FUNCTIONAL AND STRUCTURAL CONVERGENCE OF TEMPERATE GRASSLAND AND SHRUBLAND ECOSYSTEMS

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Abstract. We analyzed the similarity of structural and functional characteristics of temperate grassland and shrubland ecosystems of North and South America. We based our analyses on correlative models that describe the climatic controls of grassland and shrubland structure and functioning at regional scales. We evaluated models that describe the regional distribution of plant functional types (C_3 and C_4 grasses and shrubs), soil organic carbon (SOC), and aboveground net primary production (ANPP) and its seasonality. To evaluate the predictive power of the models, we compared their estimates against observed data. We derived data sets, independent from those used to generate the models in North America, from climatically similar areas in South America.

Our results support the notion that, in climatically similar regions, structural and functional attributes such as plant functional type composition, SOC, ANPP, and ANPP seasonality have similar environmental controls, independent of the evolutionary history of the regions. The study suggests the existence of an important degree of convergence at regional scales in both functional and structural attributes. It also points out differences in the regional patterns of some attributes that require further analyses.

Key words: ANPP; AVHRR/NOAA; ecosystem convergence; global change; grasslands; NDVI; plant functional types; regional scales; shrublands; soil organic carbon.

Introduction

An underlying hypothesis of many global vegetation models (e.g., see Box 1981, Parton et al. 1987, Prentice et al. 1992) is that, in climatically similar regions, structural and functional attributes of ecosystems have similar environmental controls, independent of the evolutionary history of their fauna and flora. This hypothesis, closely related to the idea of ecological convergence, suggests that it may be possible to predict ecosystem attributes for a region, using relationships between ecosystem attributes and environmental variables developed for geographically and evolutionarily unrelated regions. In this paper, we analyze the similarity of patterns of structural and functional characteristics of temperate grasslands and shrublands of North and South America.

The idea of ecological convergence has very important applied significance for evaluating large-scale ecological functioning in areas of the world in which no data are available. For instance, in vast areas of South America and Asia there are no available data on basic attributes, such as primary production or relative abundance of plant functional types, which are crucial for assessing ecosystem status and predicting the effects of global change. If convergence exists, we gain

sufficient confidence in applying global change simulations to these areas of the world, and can proceed with greater confidence in modeling such responses as regional or continental carbon balance. Convergence in the structure of vegetation (species richness or plant functional type (PFT) composition) has been documented for several biomes (Lowe et al. 1973, Mooney 1977, Orians and Solbrig 1977, Pielou 1979, Mares et al. 1985), with mediterranean ecosystems being the most studied (Mooney et al. 1970, Parsons and Moldenke 1975, di Castri 1981, Arroyo 1995).

The objective of this paper was to test the generality of several regional models developed for North America, using data for South America. We also present some potential applications of the models, such as the generation of scenarios of potential structure of the vegetation. Our analyses focused on correlative models that describe structural and functional characteristics of grasslands and shrublands at regional scales. We excluded from our analysis mechanistic models such as CENTURY (Parton et al. 1987), TEM (Raich et al. 1991), or Forest-BGC (Running and Coughlan 1988). These models serve a different purpose than correlative models, because they are better suited for extrapolating beyond the conditions for which they were developed. However, they require estimates of a larger number of parameters than do correlative models. Testing regional models in different geographic areas, but within the

same range of the driving variables, provides an independent assessment of their generality. Our approach in this paper consists of testing model predictions using data for a region climatically similar but geographically and evolutionarily unrelated to the region for which the models were developed.

North and South America offer a unique opportunity to test the generality of regional models. From a climatic viewpoint, temperate zones of North and South America show important similarities (Paruelo et al. 1995). In contrast, the flora and fauna of both continents are partially unrelated from an evolutionary viewpoint; North America belongs to the Holarctic realm and South America to the Neotropical realm (Udvardy 1975). North and South America remained isolated from each other until the late Pliocene ($\sim 2 \times 10^6$ of years ago), which determined different evolutionary pathways for the biota. North America shares only 67 of the 137 flowering plant families present in South America (Cox and Moore 1993). Milchunas et al. (1988) showed, for example, that the evolutionary history of grazing plays a central role in determining the response of ecosystems to grazing by domestic herbivores. North and South America differ markedly in their grazing evolutionary histories (Sala et al. 1986, Milchunas and Lauenroth 1993). Agricultural expansion started simultaneously on both continents (Cosby 1986) and land use practices have had dramatic effects on ecosystem structure and functioning over large regions of once temperate grasslands and shrublands (Burke et al. 1989, 1994, Aguiar et al. 1996). However, ecosystem responses to land use practices cannot be easily extrapolated from one temperate ecosystem to another.

We focused on models that describe the regional distribution of plant functional types (PFT) (Paruelo and Lauenroth 1996), soil organic carbon (Burke et al. 1989), and aboveground net primary production (ANPP) and its distribution throughout the year (Sala et al. 1988, Paruelo 1995, Paruelo and Lauenroth 1995). The attributes selected capture key features of ecosystem structure and functioning. The ecosystem characteristics represented by these models have a strong impact on regional and global climate (Pielke and Avissar 1990). Soil organic matter content is a critical variable in the carbon balance at both regional and global scales. Some of the attributes that the models describe also have important management applications. For example, aboveground net primary production (ANPP) and plant functional type composition affect ecosystem carrying capacity, and carbon content is tightly connected to soil fertility (Tiessen et al. 1994).

The models that we used were generated using sites in North America that corresponded to the tallgrass prairie, the Northern and Southern mixed prairie, the shortgrass steppe, the different types of shrub steppes of the intermountain west (sagebrush steppe, Great Basin sagebrush, saltbush–greasewood, etc.), and the Mo-

jave, Sonoran, and Chihuahuan deserts (Kuchler 1964, West 1983, MacMahon and Wagner 1985, Sims 1988). We tested model predictions in South America using sites that correspond to the Pampa grasslands, the Espinal savannas, and the Monte and Patagonian shrub–steppes (Cabrera 1976, Soriano 1983, Soriano 1991). Our analyses did not include mediterranean type vegetation (i.e., annual grasslands or chaparral).

METHODOLOGY

The models

The models that we used in this effort share some characteristics. First, they have a common scale and extent; they were formulated at regional scales and for grassland and shrubland areas of the temperate zones. All of the models were developed using data for central North America. For a number of reasons, this region is especially suitable for developing this kind of model: the availability of data, the range of climatic conditions, the smooth nature of the climatic gradients, and the near orthogonal distribution of precipitation and temperature gradients. All of the models analyzed are correlative models, in which soil characteristics or climatic variables with an annual or a seasonal resolution are the independent variables, and some characteristics of ecosystem structure and functioning are the dependent variables. Finally, the models are based on empirical data derived from comparative analysis of ecosystems at regional scales.

Plant functional type distribution.—Paruelo and Lauenroth (1996) described the distribution of the relative abundance of shrubs, C_3 grasses, and C_4 grasses in central North America, based on mean annual temperature (MAT), mean annual precipitation (MAP), and the proportion of the precipitation falling during summer (June, July, and August; SUM) and winter (December, January, and February; WIN) (Appendix). These correlative models were developed using field vegetation data for 73 sites distributed throughout central North America, all of which have low human impact. For each site, the relative abundance of each PFT was derived from published floristic information. We derived a relationship for the ratio of the relative abundance of C_3:C_4 grasses from the data presented by Paruelo and Lauenroth (1996) (model 1.1, Appendix). The percentage of C_4 grasses increased with MAT, MAP, and SUM. Relative abundance of shrubs (model 1.2) increased with the proportion of total precipitation occurring during winter, and decreased with total precipitation.

Patterns of soil organic carbon.—Burke et al. (1989) described the relationship between soil organic carbon and environmental variables (mean annual temperature, MAT; mean annual precipitation, MAP; percentage of silt, SLT; and percentage of clay, CLY) for the Central Grasslands region of the United States. They used data for >500 pedon descriptions for rangeland soils (model

2.1, Appendix). In general, soil organic carbon decreases with MAT and increases with MAP. Silt and clay content increase the carbon content of rangeland soils.

Soil organic carbon content results from the balance of primary production and decomposition. The positive response of organic carbon to MAP shows the effect of an increase in ANPP or carbon inputs. The negative response to temperature reflects the effect of this climatic variable on decomposition (McDaniel and Munn 1985).

Patterns of primary production.—Sala et al. (1988) developed a model (see model 3.1 in Appendix) that accounted for the regional pattern of ANPP as a function of mean annual precipitation (MAP) in the Central Grasslands of the United States. Paruelo and Lauenroth (1995) and Paruelo (1995) presented similar relationships for central North America, but they used an estimate of ANPP derived from remote sensing data: the integral through the year of the curve of the Normalized Difference Vegetation Index (NDVI), a spectral index calculated from the AVHRR/NOAA Local Area Coverage (LAC; spatial resolution of 1.1 km) reflectance data on the red and infrared bands (NDVI = (IR − R)/(IR + R)). When both field and remote sensing estimates of ANPP were used, MAP accounted for more than two-thirds of the regional variability in primary production.

For the present study, we used the relationship presented by Paruelo (1995), which was based on a 4-yr average of NDVI data (model 3.2, Appendix). This relationship was derived for 25 sites distributed over central North America. Sites covered areas of ≥ 9 km^2 and had low human impact. It has been shown both empirically and theoretically (Tucker and Sellers 1986, Box et al. 1989, Kennedy 1989, Running 1990, Prince 1991*a*, *b*) that there exists a strong correlation between the integral of the seasonal NDVI curve and ANPP. Paruelo et al. (1997) showed that, for the Central Grasslands of the United States, the 4-yr average NDVI integral (NDVI-I) used to derive model 3.2 was strongly correlated with the ANPP data from Sala et al. (1988) used to developed model 3.1. ANPP increased linearly with annual precipitation in the range 200–1300 mm/year.

Seasonality of primary production.—Paruelo and Lauenroth (1995) and Paruelo (1995) described the seasonality of the ANPP as a function of climatic variables, using two attributes of the seasonal curve of the NDVI: the difference between the maximum and minimum NDVI through the year (MAXMIN), and the date of the maximum NDVI (DOYMAX) (Appendix: models 4.1 and 4.2). Models 4.1 and 4.2 were also constructed from Large Area Coverage data from the NOAA/AVHRR satellites. They were developed for the same sites used to construct model 3.2 and for a 4-yr period. The models show that the difference between the maximum and minimum NDVI through the year

increases with mean annual precipitation (MAP) and decreases with mean annual temperature (MAT). The date of maximum NDVI (DOYMAX) occurred later in areas with high MAT and a high proportion of precipitation falling during summer (SUM) and spring (SPR).

Evaluation of model generality

We compared models' estimates against data sets independent from those used to generate the models. The new data sets corresponded to southern South America, a region climatically similar to central North America (Paruelo et al. 1995), but which belongs to a different biotic realm (Udvardy 1975) and has important differences in land use (Richards 1993) and evolutionary history (Sala et al. 1986, Milchunas and Lauenroth 1993).

We compared the relative abundance of shrubs and the proportion of C$_3$ and C$_4$ grasses derived from models 1.1 and 1.2 (Appendix) against data collected from the literature. Those data were derived from published and unpublished surveys of vegetation across South America (see Table 1). Relative abundance of the different plant functional types was based on either cover or biomass (Paruelo and Lauenroth 1996).

We compared the soil organic carbon content predicted by the model of Burke et al. (1989) against data derived from soil maps for South America (INTA 1990). For 40 sites in Argentina, we obtained the percentage of soil organic matter content for the most conspicuous soil subgroup of the map unit corresponding to each site (INTA 1990; Table 2). We also obtained information on the textural classes of the soil subgroup. Textural classes were converted into percentages of silt, sand, and clay using the USDA soil texture triangle (Rowell 1994). We used texture to calculate bulk density from Rawls (1983). We calculated soil carbon content of the upper 20 cm of the soil from the percentage of organic matter using a conversion factor of 0.58 g C/g organic matter (Rowell 1994) and bulk density values.

To test the relationship between ANPP and precipitation (MAP) (model 3.1), we compared the predictions of the Sala et al. (1988) model with ANPP data for South America reported by McNaughton et al. (1993). We obtained NDVI data for 14 sites in Argentina (Table 3), corresponding to a climatic range similar to the one used by Paruelo and Lauenroth (1995), to generate the models describing ANPP and its seasonality (models 3.2, 4.1, and 4.2). Data consisted of a 10-yr average of the NDVI calculated from NOAA/NASA Pathfinder AVHRR Land (PAL) program data (James and Kalluri 1994). Each of the 14 sites represents an area of 8 × 8 km. We compared the predictions of models 3.2, 4.1, and 4.2 against the actual NDVI data gathered for South America. Climatic data to test the models for Argentina were taken from FAO (1985), the National Meteorological Service of Argentina (SMN), the Instituto Nacional de Tecnología Agropecuaria

TABLE 1. Sites included in testing models of plant functional type distribution (Appendix, models 1.1 and 1.2), including approximate latitude (LAT) and longitude (LONG), relative abundance of shrubs (%), relative percentages of C_3 vs. C_4 grasses, the nearest weather station (WTH ST), mean annual temperature (MAT), mean annual precipitation (MAP), and the proportions of precipitation falling during summer (SUM) and winter (WIN).

LAT	LONG	Reference	Shrubs†	C_3	C_4	WTH ST	MAT	MAP	SUM	WIN
28.0	55.5	Martinez Crovetto (1965)		1	99	Posadas	21.2	1527	0.29	0.14
29.0	60.5	Lewis et al. (1990)		1	99	Corientes	21.5	1234	0.32	0.11
31.0	67.0	Cabido et al. (1993)[1]	65	0	100	San Juan	17.2	83	0.52	0.10
33.0	61.0	Lewis et al. (1985)	1	70	30	Rosario	16.7	1022	0.34	0.12
34.5	66.0	Anderson et al. (1970)[2]	11.5	30	70	San Luis	16.5	566	0.50	0.04
34.5	66.5	Anderson et al. (1970)[3]	57	31	69	San Luis	16.5	566	0.50	0.04
34.5	65.5	Leon and Marangon (1980)		26	74	San Luis	16.5	566	0.50	0.04
35.5	58.5	Leon et al. (1979)	1	52	48	Buenos Aires	16.9	986	0.27	0.19
38.0	67.0	Cano et al. (1980)[4]	32.5	100	0	Cipoletti	13.7	172	0.21	0.14
35.5	65.0	Cano et al. (1980)[5]	8	81	29	Santa Rosa	15.1	626	0.35	0.09
36.0	63.8	Cano et al. (1980)[6]		93	7	Macachin	15.2	608	0.32	0.12
36.0	63.8	Cano et al. (1980)[7]		84	16	Macachin	15.2	608	0.32	0.12
36.0	63.8	Cano et al. (1980)[8]		91	9	Macachin	15.2	608	0.32	0.12
38.0	65.5	Cano et al. (1980)[9]	42.5	89.5	10.5	Choele Choel	15.5	260	0.23	0.20
38.5	65.0	Cano et al. (1980)[10]	43.6	100	0	Choele Choel	15.5	260	0.23	0.20
38.5	65.0	Cano et al. (1980)[11]		94	6	Choele Choel	15.5	260	0.23	0.20
36.0	58.0	Burkart et al. (1990)	1	50	50	Dolores	14.7	879	0.25	0.23
36.5	63.0	Cabrera (1953)	1	49	51	Macachin	15.2	608	0.32	0.12
40.5	70.7	Paruelo et al. (*unpublished*)	35.5	100	0	Alicura	11.3	272	0.09	0.49
41.0	71.2	Golluscio et al. (*unpublished*)		100	0	San Ramon	8.6	638	0.10	0.47
41.2	70.7	Paruelo and Golluscio (1994)	22	100	0	Pilcaniyeu	7.41	304	0.06	0.37
42.9	71.1	Jobbágy et al. (1996)		100	0	Esquel	8.1	515	0.13	0.45
45.0	70.5	Golluscio et al. (1982)[12]	32	100	0	Rio Mayo	8.1	160	0.13	0.39
45.0	70.0	Golluscio et al. (1982)[13]	76.5	100	0	Sarmiento	10.8	132	0.13	0.34
45.0	71.5	Golluscio et al. (1982)[14]	7	100	0	Garzon	8.1	1100	0.12	0.47
45.8	68.5	Bertiller et al. (1981)		100	0	Sarmiento	10.8	132	0.13	0.34
48.8	70.2	Movia et al. (1987)[15]	71	100	0	Gregores	8.5	170	0.32	0.25
51.6	69.8	Borelli et al. (1988)		100	0	Rio Gallegos	6.9	222	0.36	0.21
52.0	72.0	Roig et al. (1985)		100	0	El Turbio	5.7	412	0.25	0.24
53.8	67.8	Collantes et al. (1989)		100	0	Rio Grande	5	378	0.29	0.18

Notes: Superscript numbers following the references denote the following study communities: [1] most xeric community; [2] Unit 1; [3] Unit 3; [4] open shrubland of *Larrea cuneifolia*; [5] patches of grassland in *Prosopis caldenia* forests; [6] grasslands of *Stipa tenuis* and *Piptochaetium napostaense*; [7] grasslands of *Elionurus muticus*; [8] patches of grassland in *Prosopis caldenia* forests; [9] shrubland of *Larrea divaricata*; [10] open shrubland of *Larrea divaricata*; [11] grassland with *Larrea divaricata*; [12] Community B; [13] Community C; [14] Community A; [15] average for cartographic Units E.

† Relative abundance of shrubs was not calculated for areas with patches of forest and was not available for all sites.

(INTA), WeatherDisc Associates (1994), and from data of Jobbágy et al. (1995). Relationships between simulated and observed data were evaluated by regression analyses (Dent and Blackie 1979). We specifically evaluated whether the slope and the *y*-intercept of the regression between observed and predicted values differed statistically from 1 and 0, respectively. The squared sum of the predictive error (SSPE = Σ_n (obs$_i$ − pre$_i$)^2) provides a measure of the goodness-of-fit (Smith and Rose 1995). We decompose the SSPE by calculating Theil's partial inequality coefficents (*U*) (Smith and Rose 1995). These coefficients distinguish between different sources of predictive error:

1) a proportion associated with mean differences between observed and predicted values,

$$U_{\text{bias}} = [n(\text{OBS} - \text{PRE})^2]/\text{SSPE};$$

2) a proportion associated with the slope (β) of the fitted model and the 1:1 line,

$$U_{\beta=1} = [(\beta - 1)^2 \Sigma_n (\text{pre}_i - \text{PRE})^2]/\text{SSPE};$$

3) a proportion associated with the unexplained variance,

$$U_e = \Sigma_n (\text{est}_i - \text{obs}_i)^2/\text{SSPE}$$

where obs and pre are the observed and predicted values, respectively; OBS and PRE are the means of the observed and predicted values, respectively; est are the values estimated from the fitted regression model; and *n* is the number of sites.

To evaluate biases related to sites included in the analyses, we randomly selected 20% of the South American sites, removed them from the data set, and recalculated the regression model between observed and predicted values. We repeated this procedure five times. We compared the r^2, slope, and *y*-intercept of the models generated using the incomplete data sets.

Potential applications

To illustrate the potential applications of the models, we presented a map of the potential distribution of PFT (models 1.1 and 1.2) as an example. To do that, we used a climatic database (Leemans and Cramer 1991) with a resolution of 0.5° of latitude and longitude. The database was constructed by interpolating actual climatic data from 2583 stations worldwide, including

TABLE 2. Soil organic carbon (SOC), percentages of clay (CLY) and silt (SLT), mean annual temperature (MAT), and mean annual precipitation (MAP), along with latitude (LAT), and longitude (LONG), for 40 sites in Argentina (INTA 1990).

LAT	LONG	Site	SOC†	MAT	MAP	CLY	SLT
26.8	60.5	R. Saenz Pena	2.778	21.6	1061	15	65
27.8	64.3	Stgo Del Estero	2.015	20.4	556	5	10
29.1	59.3	Goya	3.306	20.5	1131	10	15
29.2	62.0	Reconquista	4.047	19.8	1266	15	65
29.7	57.2	Paso De Los Libres	3.954	19.8	1443	20	50
31.3	58.0	Concordia	0.873	18.8	1185	5	5
31.8	60.5	Parana	3.601	18.0	1030	25	6
32.9	60.8	Rosario	4.157	16.7	1022	15	65
33.0	58.6	Gualegaychu	5.911	17.5	1054	35	55
33.1	64.3	Rio Cuarto	3.915	16.2	812	10	20
33.3	66.4	San Luis	1.894	16.5	566	20	40
34.0	63.4	Laboulaye	3.215	16.3	914	10	20
34.6	61.0	Junin	5.346	15.9	960	15	30
34.8	58.5	Ezeiza	5.697	16.2	982	15	65
35.9	61.9	Pehuajo	1.749	15.3	892	10	15
36.4	57.7	Dolores	3.699	14.7	879	20	40
36.5	63.0	Macachin	2.477	15.2	608	10	20
36.6	64.3	Sta Rosa	2.477	15.1	626	10	20
36.7	59.8	Azul	5.06	13.9	899	20	50
37.1	70.3	Chos Malal	0.9	16.2	565	15	15
37.4	64.6	Gral Acha	0.9	15.4	474	5	5
37.6	62.4	Pigue	5.059	13.5	782	20	50
37.9	57.6	Mar Del Plata	5.059	13.8	859	20	50
38.0	67.0	Cipoletti	0.945	15.6	172	50	45
38.0	65.0	Choele Choel	1.208	15.5	260	15	15
38.1	65.9	Puelches	0.873	15.2	375	10	20
38.3	60.3	Tres Arroyos	5.057	14.0	765	20	50
38.7	62.2	Com. Espora	2.332	14.7	598	35	35
39.0	68.0	Neuquen	1.208	15.9	161	5	10
40.7	65.0	San Antonio	1.208	5.1	242	5	10
41.0	71.2	San Ramon	1.042	8.6	638	5	10
41.2	70.7	Pilcaniyeu	1.042	7.4	304	5	10
41.2	71.2	Bariloche	3.215	8.2	880	15	15
41.3	68.7	Maquinchao	1.697	9.7	191	5	10
42.9	71.1	Leleque	3.215	8.4	489	10	20
43.2	65.3	Trelew	1.074	6.4	171	5	5
43.8	65.0	Paso De Indios	2.477	1.3	198	10	20
45.0	70.5	Rio Mayo	0.179	8.1	160	5	10
45.3	71.3	Media Luna	4.702	4.5	374	30	10
45.8	67.5	Comodoro	1.518	2.7	226	15	65

† Original soil organic matter content (%) for the most conspicuous soil subgroup of the map unit was converted into soil carbon content of the upper 20 cm of the soil, using a conversion factor of 0.58 g C g of organic matter (Rowell 1994) and bulk density values estimated from texture, using the equation presented by Rawls (1983).

TABLE 3. Observed data of the integral of Normalized Difference Vegetation Index (NDVI-I), the difference between maximum and minimum NDVI through the year (MAXMIN), and the date of maximum NDVI (DOYMAX) used in testing the Appendix models. Mean annual temperature (MAT), mean annual precipitation (MAP), and proportion of precipitation falling during summer (SUM) are given for the closest weather station to the site. Spectral data correspond to a 10-yr average of NOAA/NASA Pathfinder Land program data for an area of 8×8 km, with its center shown in the first two columns.

LAT	LONG	Site	NDVI-I†	MAXMIN	DOYMAX	MAT	MAP	SUM
29.2	66.5	La Rioja	0.201	0.236	261	19.8	326	0.54
31.2	66.4	Chepes	0.190	0.290	217	18.3	261	0.57
31.3	68.3	San Juan	0.014	0.025	244	17.2	83	0.52
33.2	66.2	San Luis	0.261	0.317	211	16.6	566	0.50
33.3	67.3	La Paz	0.099	0.148	246	16.0	250	0.52
36.0	59.1	Las Flores	0.373	0.353	209	15.4	919	0.26
36.2	57.4	Dolores	0.398	0.347	174	14.8	879	0.25
36.3	64.2	Santa Rosa	0.298	0.269	159	15.1	626	0.35
38.6	67.6	Neuquen	0.050	0.083	159	13.7	172	0.22
39.2	65.4	Choele	0.107	0.150	207	15.5	260	0.23
40.4	64.6	San Antonio	0.108	0.138	197	15.1	243	0.19
44.5	65.4	Camarones	0.087	0.135	109	12.5	180	0.18
45.4	71.3	Media Luna	0.288	0.442	182	4.5	374	0.13
45.4	70.2	Rio Mayo	0.083	0.140	172	8.1	160	0.13

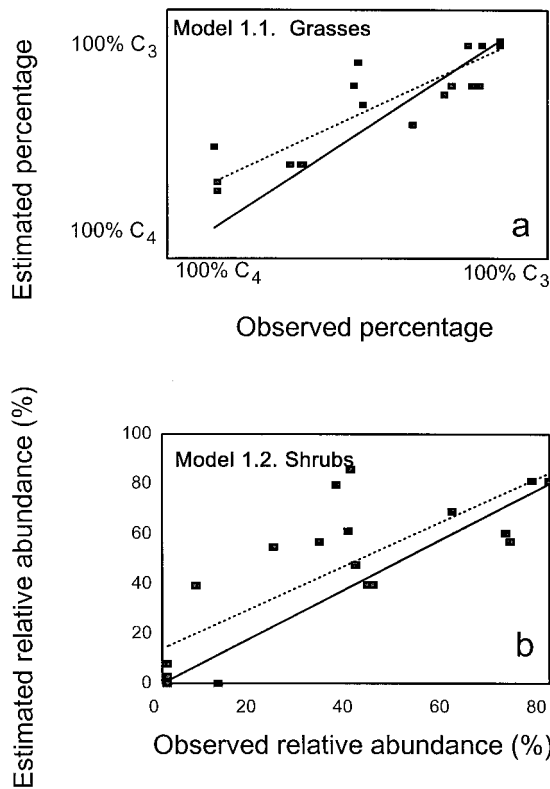† NDVI = (infrared band − red band)/(infrared band + red band).

FIG. 1. (a) Observed and predicted (model 1.1, Appendix) percentage of C_3 and C_4 grasses (Table 1). (b) Observed and predicted (model 1.2, Appendix) relative abundance of shrubs. The solid line corresponds to the 1:1 line and the dotted line to the best fit (Table 4). Solid squares represent the different sites analyzed.

monthly precipitation and temperature. We restricted our analysis to the temperate zones of North and South America occupied by grasslands or shrublands. The analyses were performed using ARC-INFO 7.0 (ESRI, Redlands, California).

RESULTS

Predicted and observed values of the percentage of C_3 and C_4 grasses showed a good agreement ($r^2 = 0.857$, $n = 30$, $P < 0.001$; see Fig. 1a and Table 4). The term associated with the unexplained variance had a large influence on the sum of squared values of the prediction error (SSPE), a measure of the goodness-of-fit (Table 5). The slope of the fitted regression line (Fig. 1a) was significantly <1 (Table 4), suggesting an overestimation of the relative proportion of C_3 grasses at the extreme of the gradient dominated by C_4 grasses. For 53% of the sites, there was a $<20\%$ mean percentage error of the prediction, MPE = ABS(pre − obs)/OBS, where pre and obs are the predicted and observed values, respectively, OBS is the mean of the observed values, and ABS is absolute value (Power 1993). For 20% of the sites, MPE was $>60\%$. The site showing the largest MPE corresponded to a shrubland

TABLE 4. *Y*-intercept, slope, and coefficient of determination of the regression model fitted to the observed and predicted values of the different ecosystem attributes analyzed (see Tables 2–4 for code definitions). All regression models were significant ($P < 0.001$). Values of the *y*-intercept and slope in boldface indicate significant differences from 0 and 1, respectively ($P < 0.01$).

Attribute	*y*-intercept	Slope	r^2
$C_3 : C_4$	0.0654	**0.7292**	0.857
Shrubs	0.1412	0.88	0.635
SOC	−0.1021	1.104	0.625
ANPP†	108.4	0.7932	0.632
NDVI-I	**0.09665**	**0.4765**	0.879
MAXMIN	0.03717	0.7139	0.577
DOYMAX	44.08	0.6229	0.533

† ANPP, aboveground net primary production.

desert with a small biomass of grasses. Some sites corresponding to the Flooding Pampa (Soriano et al. 1991) also showed a high MPE. For them, model 1.1 predicted a higher proportion of C_3 grasses. The relative proportion of C_3 and C_4 grasses of the different plant communities of the Flooding Pampa shows a high variability associated with edaphic factors (Perelman 1996).

The coefficient of determination of the regression between observed and predicted values of relative abundance of shrubs was 0.635 ($n = 19$, $P < 0.001$). The slope of the relationship did not differ significantly from 1 and the *y*-intercept did not differ from 0 (Fig. 1b, Table 4). As for the proportion of C_3 and C_4 grasses, the term associated with the unexplained variance was the most important in determining goodness-of-fit (SSPE; Table 5). For 42% of the sites, the MPE was $<20\%$; for 31% of the sites, it was $>60\%$. The Patagonian Steppe site had the largest differences between observed and predicted values. Even though it receives only 166 mm of mean annual precipitation, this site has a low relative abundance of shrubs, based either on biomass (Paruelo and Sala 1995), ANPP (Fernández et al. 1991) or on cover (Golluscio et al. 1982).

For the regression between observed and predicted values of SOC, $r^2 = 0.626$ ($n = 40$, $P < 0.001$). Most

TABLE 5. Squared sum of the predictive error (SSPE) and Theil's partial inequality coefficients (U_{bias}, $U_{\beta=1}$, and U_e) for the different attributes analyzed (codes are as in previous tables). These coefficients indicate different sources of predictive error: a proportion associated with mean differences between observed and predicted values, U_{bias}; a proportion associated with the slope (β) of the fitted model and the 1:1 line, $U_{\beta = 1}$; and a proportion associated with the unexplained variance, U_e.

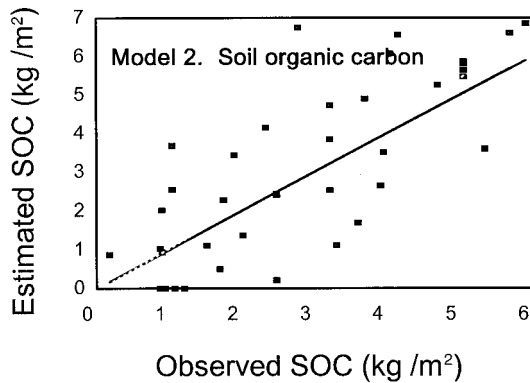| Attribute	SSPE	U_{bias}	$U_{\beta=1}$	U_e
$C_3 : C_4$	0.2225	0.086	0.107	0.807
Shrubs	0.796	0.231	0.158	0.611
SOC	78.79	0.012	0.486	0.496
ANPP	443 735	0.124	0.088	0.788
NDVI-I	0.06022	0.001	0.604	0.395
MAXMIN	0.09457	0.097	0.065	0.838
DOYMAX	22 936	0.546	0.0142	0.44

Fig. 2.   Observed and predicted (model 2, Appendix) soil organic carbon (SOC) for the upper 20 cm). The solid line corresponds to the 1:1 line and the dotted line to the best fit (Table 4).

of the observed lack of fit was associated with the unexplained variance (Table 5). The slope of the relationship did not differ significantly from 1 and the y-intercept did not differ from 0 (Fig. 2, Table 4). Of the sites, 50% showed a MPE <20% and only 2.5% had a MPE >60%.

For ANPP, the MPE was <20% for over 57% of the sites. The coefficient of determination of the regression model fitted to the observed and predicted values was 0.632 ($n = 14$, $P < 0.001$). The slope and the y-intercept of the fitted line did not differ significantly from 1 and 0, respectively (Fig. 3a, Table 4). Again, the unexplained variance made the largest contribution to the lack of fit. For our alternative descriptor of primary production, the NDVI integral, the correspondence between observed and predicted values was higher ($r^2 = 0.879$, $n = 14$, $P < 0.001$) than for ANPP. In this case, the lack of consistency (difference between the estimated slope and the 1:1 line) made the largest contribution to the lack of fit (Table 5). The slope and y-intercept of the fitted model differed significantly from 1 and 0, respectively (Fig. 3b). Differences in slope determined that even though predicted and observed values showed a high correlation, only 21% of the sites showed a MPE <20%.

Models 4.1 and 4.2 explore two aspects of the seasonality of NDVI: the difference between maximum and minimum values of NDVI, and the date of maximum NDVI. For both attributes, the correspondence between observed and predicted values was weaker than for the previous attributes considered ($r^2 = 0.577$ for the difference between maximum and minimum NDVI, and $r^2 = 0.533$ for the date of maximum NDVI; $n = 14$, $P < 0.001$). For the date of maximum NDVI, the lack of fit was mainly related to bias or mean differences between the observed and predicted values (Table 5). For the difference between maximum and minimum NDVI, the mayor contribution to SSPE was related to the unexplained variance. For both attributes of the NDVI seasonality, the slope and y-intercept of

the fitted line did not differ significantly from 1 and 0, respectively (Table 5). For 57% of the sites, MPE <20% for the difference between maximum and minimum. For the date of maximum NDVI, 47% of the sites showed a MPE <20%.

The agreement between observed and predicted values for the different attributes considered was relatively insensitive to the set of sites included in the regression model. The parameters and the coefficient of determination of regression between observed and predicted values were very similar for the five different subsets of the data (Table 6). There was, consequently, a small bias associated with the particular sites included in the analysis.

DISCUSSION

Our results support the notion that, in climatically similar regions, some structural and functional attributes (including plant functional type composition, soil organic carbon, and aboveground net primary production and its seasonality) have similar environmental controls, independent of the evolutionary history of the regions. For five out of seven attributes, the models generated for North American sites accounted for a larger fraction of the variance when applied to South
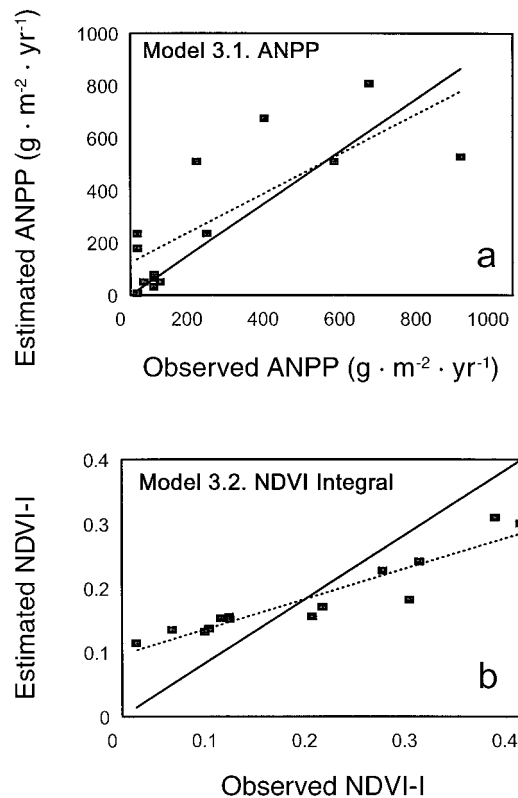

Fig. 3.   (a) Observed and predicted (model 3.1, Appendix) aboveground net primary production (ANPP) (g·m^{-2}·yr^{-1}). (b) Observed and predicted (model 3.2, Appendix) integral of NDVI throughout a year. The solid line corresponds to the 1:1 line and the dotted line to the best fit (Table 4).

TABLE 6. Coefficient of determination, slope, and *y*-intercept of the regression models between observed and predicted values for the seven attributes analyzed and for five subsets of the data. Subsets were produced by randomly deleting 20% of the points of the original data set.

	Data subsets				
Attributes	Set 1	Set 2	Set 3	Set 4	Set 5
Coefficient of determination					
$C_3:C_4$	0.798	0.903	0.793	0.846	0.904
Shrubs	0.699	0.606	0.672	0.695	0.759
SOC	0.679	0.517	0.594	0.596	0.606
ANPP	0.814	0.688	0.734	0.663	0.606
NDVI-I	0.898	0.884	0.839	0.894	0.898
MAXMIN	0.453	0.663	0.663	0.749	0.727
DOYMAX	0.403	0.493	0.553	0.649	0.548
Slope					
$C_3:C_4$	0.675	0.74	0.666	0.711	0.737
Shrubs	0.906	0.877	1	0.871	1.024
SOC	1.219	1.037	1.103	1.042	1.077
ANPP	1.1247	0.817	0.747	0.735	0.782
NDVI-I	0.481	0.484	0.445	0.478	0.604
MAXMIN	0.638	0.744	0.748	0.814	0.804
DOYMAX	0.536	0.429	0.489	0.588	0.404
y-intercept					
$C_3:C_4$	0.074	0.06	0.08	0.07	0.057
Shrubs	0.108	0.16	0.112	0.126	0.083
SOC	−0.381	−0.032	−0.188	−0.01	−0.159
ANPP	39	80	68	106	126
NDVI-I	0.098	0.095	0.101	0.097	0.053
MAXMIN	0.051	0.047	0.041	0.031	0.024
DOYMAX	68	84	73	52	99

America than when used in their original location (Appendix and Table 4).

Even though the floras of North and South America correspond to different floristic realms (the Holarctic and the Neotropic, respectively; Udvardy 1975), the distribution of plant functional types seems to respond to climate similarly in both regions. The prediction of the relative abundance of functional types was quite good for the proportion of C_3 and C_4 grasses (Fig. 1a) and less so for shrubs (Fig. 1b). It was clear that, in North and South America, the relative abundance of shrubs was higher in dry areas with precipitation concentrated in winter. In both regions, temperature, precipitation, and the distribution of precipitation seem to be the major controls of the relative proportion of C_3 and C_4 grasses.

The correlative model developed by Burke et al. (1989) for North American soils was able to represent the geographic differences in organic carbon found in grassland and shrubland soils of temperate South America (Fig. 2). This suggests that the same environmental factors are controlling the soil carbon content in both regions.

A large amount of evidence supports the existence of a linear relationship between ANPP and total precipitation for grassland and shrubland areas (Le Houéréou and Hoste 1977, Lauenroth 1979, Deshmukh 1984, McNaughton 1985, Sala et al. 1988, Milchunas and Lauenroth 1993). In spite of differences in the methods used to estimate ANPP in the field, and the effect of small-scale factors (soils, topography, etc.), the relationship between ANPP and precipitation is essentially the same in different geographic regions (McNaughton et al. 1993). ANPP is an integrative estimate of the functioning of ecosystems (McNaughton et al. 1989). Proper spatial representation of ANPP is critical at regional scales because it may allow one to infer some other ecosystem characteristics, such as hervibore biomass or secondary productivity (McNaughton et al. 1989, Oesterheld et al. 1992).

The same relationship between precipitation and ANPP based on field data was derived using the integral of the NDVI as an estimate of ANPP (Paruelo and Lauenroth 1995). Paruelo et al. (1993) for Patagonia, and Malo and Nicholson (1990) for the Sahel also reported a linear relationship between the NDVI integral and precipitation. Paruelo et al. (1997) showed a strong correlation between the NDVI-I and ANPP for the Central Grassland region of the United States. The similarity of the relationship with mean annual precipitation for both ANPP and the NDVI-I gives additional support to the interpretation of NDVI-I as an estimate of ANPP in grassland and shrubland ecosystems.

Although the observed and estimated NDVI-I showed a high correlation, the model tended to underestimate the highest values and to overestimate the lowest values (Fig. 3b). This discrepancy may have some biological reasons, but it may also be related to the data used to test the model. The NDVI-I–MAP model was generated using Local Area Coverage (LAC) data

with a 1.1-km resolution derived from the NOAA/ AVHRR satellites. To fit the model, the data of each square kilometer pixel were averaged over the area of the site, (9–36 km² (Paruelo and Lauenroth 1995). Because the same kind of LAC product (biweekly maximum composites of NDVI; see Eidenshink 1992 for details) was not available for Argentina, we used 10-d composites of Pathfinder AVHRR Land Program data (James and Kalluri 1994). Those data came from resampling the spectral reflectance measured by the AVHRR sensor of NOAA satellites, and they have a coarser resolution than LAC data (8 × 8 km). Additionally, the periods for which the North and South American data were averaged were not the same (1990–1993 for the LAC data and 1981–1992 for the South American PAL data), which implies the use of spectral data derived from different satellites of the NOAA series (NOAA 7 to NOAA 11). To check for some bias associated with the satellite data used, we analyzed the relationship between the NDVI-I derived from LAC and PAL data for seven of the 24 North American sites used to derive model 3.2 (we used only the largest sites included in Paruelo's (1995) analysis to allow for a proper localization of the area on the PAL image). The NDVI-I derived from PAL data was highly correlated with an estimate of NDVI-I derived from LAC data, NDVI-I (LAC) = 0.041 + 0.99 NDVI-I (PAL); $n = 7$, $r^2 = 0.72$, $P < 0.001$). The slope and the y-intercept of this relationship were not significantly different from 1 and 0, respectively, suggesting that both data sets give essentially the same regional picture for North America.

Model 4.2 underestimates the date of maximum NDVI. Differences in thermal amplitude between North and South America may be responsible for the delayed occurrence of the NDVI peak in South America (Fig. 4b). The larger size of North American continental masses determines a higher annual thermal amplitude in the Northern than in the Southern Hemisphere. Cooler summers in the Southern Hemisphere may delay the date of maximum NDVI by reducing evapotranspiration losses. Comparative analyses using matching sites in North and South America may provide further clues for the observed differences in NDVI seasonality.

There are uncertainties associated with the data that should be taken into account when evaluating these results. First, the models that we evaluated were based on point floristic information that was assumed to be representative of relatively large areas, based on the description of the sites. Therefore, the models did not take into account local spatial variability associated with soils or topography. The same is true for the data collected to test the models. Soil texture is a critical parameter in defining the proportion of shrubs in areas with intermediate levels of precipitation (Sala et al. 1997). Second, both for the data used to develop the models and for the data used to test them, it was assumed that relative abundance measures of functional
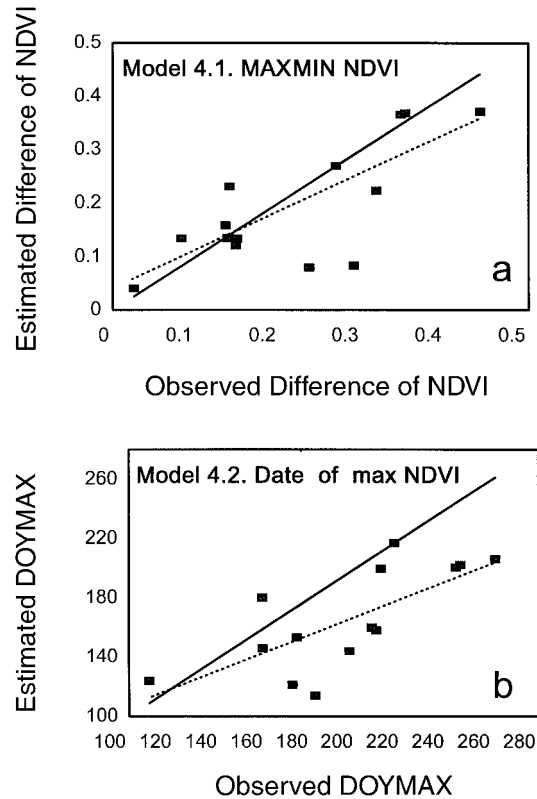

Fig. 4. (a) Observed and predicted (model 4.1, Appendix) difference between maximum and minimum NDVI. (b) Observed and predicted (model 4.2, Appendix) day of the year of the maximum value of NDVI of the year (DOYMAX). The solid line corresponds to the 1:1 line and the dotted line to the best fit (Table 4).

types calculated from cover, biomass, or frequency data were equivalent. Third, some of the South American points are located in regions with a steep precipitation gradient (Jobbágy et al. 1995); thus, the availability of weather stations did not guarantee a perfect representation of the climate of every point.

The study suggests the existence of an important degree of convergence, at regional scales, in both functional and structural attributes. It also points out differences in the regional patterns of some attributes that require further analyses. Do biases in the predicted relationships for South America indicate a partial lack of convergence between the ecosystems of North and South America, or do these biases reflect a need to include new abiotic variables in the models? Similarly, do biases result from biotic or abiotic, unaccounted-for phenomena? Do new models need to include new abiotic variables or a characterization of the evolutionary history? We currently cannot answer these questions, although we know that some climatic variables are not accounted for. North and South American sites that match on a mean annual temperature and precipitation basis may differ in some additional aspects that may account for different ecosystem patterns.
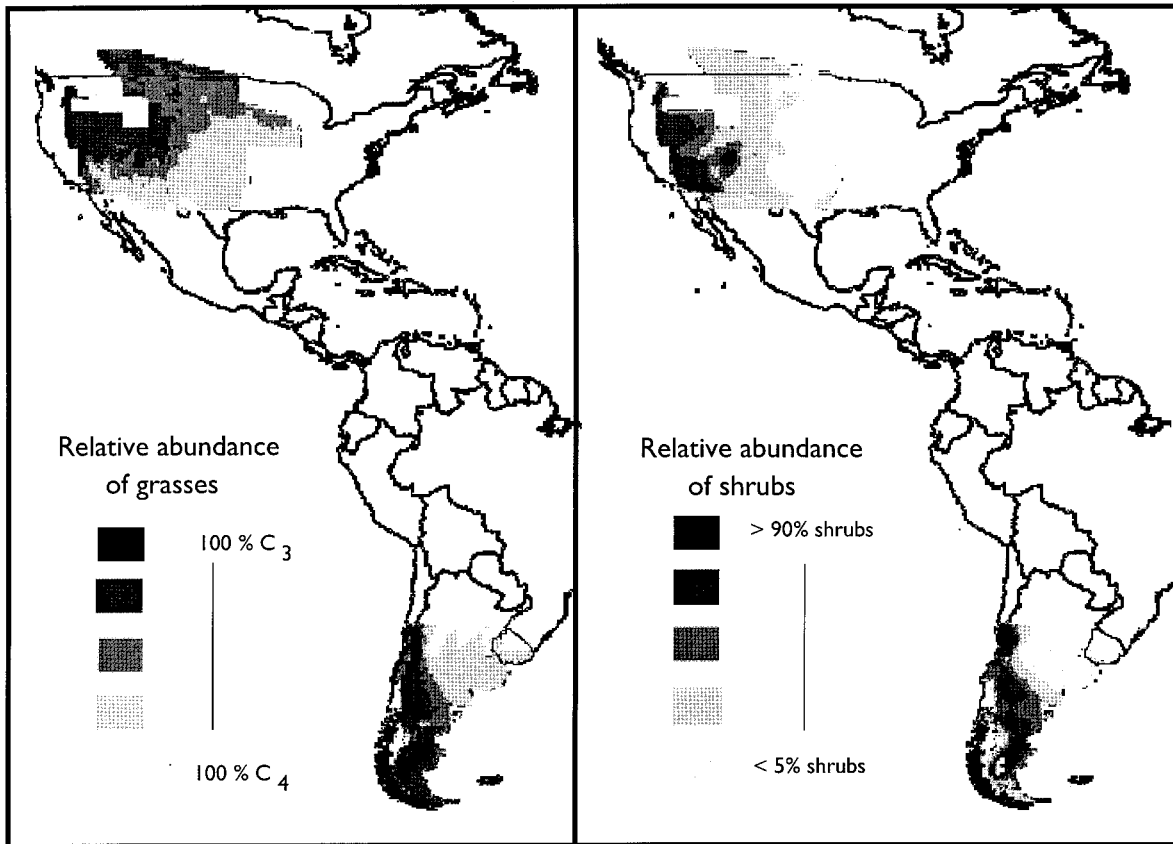
FIG. 5. Maps of (a) the relative percentage of C_3 and C_4 grasses (model 1.1, Appendix) and (b) the relative abundance of shrubs (model 1.2, Appendix) for the temperate zones of North and South America dominated by grasslands and shrublands. The equations of the respective models were applied to a climatic database with a resolution of 0.5° of latitude and longitude (Leemans and Cramer 1991).

For example, Dolores (a site in the Flooding Pampa) and Konza Prairie (a site in the tallgrass prairie) have the same MAP (879 mm and 885 mm, respectively) and a similar MAT (14°C vs. 13°C, respectively). However, they differ markedly in the annual thermal amplitude (difference between the temperature of the warmest and coldest months; 11.5°C vs. 26.5°C) and in the proportion of precipitation falling during winter (0.23 vs. 0.12). The Pampa grasslands may be able to grow more than the tallgrass prairie during winter, because they do not have strong water and temperature constraints, resulting in higher ANPP than predicted by the model.

As with any correlative models, those analyzed here do not prove causality. However, they provide a starting point for analyzing the mechanisms by which grassland and shrubland ecosystems respond to environmental variables. For example, coupling correlative and simulation models seems to be a useful way to increase our understanding of ecosystems (e.g., Burke et al. 1991). Correlative models also provide a reference point for comparing sites in different continents. Comparative analyses offer a powerful way to detect, in-

vestigate, and predict the response of ecosystems to global change.

A climatic approach to defining ecologically similar areas has the advantage that the defined units are not influenced by human use, a critical point for heavily modified ecosystems, as most grassland and shrubland areas of the world are. Our models provide a useful tool for defining similar areas on different continents, because they provide the relevant climatic dimensions for locating sites with the potential to support similar ecosystems. Moreover, integrating the models with a climatic database allows one to identify areas with particular combinations of ecological attributes.

Our results suggest that these correlative models can be used to generate baseline scenarios of ecosystem structure and functioning for grassland and shrubland areas of the world that do not have available data, such as central Asia. Maps of the potential structure and functioning of grassland and shrubland ecosystems are potentially useful for calibrating mesoclimatic models. These models (i.e., RAMS; Pielke et al. 1992) have been successful in describing the impact of land use on climate at regional scales (Pielke et al. 1997). Figure

5 presents an example of scenarios of the potential structure (based on relative abundance of plant functional types) of temperate grasslands and shrublands in both North and South America.

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APPENDIX

Regional models of the relationship between ecosystem structure and functioning and climatic variables: MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C); SUM, proportion of precipitation falling during summer (June–August for the Northern Hemisphere, and December–February for the Southern Hemisphere); WIN, proportion of precipitation falling during winter (December–February for the Northern Hemisphere and June–August for the Southern Hemisphere); SPR, proportion of precipitation falling during spring (March–May for the Northern Hemisphere, and September–November for the Southern Hemisphere); SLT, percentage silt; CLY, percentage clay; C_3 and C_4, relative abundance of C_3 and C_4 grasses, respectively; SHR, relative abundance of shrubs; ANPP, aboveground net primary production $g \cdot m^{-2} \cdot yr^{-1}$; SOC, soil organic carbon (kg/m^2); NDVI-I, integral over the year of the normalized difference vegetation index; MAXMIN, difference between maximum and minimum NDVI; DOYMAX, day of the year of the maximum NDVI.

Model 1. Plant functional types distribution:

$$\ln[(C_3 + 1)/(C_4 + 1)] \tag{1.1}$$
$$= 1.572 - 0.0468 \text{ MAT} - 1.0718 \text{ SUM}$$
$$- 0.131 \log \text{MAP}$$
$$r^2 = 0.51; \quad df = 3, 69; \quad P < 0.0001$$

(relationship calculated from data in Paruelo and Lauenroth 1996).

$$\text{SHR} = 1.710 - 0.291 \log \text{MAP} + 1.545 \text{ WIN} \tag{1.2}$$
$$r^2 = 0.62; \quad df = 2, 70; \quad P < 0.0001$$

(from Paruelo and Lauenroth 1996).

Model 2. Patterns of soil organic carbon:

$$\text{SOC} = 4.09 - 0.827 \text{ MAT} + 0.0224 \text{ MAT}^2 + 0.127 \text{ MAP} \tag{2}$$
$$- 0.000938 \text{ MAP}^2 + 0.000899 \text{ MAP} \times \text{SLT}$$
$$+ 0.0006 \text{ MAP} \times \text{CLY}$$
$$r^2 = 0.51; \quad df = 6, 555; \quad P < 0.0001$$

(from Burke et al. 1989).

Model 3. Pattern of primary production:

$$\text{ANPP} = 0.6 \times \text{MAP} - 34 \tag{3.1}$$
$$r^2 = 0.90; \quad F = 935; \quad df = 1, 98; \quad P < 0.0001$$

(from Sala et al. 1988).

$$\text{NDVI-I} = 0.0946 + 0.000235 \times \text{MAP} \tag{3.2}$$
$$r^2 = 0.75; \quad F = 70; \quad df = 1, 23; \quad P < 0.0001$$

(from Paruelo 1995).

Model 4. Seasonality of primary production:

MAXMIN
$$= 0.319 + 0.000353 \times \text{MAP} - 0.0179 \times \text{MAT} \tag{4.1}$$
$$r^2 = 0.59; \quad F = 16; \quad df = 2, 22; \quad P < 0.0001$$

(from Paruelo 1995).

$$\text{DOYMAX} = 54.71 + 173.8 \times \text{SUM} + 1.755 \text{ MAT} \tag{4.2}$$
$$+ 126.576 \text{ SPR}$$
$$r^2 = 0.69; \quad F = 17; \quad df = 3, 21; \quad P < 0.0001$$

(from Paruelo 1995).