

Woody plant diversity in seasonally dry tropical forests of Urubamba basin, a threatened biodiversity hotspot in southern Peru

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Abstract: We studied the woody flora of seasonally dry forests in the middle section of the Urubamba river, Cusco region in southern Peru. We set up twenty 0.1 ha plots at altitudes between 700 and 1300 masl and enumerated all individuals with diameter at breast height (dbh) ≥ 2.5 cm. We recorded 5259 individuals belonging to 552 species, 303 genera and 82 families. On average, we recorded 92 species/plot, with a maximum of 150 species/plot. The most species rich families in the area were Fabaceae (69 species), Bignoniaceae (30), Moraceae (27), Apocynaceae (23) and Sapindaceae (22). The most species rich genera were *Inga* (13 species), *Aspidosperma* (11), *Ficus* (11), *Machaerium* (10) and *Eugenia* (9). The five most abundant species were *Allophylus punctatus* (142 individuals), *Pogonopus tubulosus* (122), *Warszewiczia coccinea* (111), *Annona neoulei* (106) and *Anadenanthera colubrina* (95). Multivariate floristic analyses suggested three types of dry forests in the area: Amazonian pluviseasonal tropical dry forest, sub-Andean pluviseasonal tropical dry forest, and savanna-like pluviseasonal tropical dry forest. A phytogeographical analysis showed that the dry forest in the Urubamba is more related to the dry forests in the Bolivian Chiquitania, than to other Peruvian dry forests. The conservation status of these forests is critical since much of their original area has been converted to other land use. We conclude that the high diversity of woody taxa and the phytogeographical relations suggest that the Urubamba dry forests are an Andean-Amazonian and neotropical dry forest hotspot, requiring urgent protection and conservation in the face of current rapid destruction.

Key words: Amazonian, endemism, floristics, quantitative plant inventory, Quillabamba, savanna-like dry forest, species richness, sub-Andean.

Introduction

Dry forests worldwide account for about 42% of tropical and subtropical forests (Murphy & Lugo 1986; Miles *et al.* 2006). In the Neotropics they have

been proposed as a biome or metacommunity and integrate all seasonally dry forested ecosystems (Pennington *et al.* 2009; Prado 2000). Seasonally dry tropical forests (SDTF) are defined by presence of a deciduous to semi-deciduous vegetation, prevalence of thorny and succulent plants,

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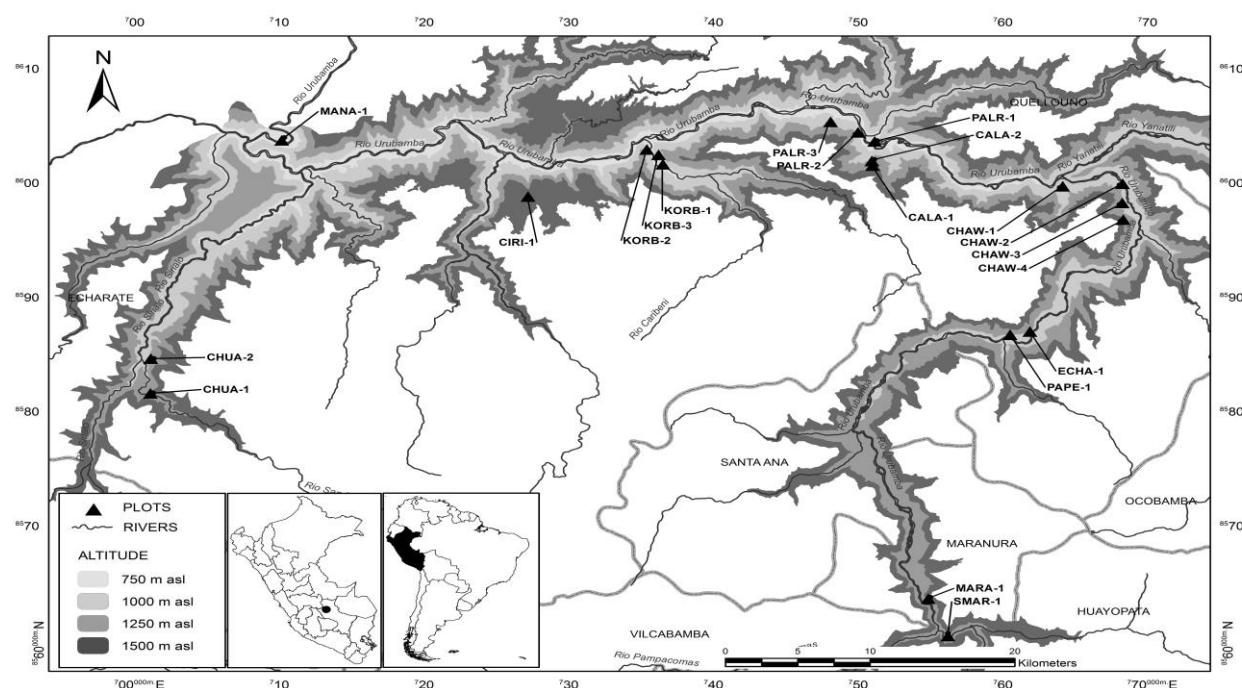


Fig. 1. Distribution of seasonally dry tropical forest inventory plots in the medium section of the Urubamba basin.

occurring in regions with average annual precipitation below 1600 mm with a period of at least 5–6 months when they receive less than 100 mm of total precipitation. These forests usually occur on rich soils (Gentry 1995; Mooney *et al.* 1995; Murphy & Lugo 1986). These ecosystems are represented in the Neotropics by a series of discontinuous patches, including the phytogeographic domains of the Caatinga and Chiquitania (Banda *et al.* 2016). Recent studies have identified up to 21 dry forests nuclei in the Neotropics, from northern Mexico and the Caribbean to Argentina and southern Brazil (García-Villacorta *et al.* 2009; Linares-Palomino *et al.* 2011; Särkinen *et al.* 2011a). Many of these nuclei are suggested to have been part of an extensive and continuous biome, somewhere during the Miocene to Pleistocene transitions, reaching its peak in the latter, and subjected to climatic events such as prolonged drought and cold, geological influences e.g. the Andean uplift and glaciations during the Quaternary (Burnham & Graham 1999; Hughes & Eastwood 2006; Bueno *et al.* 2016; Prado 2000). These areas are known as the "Pleistocenic Arc", extending from the coast of Brazil to the dry regions of Paraguay and Argentina, and the inter-Andean regions of Bolivia and Peru to SDTF in northern Peru and southern Ecuador (Linares-

Palomino *et al.* 2011; Moggi *et al.* 2015; Prado 2000; Särkinen *et al.* 2011a).

SDTFs have traditionally been under strong anthropic pressure because they are usually associated with rich soils (Blackie *et al.* 2014; Mooney *et al.* 1995). Three main SDTF areas are currently recognized in Peru: i) the equatorial SDTF along the northern coast from Tumbes to Lambayeque, ii) SDTF in inter-Andean valleys of the Marañón, Apurimac and Mantaro rivers, and iii) the Eastern SDTF south of Tarapoto (García-Villacorta *et al.* 2009; Linares-Palomino 2004; Linares-Palomino & Ponce-Alvarez 2009; Linares-Palomino *et al.* 2011). A brief mention is given to the SDTF in Quillabamba as belonging to the inter-Andean group within the Urubamba valley but only as "minor remnants", given the limited information available at the time and the inability to properly establish their phytogeographic relationships (Linares-Palomino 2006). Few studies describe the vegetation of the valley, and in particular of the SDTF. Weberbauer (1945) and Marin (1961) described this as evergreen savannas. Marin (1995) mentioned *Cereus vargasii* (Cactaceae), *Dictyoloma peruviana* (Rutaceae) and *Pseudourceolina* as endemic to this SDTF. Apart from these studies, only botanical collections are known from the area,

Table 1. Floristic and environmental characteristics of twenty 0.1 ha plots sampled in the SDTF of the Urubamba basin. (I = number of individuals, S = number of species, AB = basal area (m²/0.1 ha)). Highest values are underlined, the three highest values for each variable are shown in bold.

Locality	Code-plot	I	S	AB	Fisher's alpha	Texture	Drainage	pH	Altitude (masl)
Calaminayoc-2	CALA-2	262	106	2.62	66.22	1.5	15.1	4.7	1010
Calaminayoc-1	CALA-1	242	114	2.42	84.15	1.5	14.8	4.8	1220
Chawares-1	CHAW-1	214	72	2.58	38.11	1.5	14.2	4.7	780
Chawares-2	CHAW-2	290	81	2.07	37.29	1.5	14	4.7	790
Chawares-3	CHAW-3	258	88	2.14	47.10	1.5	13.8	4.8	890
Chawares-4	CHAW-4	207	77	2.90	44.42	1.5	14	4.8	1200
Chuankiri-2	CHUA-2	258	89	2.58	48.08	2.5	18.2	4.5	1000
Chuankiri-1	CHUA-1	275	93	2.75	49.43	2.5	18.5	4.3	1290
Cirialo-1	CIRI-1	283	101	2.83	56.17	2	17.6	4.4	1123
Echarati-1	ECHA-1	223	75	2.23	39.68	1.5	12.3	4.9	930
Koribeni-2	KORB-2	313	110	2.18	60.37	1.5	13	4.7	750
Koribeni-3	KORB-3	218	108	3.22	84.92	1.5	13.4	4.7	795
Koribeni-1	KORB-1	322	127	3.13	77.39	1.5	14.1	4.8	840
Managua	MANA-1	277	150	2.77	133.6	1.5	14	4.7	720
Maranura	MARA-1	227	54	2.27	22.41	2	16.5	5.1	1230
Palma real-2	PALR-2	254	81	2.54	41.08	1.5	13.8	4.8	780
Palma real-1	PALR-1	309	99	3.09	50.39	1.5	14.1	4.9	790
Palma real-3	PALR-3	302	78	3.02	34.08	1.5	13.8	4.8	820
Papelpata-1	PAPE-1	330	84	3.30	36.36	1.5	13.6	4.8	950
Santa María-1	SMAR-1	182	62	1.82	33.15	2	16.1	4.9	1250

mainly by César Vargas Calderon (in 1974) and more recently by a Missouri Botanical Garden project (2002–2009) in southern Peru. It is in this context that the present study aims to fill an information void of SDTF in inter-Andean valleys through extensive and detailed studies of their plant diversity and floristic composition in order to clarify their phytogeographic relationships with other SDTF in Peru and the Neotropics and place into context their conservation and management needs.

Material and methods

Study Area

This study was done in the middle section of the Urubamba basin (IMA 2001), within the La Convención province (districts of Amaybamba, Quellouno, Maranura, Santa Ana, Echarati and Vilcabamba), between 720 masl and 1550 masl. The middle section of the Urubamba is defined between the Santa Teresa and Kiteni villages. The study area was initially characterized by using Holdridge life zones as a subtropical dry forest transitional to

subtropical humid forest, a tropical dry forest transitional to subtropical and as subtropical dry forest (ONERN 1976; POT-LC 2005). These life zones represent about 13% of the area in La Convención Province (POT-LC 2005). The basin in this section has warm dry climate, with temperatures of 14 °C to 30 °C (average of 15.4 °C) in the towns of Cirialo and Chahuares (towards the lower end of the basin) and maximum temperatures of 28.8 °C (average of 23.3 °C) in the towns from Quillabamba to Echarati (toward the higher end of the basin). Total annual rainfall does not exceed 1300 mm in the basin bottom but increases as one descends through the main basin up to 1600 mm (IMA 2001). The SDTF of the Urubamba have undergone a major landscape transformation and now much of the territory of the La Convención Province includes agricultural and disturbed areas mainly surrounding the villages of Santa Maria, Maranura, the city of Quillabamba and the town of Echarati (POT-LC 2005). However, in this transformed vegetation matrix relicts of primary or little impacted forest remains, mainly due to their presence on steep slopes and consequent

inaccessibility. It is among these remaining forest patches, that we chose eleven locations for quantitative inventory plots (Fig. 1, Table 1).

Plot setup and assessment

To quantify diversity and structure of the forest, we installed twenty 50 m x 20 m plots (0.1 ha). This method is being widely used due to its balance between time and resource investment and data collection effectiveness (Macia 2008; Torrez *et al.* 2010). Within each plot we assessed all individuals with diameter at breast height (dbh) ≥ 2.5 cm, belonging to all life-forms (lianas, trees, shrubs, hemi-epiphytes and cacti). When the forest patch was big enough to accommodate more than one plot, we made sure that these were separated at least 600 m. All collected plant specimens were processed, identified and deposited at CUZ herbarium (Universidad Nacional de San Antonio Abad del Cusco), with duplicates at USM, HUT, MOL, AMAZ and MO (herbarium acronyms follow Thiers 2016). Taxonomic treatment of families followed the Angiosperm Phylogeny Group (APG 2016), and information provided by TROPICOS (www.tropicos.org) and The Plant List (www.theplantlist.org).

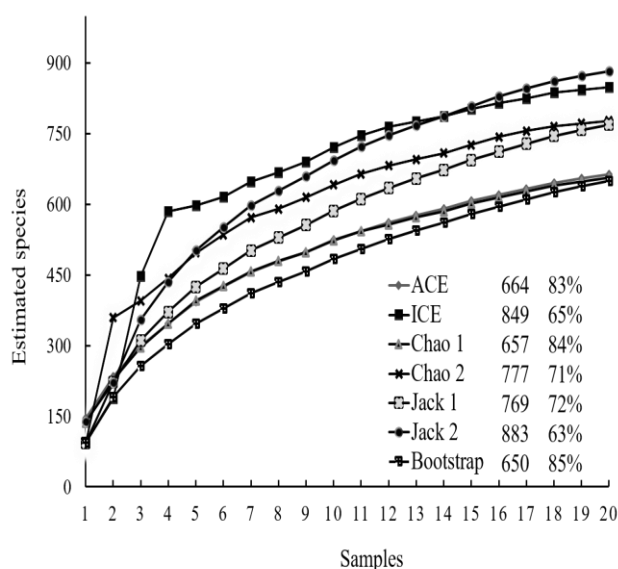


Fig. 2. Estimated species number of the SDTF in the Urubamba basin. Data is from quantitative samples from 20 sites. The inserted table provides the estimated species numbers and the estimated coverage (in %) for all 20 sites. Abbreviations; Chao, Bootstrap, ICE = incidence coverage estimator, Jack = Jackknife, ACE = abundance coverage estimator.

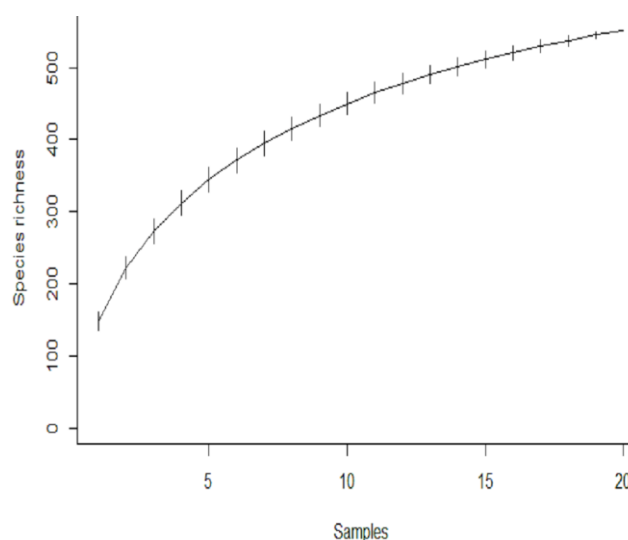


Fig. 3. Rarefaction curve showing species accumulation for the Urubamba SDTF.

Terrain and soil data

To characterize topography, we measured for each plot slope in degrees. We further collected one kilogram of soil using a trial pit of 40 cm depth from each of the four corners of each plot, mixed them and produced one single soil sample. Soils were analyzed at the Soil Analysis Laboratory of the Universidad Nacional de San Antonio Abad del Cusco for texture, pH and soil type according to ONERN (1987) and IMA (2001). We took quantitative field measurements for texture and drainage according to Soil Survey Division Staff protocols (1993), which divides drainage into seven categories based on time (minutes).

Data analysis

Diversity

Within-plot diversity was characterized by species richness and Fisher's Alpha. The latter is an index that has been shown to be robust to variations in abundances, and is widely used to compare floristic diversity among tropical forest plots (Phillips & Miller 2002; ter Steege *et al.* 2006). To estimate species richness for SDTF in the middle section of the Urubamba basin we calculated the species richness using seven different estimators (abundance coverage estimator, incidence coverage estimator, Bootstrap, Chao1 and 2, Jackknife 1 and 2; 100 randomizations) provided in the Estimate S software (Chazdon *et al.* 1998; Colwell *et al.* 2004). To assess accumulated species richness, we constructed a species accumulation curve with random

accumulation (Colwell *et al.* 2012) using R (R Core Development Team 2016) and Estimate S (Colwell *et al.* 2012).

Structure and composition

We calculated community parameters like relative abundance, relative dominance and relative frequency for each plot. We derived the importance value (*sensu* Curtis & McIntosh 1951) using the following formulas: Relative Abundance: $DeR_j = 100 \times De_j / \sum De_j$; Relative Dominance: $DoR_j = 100 \times Do_j / \sum Do_j$; Relative Frequency: $FR_j = 100 \times F_j / \sum F_j$, Importance Value Index (IVI_j) = $DeR_j + DoR_j + FR_j$, where: De_j is the total number of stems of species j in all plots, Do_j is the total basal area of species j in all plots, F_j is the number of plots where species j is present.

Similarity and association analysis

The percentage of floristic similarity between plots was calculated using the quantitative Bray-Curtis index (with abundance data) (Magurran 1988). To visually represent these similarities, we used two ordination methods. The cluster analysis used these similarities and the group averages as linkage method between groups and pairs of groups to build dendrograms. To complement this analysis, we further used a non-metric multidimensional scaling ordination (NMDS) (McCune & Grace 2002). In order to explore the relationship between the plots and the environmental variables recorded (pH, altitude, drainage, texture and slope), we performed a canonical correspondence analysis (CCA). All analyses were performed with R (R Core Development Team 2016) and PAST v3.01 (Hammer *et al.* 2001).

Results

Diversity, composition and structure

We enumerated 5259 individuals with dbh ≥ 2.5 cm. These included 552 species and morphospecies, in 303 genera and 82 families. We identified 352 taxa to species level (63.8%). We identified 302 genera (99.9%) and all families.

The most diverse plot was Managua (150 species, 277 individuals, Fisher's alpha = 133.6), followed by Koribeni-3 (Fisher's alpha = 84.92) and Calaminayoc-1 (Fisher's alpha = 84.15). In contrast, Maranura had a Fisher's alpha of only 22.41, with 54 species (Table 1). Estimated species richness values ranged between 650 (Bootstrap means) and

Table 2. Diversity, abundance and basal area of ten representative SDTF families of the Urubamba basin (I = number of individuals, S = number of species, AB = basal area (m²/0.1 ha)).

Family	S	I	AB
Fabaceae	69	587	7.32
Bignoniaceae	31	290	1.02
Moraceae	27	389	13.64
Apocynaceae	23	210	1.82
Euphorbiaceae	22	126	0.92
Sapindaceae	22	312	0.74
Myrtaceae	20	236	2.13
Rubiaceae	19	418	2.28
Malpighiaceae	18	166	0.72
Melastomataceae	16	77	0.34
Total	267	2811	30.93

883 (Jackknife 2 means). The coverage ranged between 63% and 85% (mean 75%). For a sample coverage between 73% and 86%, Brose & Martinez (2004) recommended use of the incidence coverage estimator, which gives an estimate of 769 species (Jackknife 1).

The species accumulation and rarefaction curves showed that after ten plots we were registering nearly 95% of all species (524) (Figs. 2, 3).

The most species rich families were Fabaceae (69 species), Bignoniaceae (30), Moraceae (27), Apocynaceae (23), Sapindaceae (22), Euphorbiaceae (22) and Myrtaceae (20). The ten most species rich families concentrated 48.4% of all species, 53.6% of all individuals and 50% of total basal area (Table 2).

The most species rich genera were *Inga* (Fabaceae, 13 species), *Aspidosperma* (Apocynaceae, 11), *Ficus* (Moraceae, 11), *Machaerium* (Fabaceae, 10), *Eugenia* (Myrtaceae, 9), *Miconia* (Melastomataceae, 9) and *Paullinia* (Sapindaceae, 8) (Table 3). The ten most species rich genera represent 16.7% of all species and include 16 % of total basal area (Table 3).

The five most abundant species were *Allophylus punctatus* (Sapindaceae, 142 individuals), *Pogonopus tubulosus* (Rubiaceae, 122), *Warszewiczia coccinea* (Rubiaceae, 111), *Annona neoulei* (Annonaceae, 106) and *Anadenanthera colubrina* (Fabaceae, 95). Half of all individuals (2593, 49.4%) were in the smallest dbh class (2.5–5 cm), whereas only 70 individuals (1.4%) were recorded with dbh higher than 40 cm. (Fig. 4a). Plots with highest basal area values were

Papelpata (3.3 m²), Koribeni-3 (3.22 m²) and Koribeni-1 (3.13 m²), while, Santa María (1.82 m²) and Chawares-2 (2.07 m²) had the lowest values (Table 1).

Characteristic shrubby and low diameter taxa included *Cnidoscylus urens* and *Acalypha villosa* (Euphorbiaceae), *Carica glandulosa* (Caricaceae), *Philodendron* sp. (Araceae), *Annona neoulei* (Annonaceae), *Allophylus punctatus* (Sapindaceae), *Erythroxylum ulei* (Erythroxylaceae), several species of *Machaerium* (Fabaceae), several species of Bignoniaceae, including lianas with genera like *Arrabidaea* and *Pithecoctenium*, and most of the genera in the Sapindaceae and Malpigiaceae. Arboreal and thicker taxa included *Ficus citrifolia*, *F. insipida*, *Brosimum guianense*, *Myroxylon balsamum*, *B. alicastrum* and *Pseudolmedia laevigata* (Moraceae), *Ceiba samauma* and *Ceiba insignis* cf. (Malvaceae), *Machaerium* sp. 3 and *Amburana cearensis* (Fabaceae), *Terminalia amazonia* (Combretaceae), *Ampelocera ruizii* (Ulmaceae) and *Gallesia integrifolia* (Phytolaccaceae).

In terms of height, the woody vegetation was characterized by individuals attaining between 2 m and 5 m (39.2%, 2060 individuals) (Fig. 4b). Few individuals reached heights of more than 25 m and included *Amburana cearensis*, *Myroxylon balsamum* and *Apuleia leiocarpa* (Fabaceae), *Ceiba insignis* cf. and *Cavanillesia umbellata* (Malvaceae) and *Brosimum alicastrum* (Moraceae).

Trees and shrubs dominated the SDTF in the Urubamba basin (42%, 2205 individuals and 41%, 2190 individuals, respectively), this included arborescent ferns (2 individuals), cacti (67), stranglers (14), hemi-epiphytes (20) and palms (95). The remaining 17% (864 individuals) corresponded to lianas.

Beta diversity, floristic affinities and relationship with environmental variables

The cluster and NMDS analyses showed three main groups, consistent at species and genus level (Fig. 5). The biggest and most homogeneous group included 15 plots, with the Chawares sites having the highest similarity values (56%–65% similarity at species level, 63%–76% similarity at genus level), complemented by the Palma Real-1, 2 and 3, Koribeni-1, 2 and 3, Calaminayoc-1 and 2, Echarati, Managua and Papelpata plots.

The two other groups contained two and three plots, respectively. One, including the Santa María and Maranura plots (52% and 57% similarity for

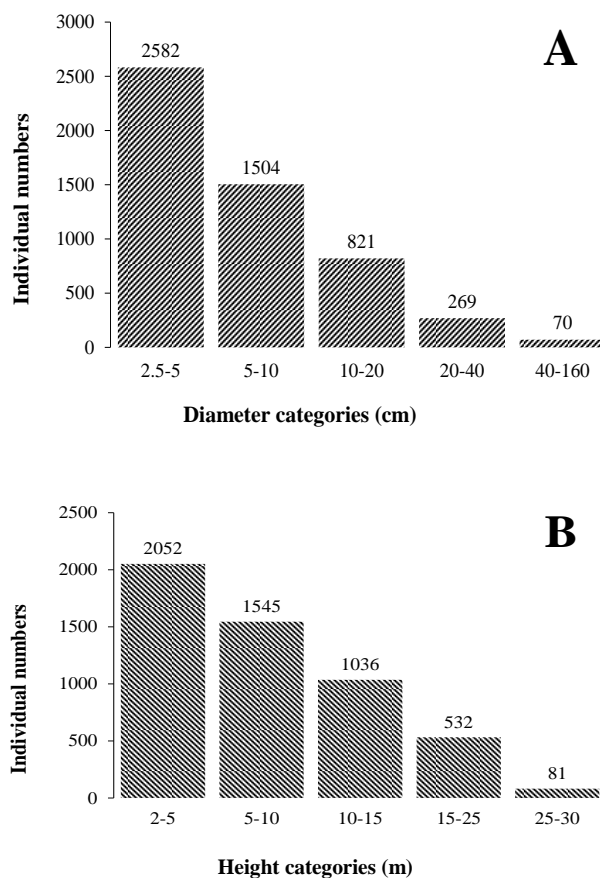


Fig. 4. Distribution of woody individuals assessed in the Urubamba basin SDTF by A) diameter at breast height and B) height.

species and genera, respectively), was located in the upper reaches of the Urubamba watershed. The other included the Chuankiri-1 and 2 and Cirialo plots, with similarities between 22% and 48% for species and 42% to 59% for genera. These plots were located towards the lower Urubamba basin, although at higher altitude than the other plots surveyed.

Three of the evaluated variables explained more than 63% of the variation in the floristic composition of the data and included pH, texture and drainage. The main group is influenced by acidic pH values (4.7–4.9), good drainage and clayey texture. The second group (Chuankiri1, 2 and Cirialo 1) is influenced by soils with a loamy-clayey texture, acidic pH (4.3–4.5) and poor drainage. The third group (Santa María and Maranura) is related to soils with slightly less acidic conditions (4.9–5.1), loamy texture and good drainage. In contrast, altitude and slope, were variables that explained little of the floristic variation in our plots.

Table 3. Diversity, abundance and basal area of ten representative SDTF genera of the Urubamba basin (I = number of individuals, S = number of species, AB = basal area (m²/0.1 ha)).

Genus	S	I	AB
<i>Inga</i>	13	66	0.44
<i>Aspidosperma</i>	11	116	1.70
<i>Ficus</i>	11	41	4.39
<i>Machaerium</i>	10	88	1.42
<i>Eugenia</i>	9	77	0.47
<i>Miconia</i>	9	43	0.16
<i>Paullinia</i>	8	36	0.06
<i>Arrabidaea</i>	7	40	0.08
<i>Casearia</i>	7	57	0.46
<i>Nectandra</i>	7	57	0.64
Total	92	623	9.82

Discussion

Diversity and composition of the SDTF in the Urubamba basin in the context of the Neotropical dry forests

The floristic knowledge of SDTF in Peru has been increasing in recent years, with the main focus on the major SDTF areas in the country (Aguirre *et al.* 2006; García-Villacorta 2009; Linares-Palomino 2006; Linares-Palomino & Ponce-Alvarez 2009; Linares-Palomino *et al.* 2011; Marcelo-Peña 2008; Marcelo-Peña *et al.* 2015). This study reports 552 woody species for the SDTF in the Urubamba, a hitherto floristically little known region which was considered as a small isolated remnant (Linares-Palomino 2006). In terms of species richness, the Urubamba plots had in average 92 species, with a range between 54 and 150 species. These variations occur along the middle section of the basin, with a distinct gradient of richer sites downstream (e.g. Managua and Koribeni sites) that decreases upstream (as in the Calaminayoc, Cirialo and Palmareal sites). However, these last sites still present richness values that are higher than values reported for other studies in SDTFs across Peru using the same survey methodology. For instance, a study in the Marañon valley in northern Peru recorded between 25 and 30 species per plot (440 species in total, Marcelo-Peña *et al.* 2015), around 50 species per plot in the SDTF in Tarapoto (García-

Villacorta 2009, with around 100 species in total, Gentry 1995) and between 43 and 61 species in the SDTF in northern coastal Peru (Gentry 1995; Phillips & Miller 2002, with some 313 woody species, Aguirre *et al.* 2006; Linares-Palomino *et al.* 2011). Especially noteworthy is the fact that even the sites with the lowest species richness values, such as Santa María and Maranura, recorded values at least similar to other SDTF inventories in Peru. Compared to other studies in the Neotropics, the Urubamba SDTF reported higher values than surveys in Bolivia (40 to 86 species per plot, Fisher's alpha values between 20 and 35, Gentry 1995; Fuentes *et al.* 2004), Venezuela (38 to 67 species per transect, Fisher's alpha values between 25 and 60, Phillips & Miller 2002) and Mexico (22 to 97 species per plot, Trejo & Dirzo 2002; Williams *et al.* 2010). Similar values to the Urubamba SDTF were, to our knowledge, only reported in dry forest surveys in Colombia (52 to 120 species per transect, Fisher's alpha values between 25 and 60, Phillips & Miller 2002).

Fabaceae was the most species-rich family (69 species), followed by Bignoniaceae (31), showing a pattern reported for most of the SDTF in the Neotropics (Gentry 1995; Linares-Palomino *et al.* 2011; Pennington *et al.* 2000; Pennington *et al.* 2006; Ratter *et al.* 2003, 2006). However, the third family in terms of species richness in our study area was Moraceae (27 species), which is unusual for Neotropical dry forests. The Moraceae are consistently recorded in SDTF surveys, especially members of the genus *Ficus*, as in northwestern Colombia, southeastern Ecuador and eastern Peru (Gentry 1995; García-Villacorta 2009), although in low numbers. Other families that characterized the Urubamba SDTF include Apocynaceae, Euphorbiaceae, Sapindaceae, Myrtaceae, Rubiaceae and Malpighiaceae, which are considered representative and dominant of Neotropical SDTF (Gentry 1995; García-Villacorta 2009). Gentry (1995) noted that Cappariaceae, Cactaceae, Erythroxylaceae, Celastraceae and Malvaceae are also characteristic of SDTF, all of which were recorded in our study area.

Considering that this quantitative study was plot-based, the 82 families recorded are exceptional in terms of diversity. The compilation by Gentry (1995), based on inventories in 28 sites across the Neotropics, listed 82 families. Geographically more closer studies recorded 61 and 25 families in inter-Andean (Marcelo-Peña *et al.* 2015) and eastern Andean (García-Villacorta 2009) SDTF in Peru,

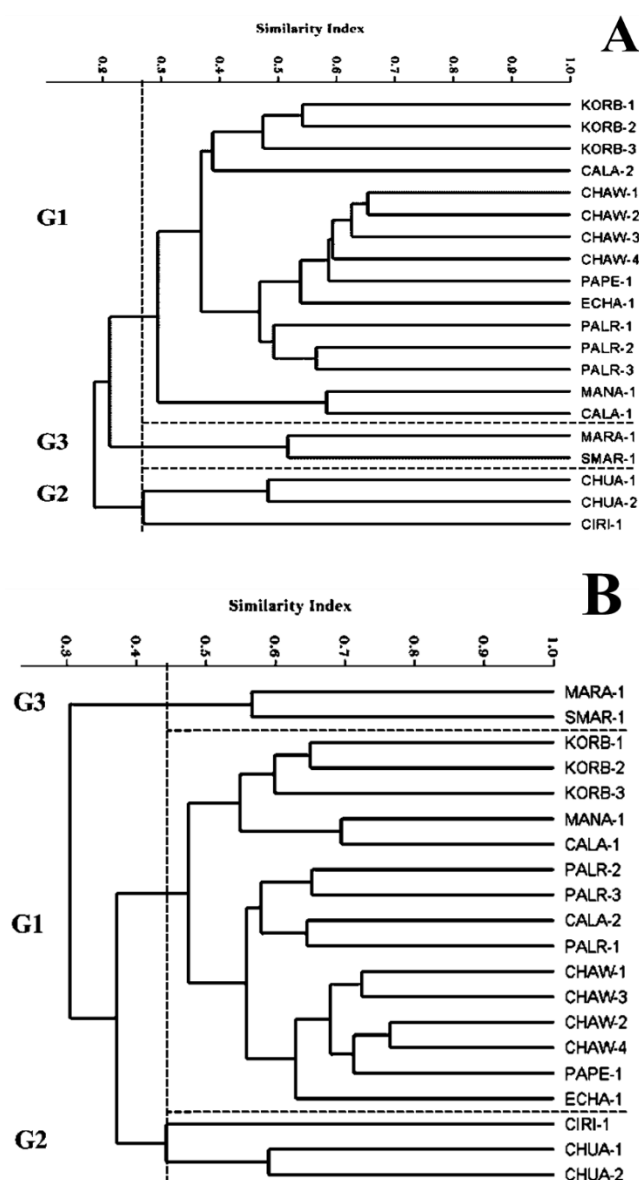


Fig. 5. Similarity dendrograms between Urubamba basin SDTF plots using **A.** species and **B.** genera.

respectively, and 50 families for the SDTF in Tuichi, northern Bolivia (Fuentes *et al.* 2004).

At genus level, the Urubamba SDTF was dominated by *Inga* (13 species), agreeing with Linares-Palomino (2006), who also listed *Inga* among the most species-rich in Peruvian dry forests. The genus *Inga* is especially diverse in humid forests, but it presents wide ecological plasticity attributed to recent diversification events to different habitats including SDTF (Kursar *et al.* 2009). Other genera rich in species in our study area, such as *Aspidosperma*, *Machaerium*, *Brosimum* and *Eugenia* are more frequent in SDTF

islands within the Brazilian Cerrado (Ratter *et al.* 2003), *Aspidosperma* and *Machaerium* are also the most species-rich in the Bolivian Chiquitania (Fuentes *et al.* 2004). Gentry (1995) listed *Tabebuia*, *Casearia*, *Bauhinia*, *Trichilia*, *Erythroxylum*, *Randia*, *Hippocratea*, *Serjania*, *Croton* and *Zanthoxylum* as dominant in the lowland SDTF, all of which (with the exception of *Hippocratea*) were present in the Urubamba. Other genera also mentioned by Gentry (1995) as being present in SDTF (although with lower species richness) and recorded in the Urubamba were *Astronium*, *Spondias*, *Forsteronia*, *Annona*, *Cydistax*, *Ceiba*, *Machaerium*, *Erythrina*, *Psidium*, *Allophylus* and *Guazuma*. Of the ten most species-rich genera listed by Linares-Palomino (2006) for the six SDTF areas identified for Peru, we recorded *Capparis*, *Erythroxylum*, *Inga*, *Trichilia* and *Tabebuia* in the Urubamba. These elements are clearly related to the semi-deciduous SDTF of the eastern Andean slopes. Following a similar pattern as for species, only some genera are shared with the inter-Andean dry forests of the Marañón, Apurímac and Mantaro and those of the Pacific coast. An in-depth study of these patterns is currently in progress.

Linares-Palomino *et al.* (2011) analyzed 21 SDTF areas across the Neotropics, compiling all available information for each area in terms of published and unpublished species lists. Of these, only the Cerrado and Caatinga areas (covering extensive areas and including several individual lists) have higher species richness than the Urubamba SDTF. Linares-Palomino *et al.* (2011) also identified ecologically versatile species (i.e. present in SDTF, but also growing in other ecosystems), generalist (species not restricted to a particular ecosystem) and SDTF specialists. Applying these same concepts, we recorded *Anadenanthera colubrina*, *Celtis iguanaea* and *Urera baccifera* (SDTF specialist), *Amburana cearensis*, *Astronium fraxinifolium*, *Cynophalla flexuosa*, *Guazuma ulmifolia*, *Luehea grandiflora*, *Luehea paniculata*, *Pterocarpus rohrii* and *Handroanthus roseo-albus* (generalists) and *Casearia sylvestris*, *Machaerium acutifolium*, *Maclura tinctoria*, *Prockia crucis*, *Randia armata*, *Sapium glandulosum*, *Handroanthus ochraceus*, *Trema micrantha* and *Trichilia elegans* (ecologically versatile). *Amburana cearensis* and *A. colubrina*, considered among the most representative SDTF species (Linares-Palomino *et al.* 2011; Moggi *et al.* 2015; Särkinen *et al.* 2011a), were frequently recorded in our plots.

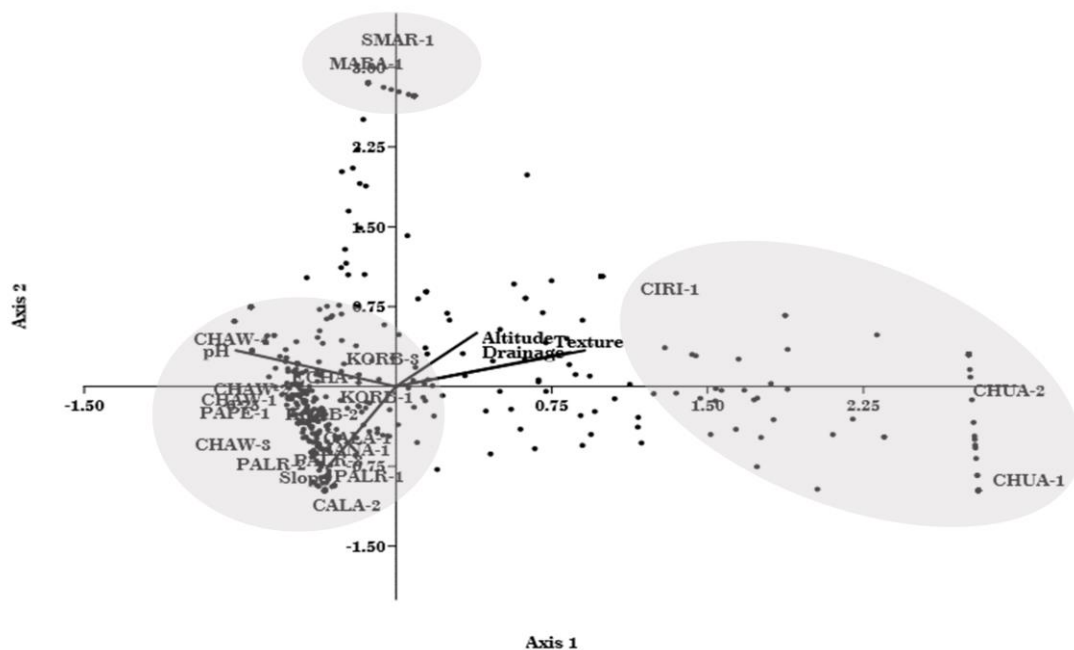


Fig. 6. Canonical correspondence analysis showing relationship between surveyed plots (the points represent the species evaluated) in SDTF of the Urubamba and five abiotic variables.

The presence of woody taxa characteristic of deciduous and semi-deciduous forests, such as Fabaceae, Bignoniaceae, Myrtaceae, Sapindaceae, Anacardiaceae and Capparidaceae, as well as species such as *Anadenanthera colubrina*, *Amburana cearensis*, *Piptadenia viridiflora*, *Cyathostegia matthewsii*, *Celtis iguanaea*, *Urea baccifera*, *Astronium fraxinifolium*, *Cynophalla flexuosa*, *Guazuma ulmifolia*, *Luehea grandiflora*, *Luehea paniculata*, *Pterocarpus rohrii*, *Handroanthus roseo-albus*, *Cariniana estrellensis*, *Maclura tinctoria*, *Dilodendron bipinnatum*, *Trichilia elegans*, *Psidium sartorianum* and *Myrcia tomentosa* confirm that the dry forests in the Urubamba belong to the SDTF biome (Fuentes *et al.* 2004; Linares-Palomino *et al.* 2011; Mogni *et al.* 2015; Pennington *et al.* 2010; Prado & Gibbs 1993; Prado 2000; Ratter *et al.* 2003; Särkinen *et al.* 2011a). This is further reinforced by other typical SDTF species such as *Myrcia tomentosa*, *Psidium sartorianum* (Myrtaceae), *Maytenus cardenasii* (Celastraceae), *Cardiopetalum calophyllum* (Annonaceae) and *Passiflora venusta* (Passifloraceae), recently described as new records for the Peruvian flora (Huamantupa *et al.* 2014).

In terms of floristics and forest structure, the Urubamba SDTF are a combination of savanna-like

forests with typical species such as *Curatella americana* (Dilleniaceae), *Handroanthus roseo-albus*, *Cybstax anticiphilitica* (Bignoniaceae) and *Astronium fraxinifolium* (Anacardiaceae), associated to dominant grasses such as *Andropogon bicornis* and *Melinis minutiflora*, and patches of dry forest including elements of montane forests (with species of *Neea* (Nyctaginaceae) and *Meliosma* (Sabiaceae)). These taxa suggest affinities with the semi-deciduous forests in the Chiquitania and, to a lesser extent, to the Bolivian and Brazilian Cerrado (Linares-Palomino 2006b; Mogni *et al.* 2015; Prado & Gibbs 1993; Ratter *et al.* 2003; Särkinen *et al.* 2011a).

Characterization of the SDTF in the middle section of the Urubamba

The abiotic variables related to soil physico-chemical characteristics allowed distinction of community composition across the altitudinal gradient (720–1290 masl). The data suggest that small variations in pH and drainage play an important role, determining low-lying areas with less acid soils and poor drainage carrying vegetation with higher species diversity, whereas areas at higher altitudes have more acidic soils,

better drainage but carry less diverse vegetation. Our results are similar to a study in the Chiquitania (Torrez *et al.* 2010), where areas located at higher altitudes also showed lower species diversity, and growing on more acidic soils. The soils of middle section of the Urubamba have low concentration of aluminum (IMA 2001), in contrast to records in the Brazilian Cerrado where aluminum levels are high, determining poor soils and a sclerophyllous, low-stature vegetation (Ratter *et al.* 1997). The SDTF in the Urubamba were dominated by soils of the Acrisol-cambisol type, which are considered fertile and appropriate for agriculture, an activity present in all the La Convención province (INRENA 2000; POT-LC 2005).

The recorded data show that for our study area the upper altitudinal limit for SDTF is at around 1500 masl, above which the characteristic dry forest flora is replaced by montane forest taxa. The lower altitudinal limit is at around 500 masl, where taxa characteristic of humid Amazonian forest appear.

The three consistent groups of SDTF in the middle section of the Urubamba basin were clearly distinguished by the multivariate analyses and we propose to term them as follows: a) Amazonian pluviseasonal tropical dry forest, b) sub-Andean pluviseasonal tropical dry forest, and c) savanna-like pluviseasonal tropical dry forest.

The Amazonian pluviseasonal tropical dry forest included most of the surveyed plots, which are mostly located in the lower areas of the basin. High species numbers characterized these plots, as well as taxa of semi-deciduous dry forests (Fig. 7) such as *Ampelocera ruizii*, *Brosimum alicastrum*, *Ceiba boliviana*, *Pogonopus tubulosus*, *Amburana cearensis*, *Allophylus punctatus*, *Annona neoulei*, *Anadenanthera colubrina* and *Psidium sartorianum* (Table 5).

The Sub-Andean pluviseasonal tropical dry forest included species characteristic of both montane and Amazonian forests (Fig. 8) and SDTF such as *Pseudolmedia laevigata*, *Helicostylis scabra*, *Ceiba samauma*, *Maclura tinctoria*, *Terminalia amazonia*, *Mollinedia killipii*, *Bathysa bathysoides* and *Warszewiczia coccinea* (Table 5).

The savanna-like pluviseasonal tropical dry forest included taxa typical of SDTF and of neotropical savannas (Fig. 9), usually associated to altered areas and to more open forests with lower canopies, such as *Cereus vargasianus*, *Anadenanthera colubrina*, *Astronium fraxinifolium*, *Ceiba boliviana*, *Urera caracasana*,

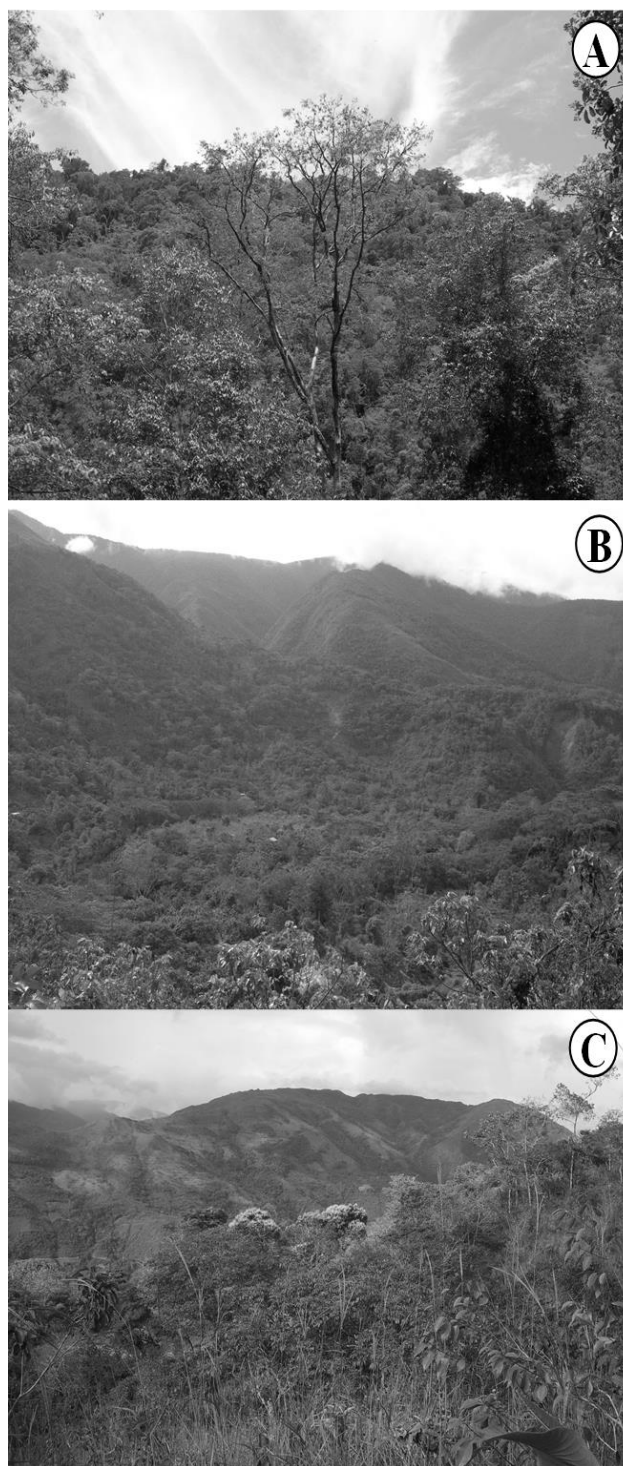


Fig. 7. A. The Amazonian pluviseasonal tropical dry forest and the characteristic tree *Amburana cearensis* (Fabaceae, in front), close to Koribeni locality. B. the Sub-Andean pluviseasonal tropical dry forest near the Chuanquiri village, and C. The Savanna-like pluviseasonal tropical dry forest around the city of Quillabamba.

Table 4. Floristic similarity between studied plots. Upper triangle shows Bray-Curtis similarity coefficients based on species abundance data. The lower triangle shows Bray-Curtis similarity coefficients based on abundance data of genera (in bold, values above 0.60).

	CALA-1	CALA-2	CHAW-1	CHAW-2	CHAW-3	CHAW-4	CHUA-1	CHUA-2	CIRI-1	ECHA-1	KORB-1	KORB-2	KORB-3	MANA-1	MARA-1	PALR-1	PALR-2	PALR-3	PAPE-1	SMAR-1
CALA-1		0.36	0.26	0.27	0.30	0.21	0.25	0.19	0.18	0.26	0.34	0.41	0.36	0.58	0.08	0.35	0.30	0.28	0.26	0.09
CALA-2	0.58		0.38	0.34	0.41	0.33	0.17	0.19	0.20	0.35	0.37	0.42	0.38	0.34	0.17	0.48	0.45	0.38	0.34	0.13
CHAW-1	0.43	0.49		0.65	0.65	0.59	0.12	0.17	0.16	0.49	0.37	0.38	0.27	0.26	0.38	0.46	0.56	0.49	0.56	0.36
CHAW-2	0.48	0.53	<u>0.72</u>		0.60	0.63	0.15	0.22	0.18	0.56	0.43	0.37	0.28	0.23	0.33	0.47	0.56	0.53	0.59	0.31
CHAW-3	0.45	0.48	0.72	0.69		0.56	0.17	0.19	0.18	0.57	0.42	0.40	0.27	0.28	0.24	0.52	0.47	0.46	0.60	0.24
CHAW-4	0.42	0.52	0.68	0.76	0.63		0.13	0.20	0.15	0.54	0.42	0.37	0.27	0.20	0.31	0.42	0.46	0.41	0.58	0.30
CHUA-1	0.49	0.39	0.24	0.27	0.29	0.25		0.48	0.32	0.19	0.23	0.24	0.28	0.21	0.05	0.24	0.20	0.14	0.15	0.06
CHUA-2	0.45	0.39	0.30	0.36	0.34	0.38	0.59		0.22	0.19	0.21	0.19	0.23	0.18	0.07	0.26	0.19	0.11	0.16	0.05
CIRI-1	0.44	0.37	0.29	0.31	0.32	0.31	0.47	0.42		0.23	0.30	0.26	0.31	0.21	0.12	0.24	0.24	0.29	0.16	0.11
ECHA-1	0.48	0.51	0.58	0.66	0.66	0.63	0.34	0.39	0.37		0.41	0.40	0.29	0.25	0.26	0.42	0.41	0.44	0.54	0.25
KORB-1	0.54	0.53	0.46	0.50	0.51	0.51	0.40	0.41	0.48	0.47		0.54	0.43	0.35	0.19	0.43	0.43	0.36	0.44	0.14
KORB-2	0.55	0.60	0.47	0.47	0.51	0.49	0.39	0.39	0.44	0.45	0.65		0.52	0.41	0.16	0.39	0.42	0.40	0.42	0.13
KORB-3	0.53	0.55	0.36	0.39	0.39	0.39	0.51	0.41	0.48	0.43	0.61	0.58		0.33	0.12	0.33	0.30	0.28	0.28	0.11
MANA-1	0.69	0.52	0.43	0.42	0.42	0.40	0.42	0.37	0.43	0.40	0.57	0.59	0.52		0.13	0.29	0.27	0.27	0.23	0.12
MARA-1	0.27	0.31	0.47	0.44	0.35	0.46	0.14	0.18	0.22	0.38	0.29	0.29	0.24	0.33		0.22	0.24	0.27	0.26	0.52
PALR-1	0.59	0.65	0.54	0.59	0.61	0.57	0.37	0.42	0.40	0.56	0.52	0.52	0.48	0.51	0.35		0.49	0.50	0.46	0.17
PALR-2	0.54	0.58	0.64	0.64	0.59	0.56	0.32	0.38	0.43	0.51	0.53	0.55	0.42	0.47	0.34	0.59		0.57	0.47	0.24
PALR-3	0.50	0.55	0.58	0.60	0.57	0.54	0.29	0.28	0.46	0.54	0.45	0.54	0.43	0.46	0.35	0.60	0.65		0.43	0.23
PAPE-1	0.47	0.53	0.65	0.70	0.71	0.72	0.27	0.34	0.32	0.60	0.52	0.52	0.41	0.43	0.37	0.59	0.57	0.53		0.21
SMAR-1	0.20	0.27	0.47	0.42	0.36	0.47	0.15	0.22	0.19	0.35	0.24	0.24	0.19	0.25	0.57	0.26	0.33	0.24	0.33	

Table 5. The 15 most conspicuous woody species in each SDTF type identified in the middle section of the Urubamba basin. IVI= importance value index.

Amazonian pluviseasonal tropical dry forest			Sub-Andean pluviseasonal tropical dry forest			Savanna-like pluviseasonal tropical dry forest		
Family	Species	IVI	Family	Species	IVI	Family	Species	IVI
Ulmaceae	<i>Ampelocera ruizii</i>	7.32	Moraceae	<i>Pseudolmedia laevigata</i>	13.93	Cactaceae	<i>Cereus vargasianus</i>	27.43
Moraceae	<i>Brosimum alicastrum</i>	6.78	Moraceae	<i>Helicostylis scabra</i>	11.98	Fabaceae	<i>Anadenanthera colubrina</i>	18.61
Malvaceae	<i>Ceiba boliviana</i>	6.78	Malvaceae	<i>Ceiba samauma</i>	9.3	Anacardiaceae	<i>Astronium fraxinifolium</i>	15.07
Rubiaceae	<i>Pogonopus tubulosus</i>	5.41	Moraceae	<i>Maclura tinctoria</i>	9.18	Malvaceae	<i>Ceiba boliviana</i>	14.38
Fabaceae	<i>Amburana cearensis</i>	5.1	Combretaceae	<i>Terminalia amazonia</i>	9.02	Urticaceae	<i>Urera caracasana</i>	11.63
Sapindaceae	<i>Allophylus punctatus</i>	4.98	Monimiaceae	<i>Mollinedia killipii</i>	4.95	Euphorbiaceae	<i>Croton baillonianus</i>	11.46
Annonaceae	<i>Annona neoulei</i>	4.85	Rubiaceae	<i>Bathysa bathysoides</i>	4.5	Moraceae	<i>Maclura tinctoria</i>	10.55
Fabaceae	<i>Anadenanthera colubrina</i>	4.37	Rubiaceae	<i>Warszewiczia coccinea</i>	4.24	Malvaceae	<i>Guazuma ulmifolia</i>	9.51
Moraceae	<i>Ficus citrifolia</i>	4.28	Fabaceae	<i>Inga auristellae</i>	3.98	Araliaceae	<i>Dilodendron bipinnatum</i>	8.88
Myrtaceae	<i>Psidium sartorianum</i>	4.25	Vochysiaceae	<i>Vochysia mapirensis</i>	3.94	Verbenaceae	<i>Duranta obtusifolia</i>	6.7
Urticaceae	<i>Myriocarpa filiformis</i> cf.	4.25	Malvaceae	<i>Bellucia pentamera</i>	3.83	Araceae	<i>Philodendron</i> sp. 1	6.08
Moraceae	<i>Brosimum guianense</i>	4.2	Moraceae	<i>Clarisia biflora</i>	3.71	Fabaceae	<i>Acacia riparia</i>	5.78
Moraceae	<i>Maclura tinctoria</i>	4.19	Moraceae	<i>Ficus</i> sp. 1	3.64	Urticaceae	<i>Cecropia engleriana</i>	5.78
Fabaceae	<i>Myroxylon balsamum</i>	4.14	Erythroxylaceae	<i>Erythroxylum citrifolium</i>	3.61	Malvaceae	<i>Luehea paniculata</i>	5.5
Lecythidaceae	<i>Cariniana estrellensis</i>	3.93	Cannabaceae	<i>Celtis schippii</i>	3.58	Capparaceae	<i>Cynophalla flexuosa</i>	5.06

Croton baillonianus, *Maclura tinctoria*, *Guazuma ulmifolia* and *Dilodendron bipinnatum* (Table 5).

The Urubamba basin, a plant diversity hotspot for Neotropical SDTF

In addition to the suite of species reported for other Neotropical SDTF, the Urubamba dry forest also contains characteristic species such as *Ceiba boliviana*, *Cereus vargasianus*, *Allophylus punctatus*, *Pogonopus tubulosus*, *Warszewiczia coccinea*, *Annona neoulei*, *Helicostylis scabra*, *Aspidosperma macrocarpon*, *Symplocos cuzcoensis*, *Stigmaphyllon cuscanon*, *Forsteronia pubescens*, *Brosimum guianense*, *Erythroxylum raimondii*, *Carica glandulosa*, *Thinouia obliqua*, *Machaerium jacarandifolium*, *Thinanthus polyanthus*, *Luehea paniculata*, *Vochysia mapirensis* and *Handroanthus ochraceus*. These species have not been previously reported for the SDTF in Peru (Linares-Palomino 2006) or the continent (Linares-Palomino *et al.* 2011; Särkinen *et al.* 2011a).

Although the region of Cusco and southern Peru in general has been considered as having high endemism values (León *et al.* 2006), endemics in our study area were few and included *Cereus vargasianus*, a columnar cactus reaching 6 m height and forming locally dense colonies and *Symplocos cuzcoensis*, a tree present in the SDTF to montane forest transition in this basin. Endemic lianas were represented by *Stigmaphyllon cuzcanon* and *Lycoseris peruviana*. Although not recorded in our quantitative survey, the hemi-epiphyte *Demosthenesia matsiguenka* (Ericaceae), restricted to this valley, should be added. The floristic links to SDTF formation further south and especially to the Chiquitania are shown by shared occurrences only reported so far for these two areas, such as *Ceiba boliviana*, *Triplaris vestita*, *Erythroxylum raimondii*, *Dyctioloma peruvianum* and *Cedrela saltensis*. The latter is frequently found in dry ecosystems of the Chuquisaca, Santa Cruz and Tarija departments in Bolivia, reaching Salta in Argentina, and has recently been reported for this valley (Huamantupa *et al.* 2014).

Endemism for SDTF at a Neotropical level are considered variable (Pennington *et al.* 2006). Compared to values in the inter-Andean SDTF of the Marañon (Marcelo-Peña *et al.* 2015), the Brazilian Caatingas (Queiroz 2006) and dry forests in Mexico (Lott & Atkinson 2006), all of which have at least a 15% of endemic species; endemism in the Urubamba was moderate to low. This is in contrast

to studies in other Peruvian inter-Andean dry valleys, which have been suggested to have had a long and stable ecological history, isolated by the Andean mountains and deep valleys from other biomes, which have allowed local speciation events, and thus, accumulation of endemics (Särkinen *et al.* 2011b). We expect that additional floristic studies in these forests will add further records of endemic species.

The high plant diversity we are reporting for the SDTF in the Urubamba, confirms that it not only belongs to the southern Peruvian Andean-Amazonian biodiversity hotspot (Myers *et al.* 2000), but also that its high diversity of species and families in the Urubamba, as well as per plot and high alpha Fisher values, the structural and floristic combination of dry forests, savanna-like forests and inter-Andean dry forests suggest that this area is an SDTF nucleus (*sensu* Linares-Palomino *et al.* 2011) by its own right, an SDTF plant diversity hotspot and probably the southernmost remain of SDTF area west of the Andes.

Conservation issues

The main threats for the SDTF in the Urubamba are similar to those reported for other dry forests worldwide (Blackie *et al.* 2014; Pennington *et al.* 2009): habitat destruction and conversion due to migrant agricultural practices, habilitation of pasture zones and timber exploitation. These factors have in combination likely produced soil erosion and compaction, and are responsible for high incidence of forest fires, scarcity of water, presence of invasive plants and the general degradation of the environment (POT-LC 2005).

This current status of the Urubamba forests results from the historical development of agricultural activities in La Convención province, dating back to the beginning of the 1950s when the first settlers coming from Andean regions in Cusco established themselves in the localities of Santa Teresa and Quillabamba. They planted fruit trees such as mango, banana and citrus, expanding later to cocoa, coffee and tea by slashing and burning dry and montane forest at higher altitudes and downstream towards the locality of Kiteni (IMA 2001; POT-LC 2005). Deforestation rates in the valley have been increasing steadily, with an estimated loss to date of 1, 410.300 Km² in the La Convención province alone and an annual rate of 20,000 hectares per year (POT-LC 2005), of which 70% correspond to SDTF (IMA 2001). Due to

selective logging, economically important species have practically disappeared in this valley, including *Myroxylon balsamum*, *Amburana cearensis* (Fabaceae), *Cedrela saltensis*, *C. angustifolia*, *C. fissilis* and *Swietenia macrophylla* (Meliaceae) (Huamantupa 2011). Our study has been able to locate small populations of these species only around the Kiteni and Managua villages.

The outcome of these deforestation events can be seen clearly in the different values of species richness and diversity of our data. Survey localities such as Santa María and Maranura had the lowest values (54 and 62 species, respectively), showing a forest structure and physiognomy reminiscent of American savannas dominated by *Curatella americana* (Dilleniaceae) (Pennington *et al.* 2004, 2006; Ratter *et al.* 2006). In addition, the introduction and colonization of exotic species is another problem for the native flora. For instance, *Melinis minutiflora* (Poaceae), a very aggressive grass favored by fires, the fern *Pteridium aquilinum* (Pteridiaceae), cultivated ornamentals like *Eryobothrium japonicum* (Rosaceae), *Melia azedarach* (Meliaceae) and the liana *Cobaea scandens* (Polemoniaceae) could lead to changes in local forest structure, species loss and homogenization of the floristic composition (Sharma & Raghubanshi 2010).

The most degraded areas are in Santa María, Maranura, Quillabamba and Echarati. Further downstream, close to the Palma Real, Koribeni, Cirialo and Kiteni villages, some areas with major primary forest patches remain, especially towards the steeper slopes. The best preserved areas are those close to Managua village and downwards and closer to the confluence with the humid rainforest.

The environmental issues discussed above seem to have a direct (game hunting) and indirect (habitat destruction and fragmentation) effect on the local fauna. To date, several species have been included into the official list of threatened species: 12 are considered vulnerable, five in danger of extinction and one considered rare (IMA 2001). The reduced presence or even absence of these animals could be having negative effects on key ecological processes in these SDTF, such as seed dispersion and reduced pollination services, which are important in some species of the Nyctaginaceae (*Neea*, *Guapira*), Araliaceae (*Dendropanax*), Sapotaceae (*Pouteria*, *Chrysophyllum*), Erythroxylaceae (*Erythroxylum*), Melastomataceae (*Miconia*) and Myrtaceae (*Psidium*, *Eugenia*), all of

which show lack of natural regeneration (absence of seedlings and saplings) (I. H. pers. obs). In contrast, these effects seem to be favoring the growth of lianas (17% of all life-forms in this study) as observed in other dry forests, e.g. in the Lomerio region in Bolivia, where woody trees populations were infested up to 75% by lianas (Carse *et al.* 2000).

The fact that the regional government in Cusco is considering several major development projects in this area will certainly not help to reduce the current situation. Planned is the construction of hydroelectric power plants and cattle production centers, as well as reforestation with exotic timber species (POT-LC 2005). It is thus necessary to implement some form of conservation areas in the Urubamba basin, prioritizing two areas. One around the villages of Santa María and Echarati, focusing on recovering vegetation cover, another in the lower parts of the basin between Koribeni and Managua, where most of the better-preserved SDTF patches exist.

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