EL	0.427	387.990	2.256
C3, C4, SA, SR, SL, EL	0.426	388.613	2.879
C2, C4, SA, SL, EL	0.416	390.262	4.528
C2, C3, C4, SA, SR, SL, EL	0.426	390.801	5.067
C2, C3, C4, SA, SL, EL	0.413	393.478	7.744
C1, C4, SA, SR, SL, EL	0.374	407.765	22.031
C1, C2, C4, SA, SR, SL, EL	0.370	411.621	25.887
C1, C3, C4, SA, SR, SL, EL	0.361	414.569	28.835
C1, C2, C3, C4, SA, SR, SL, EL	0.359	417.485	31.751

Table S9.

Summary results of the modelling of the P cycling index using spatial simultaneous autorregression (SAR). The same models presented in table S6, ranked according to its second-order Akaike information criterion (AIC_c), are presented. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c
C2, C4, SA, EL	0.294	421.939	0
C2, C4, SA, SL, EL	0.290	425.294	3.355
C2, C4, SA, SR, EL	0.290	425.323	3.384
C2, C3, C4, SA, EL	0.284	427.120	5.181
C2, C4, SA, SL, SR, EL	0.286	428.632	6.693
C2, C3, C4, SA, SL, EL	0.284	429.258	7.319
C2, C3, C4, SA, SR, EL	0.283	429.532	7.593
C1, C2, C4, SA, EL	0.224	445.193	23.254
C1, C2, C4, SA, SR, EL	0.219	448.781	26.842
C1, C2, C3, C4, SA, EL	0.191	456.768	34.829

Table S10.

Summary results of the modelling of the C cycling index using ordinary least squares linear regression and quadratic terms in some independent variables (sand content, elevation and the four components of a principal component analysis conducted with climatic data), to account for potential effects of non-linear relationships between multifunctionality and these variables (see fig. S7). The same models presented in table S4, ranked according to its second-order Akaike information criterion (AIC_c), are presented. The first model of the table is the most parsimonious; the ΔAIC_c of the same model without species richness is indicated in bold. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c
C1, C1 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.663	295.428	0
C1, C1 ² , C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.665	298.774	3.346
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.652	299.866	4.438
C1, C1 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, LA, LO	0.650	303.602	8.174
C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.632	310.240	14.812
C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.626	313.889	18.461
C2, C2 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.626	313.889	18.461
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.634	313.906	18.478
C3, C3 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.624	315.005	19.577
C1, C1 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.614	316.442	21.014

Table S11.

Summary results of the modelling of the N cycling index using ordinary least squares linear regression and quadratic terms in some independent variables (sand content, elevation and the four components of a principal component analysis conducted with climatic data), to account for potential effects of non-linear relationships between multifunctionality and these variables (see fig. S8). The same models presented in table S5, ranked according to its second-order Akaike information criterion (AIC_c), are presented. The first model of the table is the most parsimonious; the same model without species richness had $R^2 = 0.573$, $AIC_c = 334.701$, and $\Delta AIC_c = 1.367$. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c
C1, C1 ² , C2, C2 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.575	336.068	0
C1, C1 ² , C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.577	339.596	3.528
C1, C1 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.557	340.772	4.704
C1, C1 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.561	343.054	6.986
C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.509	363.626	27.558
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.514	366.047	29.979
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.508	366.205	30.137
C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.491	367.089	31.021
C2, C2 ² , C4, C4 ² , SA, SA ² , SR, SL, EL, EL ² , LA, LO	0.495	369.782	33.714
C2, C2 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.496	369.880	33.812

Table S12.

Summary results of the modelling of the P cycling index using ordinary least squares linear regression and quadratic terms in some independent variables (sand content, elevation and the four components of a principal component analysis conducted with climatic data), to account for potential effects of non-linear relationships among multifunctionality and these variables (see fig. S9). The same models presented in table S6, ranked according to second-order Akaike information criterion (AIC_c), are presented. The second model of the table is the most parsimonious. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , EL, EL ² , LA, LO	0.425	390.213	0
C2, C2 ² , C4, C4 ² , SA, SA ² , EL, EL ² , LA, LO	0.411	391.098	0.885
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SR, EL, EL ² , LA, LO	0.428	391.453	1.240
C2, C2 ² , C4, C4 ² , SA, SA ² , SR, EL, EL ² , LA, LO	0.412	392.898	2.685
C2, C2 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.411	393.352	3.139
C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.428	393.689	3.476
C1, C1 ² , C2, C2 ² , C4, C4 ² , SA, SA ² , EL, EL ² , LA, LO	0.416	393.846	3.633
C2, C2 ² , C4, C4 ² , SA, SA ² , SL, EL, EL ² , LA, LO	0.412	395.167	4.954
C1, C1 ² , C2, C2 ² , C4, C4 ² , SA, SA ² , SR, EL, EL ² , LA, LO	0.417	395.769	5.556
C1, C1 ² , C2, C2 ² , C3, C3 ² , C4, C4 ² , SA, SA ² , EL, EL ² , LA, LO	0.429	395.829	5.616

Table S13.

Best-fitting regression models of ecosystem multifunctionality using an alternative index that takes into account the variation in the individual functions (SDSE index, described in the Materials and Methods) and ordinary least squares regression. Of all 255 possible models, the best ten models are presented, ranked according to the second-order Akaike information criterion (AIC_c). The first model of the table is the most parsimonious; the ΔAIC_c of the same model without species richness is indicated in bold. w_i = Akaike weights. Rest of legend as in table S2.

Independent variables	R^2	AIC_c	ΔAIC_c	w_i
C3, C4, SA, SR, SL, EL, LA, LO	0.596	-706.873	0	0.433
C1, C3, C4, SA, SR, SL, EL, LA, LO	0.599	-706.177	0.696	0.306
C2, C3, C4, SA, SR, SL, EL, LA, LO	0.596	-704.661	2.212	0.143
C1, C2, C3, C4, SA, SR, SL, EL, LA, LO	0.599	-704.079	2.794	0.107
C4, SA, SR, SL, EL, LA, LO	0.575	-697.607	9.266	0.004
C1, C4, SA, SR, SL, EL, LA, LO	0.576	-695.929	10.944	0.002
C2, C4, SA, SR, SL, EL, LA, LO	0.575	-695.475	11.398	0.001
C3, C4, SA, SL, EL, LA, LO	0.568	-694.051	12.822	< 0.001
C1, C2, C4, SA, SR, SL, EL, LA, LO	0.576	-693.942	12.931	< 0.001
C2, C3, C4, SA, SL, EL, LA, LO	0.571	-693.545	13.328	< 0.001

Table S14.

Multimodel averaged parameter estimates of the analyses conducted with the multifunctionality index (*M*) as dependent variable and all possible combinations of the independent variables used. The results shown are the parameter estimates averaged across 255 models using Akaike weights (130) and ordinary least squares regression. STE = Standardized coefficient, SE = Standard error, and CI = confidence interval. Rest of legend as in table S2.

Variable	Coefficient	STE	SE	t	95% Lower CI	95% Upper CI
C1	-0.059	-0.091	0.021	-2.865	-0.1	-0.019
C2	-0.045	-0.068	0.018	-2.482	-0.08	-0.009
C3	0.057	0.086	0.02	2.882	0.018	0.095
C4	-0.235	-0.358	0.037	-6.409	-0.306	-0.163
SA	-0.017	-0.461	0.002	-8.319	-0.021	-0.013
SR	0.112	0.191	0.032	3.525	0.05	0.175
SL	0.116	0.224	0.032	3.593	0.053	0.18
EL	-0.014	-0.282	0.004	-3.719	-0.021	-0.007

Table S15.

Variance inflation factors of the different predictors included in the best (B) and most parsimonious (MP) ordinary least squares regression models of the multifunctionality index (*M*), and carbon, nitrogen and phosphorus cycling indices. See Table 1 in the main text and tables S4, S5 and S6 for additional details on these models. Rest of legend as in table S2.

Variable	<i>M</i>		Carbon cycling	Nitrogen cycling		Phosphorus cycling
	B	MP	B*	B	MP	B*
C1	1.514	-	-	1.484	-	-
C2	-	-	-	-	-	2.423
C3	1.514	-	1.515	-	-	-
C4	1.399	1.361	1.373	1.382	1.361	1.381
SA	1.446	1.325	1.400	1.388	1.325	1.241
SR	1.333	1.101	1.752	1.124	1.101	-
SL	1.865	1.677	1.752	1.765	1.677	-
EL	1.633	1.583	1.592	1.629	1.583	3.452
LA	1.757	1.291	1.362	1.634	1.291	1.327
LO	1.672	1.484	1.562	1.568	1.484	1.847

* The best model is also the most parsimonious in this case.

Database S1

1215442_DatabaseS1.xls: Data used in the primary analyses of this article. The data appear in the Data spreadsheet; the description and units of each variable appear in the Metadata spreadsheet.

Map S1

1215442_mapS1.kml: Interactive map showing the location of all the 224 study sites. Each site is represented by a red icon and a number, corresponding with the number given in Database S1. The following information of every study site appears after clicking on each icon: name, vegetation type, soil type (38), soil texture (USDA classification, obtained from <http://soils.usda.gov/technical/aids/investigations/texture/>), slope, annual mean precipitation, annual mean temperature, species richness, multifunctionality index, carbon cycling index, nitrogen cycling index, and phosphorus cycling index. The free software Google Earth (<http://www.google.com/earth/index.html>) is needed to view the file.

References and Notes

1. B. J. Cardinale *et al.*, The functional role of producer diversity in ecosystems. *Am. J. Bot.* **98**, 572 (2011). [doi:10.3732/ajb.1000364](https://doi.org/10.3732/ajb.1000364) [Medline](#)
2. D. U. Hooper *et al.*, Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* **75**, 3 (2005). [doi:10.1890/04-0922](https://doi.org/10.1890/04-0922)
3. A. Hector *et al.*, Plant diversity and productivity experiments in European grasslands. *Science* **286**, 1123 (1999). [doi:10.1126/science.286.5442.1123](https://doi.org/10.1126/science.286.5442.1123) [Medline](#)
4. P. Flombaum, O. E. Sala, Higher effect of plant species diversity on productivity in natural than artificial ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 6087 (2008). [doi:10.1073/pnas.0704801105](https://doi.org/10.1073/pnas.0704801105) [Medline](#)
5. Millennium Ecosystem Assessment, *Ecosystems and Human Well-Being: Biodiversity Synthesis* (World Resources Institute, Washington, DC, 2005).
6. S. Naeem, D. E. Bunker, A. Hector, M. Loreau, C. Perrings, Eds., *Biodiversity, Ecosystem Functioning and Human Wellbeing. An Ecological and Economic Perspective* (Oxford Univ. Press, Oxford, 2009).
7. Z. Guo, L. Zhang, Y. Li, Increased dependence of humans on ecosystem services and biodiversity. *PLoS ONE* **5**, e13113 (2010). [doi:10.1371/journal.pone.0013113](https://doi.org/10.1371/journal.pone.0013113)
8. E. S. Zavaleta, J. R. Pasari, K. B. Hulvey, G. D. Tilman, Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 1443 (2010). [doi:10.1073/pnas.0906829107](https://doi.org/10.1073/pnas.0906829107) [Medline](#)
9. F. Isbell *et al.*, High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199 (2011). [doi:10.1038/nature10282](https://doi.org/10.1038/nature10282) [Medline](#)
10. A. Hector, R. Bagchi, Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188 (2007). [doi:10.1038/nature05947](https://doi.org/10.1038/nature05947) [Medline](#)
11. L. Gamfeldt, H. Hillebrand, P. R. Jonsson, Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* **89**, 1223 (2008). [doi:10.1890/06-2091.1](https://doi.org/10.1890/06-2091.1) [Medline](#)
12. F. T. Maestre, A. P. Castillo-Monroy, M. Bowker, R. Ochoa-Hueso, Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. *J. Ecol.* 10.1111/j.1365-2745.2011.01918.x (2011).
13. F. T. Maestre *et al.*, Do biotic interactions modulate ecosystem functioning along stress gradients? Insights from semi-arid plant and biological soil crust communities. *Phil. Trans. R. Soc. B* **365**, 2057 (2010). [doi:10.1098/rstb.2010.0016](https://doi.org/10.1098/rstb.2010.0016) [Medline](#)
14. J. A. Godbold, M. Solan, Relative importance of biodiversity and the abiotic environment in mediating an ecosystem process. *Mar. Ecol. Prog. Ser.* **396**, 273 (2009). [doi:10.3354/meps08401](https://doi.org/10.3354/meps08401)
15. D. A. Wardle, M. Jonsson, Biodiversity effects in real ecosystems—a response to Duffy. *Front. Ecol. Environ* **8**, 10 (2010). [doi:10.1890/10.WB.002](https://doi.org/10.1890/10.WB.002)

16. J. F. Reynolds *et al.*, Global desertification: Building a science for dryland development. *Science* **316**, 847 (2007). [doi:10.1126/science.1131634](https://doi.org/10.1126/science.1131634) [Medline](#)
17. R. P. White, J. Nackoney, *Drylands, People, and Ecosystem Goods and Services: A Web-Based Geospatial Analysis* (World Resources Institute, Washington, DC, 2003); www.wri.org/publication/content/8241.
18. Millennium Ecosystem Assessment, *Ecosystems and Human Well-being: Desertification Synthesis* (World Resources Institute, Washington, DC, 2005).
19. A search on the Institute for Scientific Information's Web of Science (18 November 2011) using the keywords "species AND (diversity OR richness) AND (community OR ecosystem) AND (function OR functioning OR production OR productivity OR biomass OR predation OR decomposition OR herbivory)" yielded 14,136 documents, only 2.5% of which contained the word "arid."
20. Materials and methods are available as supporting material on *Science* Online.
21. F. T. Maestre, A. Escudero, Is the patch size distribution of vegetation a suitable indicator of desertification processes? *Ecology* **90**, 1729 (2009). [doi:10.1890/08-2096.1](https://doi.org/10.1890/08-2096.1) [Medline](#)
22. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach* (Springer, New York, ed. 2, 2002).
23. J. A. F. Diniz-Filho, T. F. L. V. B. Rangel, L. M. Bini, Model selection and information theory in geographical ecology. *Glob. Ecol. Biogeogr.* **17**, 479 (2008). [doi:10.1111/j.1466-8238.2008.00395.x](https://doi.org/10.1111/j.1466-8238.2008.00395.x)
24. R. M. Pringle, T. P. Young, D. I. Rubenstein, D. J. McCauley, Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 193 (2007). [doi:10.1073/pnas.0609840104](https://doi.org/10.1073/pnas.0609840104) [Medline](#)
25. P. B. Adler *et al.*, Productivity is a poor predictor of plant species richness. *Science* **333**, 1750 (2011). [doi:10.1126/science.1204498](https://doi.org/10.1126/science.1204498) [Medline](#)
26. T. G. O'Connor, L. M. Haines, H. A. Snyman, Influence of precipitation and species composition on phytomass of a semi-arid African grassland. *J. Ecol.* **89**, 850 (2001). [doi:10.1046/j.0022-0477.2001.00605.x](https://doi.org/10.1046/j.0022-0477.2001.00605.x)
27. D. U. Hooper, P. M. Vitousek, Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* **68**, 121 (1998). [doi:10.1890/0012-9615\(1998\)068\[0121:EOPCAD\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1998)068[0121:EOPCAD]2.0.CO;2)
28. W. G. Whitford, *Ecology of Desert Systems* (Academic Press, San Diego, CA, 2002).
29. T. Wu, E. Ayres, R. D. Bardgett, D. H. Wall, J. R. Garey, Molecular study of worldwide distribution and diversity of soil animals. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 17720 (2011). [doi:10.1073/pnas.1103824108](https://doi.org/10.1073/pnas.1103824108) [Medline](#)

30. R. D. Evans, R. Rimer, L. Sperry, J. Belnap, Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecol. Appl.* **11**, 1301 (2001). [doi:10.1890/1051-0761\(2001\)011\[1301:EPIAND\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1301:EPIAND]2.0.CO;2)
31. S. Solomon *et al.*, *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, Cambridge, 2007).
32. O. E. Sala *et al.*, Global biodiversity scenarios for the year 2100. *Science* **287**, 1770 (2000). [doi:10.1126/science.287.5459.1770](https://doi.org/10.1126/science.287.5459.1770) [Medline](#)
33. J. A. Morgan *et al.*, C4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* **476**, 202 (2011). [doi:10.1038/nature10274](https://doi.org/10.1038/nature10274) [Medline](#)
34. F. I. Woodward, C. K. Kelly, Responses of global plant diversity capacity to changes in carbon dioxide concentration and climate. *Ecol. Lett.* **11**, 1229 (2008). [Medline](#)
35. N. J. Middleton, D. S. G. Thomas, Eds., *World Atlas of Desertification* (United Nations Environment Programme, Edward Arnold, New York, 1997).
36. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965 (2005). [doi:10.1002/joc.1276](https://doi.org/10.1002/joc.1276)
37. W. G. Whitford, *Ecology of Desert Systems* (Academic Press, San Diego, CA, 2002)
38. Food and Agriculture Organization (FAO), *World Reference Base for Soil Resources* (FAO, Rome, 1998).
39. P. Kutiel, Slope aspect effect on soil and vegetation in a Mediterranean Ecosystem. *Isr. J. Bot.* **41**, 243 (1992).
40. P. Kutiel, H. Lavee, Effect of slope aspect on soil and vegetation properties along an aridity transect. *Isr. J. Plant Sci.* **47**, 169 (1999).
41. M. Sternberg, M. Shoshany, Influence of slope aspect on Mediterranean woody formations: Comparison of a semiarid and an arid site in Israel. *Ecol. Res.* **16**, 335 (2001). [doi:10.1046/j.1440-1703.2001.00393.x](https://doi.org/10.1046/j.1440-1703.2001.00393.x)
42. A. Gómez-Plaza, M. Martínez, J. Albaladejo, V. M. Castillo, Factors regulating spatial distribution of soil water content in small semiarid catchments. *J. Hydrol. (Amst.)* **253**, 211 (2001). [doi:10.1016/S0022-1694\(01\)00483-8](https://doi.org/10.1016/S0022-1694(01)00483-8)
43. J. Bellot, F. T. Maestre, N. Hernandez, J. M. Ortiz de Urbina, Spatio-temporal dynamics of chlorophyll fluorescence in a semiarid Mediterranean shrubland. *J. Arid Environ.* **58**, 295 (2004). [doi:10.1016/j.jaridenv.2003.08.009](https://doi.org/10.1016/j.jaridenv.2003.08.009)
44. S. Matesanz, A. Escudero, F. Valladares, Impact of three global change drivers on a Mediterranean shrub. *Ecology* **90**, 2609 (2009). [doi:10.1890/08-1558.1](https://doi.org/10.1890/08-1558.1) [Medline](#)

45. D. J. Tongway, N. Hindley, *Landscape Function Analysis: Procedures for Monitoring and Assessing Landscapes* (Commonwealth Scientific and Industrial Research Organisation Publishing, Brisbane, Australia, 2004).
46. F. T. Maestre, A. Escudero, Is the patch size distribution of vegetation a suitable indicator of desertification processes? *Ecology* **90**, 1729 (2009). [doi:10.1890/08-2096.1](https://doi.org/10.1890/08-2096.1) [Medline](#)
47. C. E. Pake, D. L. Venable, Seed banks in desert annuals: Implications for persistence and coexistence in variable environments. *Ecology* **77**, 1427 (1996). [doi:10.2307/2265540](https://doi.org/10.2307/2265540)
48. N. J. Gotelli, R. K. Colwell, Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379 (2001). [doi:10.1046/j.1461-0248.2001.00230.x](https://doi.org/10.1046/j.1461-0248.2001.00230.x)
49. B. J. Cardinale *et al.*, The functional role of producer diversity in ecosystems. *Am. J. Bot.* **98**, 572 (2011). [doi:10.3732/ajb.1000364](https://doi.org/10.3732/ajb.1000364) [Medline](#)
50. A. E. Magurran, *Measuring Biological Diversity* (Blackwell, Oxford, 2004).
51. J. Reiss, J. R. Bridle, J. M. Montoya, G. Woodward, Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* **24**, 505 (2009). [doi:10.1016/j.tree.2009.03.018](https://doi.org/10.1016/j.tree.2009.03.018) [Medline](#)
52. K. Jax, *Ecosystem Functioning* (Cambridge Univ. Press, Cambridge, 2010).
53. A. Hector, R. Bagchi, Biodiversity and ecosystem multifunctionality. *Nature* **448**, 188 (2007). [doi:10.1038/nature05947](https://doi.org/10.1038/nature05947) [Medline](#)
54. L. Gamfeldt, H. Hillebrand, P. R. Jonsson, Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* **89**, 1223 (2008). [doi:10.1890/06-2091.1](https://doi.org/10.1890/06-2091.1) [Medline](#)
55. E. S. Zavaleta, J. R. Pasari, K. B. Hulvey, G. D. Tilman, Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 1443 (2010). [doi:10.1073/pnas.0906829107](https://doi.org/10.1073/pnas.0906829107) [Medline](#)
56. K. H. Orwin *et al.*, Linkages of plant traits to soil properties and the functioning of temperate grassland. *J. Ecol.* **98**, 1074 (2010). [doi:10.1111/j.1365-2745.2010.01679.x](https://doi.org/10.1111/j.1365-2745.2010.01679.x)
57. F. T. Maestre *et al.*, Do biotic interactions modulate ecosystem functioning along stress gradients? Insights from semi-arid plant and biological soil crust communities. *Philos. Trans. R. Soc. London Ser. B* **365**, 2057 (2010). [doi:10.1098/rstb.2010.0016](https://doi.org/10.1098/rstb.2010.0016) [Medline](#)
58. P. Balvanera *et al.*, Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* **9**, 1146 (2006). [doi:10.1111/j.1461-0248.2006.00963.x](https://doi.org/10.1111/j.1461-0248.2006.00963.x) [Medline](#)

59. F. Isbell *et al.*, High plant diversity is needed to maintain ecosystem services. *Nature* **477**, 199 (2011). [doi:10.1038/nature10282](https://doi.org/10.1038/nature10282) [Medline](#)
60. Millennium Ecosystem Assessment, *Ecosystems and Human Well-being: Synthesis* (Island Press, Washington, DC, 2005).
61. R. Zornoza *et al.*, Assessing air-drying and rewetting pre-treatment effect on some soil enzyme activities under Mediterranean conditions. *Soil Biol. Biochem.* **38**, 2125 (2006). [doi:10.1016/j.soilbio.2006.01.010](https://doi.org/10.1016/j.soilbio.2006.01.010)
62. R. Zornoza, J. Mataix-Solera, C. Guerrero, V. Arcenegui, J. Mataix-Beneyto, Storage effects on biochemical properties of air-dried soil samples from southeastern Spain. *Arid Land Res. Manage.* **23**, 213 (2009). [doi:10.1080/15324980903038727](https://doi.org/10.1080/15324980903038727)
63. Z. Jin, Y. S. Dong, Y. C. Qi, Z. S. An, Soil respiration and net primary productivity in perennial grass and desert shrub ecosystems at the Ordos Plateau of Inner Mongolia, China. *J. Arid Environ.* **74**, 1248 (2010). [doi:10.1016/j.jaridenv.2010.05.018](https://doi.org/10.1016/j.jaridenv.2010.05.018)
64. C. Hbirkou *et al.*, Reducing topsoil salinity and raising carbon stocks through afforestation in Khorezm, Uzbekistan. *J. Arid Environ.* **75**, 146 (2011). [doi:10.1016/j.jaridenv.2010.09.018](https://doi.org/10.1016/j.jaridenv.2010.09.018)
65. L. Zedda *et al.*, Distribution patterns of soil lichens across the principal biomes of southern Africa. *J. Arid Environ.* **75**, 215 (2011). [doi:10.1016/j.jaridenv.2010.10.007](https://doi.org/10.1016/j.jaridenv.2010.10.007)
66. Y. Qiu, B. Fu, J. Wang, L. Chen, Spatial variability of soil moisture content and its relation to environmental indices in a semi-arid gully catchment of the Loess Plateau, China. *J. Arid Environ.* **49**, 723 (2001). [doi:10.1006/jare.2001.0828](https://doi.org/10.1006/jare.2001.0828)
67. F. T. Maestre *et al.*, Microsite and mycorrhizal inoculum effects on the establishment of *Quercus coccifera* in a semi-arid degraded steppe. *Ecol. Eng.* **19**, 289 (2002). [doi:10.1016/S0925-8574\(02\)00097-6](https://doi.org/10.1016/S0925-8574(02)00097-6)
68. Y. Cantón, A. Solé, F. Domingo, Temporal and spatial patterns of soil moisture in semiarid badlands of SE Spain. *J. Hydrol. (Amst.)* **285**, 199 (2004). [doi:10.1016/j.jhydrol.2003.08.018](https://doi.org/10.1016/j.jhydrol.2003.08.018)
69. A. P. Castillo-Monroy, F. T. Maestre, A. Rey, S. Soliveres, P. Garcia-Palacios, Biological soil crust microsites are the main contributor to soil respiration in a semiarid ecosystem. *Ecosystems (N. Y.)* **14**, 835 (2011). [doi:10.1007/s10021-011-9449-3](https://doi.org/10.1007/s10021-011-9449-3)
70. J. M. Anderson, J. S. I. Ingram, Eds., *Tropical Soil Biology and Fertility: A Handbook of Methods* (CABI, Wallingford, UK, ed. 2, 1993).
71. S. R. Olsen, L. E. Sommers, in *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties*, A. L. Page, R. H. Miller, D. R. Keeney, Eds. (American Society of Agronomy and Soil Science Society of America, Madison, WI, 1982), pp. 403–427.

72. R. H. Bray, L. T. Kurtz, Determination of total, organic, and available forms of phosphorus in soils. *Soil Sci.* **59**, 39 (1945). [doi:10.1097/00010694-194501000-00006](https://doi.org/10.1097/00010694-194501000-00006)
73. M. A. Tabatabai, J. M. Bremner, Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. *Soil Biol. Biochem.* **1**, 301 (1969). [doi:10.1016/0038-0717\(69\)90012-1](https://doi.org/10.1016/0038-0717(69)90012-1)
74. M. A. Tabatabai, in *Methods of Soil Analyses Part 2, Chemical and Microbiological Properties*, A. L. Page, R. H. Miller, D. R. Keeney, Eds. (American Society of Agronomy, Madison, WI, 1982), pp. 903–947.
75. D. L. Jones, V. B. Willett, Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. *Soil Biol. Biochem.* **38**, 991 (2006). [doi:10.1016/j.soilbio.2005.08.012](https://doi.org/10.1016/j.soilbio.2005.08.012)
76. M. H. Chantigny, D. A. Angers, K. Kaiser, K. Kalbitz, in *Soil Sampling and Methods of Analysis*, M. R. Carter, E. G. Gregorich, Eds. (Canadian Society of Soil Science, 2006), pp. 617–635.
77. G. K. Sims, T. R. Ellsworth, R. L. Mulvaney, Microscale determination of inorganic nitrogen in water and soil extracts. *Commun. Soil Sci. Plan* **26**, 303 (1995). [doi:10.1080/00103629509369298](https://doi.org/10.1080/00103629509369298)
78. M. Delgado-Baquerizo, A. Gallardo, Depolymerization and mineralization rates at 12 Mediterranean sites with varying soil N availability. A test for the Schimel and Bennett model. *Soil Biol. Biochem.* **43**, 693 (2011). [doi:10.1016/j.soilbio.2010.11.030](https://doi.org/10.1016/j.soilbio.2010.11.030)
79. C. H. Körner, The use of ‘altitude’ in ecological research. *Trends Ecol. Evol.* **22**, 569 (2007). [doi:10.1016/j.tree.2007.09.006](https://doi.org/10.1016/j.tree.2007.09.006) [Medline](#)
80. Y. Cantón, F. Domingo, A. Solé, J. Puigdefábregas, Influence of soil-surface types on the overall runoff of the Tabernas badlands (south-east Spain): Field data and model approaches. *Hydrol. Processes* **16**, 2621 (2002). [doi:10.1002/hyp.1052](https://doi.org/10.1002/hyp.1052)
81. D. L. Dunkerley, Infiltration rates and soil moisture in a groved mulga community near Alice Springs, arid central Australia: Evidence for complex internal rainwater redistribution in a runoff-runon landscape. *J. Arid Environ.* **51**, 199 (2002). [doi:10.1006/jare.2001.0941](https://doi.org/10.1006/jare.2001.0941)
82. E. Bochet, P. Garcia Fayos, Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia, Spain. *Restor. Ecol.* **12**, 166 (2004). [doi:10.1111/j.1061-2971.2004.0325.x](https://doi.org/10.1111/j.1061-2971.2004.0325.x)
83. M. Boer, J. Puigdefábregas, Effects of spatially structured vegetation patterns on hillslope erosion in a semiarid Mediterranean environment: A simulation study. *Earth Surf. Process. Landf.* **30**, 149 (2005). [doi:10.1002/esp.1180](https://doi.org/10.1002/esp.1180)

84. T. A. Kettler, J. W. Doran, T. L. Gilbert, Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Sci. Soc. Am. J.* **65**, 849 (2001). [doi:10.2136/sssaj2001.653849x](https://doi.org/10.2136/sssaj2001.653849x)
85. F. Qi, E. Kuniyiko, C. Guodong, Soil water and chemical characteristics of sandy soils and their significance to land reclamation. *J. Arid Environ.* **51**, 35 (2002). [doi:10.1006/jare.2001.0928](https://doi.org/10.1006/jare.2001.0928)
86. F. T. Maestre, J. Cortina, S. Bautista, J. Bellot, R. Vallejo, Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. *Ecosystems (N. Y.)* **6**, 630 (2003). [doi:10.1007/s10021-002-0222-5](https://doi.org/10.1007/s10021-002-0222-5)
87. A. Mills, M. Fey, J. Donaldson, S. Todd, L. Theron, Soil infiltrability as a driver of plant cover and species richness in the semi-arid Karoo, South Africa. *Plant Soil* **320**, 321 (2009). [doi:10.1007/s11104-009-9904-5](https://doi.org/10.1007/s11104-009-9904-5)
88. J. M. Cable *et al.*, The temperature responses of soil respiration in deserts: A seven desert synthesis. *Biogeochemistry* **103**, 71 (2011).
89. R. J. Zomer, A. Trabucco, O. van Straaten, D. A. Bossio, *Carbon, Land and Water: A Global Analysis of the Hydrologic Dimensions of Climate Change Mitigation Through Afforestation/Reforestation* [International Water Management Institute (IWMI) Research Report 101, IWMI, Colombo, Sri Lanka, 2006].
90. G. P. Quinn, M. J. Keough, *Experimental Design and Data Analysis for Biologists* (Cambridge Univ. Press, Cambridge, 2002).
91. M. J. Metzger, R. G. H. Bunce, R. H. G. Jongman, C. A. Mucher, J. W. Watkins, A climatic stratification of the environment of Europe. *Glob. Ecol. Biogeogr.* **14**, 549 (2005). [doi:10.1111/j.1466-822X.2005.00190.x](https://doi.org/10.1111/j.1466-822X.2005.00190.x)
92. M. A. Bowker, S. Soliveres, F. T. Maestre, Competition increases with abiotic stress and regulates the diversity of biological soil crusts. *J. Ecol.* **98**, 551 (2010). [doi:10.1111/j.1365-2745.2010.01647.x](https://doi.org/10.1111/j.1365-2745.2010.01647.x)
93. S. Maltez-Mouro, F. T. Maestre, H. Freitas, Co-occurrence patterns and abiotic stress in sand-dune communities: Their relationship varies with spatial scale and the stress estimator. *Acta Oecol.* **36**, 80 (2010). [doi:10.1016/j.actao.2009.10.003](https://doi.org/10.1016/j.actao.2009.10.003)
94. F. S. de Albuquerque, P. Castro-Díez, M. Á. Rodríguez, L. Cayuela, Assessing the influence of environmental and human factors on native and exotic species richness. *Acta Oecol.* **37**, 51 (2011). [doi:10.1016/j.actao.2010.11.006](https://doi.org/10.1016/j.actao.2010.11.006)
95. J. J. Stachowicz, J. Bruno, J. E. Duffy, Understanding the effects of marine biodiversity on communities and ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **38**, 739 (2007). [doi:10.1146/annurev.ecolsys.38.091206.095659](https://doi.org/10.1146/annurev.ecolsys.38.091206.095659)
96. A. Gallardo, W. H. Schlesinger, Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. *Biogeochemistry* **18**, 1 (1992). [doi:10.1007/BF00000423](https://doi.org/10.1007/BF00000423)

97. A. Gallardo, W. H. Schlesinger, Factors determining soil microbial biomass and nutrient immobilization in desert soils. *Biogeochemistry* **28**, 55 (1995). [doi:10.1007/BF02178061](https://doi.org/10.1007/BF02178061)
98. J. Abadín, S. J. Gonzalez-Prieto, T. Carballas, Relationships among main soil properties and three N availability indices. *Plant Soil* **339**, 193 (2011). [doi:10.1007/s11104-010-0568-y](https://doi.org/10.1007/s11104-010-0568-y)
99. M. J. Merrick, R. A. Edwards, Nitrogen control in bacteria. *Microbiol. Rev.* **59**, 604 (1995). [Medline](#)
100. G. A. Marzluf, Genetic regulation of nitrogen metabolism in the fungi. *Microbiol. Mol. Biol. Rev.* **61**, 17 (1997). [Medline](#)
101. R. Aerts, F. S. Chapin III, The mineral nutrition of wild plants revisited: A reevaluation of processes and patterns. *Adv. Ecol. Res* **30**, 1 (1999). [doi:10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1)
102. D. Geisseler, W. R. Horwath, R. G. Joergensen, B. Ludwig, Pathways of nitrogen utilization by soil microorganisms—A review. *Soil Biol. Biochem.* **42**, 2058 (2010). [doi:10.1016/j.soilbio.2010.08.021](https://doi.org/10.1016/j.soilbio.2010.08.021)
103. F. J. Stevenson, *Nitrogen in Agricultural Soils* (Soil Science Society of America, Madison, WI, 1982).
104. D. L. Jones, J. R. Healey, V. B. Willett, J. F. Farrar, A. Hodge, Dissolved organic nitrogen uptake by plants—an important N uptake pathway? *Soil Biol. Biochem.* **37**, 413 (2005). [doi:10.1016/j.soilbio.2004.08.008](https://doi.org/10.1016/j.soilbio.2004.08.008)
105. F. S. Chapin III, L. Moilanen, K. Kielland, Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature* **361**, 150 (1993). [doi:10.1038/361150a0](https://doi.org/10.1038/361150a0)
106. K. Kalbitz, S. Solinger, J. H. Park, B. Michalzik, E. Matzner, Controls on the dynamics of dissolved organic matter in soils: A review. *Soil Sci.* **165**, 277 (2000). [doi:10.1097/00010694-200004000-00001](https://doi.org/10.1097/00010694-200004000-00001)
107. J. C. Neff, F. S. Chapin, P. M. Vitousek, The role of dissolved organic nitrogen in nutrient retention and plant mineral nutrition; reconciling observations with ecological theory. *Front. Ecol. Environ* **1**, 42 (2003).
108. J. P. Schimel, J. Bennett, Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* **85**, 591 (2004). [doi:10.1890/03-8002](https://doi.org/10.1890/03-8002)
109. D. L. Jones, D. Shannon, T. Junvee-Fortune, J. F. Farrar, Plant capture of free amino acids is maximized under high soil amino acid concentrations. *Soil Biol. Biochem.* **37**, 179 (2005). [doi:10.1016/j.soilbio.2004.07.021](https://doi.org/10.1016/j.soilbio.2004.07.021)
110. Y. P. Chen, G. Lopez-de-Victoria, C. R. Lovell, Utilization of aromatic compounds as carbon and energy sources during growth and N₂-fixation by freeliving nitrogen fixing bacteria. *Arch. Microbiol.* **159**, 207 (1993). [doi:10.1007/BF00248473](https://doi.org/10.1007/BF00248473)

111. J. P. Schimel, K. Van Cleve, R. G. Cates, T. P. Clausen, P. B. Reichardt, Effects of balsam poplar (*Populus balsamifera*) tannins and low molecular weight phenolics on microbial activity in taiga floodplain soil: Implications for changes in N cycling during succession. *Can. J. Bot.* **74**, 84 (1996). [doi:10.1139/b96-012](https://doi.org/10.1139/b96-012)
112. X. C. Souto, G. Chiapusio, F. Pellissier, Relationships between phenolics and soil microorganisms in spruce forests: significance for natural regeneration. *J. Chem. Ecol.* **26**, 2025 (2000). [doi:10.1023/A:1005504029243](https://doi.org/10.1023/A:1005504029243)
113. R. L. Sinsabaugh *et al.*, Stoichiometry of soil enzyme activity at global scale. *Ecol. Lett.* **11**, 1252 (2008). [Medline](#)
114. E. L. Rice, S. K. Pancholy, Inhibition of nitrification by climax ecosystems. II. Additional evidence and possible role of tannins. *Am. J. Bot.* **60**, 691 (1973). [doi:10.2307/2441448](https://doi.org/10.2307/2441448)
115. I. T. Baldwin, R. K. Olson, W. A. Reiners, Protein binding phenolics and the inhibition of nitrification in subalpine balsam fir soils. *Soil Biol. Biochem.* **15**, 419 (1983). [doi:10.1016/0038-0717\(83\)90006-8](https://doi.org/10.1016/0038-0717(83)90006-8)
116. G. P. Robertson, H. A. Vitousek, Nitrification potentials in primary and secondary succession. *Ecology* **62**, 376 (1981). [doi:10.2307/1936712](https://doi.org/10.2307/1936712)
117. T. DeLuca, M.-C. Nilsson, O. Zackrisson, Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia* **133**, 206 (2002). [doi:10.1007/s00442-002-1025-2](https://doi.org/10.1007/s00442-002-1025-2)
118. D. Mouillot, S. Villéger, M. Scherer-Lorenzen, N. W. H. Mason, Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE* **6**, e17476 (2011). [doi:10.1371/journal.pone.0017476](https://doi.org/10.1371/journal.pone.0017476) [Medline](#)
119. J. Z. He, Y. Ge, Z. Xu, C. Chen, Linking soil bacterial biodiversity to ecosystem multi-functionality using backward-elimination boosted trees analysis. *J. Soils Sediments* **9**, 547 (2009). [doi:10.1007/s11368-009-0120-y](https://doi.org/10.1007/s11368-009-0120-y)
120. H. Peter *et al.*, Multifunctionality and diversity in bacterial biofilms. *PLoS ONE* **6**, e23225 (2011). [doi:10.1371/journal.pone.0023225](https://doi.org/10.1371/journal.pone.0023225) [Medline](#)
121. J. Pasari, T. Levi, E. S. Zavaleta, G. D. Tilman, paper presented at the 89th Annual Meeting of the Ecological Society of America, Austin, TX, 8 August 2011.
122. N. J. Gotelli, W. Ulrich, F. T. Maestre, Randomization tests for quantifying species importance to ecosystem function. *Method. Ecol. Evol.* 10.1111/j.2041-210X.2011.00121.x (2011).
123. M. Etienne, Non destructive methods for evaluating shrub biomass: A review. *Acta Oecol.* **10**, 115 (1989).
124. N. Montès, T. Gauquelin, W. Badri, V. Bertaudiere, E. H. Zaoui, A nondestructive method for estimating above-ground forest biomass in threatened woodlands. *For. Ecol. Manage.* **130**, 37 (2000). [doi:10.1016/S0378-1127\(99\)00188-7](https://doi.org/10.1016/S0378-1127(99)00188-7)

125. J. M. Paruelo, W. K. Lauenroth, P. A. Roset, Estimating aboveground plant biomass using a photographic technique. *J. Range Manage.* **53**, 190 (2000). [doi:10.2307/4003281](https://doi.org/10.2307/4003281)
126. P. Flombaum, O. E. Sala, A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments. *J. Arid Environ.* **69**, 352 (2007). [doi:10.1016/j.jaridenv.2006.09.008](https://doi.org/10.1016/j.jaridenv.2006.09.008)
127. C. F. Dormann *et al.*, Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography* **30**, 609 (2007). [doi:10.1111/j.2007.0906-7590.05171.x](https://doi.org/10.1111/j.2007.0906-7590.05171.x)
128. W. D. Kissling, G. Carl, Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.* **17**, 59 (2008).
129. L. M. Bini *et al.*, Coefficient shifts in geographical ecology: An empirical evaluation of spatial and non-spatial regression. *Ecography* **32**, 193 (2009). [doi:10.1111/j.1600-0587.2009.05717.x](https://doi.org/10.1111/j.1600-0587.2009.05717.x)
130. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodel Inference. A Practical Information-Theoretical Approach* (Springer-Verlag, New York, 2002).
131. J. B. Johnson, K. S. Omland, Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**, 101 (2004). [doi:10.1016/j.tree.2003.10.013](https://doi.org/10.1016/j.tree.2003.10.013) [Medline](#)
132. J. A. F. Diniz-Filho, T. F. L. V. B. Rangel, L. M. Bini, Model selection and information theory in geographical ecology. *Glob. Ecol. Biogeogr.* **17**, 479 (2008). [doi:10.1111/j.1466-8238.2008.00395.x](https://doi.org/10.1111/j.1466-8238.2008.00395.x)
133. B. A. Hawkins, J. A. F. Diniz-Filho, L. M. Bini, P. De Marco, T. M. Blackburn, Red herrings revisited: Spatial autocorrelation and parameter estimation in geographical ecology. *Ecography* **30**, 375 (2007).
134. J. A. Hoeting, R. A. Davis, A. A. Merton, S. E. Thompson, Model selection for geostatistical models. *Ecol. Appl.* **16**, 87 (2006). [doi:10.1890/04-0576](https://doi.org/10.1890/04-0576) [Medline](#)
135. A. S. Fotheringham, C. Brunsdon, M. Charlton, *Geographically Weighted Regression: The Analysis of Spatially Varying Relationships* (Wiley, Hoboken, NJ, 2002).
136. S. Chatterjee, B. Price, *Regression Analysis by Example* (Wiley, New York, ed. 2, 2001).
137. T. F. Rangel, J. A. F. Diniz-Filho, L. M. Bini, SAM: A comprehensive application for spatial analysis in macroecology. *Ecography* **33**, 46 (2010). [doi:10.1111/j.1600-0587.2009.06299.x](https://doi.org/10.1111/j.1600-0587.2009.06299.x)