

## Land use in the dry subtropics: Vegetation composition and production across contrasting human contexts

G. Baldi\*, E.G. Jobbágy

Grupo de Estudios Ambientales – IMASL, Universidad Nacional de San Luis & CONICET, Ejército de los Andes 950, D5700HHW San Luis, Argentina

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### ABSTRACT

Dry subtropical regions, originally hosting xerophytic vegetation, are currently characterized by diverse land cover/use patterns. Using existing biophysical and socio-economic databases, we explored how human contexts influenced land cover, vegetation composition and agricultural production in five distant regions. On average, cultivated areas represented a minor proportion (<16%) of all the regions, except in Asia (74%). This proportion was positively associated with population density when considering all regions together (slope =  $0.2 \text{ ha}^* \text{inh}^{-1}$ ), but the association became weaker in low-population regions. While protected areas displayed highly similar life-forms across regions, non-protected natural vegetation areas presented large contrasts, suggesting different imprints of land management. The observed contrasts were more marked for cultivated vegetation, with different species and species diversities being found in each region. These contrasts likely reflect orientation toward national/global markets in the Australian and American regions and toward local markets/subsistence in Asian and African regions. Africa and Asia were characterized by low and similar per capita levels of food production ( $\sim 50 \text{ kg grain}^* \text{y}^{-1} \text{inh}^{-1}$  and  $\sim 0.14 \text{ livestock units}^* \text{inh}^{-1}$ ), in contrast to South America and Australia ( $585 \text{ kg grain}^* \text{y}^{-1} \text{inh}^{-1}$  and  $10.2 \text{ units}^* \text{inh}^{-1}$ , respectively). This comparative perspective assisted in exploring the reciprocal influences between social-economic development and ecosystems that lead to alternative strategies of land management.

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### 1. Introduction

Dry subtropical (DST) regions can be considered as valuable settings to explore how societies shape land cover/use (and consequently vegetation composition, and the production of goods), as they are subjected to a large diversity of socio-economical contexts under a physical environment that constrains agriculture or livestock production due to water-associated limitations (with respect to amounts, interannual variability, and unpredictability). Current patterns of land cover/use differ among different hemispheres, continents and countries. While some DST regions have been recognized as cultivation frontiers, especially in South America and Sub-Saharan Africa (Lambin et al., 2003), Asian DST areas, such as the Indo-Gangetic plains, were ancient foci of plant domestication and are crucial world breadbaskets since preindustrial times (Gadgil and Guha, 1992; Gupta, 2004). Additionally, very few comparative studies deal with the land use, land cover, or conservation status of tropical

or subtropical systems (e.g., Miles et al., 2006), with most studies being focused in individual regions, such as the intensely explored Sahel (e.g., Culf et al., 1993).

The human imprint on these regions stems from pressure on land resources and from the complex array of interventions that allow the appropriation of plant and animal products. Pressure from local populations was a dominant driver of ecosystem changes in preindustrial times in the dry subtropics, and this is still the case in areas associated with high rates of population growth and low incomes. However, global population pressures, transmitted through complex market and policy signals, are now gaining importance as societies become more economically stable, connected, and urbanized (Lambin et al., 2003). Thus, within biophysically similar areas, the current ecological divergences that exist across political boundaries and social realms could be attributable to a different timing of these societal changes (Foley et al., 2005).

The dry subtropics, similar to most dryland or subhumid areas, are characterized by competing or coexisting uses produced by historical and present interactions between socio-economic and intrinsic biophysical characteristics (Noy-Meir, 1973; Millennium Ecosystem Assessment, 2005). In preindustrial times, and in

\* Corresponding author. Tel.: +54 2652 424740; fax: +54 2652 422803.  
E-mail addresses: baldi@unsl.edu.ar, germanbaldi@gmail.com (G. Baldi).

current areas associated with a less-affluent social context, shifting cultivation, extensive livestock rearing, and wood extraction have given form to the landscape, leading to spatially dynamic land segmentation characterized by croplands and grassy and woody vegetation in different stages of succession and with different degrees of biomass depletion or appropriation (Chidumayo, 1987; Kunst et al., 2006). In richer and more populated areas, rainfed and irrigated agriculture and mixed crop/livestock production systems occupy the most productive and connected (to markets) areas at present, while extensive grazing and wood extraction are restricted to areas with lower environmental quality or accessibility (Chidumayo, 2002; Grau et al., 2008).

The type and intensity of interventions carried out in the resultant cultivated and natural to semi-natural ecosystems depend on technology access (e.g., fertilizers, tractors), production organization (e.g., labor availability), government policies (e.g., conservation, price controls), and culture or ideological attitudes (e.g., religion, community feelings), among other factors. Human interventions lead to disruption of natural ecosystem structure through activities such as forest harvesting and clearing, grazing, biomass burning, fertilization, and irrigation (DeFries et al., 2006; Bucini and Hanan, 2007). Ultimately, interventions determine the provision of food (vegetables and meat) and other goods (fibers, fuels, construction materials) and thus the well-being of local inhabitants (who are mostly poor and dependent on local production in the case of drylands) (Millennium Ecosystem Assessment, 2005; Snyman, 1998).

The dry subtropics are shaped by competition among land uses, management practices, and consequent goods production, which are often constrained by the degree of water limitation that these areas experience (Bucini and Hanan, 2007). Global analyses have shown that rainfed agriculture tends to be concentrated in subhumid climates (with a ratio of precipitation to evapotranspiration ranging from 0.5 to 1), becoming limited by insufficient and unpredictable precipitation toward arid extremes (presenting only scattered farming systems, Noy-Meir, 1973) and by soil fertility and/or waterlogging and flooding toward humid extremes (Woodward et al., 2004; Millennium Ecosystem Assessment, 2005). Grazing operations based on natural vegetation tend to peak in semiarid climates (ratio ranging from 0.2 to 0.5), where rainfed agriculture is less productive and highly risky, but forage productivity is still sufficient to maintain animal production (Oesterheld et al., 1992; Millennium Ecosystem Assessment, 2005). However, the influence of these climatic restrictions can lose strength under growing human demands, which coupled with access to irrigation, fertilization, and other technologies, can cause agriculture to expand to the most arid environments (Qi et al., 2007).

Under an abiotic framework characteristic of DST regions, our guiding questions are as follows: How do land cover/use patterns vary across territories with similar environmental settings? Is this variability related to contrasting human contexts? How does aridity constrain land cover/use? What are the productive outputs per area and per capita of these regions? To address these questions, we apply a cross-continental comparative and quantitative approach using existing databases from different sources. Our specific goals are to (a) characterize the global distribution of DST regions based on common climatic and topographic conditions; (b) synthesize current land cover patterns considering the proportions under cultivation, (semi)natural vegetation, urban areas, and water bodies; (c) describe the composition of uncultivated (semi)natural (relative dominance of life forms) and cultivated vegetation (relative dominance of species, crop types, and diversity); and (d) quantify crop and animal production and exploring their relationship with demography, using cartographic, photographic, and statistical databases.

**Table 1**

List of variables and value ranges used to identify and map similar regions. Areas at latitudes of less than 10° were not considered. \* October to March or April to September, depending on the hemisphere. Acronym: PET, mean annual potential evapotranspiration.

Group	Variable	Range
Climatic	Mean annual precipitation (PPT)	350–1500 mm
	Precipitation seasonality*	≥66%
	Mean annual temperature	20–25 °C
	Climatic water balance (PPT:PET)	≥0.2 ^ ≤1
Topographic	Altitude	≤1200 masl
	Slope	≤0.7°

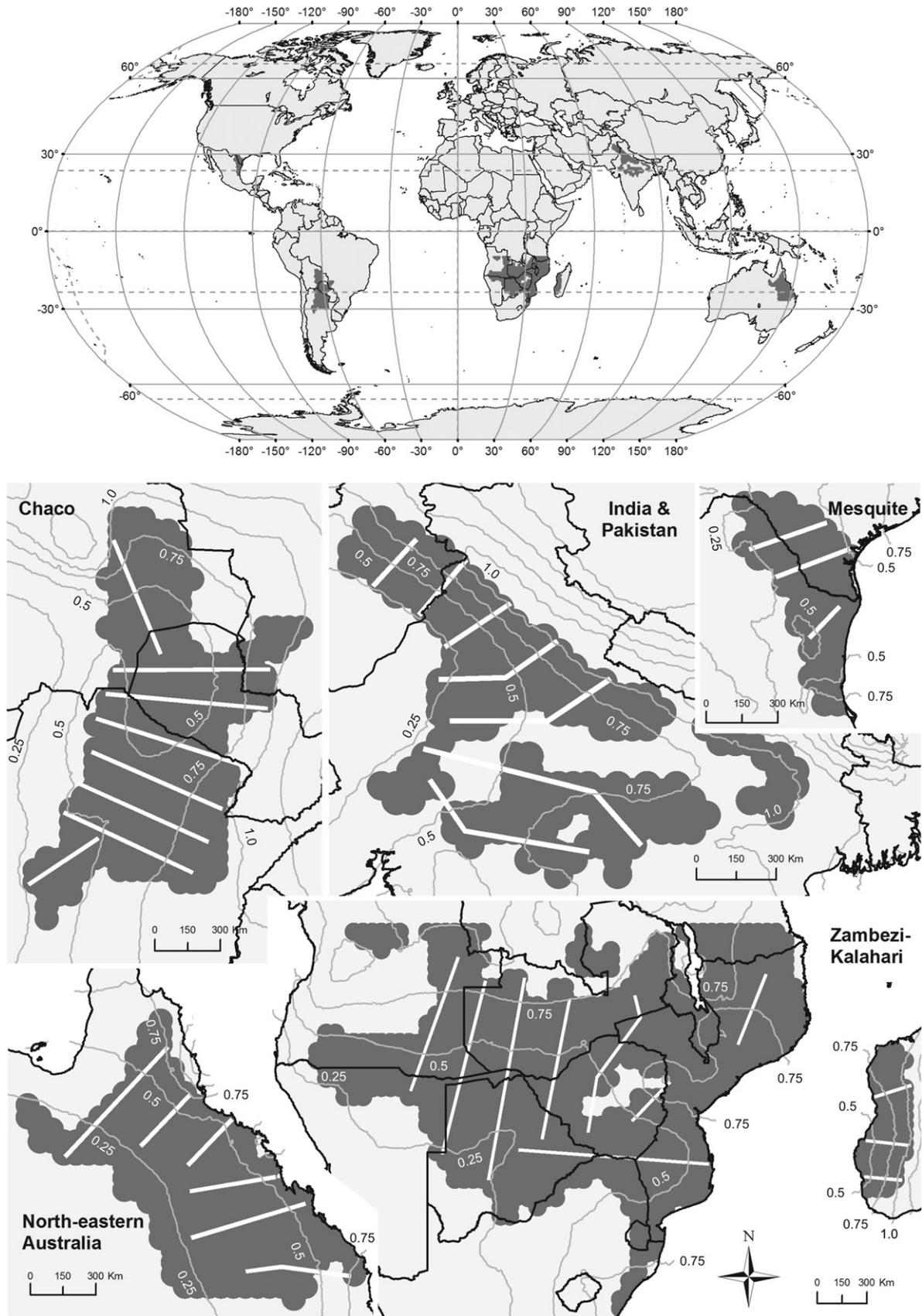
## 2. Methods

### 2.1. Distribution of DST regions

To compare biophysically similar areas, we defined the limits of dry regions, particularly those with summer rains, based on a small set of climatic and topographic attributes (Table 1). These regions encompassed a wide water balance gradient (values of 0.2–1.0 for the ratio of mean annual precipitation to mean annual potential evapotranspiration, PPT:PET), including semiarid (0.2–0.5), dry subhumid (0.5–0.7) and subhumid (0.7–1.0) conditions. Climatic data were obtained from the Ten Minute Climatology database (CRU-UEA, New et al., 2002) representing average monthly figures for the period 1961–1990. We calculated potential evapotranspiration using the Penman-Monteith algorithm (Allen et al., 2004). Topographic variables were generated through the “Shuttle Radar Topography Mission” (SRTM) digital elevation model (USGS, 2004). Information was rescaled at a spatial resolution of 30 min through averaging the original data. We applied a buffer of 30 min and discarded small or discontinuous areas (<5 contiguous grid cells). Once the regions were delimited, we characterized their soil texture and chemical fertility using the 5–30 min spatial resolution ISRIC-WISE databases (Fairhurst et al., 1999; Batjes, 2006), recognizing that they can present inconsistencies among countries or continents and be inaccurate at the scale at which landscape management decisions are made. A few regions that matched our search criteria were excluded from the analysis because of their reduced area and/or lack of water balance gradients (some areas in the Caribbean and along the west coasts of Mexico and India) and the spatial patchiness of the delimited areas (Brazilian Cerrado).

### 2.2. Sampling procedure

To compare human contexts, land cover patterns, and vegetation composition across regions and climatic gradients, we used three levels of data sampling and/or integration according to the variable being addressed. The first level involved the calculation of an average value for each region to describe general traits (such as population density, historical cultivation trends, and uncultivated vegetation characteristics). The second level allowed association of land cover, vegetation composition and production variables with water availability based on 35 transects covering regional gradients of water balance (Fig. 1). The data were aggregated within PPT:PET intervals of 0.1 ( $n = 186$ ). The transects covered  $3.7 \times 10^5$  km<sup>2</sup> and were 20 km wide and, when parallel to each other, were separated by a distance of 125–250 km (Table 2). A third level of analysis involved the selection of 2031 sampling points to confirm the presence of cultivated areas within transects, and for cultivation composition and productivity analyses. Points were selected by combining visual inspections of high-resolution satellite images (supported by the Google Earth system) and online photographic



**Fig. 1.** Dry subtropical (DST) summer-rain regions: Chaco, India & Pakistan, Mesquite, NE Australia and Zambezi-Kalahari. White strips represent 20-km wide transects along water balance gradients used to describe land uses; light gray lines represent water balance isolines; and numbers show the PPT:PET value.

**Table 2**  
Data samples and sources of information for land use/cover maps (LUC).

Region	Transect length (km)	Cultivated points (n)	LUC main source
Chaco	5250 (n = 8)	497	Eva et al. (2004)
India & Pakistan	3300 (n = 7)	806	Agrawal et al. (2003)
Mesquite	1040 (n = 3)	97	Homer et al. (2004), Latifovic et al. (2004)
NE Australia	3400 (n = 6)	94	BRS (2006)
Zambezi-Kalahari	7700 (n = 11)	537	Mayaux et al. (2004)

archives (“Confluence Project”, <http://www.confluence.org>, and “Panoramio”, <http://www.panoramio.com>, accessed in February 2008), maintaining a point-to-point distance of ~7 km. The data intersected by these points were summarized at a regional level (i.e., average figures for each region).

### 2.3. Data sources and statistical analyses

We characterized population density using the CIESIN-CIAT 2.5 min spatial resolution map based on 1990–1995 estimates (2005) and infant mortality rates using CIESIN sub-national statistics for year 2000 estimates (2005). We used ancillary data at a national scale from the Food and Agriculture Organization (FAO, 2009) to characterize national production and consumption for different crops, fertilizer uses, and international trade at the regional level for the 2000–2005 period. We further linked population density and current cultivation rates (amount of cultivated area) at the transect level by applying linear regression models.

We focused our investigation on uncultivated and cultivated vegetation, distinguishing between rainfed and irrigated land in the latter case. Land cover was characterized through synthesis of six available land use/cover products (Table 2) and the proportion of protected area (all IUCN categories) through the World Database on Protected Areas (UNEP-WCMC, 2009). We calculated the proportion of cultivated areas under irrigation based on the “Global map of irrigated areas” (Siebert et al., 2007), which depicts the proportion of area equipped for irrigation with a 5 min resolution. In the present study, an area was considered irrigated when this proportion was >5%. Changes in cultivated areas from 1700 to 1990 were described based on the 30 min spatial resolution “Historical Croplands Dataset” (SAGE and Ramankutty and Foley, 1999) and updated to 2000 using current regional databases (Table 2). For Mesquite, historical data were adjusted using the “National Land Cover Dataset 1992” for the USA (Vogelman et al., 2001) (a year in which the two datasets overlap) due to unexpectedly high cultivation values in historical data that are not supported by current information and historical narratives (Tinkler, 2004).

We characterized the composition of cultivated land cover types (rainfed + irrigated) using four metrics: (1) crop species present, (2) category (cereals; pulses; roots and tubers; industrial; oil; and fruits, vegetables and others), (3) growing season (cool/dry vs. warm/humid), and (4) diversity. The crop species composition circa the year 2000 was obtained from global maps produced by Monfreda et al. (2008) addressing the harvested area and yield of 157 species (5 min spatial resolution). This database was created by combining national and subnational level census statistics and satellite-derived land cover maps (Monfreda et al., 2008; Ramankutty et al., 2008). All measures were calculated by extracting the information for each sampling point regarding the fraction of the pixel covered by each available species and later classifying the results by point into the above mentioned crop groups (category and growing season). Crop diversity was estimated using the “Shannon index” (H), calculated as follows:

$$H_j = - \sum_{i=1}^n P_{ij} \cdot \ln P_{ij} \quad (1)$$

where  $P_{ij}$  is the percentage of crop  $i$  in region  $j$  and  $n$  is the number of crops. This index adopts a value of zero for a unique dominant species and 0.7 or 2.3 when there are two or ten evenly distributed species, respectively. We averaged each metric at the regional level. We also analyzed the individual occurrence of each crop species across the water balance gradient using the same information.

We characterized the vegetation composition of uncultivated land cover types based on the relative dominance of trees, grasses and shrubs. We determined the composition at the regional level based on the intersection of the areas of interest and cartographic information (Table 2), categorizing it into four classes: woodland, shrubland, grassland, and barren ground. We complementarily explored the vegetation composition in protected areas (IUCN categories I to V, <http://www.iucn.org>) by inspecting the same cartographic information and online photographic archives. Though unevenly distributed within regions, these areas most likely represent original vegetation. Photographic information was obtained from “Panoramio” and “Flickr” (<http://www.flickr.com>) uploaded at the web site of the WDPA (<http://www.wdpa.org>), and from the “Confluence Project” (assessment performed in February 2009); each photograph was visually inspected and classified into one of the four classes listed above. Photographs provide detailed information about landscape elements and, thus, vegetation traits (Ode et al., 2008; Palmer and Hoffman, 2001), but we acknowledge that their spatial locations, except for those from the “Confluence Project”, could be biased by scenic preferences of photographers across landscapes and regions.

We characterized animal and crop production at regional and transect levels. Livestock density (unit\*km<sup>-2</sup>) was estimated using FAO-AGA (2010) global databases with a 3 min spatial resolution. We considered data for buffalo, cattle, goats, and sheep, assuming that 1 cattle unit = 1 buffalo = 8 goats/sheep and adjusting the values across regions using the criteria of 1 cattle unit in “developed” countries equaling 0.75, 0.46, and 0.42 units in South American, Sub-Saharan Africa, and Asian regions, respectively (FAO, 1995). In the case of crops, we focused on an area-weighted yield value for all cereal and oil crop species based on information provided by Monfreda et al. (2008) for the cultivated sampling points. An important factor in the calculation of agricultural productivity is the number of crops grown in a year (i.e., rotation intensity), which is not shown by the available statistics. While reported crop yields could be assigned to a whole annual cycle in most cases, cropping sequences can involve less intense rotations with long fallow periods, as occurs in the drier areas of Africa and Australia (Nandwa and Bekunda, 1998; Sadras and Roget, 2004). In contrast, areas with intense rotations can involve two or, more rarely, three cropping cycles in one year, as has been reported for India (Frolking et al., 2006). To overcome this problem, we considered typical double-cropping schemes for South America and South Asia (where this practice is common) based on the literature and local expert knowledge (AJ Hall, JM Mercau, personal communication). We identified five schemes for India & Pakistan (rice-wheat, millet-wheat, millet-rapeseed, maize-wheat, and sorghum-wheat) and one for Chaco (soybean-wheat). For these cases, we assumed that all of the land capable of supporting double-cropping was subjected to this practice based on the following equation:

$$Y_j = \frac{\sum_{j=1}^2 C_{ij} \cdot Y_{ij}}{\sum_{j=1}^2 C_{ij} - F} \quad (2)$$

**Table 3**

Some relevant soil characteristics across dry subtropical regions. Mean values for surface soil (0–20 cm) according to ISRIC-WISE databases (Fairhurst et al., 1999; Batjes, 2006).

Region	Texture (100-sand %)	Base saturation (% CEC soil)	Total carbon content (%)	Land proportion with phosphorus deficiency (%)
Chaco	56.1	90.2	1.03	18.6
India & Pakistan	53.8	94.6	0.80	26.2
Mesquite	67.4	96.9	1.24	17.2
NE Australia	51.7	87.2	0.75	40.9
Zambezi-Kalahari	36.5	74.6	0.90	46.0

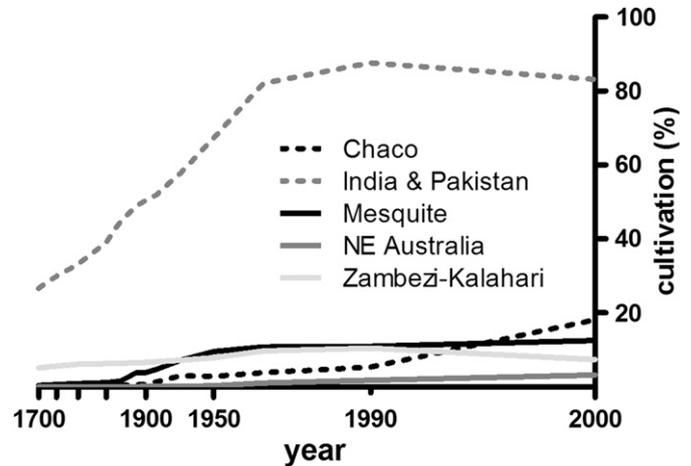
where  $C_{ij}$  is the area of crop  $i$  in region  $j$ ;  $Y_{ij}$  is the yield of crop  $i$  in region  $j$ ; and  $F$  is a factor that accounts for the area subjected to double-cropping (i.e., the area of warm-season crops when the area of cool-season crops exceed the first and vice versa, considering only species involved in double-cropping). Additionally, we calculated maize (*Zea mays*) and sorghum (*Sorghum spp.*) yields, as these two species are widely distributed and rarely included in double-cropping schemes.

### 3. Results

#### 3.1. Distribution and biophysical/human context

We identified five regions, accounting for  $6.4 \times 10^6$  km<sup>2</sup>, i.e., 5% of the global land area (excluding Antarctica), in Africa (referred to as Zambezi-Kalahari), Asia (India & Pakistan), Australia (North-eastern Australia), North America (Mesquite), and South America (Chaco) (Fig. 1). These abiotically defined regions presented a good match with the “Tropical and subtropical dry broadleaf forests” and “Tropical and subtropical grasslands, savannas, and shrublands” biomes mapped by Olson et al. (2001), with 75% of their area lying within these biomes. DST dry winter season lasted 9.3–11.5 months on average (a period with precipitation lower than potential evapotranspiration, PPT < PET), and their mean annual temperature ranged from 22.4 to 24.7 °C. Although all regions included semiarid, dry subhumid, and subhumid conditions, India & Pakistan and Zambezi-Kalahari were the only two that covered the full range of the gradient ( $0.2 \geq \text{PPT}:\text{PET} \leq 1$ ).

These regions display soil fertility differences that can play an important role in shaping the structure of their natural ecosystems and, more importantly, their response to cultivation (Table 3). The long-term stability and exposure of surface rocks to weathering and leaching in NE Australia and Zambezi-Kalahari (Paton et al., 1995), have resulted in greater phosphorus and base cation deficiencies in comparison to the other regions, where soils have been renewed by Pleistocene transport of fluvio-aolian sediments in Chaco and



**Fig. 2.** Regional rates of cultivation throughout the last three centuries in dry subtropical regions. Time is shown in a logarithmic scale with markers indicating 50-year intervals.

India & Pakistan and marine incursions in Mesquite (Paton et al., 1995).

The DST regions encompassed contrasting human conditions (Table 4). The most striking difference was with regard to population density, with a 500-fold difference being observed between India & Pakistan and NE Australia, which was reduced to a (still large) 15-fold difference when population density was calculated on the basis of cultivated land. In agreement with the observed population patterns, the agricultural production of these regions presented contrasting orientations, with India & Pakistan and Zambezi-Kalahari being characterized by a focus on subsistence and local markets (97% of the goods produced in these regions are locally consumed; FAO, 2009), while the others were oriented to national (Mesquite) or national-to-global markets (Chaco and NE Australia). For poverty, as indicated by infant mortality (sensu CIESIN, 2005), two very different scenarios were observed: low to medium values ( $\leq 28\%$ ) in Chaco, Mesquite, and NE Australia, and very high values ( $\sim 100\%$ ) in India & Pakistan and Zambezi-Kalahari.

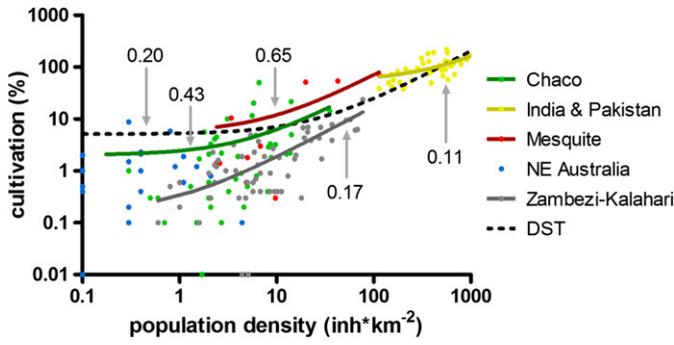
#### 3.2. Land cover and use

Different temporal trends and current rates of cultivation emerged across DST regions. Densely-populated India & Pakistan exhibited the highest proportion of land under cultivation (74%, Table 4) and the longest cultivation history (Gadgil and Guha, 1992; Gupta, 2004) (Fig. 2). This region achieved its maximum cropped area in the 1950s, with remaining uncultivated areas most likely

**Table 4**

General characteristics of the five regions selected through the classification process. \* Data missing for western Paraguay.

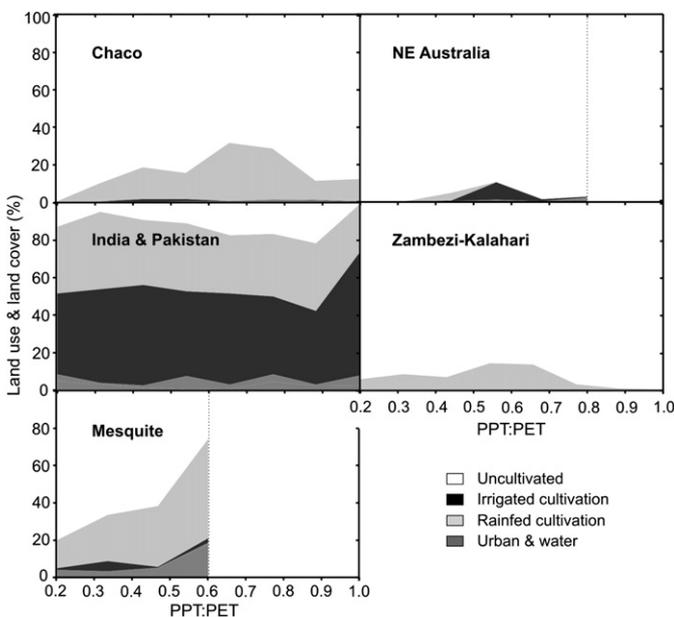
Region	Countries	Area (thousand km <sup>2</sup> )	Cultivated area (%)	Irrigated area (% of cultivated)	Protected area (%)	Population density (inh*km <sup>2</sup> )	Inhabitants/cultivated area (inh*km <sup>-2</sup> )	Infant mortality rates (‰)
Chaco	Argentina/Bolivia/Paraguay	1061	15.9	3.0	5.5	7.3	460	28*
India & Pakistan	India/Pakistan	834	73.9	57.0	2.1	465.5	6300	101
Mesquite	Mexico/United States of America	237	12.5	11.5	0.3	25.3	2023	17
NE Australia	Australia	823	2.4	23.8	0.9	1.0	429	6
Zambezi-Kalahari	Angola/Botswana/Malawi/Madagascar/Mozambique/Namibia/South Africa/Tanzania/Zambia/Zimbabwe	3483	11.4	2.5	13.7	21.6	1892	102



**Fig. 3.** Relationship between cultivation and population density in dry subtropical regions and for their sum (on a logarithmic scale). Each point represents a transect segment (intervals of 0.1 PPT:PET,  $n = 186$ ). Values are shown on a logarithmic scale. The results of all linear regression models were significant ( $p < 0.05$ ), except for NE Australia (not shown). Numbers represent the slopes ( $\beta$ ) of significant linear regression models and correspond to hectares of cultivated land per inhabitant (ratio of % to  $\text{inh} \cdot \text{km}^{-2}$ ). Double-cropping explains cultivation rates in excess of 100%. The regression coefficients were: 0.78, 0.09, 0.29, 0.71, and 0.67, for the pool of all DST regions, Chaco, India & Pakistan, Mesquite, and Zambezi-Kalahari regions, respectively; whereas a non-significant result was found for NE Australia.

being preserved for forest use and grazing activities and as a result of environmental or religious restrictions (Gadgil and Guha, 1992; Singh, 2000). In Zambezi-Kalahari, the low population density of rural areas has led to a long history of scattered and small-scale cultivation, with crops occupying 7–11% of the territory throughout the last 100 years. The lack of expansion of cultivation in this region is likely related to considerable social, economic and political impediments to agricultural development (e.g., poverty, poor integration between research and development, transportation costs, political instability), which are conditions differing markedly across countries (Sanchez, 2002).

In Mesquite, the greatest expansion of agriculture took place between 1870 and 1930. Immigration into the region and transportation development during this period accompanied the growth of agricultural systems oriented to external markets (Tinkler, 2004). Since this initial expansion, the amount of cultivated area has



**Fig. 4.** Land use across water balance gradients (PPT:PET) in dry subtropical regions. Mesquite and NE Australia only encompassed a fraction of the gradient.

**Table 5** Uncultivated vegetation composition (%) across points in the entire region (overall) and in protected areas using land use/cover cartographic information (LUC) and online photographic archives (PhA). \* In the map used for this region (see Table 2), the barren ground class encompassed regrowth, non-native and modified vegetation areas, in addition to cleared areas.

Region	Protected areas LUC				Protected areas PhA				Protected areas (n)	Photos (n)
	Woodland	Shrubland	Grassland	Barren ground*	Woodland	Shrubland	Grassland	Barren ground		
Chaco	75.4	24	0.5	0	100	0	0	0	14	13
India & Pakistan	80.2	17.7	0.1	2.0	81.5	16.3	2.2	1.3	60	121
Mesquite	13	76.9	9.9	0.2	—	—	—	—	8	0
NE Australia	96.5	1.8	1.4	0.4	100	0	0	0	67	14
Zambezi-Kalahari	43.6	40.8	13.9	1.8	53.9	23.5	19.6	2.6	142	732
Overall	71.2	15.4	13.4	0	71.2	15.4	13.4	0	—	—
	83.5	15.7	0	0.9	83.5	15.7	0	0.9	—	—
	1.6	79.6	18.3	0.5	—	—	—	—	—	—
	61.4	16.2	0.1	22.3	—	—	—	—	—	—
	34.1	32.5	33.4	0	—	—	—	—	—	—

remained relatively stable at 12.5% of the territory to the present. Although it was cultivated by European settlers since the 16th century, the South American Chaco hosted only scattered and very small cultivated areas devoted to local markets until the 1970s (Morello et al., 2005). Since then, increasingly globalized markets and rising grain prices have contributed to triggering the fastest rate of agricultural expansion seen across all of the examined regions, with 16% of the land being under cultivation at present (Steininger et al., 2001; Grau et al., 2008). Cultivation in NE Australia dates from the last decades of the 18th century, when European settlement began (Seabrook et al., 2006; Henzell, 2007). Due to the extremely low population density and low level of available labor in this region, this activity was negligible until 1930 to 1950, when mechanized forest-clearing programs and available technology favored the development of small coastal and inland agricultural foci (<3% of the region) (Fensham and Fairfax, 2003; Seabrook et al., 2006).

Using linear regression models, we found a strong positive association between current cultivation rates and population density when the entire DST territory was analyzed by transects ( $r^2 = 0.78$ ,  $n = 186$ ,  $p < 0.0001$ , Fig. 3). Within regions, the same relationship was detected for India & Pakistan, Mesquite, and Zambezi-Kalahari ( $r^2 = 0.29$ , 0.71, and 0.67, respectively), with Mesquite and India & Pakistan being the regions with the highest and lowest regression slopes (0.65 vs. 0.11 ha\*inh<sup>-1</sup>, respectively). The population-cultivation association was weaker in Chaco and NE Australia, which are two of the three regions associated with agricultural production oriented to national-to-global markets and short cultivation histories (Fig. 2).

The DST regions showed contrasting land cover patterns across water balance gradients (Fig. 4). In Chaco, NE Australia, and Zambezi-Kalahari, cultivation peaked under intermediate water balance conditions (0.5–0.6 of the gradient), decreasing (especially in the African region) or even disappearing toward the subhumid and semiarid extremes. In these three regions, cultivation never

surpassed one-fifth of the territory. In contrast, India & Pakistan showed widespread cultivation along the entire gradient. The proportion of cultivated land under irrigation was virtually nil in Chaco and Zambezi-Kalahari, low in Mesquite and high in India & Pakistan and NE Australia (Table 4 and Fig. 4). Notably, in India & Pakistan irrigation occupied 57% of the territory, with no trends along the water balance gradient being observed.

### 3.3. Vegetation composition

While all of these regions originally hosted xerophytic woodlands and savannas as natural vegetation (Olson et al., 2001), we found that all of the uncultivated territories and protected areas (assumed to provide the closest representation of the original vegetation) revealed a convergence of tree-dominated systems (woodlands) in Chaco, India & Pakistan, and NE Australia (>61% for the entire region, >75% for protected areas) (Table 5). This pattern was supported by independent photographic data examined for protected areas, which revealed no signs of vegetation classes other than woodlands occupying Chaco (13 photos) or NE Australia (14 photos). In Zambezi-Kalahari, both inside and outside protected areas, we observed co-dominance of woodlands, shrublands and grasslands. An evident patchiness of the landscape was noted in a large proportion of the 732 photos from this region, with trees being intermixed with shrubs and/or grasses. We found that in Mesquite shrublands were the dominant vegetation class (>77%), based exclusively on cartographic information. Interestingly, shared genera could be found in all regions, including dominant leguminous trees, such as *Acacia* (all regions) and *Prosopis* (all regions except NE Australia) (Cabrera, 1971; Archer, 1995; Kaushik and Kumar, 2003; Menaut, 1983).

In spite of their abiotic similarities, the vegetation composition on cultivated land (relative dominance of crop species, crop categories, crop growing season, and diversity) differed markedly across the study regions (Table 6). The distinctive feature of the

**Table 6**

Main crops ( $\geq 1\%$  of the cultivated land) found in dry subtropical regions. The values indicate the percentage of the total cultivated area occupied by each species. Values over 10% are highlighted with bold characters. Group refers to crop type: C cereals, P pulses, R roots and tubers, I industrial (fibers, sugar, and luxury crops), O oil crops, and F fruits, vegetables and others; and to the growing season: c cool/dry, and w warm/humid. Group composition and diversity were calculated using the crop percentage for the whole region. Values for all regions come from weighting of regional values by the regional cultivated area. \* Indicates a group of several unspecified crops according to the databases of Monfreda et al. (2008).

Crop	Group	Chaco	India & Pakistan	Mesquite	NE Australia	Zambezi-Kalahari	All regions
Barley	Cc	0.4	0.7	0	2.8	0	0.5
Bean	Pw	1.3	3.7	0.1	0	2.0	2.7
Cassava	Rw	0.2	0	0	0	5.1	1.0
Chickpea	Pc	0	3.1	0	0.1	0	1.8
Cotton	Iw	<b>12.8</b>	3.8	<b>20.6</b>	2.8	<b>10.1</b>	7.3
Forage*	?	0.8	3.3	0	0	0	2.0
Groundnut	Pw	0	0.8	0.5	1.3	8.7	2.1
Maize	Cw	8.0	3.5	6.9	1.4	<b>48.5</b>	<b>12.7</b>
Millet	Cw	0	9.8	0	0.1	6.2	6.8
Oats	Cc	0.7	0	0.1	3.1	0	0.2
Pulses*	P?	0	0.8	0	0	1.2	0.7
Rapeseed	Oc	0	6.6	0	0	0	3.8
Rice	Cw	0.9	<b>12.9</b>	0	0	0.2	7.6
Sorghum	Cw	6.4	1.3	<b>68.5</b>	<b>26.9</b>	5.3	6.2
Soybean	Ow	<b>36.9</b>	5.6	0	0.3	1.9	<b>10.3</b>
Sugarcane	Iw	4.0	3.7	0.8	<b>27.1</b>	1.5	3.6
Sunflower	Ow	<b>10.7</b>	0.1	0.2	5.0	1.8	2.4
Tobacco	Iw	0	0.1	0	0	2.7	0.5
Tomato	Fw	0	1.2	0	0	0	0.7
Wheat	Cc	<b>13.9</b>	<b>31.1</b>	0.8	<b>28.6</b>	1.6	<b>21.2</b>
Others		3.0	7.9	1.5	0.5	3.2	5.9
% cool/dry season crops		16	43	1	35	2	30
% oil & industrial crops		66	20	22	35	19	29
Shannon's diversity index		2.1	2.8	1.1	1.7	2.1	2.9

Chaco was that the oil/industrial crop area equaled that of cereals due to the importance of soybean and sunflower production. The other regions produced three to five times more cereals and pulses than oil and industrial crops. Mesquite was highly specialized toward sorghum cultivation (68%), showing the lowest diversity value ( $H = 1.1$ ). Three crop species dominated NE Australia: wheat, sugarcane, and sorghum, with each covering  $\sim 27\%$  of the crop cultivation area. In India & Pakistan, wheat was the main crop, closely followed by rice and millet (together representing more than half of the cultivated area). The rest of the region was devoted to several secondary crops, including minor proportions of some industrial and luxury species destined for export (sugarcane, tobacco). In Zambezi-Kalahari, maize occupied half of the cultivated area of the region, followed by a long list of species with much smaller areas. It is likely that the importance of local consumption in the last two regions (including subsistence to local market systems) is driving diversified cultivation including a large combination of pulses, nuts, roots and tubers ( $H = 2.8$  and  $2.1$ , respectively) (Table 6).

Cool-season crops, which can only be grown during the dry season in these regions, were virtually absent in Zambezi-Kalahari and Mesquite but were important in India & Pakistan and NE Australia, where irrigation is more abundant (Table 4). In spite of its small amount of irrigated area, Chaco was characterized by 16% cool-season crops (mainly wheat). Considering all of the DST territories together, ten crop species covered 85% of the cultivated land, with summer cereals being the dominant group (33%), followed by winter cereals (22%), summer oil crops (13%), industrial crops (11%), and great cross-regional variation of pulses, roots and tubers (8%).

Crop composition showed higher convergence toward more arid areas (Fig. 5), with relative increases of sorghum (Mesquite, NE Australia, Chaco) and millet (India & Pakistan and Zambezi-Kalahari) in semiarid belts. These two summer-season crops of African origin are well known for their drought resistance (Blum and Sullivan, 1986). Other species were only found in subhumid belts but not shared across regions, such as cassava in Zambezi-Kalahari and rice in India & Pakistan.

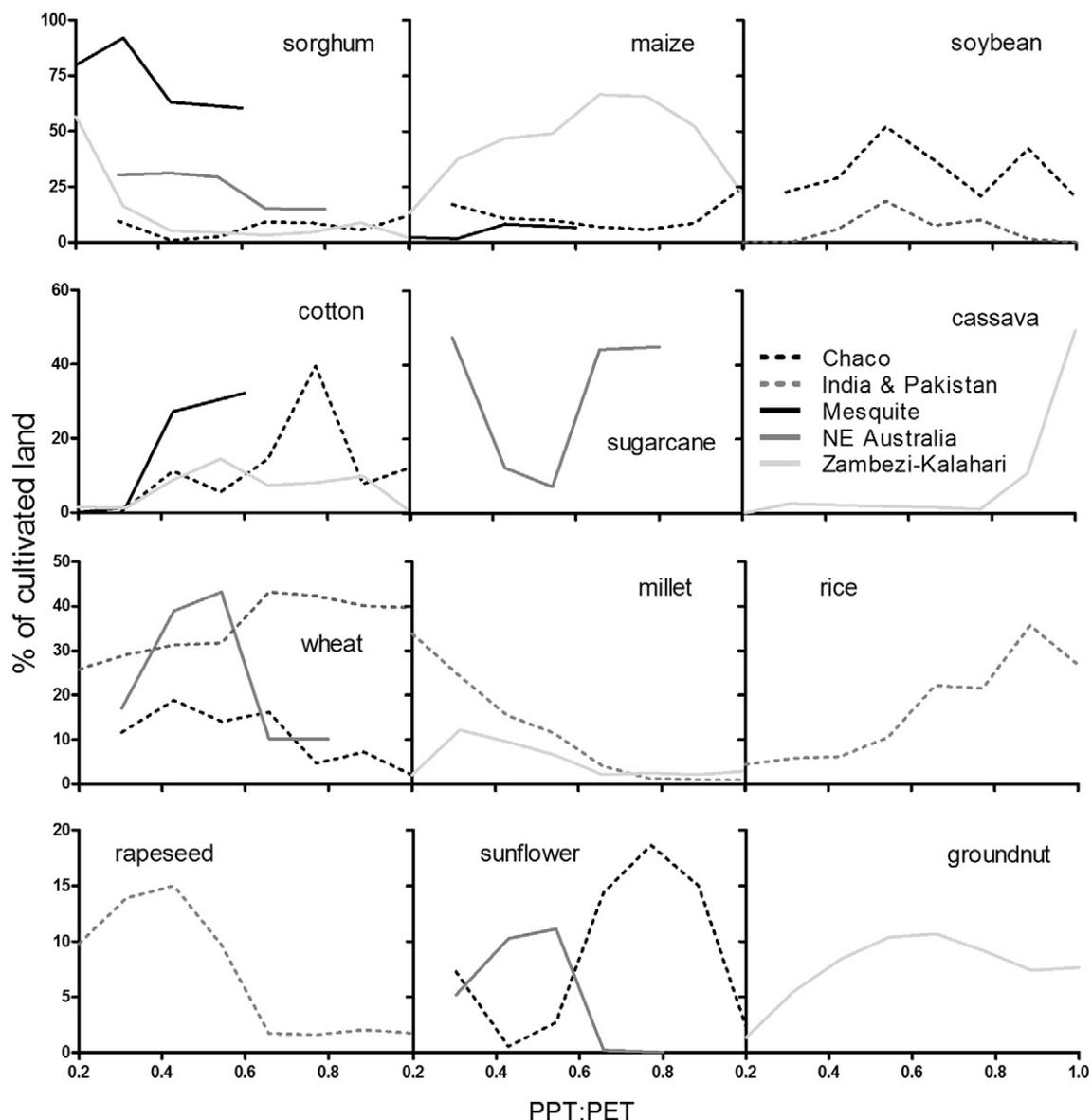
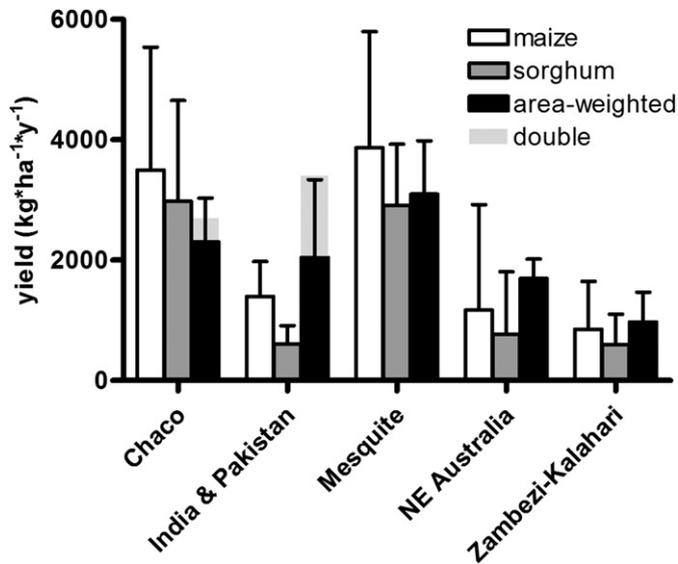


Fig. 5. Distribution of the most important crops ( $\geq 5\%$  of cultivated land) along water balance gradients (PPT:PET) in dry subtropical regions.



**Fig. 6.** Mean yields for maize, sorghum, and area-weighted (cereal + oil) crops. Adjustments for double-cropping are made based on the yields of area-weighted crops and region-specific criteria applied to Chaco and India & Pakistan, where this practice is frequent.

### 3.4. Production of goods

Agricultural productivity showed large differences across regions of up to 5- and 4.5-fold in the cases of sorghum and maize, respectively (Fig. 6 and Table 7). In particular, Mesquite and Chaco presented the highest yields of maize and sorghum, of  $>3.5$  and  $>2.9 \text{ Mg*ha}^{-1}\text{*y}^{-1}$ , respectively, while Zambezi-Kalahari exhibited the lowest values, with  $<1 \text{ Mg*ha}^{-1}\text{*y}^{-1}$  being observed for both crops. The regions were ranked according to the area-weighted crop yield as follows: Mesquite  $>$  Chaco  $>$  India & Pakistan  $\gg$  NE Australia  $\gg$  Zambezi-Kalahari, with a 3.2-fold difference being detected between the first and the last region. Low to intermediate yields in the Asian region must be treated as a special case, as double-cropping is the prevailing cultivation practice there (Das, 2006; Alauddin and Quiggin, 2008). Thus, if we assumed for this region that the annual yield was not the yield of a single crop but instead was the sum of the two crops grown in a single year, the area-weighted crop yield in India & Pakistan would match the values found in Mesquite, raising the region to the top of the ranking.

Livestock density, which is our closest proxy for animal productivity, was similar in Chaco, Mesquite, and NE Australia ( $10\text{--}15 \text{ units*km}^{-2}$ ) and lower in Zambezi-Kalahari ( $3 \text{ units*km}^{-2}$ ) (Table 7). Nevertheless, the largest contrasts were found between India & Pakistan ( $62 \text{ units*km}^{-2}$ ) and the latter regions (20-fold difference between Asia and Africa). Cattle were dominant in all regions, especially in Chaco and Mesquite, while in India & Pakistan, cattle and buffalo together represented the dominant type of

animal production (Fig. 7a). Peaks of maximum livestock density were found at intermediate water balance ranges (dry subhumid areas) in all regions except India & Pakistan, where density was maintained through the entire gradient (Fig. 7b).

## 4. Discussion

The comparative and quantitative approach followed in this study identified a major land use contrast across dry subtropical regions in the dominance of uncultivated vegetation in Chaco, Mesquite, NE Australia, and Zambezi-Kalahari (with most of their territories being dedicated to grazing, wood extraction and conservation) (Chidumayo, 2002; Fensham and Fairfax, 2003) vs. the almost complete cultivation observed in India & Pakistan (Table 4). The causes for historical and current differences in cultivation rates appeared to be linked to three factors: population density, orientation of agricultural production (i.e., global/national/local markets or subsistence), and water availability. The first of these factors, population density, presented great explanatory power when all of the regions were aggregated ( $r^2 = 0.78$ ) and when the DST regions of Asia, Africa and North America were considered individually, in agreement with previous results regarding subsistence or local market-oriented agriculture (Turner et al., 1977). This relationship exhibits a circular nature because the current population density determines local food demand and pressure to cultivate the land, as likely happens in Asia and Africa, whereas in other cases, cultivation can favor population growth both through increased food availability and labor demand. This last case might explain the association observed in the Mesquite region, where the local population no longer relies on local food production but may have migrated to cultivated areas (Tinkler, 2004).

A second factor associated with cultivation rates that has been of increasing importance in the last half-century is the orientation of agricultural production to fulfill external demands for food and other goods. The expansion of international trade and the consequent geographical decoupling of food demand and production could explain why Chaco presents high (and rapidly increasing) cultivation rates in spite of its relatively low population density (Fig. 2) (Grau et al., 2008). A similar situation would explain the smaller, yet significant, cultivation rates observed in unpopulated NE Australia in the middle of the last century (Seabrook et al., 2006). The amount of cultivated area in these two regions represents an important piece of evidence that woodland deforestation in the tropics and subtropics is driven by other factors in addition to local social and demographic conditions (Lambin et al., 2001).

The third factor, aridity, constrained land use in less populated regions, but not as expected for the portion of the water balance gradient under analysis, as both the cultivated area and livestock production peaked under dry subhumid climates. With respect to cultivated area, this behavior could be associated with a trade-off between the increasing fulfillment of crop water requirements

**Table 7**

Agricultural and animal productivity per unit of area and per capita. The area-weighted yield values consider double-cropping schemes.

Region	Area-weighted yield ( $\text{kg*ha}^{-1}\text{*y}^{-1}$ )	Cereal + oil crops production/total population ( $\text{kg*y}^{-1}\text{*inh}^{-1}$ )	Livestock density ( $\text{units*km}^{-2}$ )	Livestock density/total population ( $\text{units*inh}^{-1}$ )
Chaco	2692	585	14.9	2.0
India & Pakistan	3401	54	61.9	0.13
Mesquite	3098	153	13.3	0.53
NE Australia	1696	395	10.3	10.2
Zambezi-Kalahari	973	51	3.1	0.14

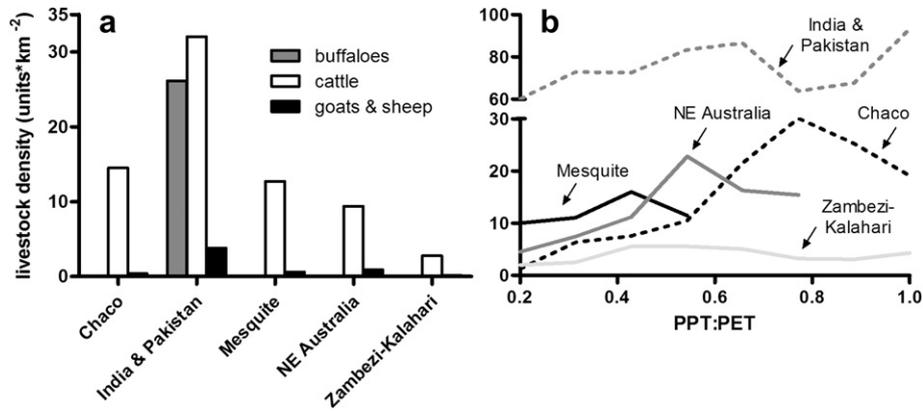


Fig. 7. Livestock density (a) regional values considering buffaloes, cattle, and goats and sheep\*, and (b) a combined value along the water balance gradient (PPT:PET) across the five dry subtropical regions. \* No goats are found in NE Australia.

toward humid areas and the decline of waterlogging and biotic stresses (pests and diseases) toward dry areas (Boling et al., 2004) (Fig. 4). In the more populated region of India & Pakistan, this trade-off has been blurred for croplands by widespread high local food demand and labor availability and a massive reliance on irrigation (Table 4). Even though grazing activities in DST regions are more frequently performed over uncultivated vegetation (Millennium Ecosystem Assessment, 2005), the peak of this activity in dry subhumid areas can be attributed to the still-large proportion of uncultivated land in all regions, except India & Pakistan. In the Asian region, a high level of livestock pressure across climatic gradients is sustained mainly by harvest residues and, to a lesser extent, by fodder crops (rainfed and irrigated), explaining the similar density throughout the entire gradient (Chakravarti, 1984).

The convergence of structural patterns of unmanaged (natural) ecosystems sharing abiotic conditions has historically been recognized by biogeographers (Schimper, 1903; Udvardy, 1975) (Fig. 8, left). However, in this study, we showed that a growing and higher

resource-demanding human population has imposed a new set of controls over ecosystems, leading to departures of ecosystem structure from natural conditions (Fig. 8, right). Even though the human imprint over ecosystems is ubiquitous (Vitousek et al., 1997), when moving from natural (protected areas) to semi-natural conditions (wild grazing areas), we found increasingly different ecosystems in terms of vegetation composition, as suggested by cartographic and photographic archives (Table 5). In protected areas, tree-dominated systems prevailed in all regions, except Mesquite. However, in Zambezi-Kalahari, we found a considerably large proportion of shrubs and grasses as well as trees. In addition to the existence of large extents of pure woodlands, shrublands, and grasslands, these vegetation classes usually co-occurred in a formation of a grassland matrix with scattered clusters of shrubs or trees (as shown by photographs). In Africa, this pattern, which is generally described as savanna or savanna woodland, may arise as a result of a long evolutionary history of foraging by wild animals and/or burning by humans (Menaut,

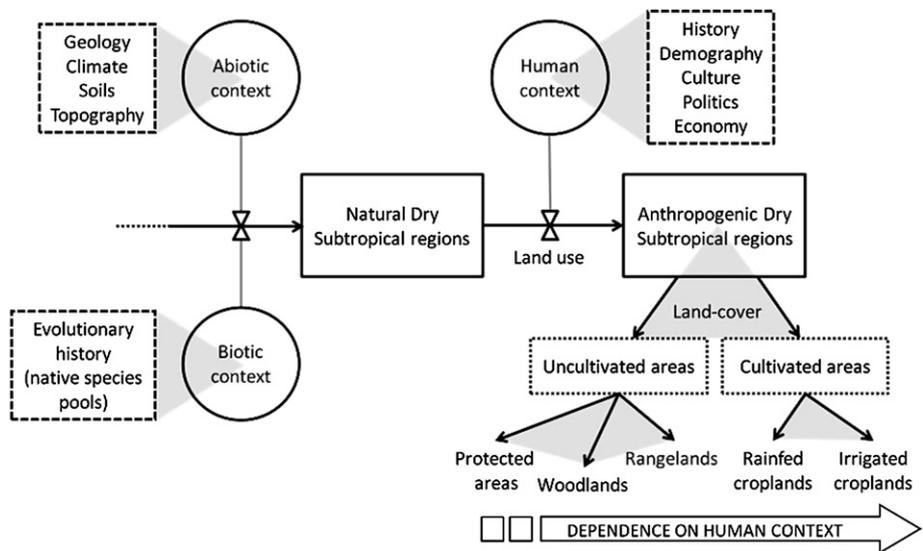


Fig. 8. Controls of ecosystem structure and function under natural and anthropogenic conditions. Driving contexts (circles) and their main dimensions (dotted boxes) are shown. While abiotic and, to a lesser extent, biotic controls shaped natural ecosystems in the past, the human context has gained importance with time through its influence on land cover and uses. As land uses subject to increasing anthropogenic intervention are examined (i.e., gradient from protected areas to croplands), the human context gains importance over abiotic and biotic contexts, introducing greater structural divergences across regions with similar environmental but contrasting social conditions. Among regions, due to the relative impact of human controls, we expect increasing divergence from protected areas to croplands (white arrow).

1983). Although the Mesquite region is defined as a shrubland area by continental vegetation maps, it shares similar traits with the remaining regions, presenting vegetation structured similarly to savanna shrublands or xerophytic woodlands often dominated by the legume tree *Prosopis glandulosa* (Archer, 1995; Owens et al., 1995). These common characteristics in the original or potential vegetation between the five DST regions were emphasized more than a century ago, when vegetation was less transformed than at present (Schimper, 1903).

The observed similarities decreased in non-protected areas, with substantial contrasts being detected in the barren ground proportion between NE Australia and the other regions (22% vs. <1%) and in the shrubland cover between Mesquite and Zambezi-Kalahari compared to the other regions (80 and 32% vs. ~15%). The barren ground expansion in Australia likely stems from a history of intensive cattle and sheep grazing in the early 20th century, followed by large-scale woody vegetation eradication programs carried out with the intention of favoring grasses (which included the use of blade ploughs and herbicides), perhaps in interaction with the particularly poor fertility (and low resilience) of the region (Henzell, 2007; McAlpine et al., 2009; Seabrook et al., 2006) (Table 5, Fig. 1, supplementary material). In Zambezi-Kalahari and Mesquite, anthropogenic fire disturbances, wood extraction, and a long-term history of cattle rearing could have reshaped the vegetation, leading to an encroachment of shrubs into open savannas and woodlands (Archer, 1995; Roques et al., 2001), which is a process that has also been described for India & Pakistan (Pandey and Singh, 1991).

With the exception of the most arid areas of our study regions, where species such as sorghum and millet showed a generally increasing trend (Fig. 5), the crop composition differed greatly across DST regions (Fig. 8, right). These divergences can partly be explained by the orientation of agricultural production toward subsistence and local markets vs. national/global markets, with Chaco, Mesquite, and NE Australia being dedicated to the production of commodity crops that greatly exceeded potential (human) regional demands. Soybean cultivation, which dominates in Chaco, supplies Asian pork and poultry production (Grua et al., 2005), while NE Australian sugarcane production exceeds national consumption by 20 times (AGSI-FAO, 1999; FAO, 2009). Sorghum and wheat from NE Australia and sorghum from Mesquite are mainly used for national intensive animal production systems, with the animal production ultimately being exported (FAO, 1996; McAlpine et al., 2009). In contrast, India & Pakistan and Zambezi-Kalahari hosted a more diversified set of crops that balanced grains and pulses, likely responding to their domestic demands (Table 6). As an example, 96% of the sorghum produced in Zambezi-Kalahari is locally consumed (FAO, 2009), while only a small proportion of the cultivated area is dedicated to crops for global markets, such as coffee, cotton and tobacco (Snapp et al., 2002; You et al., 2009). Although being characterized by the cultivation of a diversified group of crops, India & Pakistan showed a predominance of wheat and rice production, likely stemming from the Green Revolution, which favored their expansion over that of pulses, millet and sorghum (Singh, 2000; Ladha et al., 2003; Frolking et al., 2006) without an overall significant shift in the regional sown area (Alauddin and Quiggin, 2008). This technological leap in the 1960s, which included new crop varieties, fertilization, mechanization, and, most significantly, irrigation, allowed an increase of rotation intensity, with two or three cropping cycles per year being carried out (Das, 2006; Frolking et al., 2006).

The effects of irrigation and fertilization inputs and land degradation contribute to explaining the similarities and differences of agricultural productivity observed across regions

(Fig. 6). A qualitative assessment of the integrated contribution of irrigation (Table 4 and Fig. 4) and fertilization (FAO, 2009) suggests the following decreasing ranking of inputs: Mesquite = India & Pakistan > NE Australia >> Chaco = Zambezi-Kalahari. A global land degradation assessment (Oldeman et al., 1991) suggests the following decreasing ranking: Zambezi-Kalahari = India & Pakistan > Mesquite > NE Australia >> Chaco. Based on these two rankings, we speculate that Chaco, Mesquite, and India & Pakistan are currently able to achieve similar grain yields ( $\sim 3 \text{ Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ ) by compensating for their increasing degradation with parallel increases of irrigation and fertilization inputs (Fig. 2). Without achieving this compensation, Zambezi-Kalahari showed the lowest yields, likely as a result of the combined effects of high degradation and low addition of resources (this region consumes six times less nitrogen than Mesquite, in  $\text{ha}^{-1} \cdot \text{y}^{-1}$ ; FAO, 2009). In NE Australia, unconsidered soil restrictions (Chapman et al., 2000) and predominant opportunistic and low-input approaches to agriculture may explain the low rainfed crop yields (Sadras and Roget, 2004), though they coexist with conservation efforts in grain crop areas and highly subsidized and productive sugarcane systems (Thomas et al., 2007). It is important to highlight that these two last regions exhibit the poorest soils across the examined territories (Table 3).

Contrasting irrigation and fertilization patterns may respond to different needs and/or accessibility to inputs of farmers, as illustrated by the cases of Chaco and Zambezi-Kalahari, the two least-fertilized regions. In Chaco, the agricultural systems sustain almost the same grain outputs as Mesquite, with Chaco consuming six times less nitrogen and two times less phosphorus than Mesquite (FAO, 2009). High fertilization rates may not yet be strongly demanded in Chaco as a result of its short cultivation and nutrient depletion history, accompanied by the N-fixing effect of soybeans (Álvarez and Lavado, 1998). In contrast, in Zambezi-Kalahari, where imbalances between harvests (outputs) and fertilization (inputs) and associated declines in primary productivity and erosion protection are well known (Nandwa and Bekunda, 1998; Drechsel et al., 2001), fertilizers remain little-used, most likely as a result of the combination of high costs (two-to-six times higher than in Europe, America, or Asia) and low affluence of the farmers in the region (Sanchez, 2002; Snapp et al., 2002).

In India & Pakistan, the region with the longest history of cultivation, current soil degradation represents a response to the opposite situation regarding resource additions when compared to Zambezi-Kalahari. In this Asian region, high and inefficient use of water and nutrient subsidies has caused widespread hydrological alterations leading to waterlogging and salinization/alkalinization as well as soil acidification (Singh, 2000; Wichelns, 2004). These inefficiencies have at least two significant environmental consequences for water resources that involve sustained depletion of deep aquifers (Tiwari et al., 2008) and pollution of water with soluble nitrogen (Painuly and Mahendra Dev, 1998).

Production rates analyzed on a per capita basis showed unique patterns across regions (Table 7). The per capita agriculture output for Chaco and NE Australia exceeded those found for India & Pakistan and Zambezi-Kalahari by seven to eleven times. The per capita livestock availability in NE Australia displayed a 72-fold difference compared to the African and Asian regions ( $10.2$  vs.  $0.13 \text{ units} \cdot \text{inh}^{-1}$ ). Notably, Africa and Asia presented very close values for grain output ( $\sim 50 \text{ kg} \cdot \text{y}^{-1} \cdot \text{inh}^{-1}$ ) and livestock density ( $\sim 0.14 \text{ units} \cdot \text{inh}^{-1}$ ). These results could be related to the basal nutritional requirements of individuals (and the carrying capacity of a region under a certain production level) (Welch and Graham, 1999) as well as the basic labor needs to produce goods on a piece of land under a determined technical production scheme, as in Chaco or NE Australia.

## 5. Conclusions

In the dry subtropics, which are abiotically similar by definition, current and past human contexts lead to differences in the current land use conditions of individual regions in terms of the proportion of land under cultivation, the vegetation composition of cultivated and uncultivated areas, and grazing pressure. We found that this variability was related to historical vs. recent and local vs. external pressures. Thus, India & Pakistan and Zambezi-Kalahari presented long cultivation histories tied to local demands for goods, but with remarkable differences in the amount of land transformed for cultivation use due to the large contrasts in population density. In Chaco, Mesquite and NE Australia, the observed changes in cultivation rates are of modern origin and associated with external demands. The DST regions presented different uses of uncultivated lands that indicated changes from the original woody conditions to shrubby or grassy coverage (which was especially noticeable in NE Australia). Aridity (a major constraint in drylands) did not appear to drive the different land uses in the encompassed gradients, as shown by the presence of cultivation and livestock production in the most arid environments considered in this study. This would appear to indicate that global markets are not yet demanding the cultivation of arid lands in these regions, as is seen for the local populations in India & Pakistan and Zambezi-Kalahari. Regions subject to local needs for vegetable and animal products exhibited low and similar per capita outputs in Asia and Africa, in spite of the ongoing large-scale degradation occurring in these regions and the differences in their technological settings. In the remaining regions, the production of goods was almost completely decoupled from local demands.

In the last several decades, scientists have increasingly introduced human processes into attempts to understand, predict, and manage terrestrial ecosystems, expanding our knowledge regarding the complex interactions that ultimately drive their capacity to provide goods and services. Considerable contributions have been made by studies addressing the vulnerability/sustainability of supply goods and services (Turner et al., 2003), local-scale environmental narratives related to land cover and vegetation structure changes combining statistics with remotely sensed information (Hessburg and Agee, 2003; Seabrook et al., 2006), and global narratives presenting future scenarios involving these interactions and the resulting development of humanity (Raskin, 2005). Using existing data sources, we quantified how different societies (associated with diverse land uses and users) inhabiting what are currently (or were in the recent past) woodlands or savannas have generated different ecological and food production patterns. Analyses of these associations are still greatly limited by data availability at a subnational scale; thus, the production of well-supported data (both rural and urban) on population density and affluence as well as landscape connectivity is critically required. New and more reliable comparative perspectives would therefore contribute to the exploration of alternative paths and strategies for ecosystem use and management in a world with increasing demands for food where sustaining natural and social capital is one of the most urgent challenges.

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## Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2011.08.016.

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