

IDENTIFYING CONSERVATION PRIORITY AREAS IN THE MARAÑÓN VALLEY (PERU) BASED ON FLORISTIC INVENTORIES

J. L. MARCELO-PEÑA^{1,4}, I. HUAMANTUPA², T. SÄRKINEN³ & M. TOMAZELLO⁴

In this study, we report species diversity and endemism of the poorly known but highly diverse Seasonally Dry Tropical Forest (SDTF) flora of the Marañón valley in northern Peru. We characterise woody vascular plant species diversity across the valley in order to define the conservation value of the area at national and international level. Based on 32 rapid botanical inventories, 92 plots of 50 × 20 m, and a herbarium study across local and international herbaria, we report 440 woody vascular plant species of which 143 (33%) are endemic to the valley. Two centres of endemism within the valley are identified, each with clear elevational zonation of diversity. Data show that the Marañón valley is a good representative of Peruvian SDTFs as a whole, with an average of 56% SDTF species and 78% SDTF genera found in the one valley. The results show that there is wide variation in the set of dominant species across the valley, and that many local endemics are locally abundant unlike in neighbouring SDTFs where the dominant species are all geographically widespread. Our results demonstrate that the Marañón includes a rare combination of both nationally representative yet globally unique plant species, which makes the valley an ideal conservation target. The high level of endemism structured within elevational zones implies that conservation areas should be established across elevational zones in order to maximise the protection of this globally unique flora.

Keywords. Dry Andean valleys, endemism, floristic inventory, Huancabamba depression, Seasonally Dry Tropical Forests (SDTFs), woody plant diversity.

INTRODUCTION

Seasonally Dry Tropical Forests (SDTFs) in Latin America are highly fragmented due to both natural and anthropogenic factors (Pennington *et al.*, 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010; Werneck, 2011). Because SDTFs occur on fertile soils, recent expansion of agriculture, farming and charcoal production have further

¹ Herbario Forestales (MOL), Manejo Forestal, Facultad de Ciencias Forestales, Universidad Nacional Agraria La Molina, Avenida La Universidad, Apartado 456, Lima 12, Peru. E-mail for correspondence: jlmarcelop@lamolina.edu.pe

² Herbario Vargas (CUZ), Facultad de Ciencias Biológicas, Universidad Nacional San Antonio Abad del Cusco, Apartado 367, Cusco, Peru. E-mail: andeanwaya@gmail.com

³ Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, UK.

⁴ Departamento de Ciências Florestais, Escola Superior de Agricultura Luiz de Queiroz, Universidade de São Paulo, Avenida Pádua Dias 11, CEP 13418-900, Caixa postal 09, Piracicaba, São Paulo, Brazil.

fragmented them (Ratter *et al.*, 1978; Pennington *et al.*, 2000). It is now estimated that only c.5% of the original SDTFs remains in the Neotropics (Portillo-Quintero & Sánchez-Azofeifa, 2010).

Unlike the continuous Amazon, SDTF nuclei are scattered across the continent and are characterised by a high level of endemism and floristic dissimilarity between distinct nuclei (Prado & Gibbs, 1993; Prado, 2000; Linares-Palomino *et al.*, 2011). The pattern of high floristic dissimilarity and endemism poses challenges for conservation science, where a relatively large number of smaller conservation units will be needed to represent the unique flora of each nucleus. Thus far, SDTFs have been generally poorly represented in global and national conservation plans, and only a few conservation areas exist. The challenge now is to identify conservation priority areas to start preserving what remains, especially in the face of climate change where dry-adapted ecosystems such as SDTFs might provide solutions in the face of increasing temperatures and severe droughts predicted in the future (Shaver *et al.*, 2000; Jackson *et al.*, 2009).

The inter-Andean valleys found between the Eastern and Western Andean Cordilleras are amongst the smallest SDTF nuclei in South America (Linares-Palomino *et al.*, 2011). Despite their small size, inter-Andean SDTFs have been shown to be important for SDTF conservation due to the high level of endemism in the flora and fauna (Linares-Palomino *et al.*, 2011; Särkinen *et al.*, 2011a,b). Molecular phylogenetic studies have revealed that some of these endemics date back more than 10 million years (Pennington *et al.*, 2010; Särkinen *et al.*, 2012), indicating that the endemic flora has evolved in an island-like manner in response to the extreme isolation and dispersal limitation of the valleys since the mountains rose up (Pennington *et al.*, 2010; Särkinen *et al.*, 2012).

Amongst the inter-Andean valleys, the Marañón valley in northern Peru has been highlighted as the most diverse, with a high level of endemism (Fig. 1; Linares-Palomino *et al.*, 2010; Särkinen *et al.*, 2011b). The valley is the largest of the inter-Andean SDTFs and lies within the Huancabamba depression where the northern and central Andean floristic elements meet (Equatorial, Marañón and Tarapoto nuclei, and Apurimac and Mantaro nuclei, respectively; Fig. 1) (Weigend, 2002; Linares-Palomino *et al.*, 2010). Within the Marañón, over 50% of the reptile and bird fauna is endemic, with 16 endemic birds found in the narrow valley that comprises only 3750 km² (BirdLife International, 2006; WWF, 2009; MINAM, 2012). Preliminary data indicate 28% endemism in the woody flora alone, with 52 endemic tree species (Linares-Palomino & Pennington, 2007), but detailed taxonomic studies indicate that these are likely to be underestimates (Hensold, 1999; Weigend, 2002; Young *et al.*, 2002; Bridgewater *et al.*, 2003; Hughes *et al.*, 2003, 2004; Koch *et al.*, 2006; Linares-Palomino, 2006; Angulo *et al.*, 2008; Venegas *et al.*, 2008; Lewis *et al.*, 2010; Marcelo-Peña *et al.*, 2010; Särkinen *et al.*, 2011b).

Here, we present a detailed floristic survey of the Marañón valley based on plot, survey and herbarium data, and explore patterns of endemic species diversity in the woody vascular plant flora in the valley in order to quantify the conservation value of

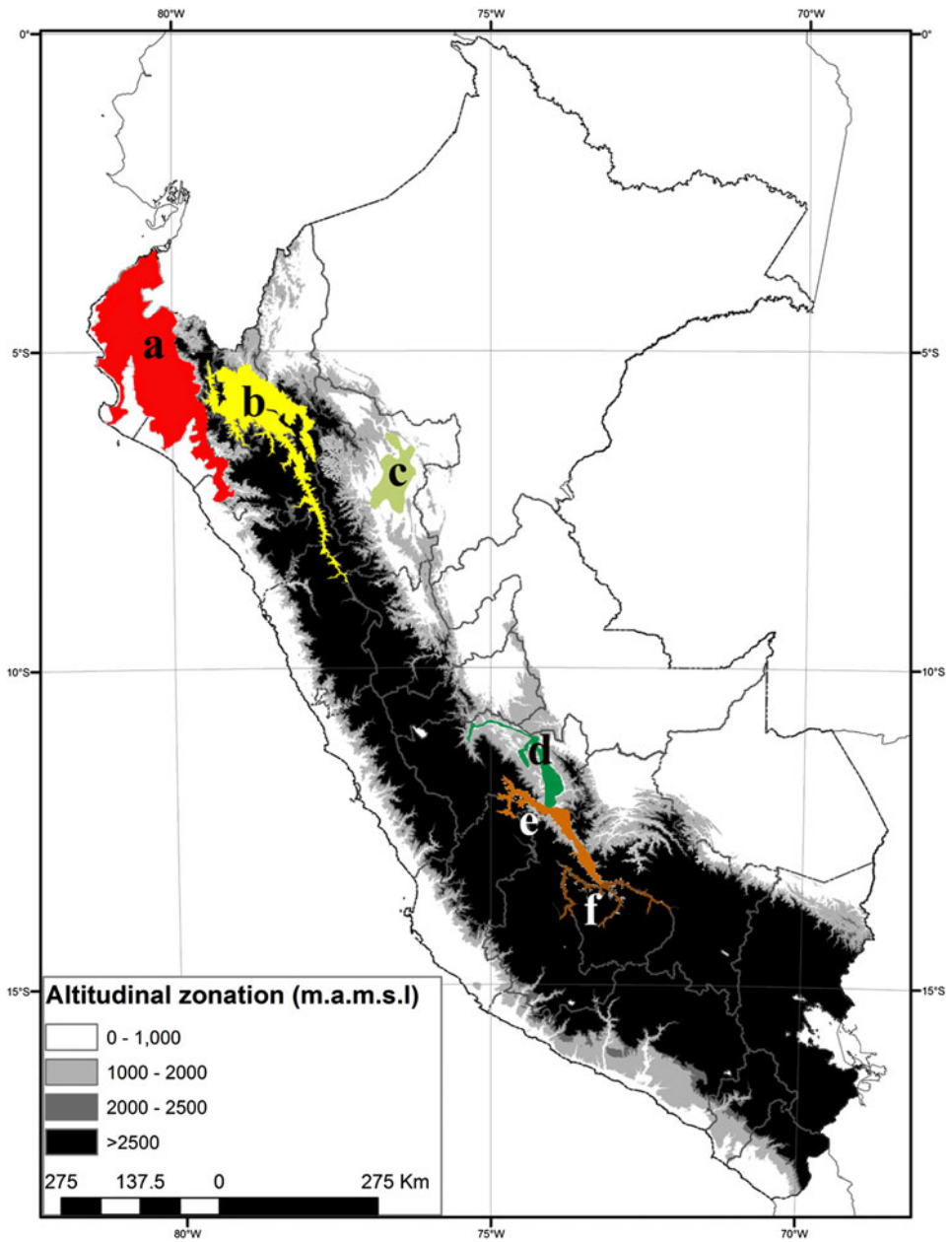


FIG. 1. Map of Seasonally Dry Tropical Forests (SDTFs) in Peru, modified from Linares-Palomino (2004). The six recognised SDTF nuclei are labelled and colour coded: (a) Equatorial SDTF (red); (b) Marañón SDTF (yellow); (c) Tarapoto SDTF (light green); (d) Chanchamayo and Tambo river valley SDTF (dark green); (e) Mantaro SDTF (orange); and (f) Apurímac (brown).

the area at national and international level. We test the prediction that the Marañón valley is well suited as a conservation target due to its position between the northern and southern Andean floristic elements within the Huancabamba depression, and the high representation of the Peruvian SDTF flora as a whole. We present an updated checklist of the woody flora of the Marañón valley, including the three watersheds of Rio Utcubamba, Rio Huancabamba and Rio Marañón, and identify centres of endemism within the valley. The results provide data for biodiversity management in the face of future changes in the Marañón valley, and help to highlight the conservation value of the area at both national and international level.

METHODS

Study area

The study area lies in the departments of Amazonas, Cajamarca and La Libertad in Peru at 400–2200 m in elevation (Fig. 2). The extreme dryness of the Marañón valley is due to its location in relation to the leeward trade winds from the east and the circulation pattern of cold air masses to the central regions of the lowest valleys

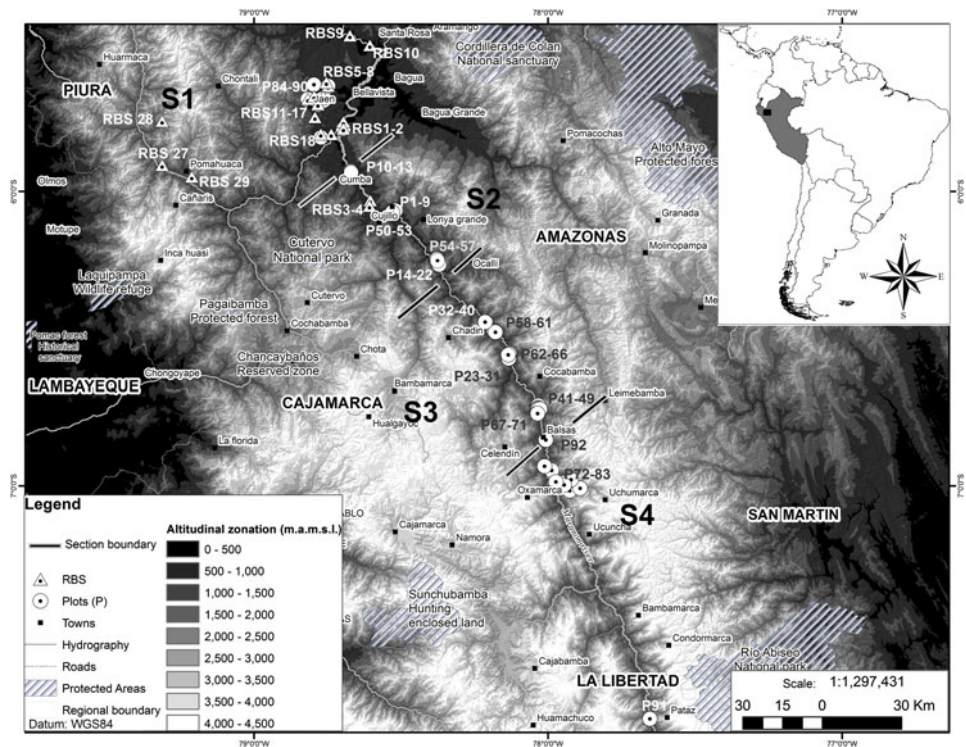


FIG. 2. Map of the Marañón valley of northern Peru with the study sites highlighted. RBS = Rapid Botanical Survey; P = plot.

(Killeen *et al.*, 2007). Additionally, scarce cloudiness and high temperature lead to increased evapotranspiration. Climate data from two weather stations located in the Marañón at Balsas (Dept. of Amazonas, 840 m elevation) and Pimpincos (Dept. of Cajamarca, 450 m elevation) from 2008 to 2013 show that the area receives an average annual rainfall of 550 mm. Maximum mean temperatures (28°C) are reached in August, whilst minimum temperatures of 25°C occur in March (SENAMHI, 2013). Relative humidity is highest in April (73%) and lowest in August (37%). In terms of geology, the Marañón valley is composed mostly of sedimentary rocks of the Mesozoic-Cenozoic (INGEMET, 1999; see www.ingemmet.gob.pe). The landscape is relatively dramatic, some areas containing sharp limestone peaks with vertical cliffs occurring amongst large sections of sandstone and limestone sequences.

Botanical surveys

A total of 124 inventory sites were established across the departments of Amazonas, Cajamarca and La Libertad (Fig. 2). These were identified using Rapid Botanical Surveys (RBS) that focused on quantifying species diversity across the valley and across elevational zones, while 50 m × 20 m plots, 12 of which were established as permanent plots, were used to study vegetation structure and composition within each zone. Herbarium studies were done to understand endemism and species distribution more fully within the valley.

The RBS surveys ($n = 32$) followed the methodology of Hawthorne & Abu-Juam (1995) and Gordon *et al.* (2004) with modifications proposed by Marcelo-Peña (2008). RBS surveys covered all woody species with stem diameter at ground level ≥ 2 cm, including vines and lianas. All species encountered in each RBS were vouchered. The time of each survey was 90 minutes in denser areas (e.g. S1, see below) and 60 minutes in less dense vegetation (e.g. S4, see below). Surveys were done by walking through the selected area without an established direction, recording all encountered species.

The 50 m × 20 m plots ($n = 92$) focused on individuals ≥ 5 cm DBH only. Only selected species were vouchered from plots when new records were encountered. Woody species not encountered in the inventory areas but found close to sampling sites were also collected to contribute towards the checklist. All botanical collections are deposited in the herbarium of the Universidad Nacional Agraria La Molina (MOL) in Lima, Peru.

The Marañón valley was divided into four geographical and five elevational sections in order to study species distribution patterns and endemism within the area. The four geographical sections were: (1) S1 in the northernmost area of the valley including Jaén, Bagua, Chachapoyas and Utcubamba (22 RBS, 7 plots); (2) S2 in the north-central part of the valley between Cumba and Cujillo (3 RBS, 17 plots); (3) S3 in the south-central part of the valley around Ocalli (2 RBS, 54 plots); and (4) S4 in the southernmost areas including Balsas, San Vicente and Chagual (5 RBS, 14 plots) (Fig. 2). The five elevational zones were: (1) Z1: 340–700 m; (2) Z2: 700–1100 m;

(3) Z3: 1100–1500 m; (4) Z4: 1500–1900 m; and (5) Z5: 1900–2300 m. The geographical and elevational limits were determined based on collection density of herbarium records and field experience.

Sampling efficiency was analysed using species accumulation curves. Smoothed accumulation curves of estimated species were calculated according to four non-parametric estimators: (1) Chao 2; (2) First order Jackknife; (3) Second order Jackknife; and (4) Bootstrap (Colwell & Coddington, 1994; Chazdon *et al.*, 1998). A total of 100 randomisations were done in all calculations involving multiple rearrangements using the R statistical environment (Development Core Team, 2008).

Species checklist

In addition to plot and survey data, previous recordings of vascular plants from herbarium records and a literature survey (Humboldt *et al.*, 1815–1825; Weberbauer, 1945; Ferreyra, 1996; Bridgewater *et al.*, 2003; Marcelo-Peña, 2008; Linares-Palomino *et al.*, 2010; Marcelo-Peña *et al.*, 2010) were used to compile an updated checklist of woody plants for the Marañón valley SDTF. The herbarium records were also used to form a complete picture of species distributions, in order to assess endemism more accurately. All records from selected major herbaria relevant for the study area were reviewed, including MOL, CPUN and USM, as well as the online databases of the Missouri Botanical Garden (www.tropicos.org), the Field Museum (<http://fm1.fieldmuseum.org/vrrc/>), the New York Botanical Garden (sciweb.nybg.org/science2/vii2.asp), Muséum national d'histoire naturelle (<http://science.mnhn.fr/institution/mnhn/collection/p/item/search/form>) and the Peruvian seasonally dry forest database (<http://rbg-web2.rbge.org.uk/dryforest/database.htm>). Data for generic and species-level diversity for Peruvian SDTFs as a whole were taken from the most recent literature by Linares-Palomino & Pennington (2007) with additions from collections made by the authors during recent years in the Marañón, Tarapoto, Mantaro, Apurimac, Chanchamayo and Puerto Ocopa areas (unpublished data). Endemism was assessed based on data from Brako & Zarucchi (1993), León *et al.* (2006), and the online IUCN Red List database (IUCN, 2001). Taxonomic treatment of families follows the phylogenetic approaches of the Angiosperm Phylogeny Group (APG III, 2009).

RESULTS

Species diversity

The Marañón valley woody flora consists of 440 species, 221 genera and 61 families of vascular plants based on the RBS and plot surveys, herbarium study, and previous literature records. Of the woody species recorded, 241 are shrubs, 177 trees and 22 lianas or scandent shrubs. Most of the species reach >3 m height ($n = 350$), while 89 species are low-growing shrubs or lianas.

The most diverse families of the Marañón in terms of species are Leguminosae (78 spp.), Euphorbiaceae (39 spp.), Compositae (35 spp.), Cactaceae (34 spp.) and Malvaceae (21 spp.; Fig. 3). At generic level, Leguminosae is the richest family with 32 genera, followed by Malvaceae (14), Cactaceae (13), Compositae (13), Apocynaceae and Euphorbiaceae (10) (Fig. 3). The most diverse genera include *Croton* (12 spp.), *Senna* (11 spp.), *Mimosa* and *Verbesina* (10 spp.), *Espostoa* and *Cnidioscolus* (9 spp.) and *Cordia* (8 spp.; Table 2). In terms of the Peruvian SDTF flora as a whole, Marañón represents an average of 56% (36–88%) of species and 78% (40–100%) of generic diversity (Tables 1 and 2). A total of 131 genera (30%) are represented by a single species in the Marañón.

At more local level, species diversity varies greatly across the valley. Individual RBS surveys recovered more species per survey (16–56 spp.), with a mean of 39 species in the most diverse areas and 21 species in the least diverse areas, compared with plots which captured 2–29 species per plot. As expected, the RBS surveys covered more species diversity as a whole (165 species, 116 genera and 40 families) compared with the plot dataset (91 species, 72 genera and 30 families) despite a larger number of established plots.

We also used accumulation curves from non-parametric estimators to assess and compare the sampling efficiency of our survey and plot inventories. The results show that there is a steady increase of species richness without reaching the asymptote, and suggest that the full richness of the woody flora has not been reached with the number

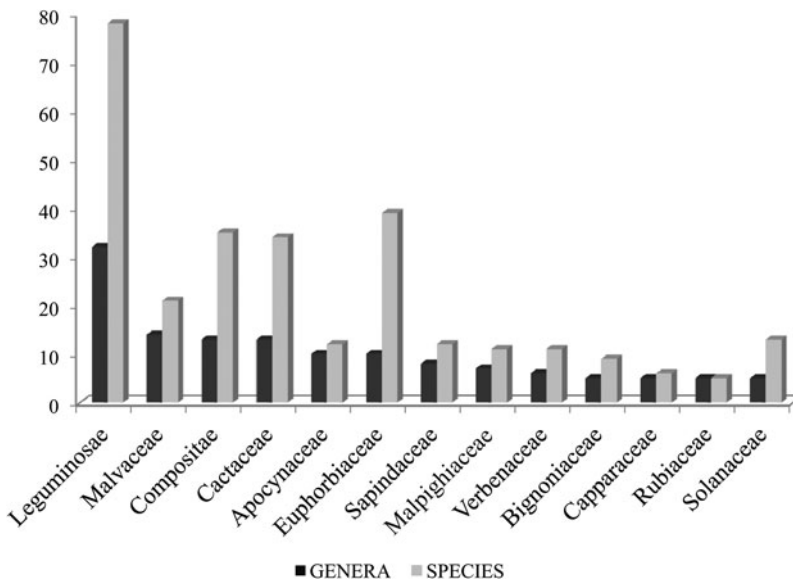


FIG. 3. Most diverse woody vascular plant families of the Marañón SDTFs based on plot and survey data presented here, combined with results from previous studies and herbarium work.

TABLE 1. Number of species for the most species-rich families of the Marañón valley in relation to Peruvian SDFT diversity as a whole

Family	No. of species		% Marañón from Peru SDFT
	SDTF Peru	SDTF Marañón	
Leguminosae	166	78	47
Euphorbiaceae	63	39	63
Compositae	44	35	80
Cactaceae	68	34	50
Malvaceae	45	21	47
Boraginaceae	17	13	77
Solanaceae	21	13	62
Apocynaceae	20	12	60
Sapindaceae	19	12	63
Malpighiaceae	16	11	69
Verbenaceae	18	11	61
Bignoniaceae	30	9	30
Meliaceae	18	8	44
Rutaceae	22	8	36
Piperaceae	8	7	88
Polygonaceae	17	7	41
Anacardiaceae	15	6	40
Capparaceae	15	6	40
Rhamnaceae	10	6	60
Nyctaginaceae	10	5	50
Urticaceae	6	5	83

of sampling units used (Jackknife 1 and Bootstrap, Fig. 4). Plots recovered fewer shrubby species due to the diameter limit of ≥ 5 cm DBH, while the RBS surveys gave a better understanding of overall diversity measures including shrubs and lianas. Species not recovered in either plot or RBS survey data included a set of rare species known only from type localities: *Cynanchum calycinum* (Schltr.) Morillo, *Monactis rhombifolia* Sagást. & Dillon, *Verbesina plowmanii* Sagást., *Hylocereus microcladus* Backeb., *Mimosa lamolina* C.E.Hughes & G.P.Lewis, *Piptadenia weberbaueri* Harms, *Eriotheca peruviana* A.Robyns, *Gossypium raymondii* Ulbr., *Eugenia curvipilosa* McVaugh, *Johnstonia axilliflora* (M.C.Johnst.) Tortosa, *Pradosia argentea* (Kunth) T.D.Penn. and *Cestrum weberbaueri* Francey.

Species composition and abundance

The plot data show that the most frequent families across the Marañón are Cactaceae (52%), Leguminosae (17%), Euphorbiaceae (5%), Capparaceae (4%), Malvaceae (3%), Apocynaceae (3%) and Boraginaceae (2%) based on the 15,400 measured individuals across the 124 inventory sites (Table 3). The high abundance of Cactaceae is mainly due to a small group of three species (*Browningia altissima* (F.Ritter) Buxb.,

TABLE 2. Species diversity in the most species-diverse genera of the Marañón valley compared with Peruvian SDTF diversity as a whole

Genus	No. of species		% Marañón from Peru SDTF
	SDTF Peru	SDTF Marañón	
<i>Croton</i>	23	12	52
<i>Senna</i>	14	11	79
<i>Mimosa</i>	14	10	71
<i>Verbesina</i>	10	10	100
<i>Cnidioscolus</i>	11	9	82
<i>Espositoa</i>	9	9	100
<i>Cordia</i>	10	8	80
<i>Piper</i>	8	7	88
<i>Solanum</i>	11	7	64
<i>Acacia</i>	8	6	75
<i>Armatocereus</i>	8	6	75
<i>Pappobolus</i>	6	6	100
<i>Acalypha</i>	5	5	100
<i>Buddleja</i>	5	5	100
<i>Caesalpinia</i>	5	5	100
<i>Erythroxylum</i>	11	5	45
<i>Ferreyranthus</i>	5	5	100
<i>Tournefortia</i>	7	5	71
<i>Bauhinia</i>	7	4	57
<i>Lantana</i>	7	4	57
<i>Zanthoxylum</i>	10	4	40

Espositoa mirabilis F.Ritter and *Armatocereus rauhii* Backeb.) dominating the vegetation; together, these three species make up nearly half the total individuals (42%; Table 3). A total of 18% (64 spp.) are represented by two or fewer individuals in the survey data.

The combined RBS and plot data show that *Acacia aroma* Gillies ex Hook. & Arn. and *Eriotheca discolor* (Kunth) A.Robyns are the most frequent species in the valley, followed by *Browningia pilleifera* (F.Ritter) Hutchison, *Cynophalla flexuosa* (L.) J.Presl, *Armatocereus rauhii*, *Sideroxylon obtusifolium* (Humb. ex Roem. & Schult.) T.D.Penn., *Jacquinia mucronata* Roem. & Schult., *Parkinsonia praecox* (Ruiz & Pav.) Hawkins, *Ruprechtia aperta* Pendry and *Browningia altissima* (Table 3). There is large variation, however, in the set of the most frequent species across the valley from north to south. The most abundant species in the northernmost Marañón (S1) include *Cordia iguaguana* Melch. ex I.M.Johnst., *Cynophalla flexuosa* and *Croton thurifer* Kunth, whilst *Acacia aroma* and *Browningia altissima* dominate further south in S2. Six species dominate across both S1 and S2 but do not occur in the southernmost sectors (*Tetrasida chachapoyensis* (Baker f.) Fryxell & Fuertes, *Ruprechtia aperta*, *Aspidosperma polyneuron* Müll.Arg., *Eugenia* sp., *Neea* sp. nov. and *Jacquinia mucronata*). The most abundant species in S3 include three species of Cactaceae (*Browningia*

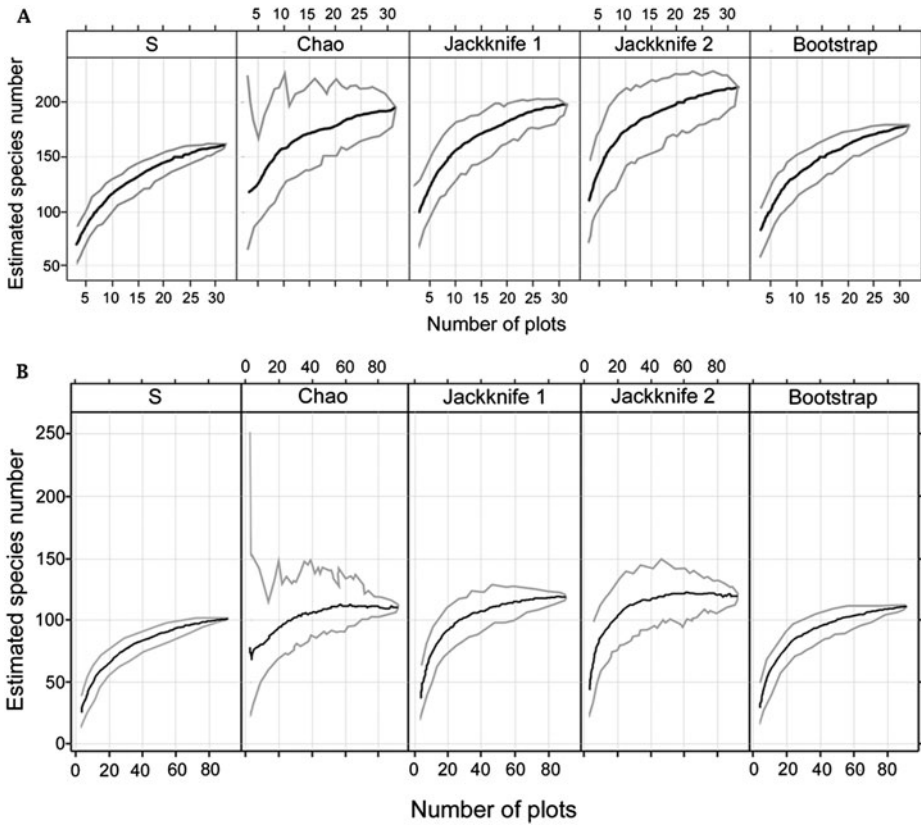


FIG. 4. Smoothed accumulation curves of species richness according to non-parametric estimators Chao 2, Jackknife 1, Jackknife 2 and Bootstrap. A. Rapid Botanical Surveys (RBS). B. Plot surveys. Each panel shows the mean (grey) with a confidence interval (black) after 100 resamplings with replacement, following increasing sampling efforts (minimum and maximum census units). Number of maximum census units was 32 in the RBS and 92 in the plot survey dataset.

altissima, *Espostoa lanata* (Kunth) Britton & Rose and *Praecereus euchlorus* subsp. *jaenensis* (Rauh ex Backeb.) Ostolaza), while a different set of Cactaceae species dominates in S4 (*Browningia pilleifera*, *Armatocereus rauhii* and *Espostoa mirabilis*). Six further species dominate in both S3 and S4 but not in the northernmost sectors (*Acacia aroma*, *Colicodendrum scabridon* (Kunth) Seem., *Parkinsonia praecox*, *Vallesia glabra* (Cav.) Link, *Cnidoscolus diacanthus* (Pax & K.Hoffm.) J.F.Macbr. and *Leucaena trichodes* (Jacq.) Benth.).

Vegetation density varies greatly across the Marañón as exemplified by the number of individuals recorded per plot (17–619). The densest vegetation is found in San Vicente in S4 with 619 individuals per plot, where *Browningia pilleifera* dominates with 574 individuals. The lowest stem density is found in Chagual, Balsas and La Pizarra, also in S4 in southern Marañón, where the climate is drier with sparser

TABLE 3. Most frequent and abundant species of the Marañón valley based on plot and survey data. Endemic dominant species are highlighted in bold

Species	No. of records	No. of individuals
<i>Acacia aroma</i> Gillies ex Hook. & Arn.	55	817
<i>Eriotheca discolor</i> (Kunth) A.Robyns	55	228
<i>Browningia pilleifera</i> (F.Ritter) Hutchison	53	4061
<i>Cynophalla flexuosa</i> (L.) J.Presl	49	392
<i>Armatocereus rauhii</i> Backeb.	46	919
<i>Sideroxylon obtusifolium</i> (Humb. ex Roem. & Schult.) T.D.Penn.	43	193
<i>Jacquinia mucronata</i> Roem. & Schult.	42	199
<i>Parkinsonia praecox</i> (Ruiz & Pav. ex Hook.) Hawkins	41	380
<i>Ruprechtia aperta</i> Pendry	39	309
<i>Browningia altissima</i> Buxb.	37	696
<i>Colicodendron scabridum</i> (Kunth) Seem.	37	301
<i>Acacia macracantha</i> Willd.	34	358
<i>Handroanthus chrysantha</i> (Jacq.) S.O.Grose	33	161
<i>Bougainvillea peruviana</i> Bonpl.	32	87
<i>Pithecellobium excelsum</i> (Kunth) Benth.	32	145
<i>Croton thurifer</i> Kunth	31	141
<i>Tetrasida chachapoyensis</i> (Baker f.) Fryxell & Fuertes	29	117
<i>Cordia saccellia</i> Gottschling & J.S.Mill.	27	120
<i>Cyathostegia mathewsii</i> (Benth.) Schery	27	205
<i>Zanthoxylum rigidum</i> Humb. & Bonpl. ex Willd.	27	64
<i>Praecereus euchlorus</i> (F.A.C.Weber ex K.Schum.) N.P.Taylor subsp. <i>jaenensis</i> (Rauh ex Backeb.) Ostolaza	26	151
<i>Rauhocereus riosaniensis</i> Backeb. subsp. <i>jaenensis</i>	26	126
<i>Ceiba insignis</i> (Kunth) P.E.Gibbs & Semir	25	82

vegetation. Here, the endemic *Parkinsonia peruviana* C.E.Hughes, Daza & Hawkins, restricted to the southern parts of the valley, dominates, with 13 individuals (43% of total stems).

Endemism

Of the 440 woody species recorded in the valley, 143 are endemic to the Marañón, representing 33% endemism in the woody vascular plant flora (Table 4). The families with the highest level of endemism are Compositae and Cactaceae (27 spp.), followed by Leguminosae and Euphorbiaceae (16 spp.), and Malvaceae (10 spp.). The six most endemic-rich genera are *Verbesina* (10 spp.), *Espostoa* (8 spp.), *Mimosa* (7 spp.), *Pappobolus* (6 spp.), and *Armatocereus*, *Cnidoscolus* and *Ferreyranthus* (4 spp.). Eight species new to science endemic to the Marañón were found during the study; these include four species of *Croton* (Ricarda Riina, pers. comm.) and two species of *Clusia* (Mats Gustafsson, pers. comm.). Four endemic genera are found in the

TABLE 4. List of woody endemic species recorded from the Marañón valley SDTFs, northern Peru

No.	Scientific name	Family	Habit
1	<i>Tetramerium peruvianum</i> (Lindau) T.F.Daniel	Acanthaceae	Shrub
2	<i>Iresine weberbaueri</i> Suess.	Amaranthaceae	Shrub
3	<i>Allamanda weberbaueri</i> Markg.	Apocynaceae	Shrub
4	<i>Cynanchum calycinum</i> (Schltr.) Morillo	Apocynaceae	Shrub
5	<i>Marsdenia oligantha</i> K.Schum.	Apocynaceae	Woody climbing vine
6	<i>Mesechites acuminatus</i> (Ruiz & Pav.) Müll.Arg.	Apocynaceae	Woody climbing vine
7	<i>Tecoma rosifolia</i> Kunth	Bignoniaceae	Shrub
8	<i>Cordia iguaguana</i> Melch. ex I.M.Johnst.	Boraginaceae	Tree
9	<i>Cordia varronifolia</i> I.M.Johnst.	Boraginaceae	Tree
10	<i>Tournefortia ternifolia</i> Kunth	Boraginaceae	Shrub
11	<i>Armatocereus arduus</i> F.Ritter	Cactaceae	Tree
12	<i>Armatocereus laetus</i> (Kunth) Backeb. ex A.W.Hill	Cactaceae	Tree
13	<i>Armatocereus oligogonus</i> Rauh & Backeb.	Cactaceae	Tree
14	<i>Armatocereus rauhii</i> Backeb. subsp. <i>rauhii</i>	Cactaceae	Tree
15	<i>Armatocereus rauhii</i> subsp. <i>balsasensis</i> (F.Ritter) Ostolaza	Cactaceae	Tree
16	<i>Browningia altissima</i> (F.Ritter) Buxb.	Cactaceae	Tree
17	<i>Browningia chlorocarpa</i> (Kunth) W.T.Marshall	Cactaceae	Tree
18	<i>Browningia pilleifera</i> (F.Ritter) Hutchison	Cactaceae	Tree
19	<i>Calymmanthium fertile</i> F.Ritter	Cactaceae	Tree
20	<i>Calymmanthium substerile</i> F.Ritter	Cactaceae	Tree
21	<i>Cleistocactus plagiostroma</i> (Vaupel) D.R.Hunt	Cactaceae	Shrub
22	<i>Cleistocactus tenuiserpens</i> Rauh & Backeb.	Cactaceae	Shrub
23	<i>Espostoa blossfeldiorum</i> (Werderm.) Buxb.	Cactaceae	Tree
24	<i>Espostoa calva</i> F.Ritter	Cactaceae	Tree
25	<i>Espostoa hylaea</i> F.Ritter	Cactaceae	Tree
26	<i>Espostoa lanianuligera</i> F.Ritter	Cactaceae	Tree
27	<i>Espostoa mirabilis</i> F.Ritter	Cactaceae	Tree
28	<i>Espostoa ritteri</i> Buining	Cactaceae	Tree
29	<i>Espostoa superba</i> F.Ritter	Cactaceae	Tree

TABLE 4. (Cont'd)

No.	Scientific name	Family	Habit
30	<i>Espostoa utcubambensis</i> G.J.Charles	Cactaceae	Tree
31	<i>Hylocereus microcladus</i> Backeb.	Cactaceae	Shrub
32	<i>Hylocereus peruvianus</i> Backeb.	Cactaceae	Shrub
33	<i>Lasiocereus fulvus</i> F.Ritter	Cactaceae	Shrub
34	<i>Lasiocereus rupicola</i> F.Ritter	Cactaceae	Shrub
35	<i>Loxanthocereus sulcifer</i> Rauh & Backeb.	Cactaceae	Shrub
36	<i>Pereskia horrida</i> (Kunth) DC.	Cactaceae	Shrub
37	<i>Praecereus euchlorus</i> subsp. <i>jaenensis</i> (Rauh ex Backeb.) Ostolaza	Cactaceae	Shrub
38	<i>Rauhocereus riosaniensis</i> Backeb. subsp. <i>riosaniensis</i>	Cactaceae	Shrub
39	<i>Rauhocereus riosaniensis</i> subsp. <i>jaenensis</i> (Rauh ex Backeb.) Ostolaza	Cactaceae	Shrub
40	<i>Capparidastrum sprucei</i> (Eichler) Hutch.	Capparaceae	Tree
41	<i>Carica aprica</i> V.M.Badillo	Caricaceae	Tree
42	<i>Maytenus durifolia</i> Briq.	Celastraceae	Tree
43	<i>Clusia rigida</i> M.Gustaffson	Clusiaceae	Tree
44	<i>Clusia</i> sp. nov.	Clusiaceae	Tree
45	<i>Arnaldoa macbrideana</i> Ferreyra	Compositae	Shrub
46	<i>Arnaldoa weberbaueri</i> (Muschl.) Ferreyra	Compositae	Shrub
47	<i>Baccharis grandicapitulata</i> Hieron. var. <i>subdentata</i> Hieron.	Compositae	Shrub
48	<i>Barnadesia hutchisoniana</i> Ferreyra	Compositae	Shrub
49	<i>Ferreyranthus fruticosus</i> (Muschl.) H.Rob.	Compositae	Shrub
50	<i>Ferreyranthus gentryi</i> H.Rob.	Compositae	Shrub
51	<i>Ferreyranthus rugosus</i> (Ferreyra) H.Rob. & Brettell	Compositae	Shrub
52	<i>Ferreyranthus vernonioides</i> (Muschl.) H.Rob. & Brettell	Compositae	Shrub
53	<i>Gochnatia vernonioides</i> Kunth	Compositae	Shrub
54	<i>Monactis rhombifolia</i> Sagást. & Dillon	Compositae	Shrub
55	<i>Pappobolus amoenus</i> Panero var. <i>amoenus</i>	Compositae	Shrub
56	<i>Pappobolus hutchisonii</i> (H.Rob.) Panero	Compositae	Shrub
57	<i>Pappobolus mathewsii</i> (Hochr.) Panero var. <i>mathewsii</i>	Compositae	Shrub
58	<i>Pappobolus mathewsii</i> (Hochr.) Panero var. <i>viridifolius</i> Panero	Compositae	Shrub

TABLE 4. (Cont'd)

No.	Scientific name	Family	Habit
59	<i>Pappobolus sagasteguii</i> (H.Rob.) Panero	Compositae	Shrub
60	<i>Pappobolus youngiorum</i> Panero	Compositae	Shrub
61	<i>Perymenium celendinianum</i> B.L.Turner	Compositae	Shrub
62	<i>Verbesina andina</i> Sagást.	Compositae	Shrub
63	<i>Verbesina auriculigera</i> S.F.Blake	Compositae	Shrub
64	<i>Verbesina cajamarcensis</i> Sagást.	Compositae	Shrub
65	<i>Verbesina capituliparva</i> Sagást.	Compositae	Shrub
66	<i>Verbesina chachapoyensis</i> Sagást. & Quipuscoa	Compositae	Shrub
67	<i>Verbesina hexantha</i> Sagást.	Compositae	Shrub
68	<i>Verbesina lopez-mirandae</i> Sagást.	Compositae	Shrub
69	<i>Verbesina ochroleucotricha</i> Sagást.	Compositae	Shrub
70	<i>Verbesina pentalobifolia</i> Sagást.	Compositae	Shrub
71	<i>Verbesina plowmanii</i> Sagást.	Compositae	Shrub
72	<i>Agarista subcordata</i> (Dunal) Judd	Ericaceae	Shrub
73	<i>Erythroxylum dillonii</i> Plowman ex Jara	Erythroxylaceae	Shrub
74	<i>Erythroxylum</i> sp. nov.	Erythroxylaceae	Shrub
75	<i>Cnidoscolus cajamarcensis</i> Fern.Casas & J.M.Pizarro var. <i>cajamarcensis</i>	Euphorbiaceae	Shrub
76	<i>Cnidoscolus cajamarcensis</i> var. <i>crenatus</i> Fern.Casas & J.M.Pizarro	Euphorbiaceae	Shrub
77	<i>Cnidoscolus hypoleucus</i> (Pax) Pax	Euphorbiaceae	Shrub
78	<i>Cnidoscolus liesneri</i> Fern.Casas & J.M.Pizarro	Euphorbiaceae	Shrub
79	<i>Croton adipatus</i> Kunth	Euphorbiaceae	Shrub
80	<i>Croton rubiginosus</i> Croizat	Euphorbiaceae	Shrub
81	<i>Croton</i> sp. nov.	Euphorbiaceae	Shrub
82	<i>Dalechampia hutchinsoniana</i> G.L.Webster	Euphorbiaceae	Shrub
83	<i>Dalechampia weberbaueri</i> Pax & K.Hoffm.	Euphorbiaceae	Shrub
84	<i>Ditaxis dioica</i> Kunth	Euphorbiaceae	Shrub
85	<i>Ditaxis katharinae</i> Pax	Euphorbiaceae	Shrub
86	<i>Jatropha humboldtiana</i> McVaugh	Euphorbiaceae	Shrub
87	<i>Jatropha weberbaueri</i> Pax & K.Hoffm.	Euphorbiaceae	Shrub

TABLE 4. (Cont'd)

No.	Scientific name	Family	Habit
88	<i>Sebastiania haploclada</i> Briq.	Euphorbiaceae	Shrub
89	<i>Sebastiania</i> sp. nov.	Euphorbiaceae	Shrub
90	<i>Stillingia parviflora</i> Sanchez Vega, Sagastegui & Huft	Euphorbiaceae	Shrub
91	<i>Aeschynomene weberbaueri</i> Ulbr.	Leguminosae	Shrub
92	<i>Caesalpinia celendiniana</i> G.P.Lewis & C.E.Hughes	Leguminosae	Shrub
93	<i>Caesalpinia pluviosa</i> DC. var. <i>maraniona</i> G.P.Lewis & C.E.Hughes	Leguminosae	Tree
94	<i>Calliandra mollissima</i> (Willd.) Benth.	Leguminosae	Shrub
95	<i>Coursetia cajamarcana</i> Lavin	Leguminosae	Shrub
96	<i>Coursetia maraniona</i> Lavin	Leguminosae	Shrub
97	<i>Maraniona lavinii</i> C.E.Hughes, G.P.Lewis, Daza & Reynel	Leguminosae	Tree
98	<i>Mimosa ctenodes</i> Barneby	Leguminosae	Shrub
99	<i>Mimosa incarum</i> Barneby	Leguminosae	Shrub
100	<i>Mimosa jaenensis</i> Särkinen, Marcelo-Peña & C.E.Hughes	Leguminosae	Shrub
101	<i>Mimosa lamolina</i> C.E.Hughes & G.P.Lewis	Leguminosae	Shrub
102	<i>Mimosa pectinatipinna</i> Burkart	Leguminosae	Shrub
103	<i>Mimosa polycarpa</i> Kunth var. <i>polycarpa</i>	Leguminosae	Shrub
104	<i>Mimosa polycarpa</i> var. <i>redundans</i> Barneby	Leguminosae	Shrub
105	<i>Parkinsonia peruviana</i> C.E.Hughes, Daza & Hawkins	Leguminosae	Tree
106	<i>Piptadenia weberbaueri</i> Harms	Leguminosae	Tree
107	<i>Mentzelia heterosepala</i> Weigend & E.Rodr.	Loasaceae	Shrub
108	<i>Banisteriopsis parvifolia</i> (Nied.) B.Gates	Malpighiaceae	Woody climbing vine
109	<i>Bunchosia bonplandiana</i> A.Juss.	Malpighiaceae	Tree
110	<i>Diplopterys leiocarpa</i> (Cav.) DC.	Malpighiaceae	Woody climbing vine
111	<i>Diplopterys populifolia</i> (Nied.) W.R.Anderson & C.Davis	Malpighiaceae	Woody climbing vine
112	<i>Heteropterys andina</i> Amorim	Malpighiaceae	Woody climbing vine
113	<i>Heteropterys tiinae</i> W.R.Anderson	Malpighiaceae	Woody climbing vine
114	<i>Stigmaphyllon peruvianum</i> Nied.	Malpighiaceae	Woody climbing vine
115	<i>Abutilon pedunculare</i> Kunth	Malvaceae	Shrub
116	<i>Abutilon piurense</i> Ulbr.	Malvaceae	Shrub

TABLE 4. (Cont'd)

No.	Scientific name	Family	Habit
117	<i>Eriotheca peruviana</i> A.Robyns	Malvaceae	Tree
118	<i>Gaya weberbaueri</i> Ulbr.	Malvaceae	Shrub
119	<i>Gossypium raimondii</i> Ulbr.	Malvaceae	Shrub
120	<i>Pseudabutilon nigropunctulatum</i> (Ulbr.) R.E.Fr.	Malvaceae	Shrub
121	<i>Pseudobombax cajamarcanus</i> Fern.Alonso	Malvaceae	Tree
122	<i>Tetrasida chachapoyensis</i> (Baker f.) Fryxell & Fuertes	Malvaceae	Tree
123	<i>Tetrasida serrulata</i> Fryxell & Fuertes	Malvaceae	Shrub
124	<i>Tetrasida weberbaueri</i> (Ulbr.) Fryxell & Fuertes	Malvaceae	Shrub
125	<i>Cedrela kuelapensis</i> T.D.Penn. & Daza	Meliaceae	Tree
126	<i>Cedrela molinensis</i> T.D.Penn. & Reynel	Meliaceae	Tree
127	<i>Eugenia curvipilosa</i> McVaugh	Myrtaceae	Tree
128	<i>Guapira</i> sp. nov.	Nyctaginaceae	Tree
129	<i>Schrebera americana</i> (Zahlbr.) Gilg	Oleaceae	Tree
130	<i>Ruprechtia albida</i> Pendry	Polygonaceae	Tree
131	<i>Ruprechtia aperta</i> Pendry	Polygonaceae	Tree
132	<i>Clavija myrmeciocarpa</i> Stahl	Primulaceae	Shrub
133	<i>Johnstonia axilliflora</i> (M.C.Johnst.) Tortosa	Rhamnaceae	Shrub
134	<i>Exostema corymbosum</i> (Ruiz & Pav.) Spreng.	Rubiaceae	Tree
135	<i>Esenbeckia cornuta</i> Engl.	Rutaceae	Tree
136	<i>Urvillea peruviana</i> Ferrucci	Sapindaceae	Woody climbing vine
137	<i>Pradosia argentea</i> (Kunth) T.D.Penn.	Sapotaceae	Tree
138	<i>Cestrum weberbaueri</i> Francey	Solanaceae	Shrub
139	<i>Nicotiana setchelli</i> Goodsp.	Solanaceae	Shrub
140	<i>Solanum arcanum</i> Peralta	Solanaceae	Shrub
141	<i>Solanum hutchisonii</i> (J.F.Macbr.) Bohs	Solanaceae	Shrub
142	<i>Lippia tayacajana</i> Moldenke	Verbenaceae	Shrub
143	<i>Stachytarpheta weberbaueri</i> Moldenke	Verbenaceae	Shrub

Marañón: *Calymmanthium* and *Lasiocereus* (Cactaceae, each with two species), *Johnstonia* (Rhamnaceae, 1 sp.) and *Maraniona* (Leguminosae, 1 sp.).

The survey and plot data show that many of the endemic species are locally abundant (Table 3). Examples of endemic species with high local abundance include *Browningia pilleifera*, *B. altissima*, *Armatocereus rauhii*, *Ruprechtia aperta*, *Tetrasida chachapoyensis*, *Praecereus euchlorus* subsp. *jaenensis* and *Rauhocereus riosaniensis* var. *jaenensis* (Rauh ex Backeb.) Ostolaza (Table 3). Endemic species that show the opposite pattern of low local abundance include *Tetramerium peruvianum* (Lindau) T.F.Daniel, *Gochnatia vernonioides* Kunth, *Cnidoscolus hypoleucus* (Pax) Pax, *Mimosa jaenensis* Särkinen, Marcelo-Peña & C.E.Hughes, and *Solanum hutchisonii* (J.F.Macbr.) Bohs: these species are always found in low numbers of individuals at each site. Endemic species that are only known from a single population include *Caesalpinia celendiniana* G.P.Lewis & C.E.Hughes, *Heteropterys tiinae* W.R.Anderson, *Mimosa ctenodes* Barneby and *Schrebera americana* (Zahlbr.) Gilg.

Analysis of the geographical distribution pattern of the endemic species indicates that the northernmost area of the river valley (S1) contains the highest number of endemic species (Fig. 5). Fifty-two endemic species are restricted to S1, whilst a further 24 endemics found in S1 occur across a wider area within the Marañón (Fig. 5). A set of 13 endemic species occurs across the entire valley from S1 to S4 (Fig. 5). Six species are restricted to S2, 16 to S3, and 17 to S4 (Fig. 5).

The analysis of the elevational distribution of endemic species shows that, within S1, most of the endemic species are confined to the lowest elevational zones below 1100 m (27 spp.; Fig. 6). Sixteen of these species are restricted to the lowest elevations, 300–700 m (Fig. 6). The elevational pattern of endemic diversity appears opposite in the southernmost parts of the valley in S3 and S4, where most endemic species are found in the highest elevational zone, 1900–2300 m (Fig. 6).

Our sampling in the southernmost areas of the valley in Pataz was poor, and further sampling of the southernmost limits of the Marañón SDTFs and their species composition will be needed to confirm the patterns observed here. The plot data from Chagual show floristic similarity with Balsas, with a similar set of dominant species including *Acacia macracantha* Willd., *A. aroma*, *Parkinsonia praecox*, *Armatocereus rauhii*, *Browningia pilleifera*, *Espostoa blossfeldiorum* (Werderm.) Buxb., *E. mirabilis*, *Cnidoscolus basiacanthus* (Pax & K.Hoffm.) J.F.Macbr. and *Jatropha weberbaueri* Pax & K.Hoffm. Further studies are needed, however, to confirm these patterns and discover whether a possible third centre of endemism might exist in the southernmost areas of the valley.

DISCUSSION

Quantitative vegetation surveys of Neotropical SDTFs have been historically sparse but over the past decades studies have been gradually moving towards large-scale analyses of diversity patterns across SDTF nuclei (e.g. Gentry, 1995; Ratter *et al.*,

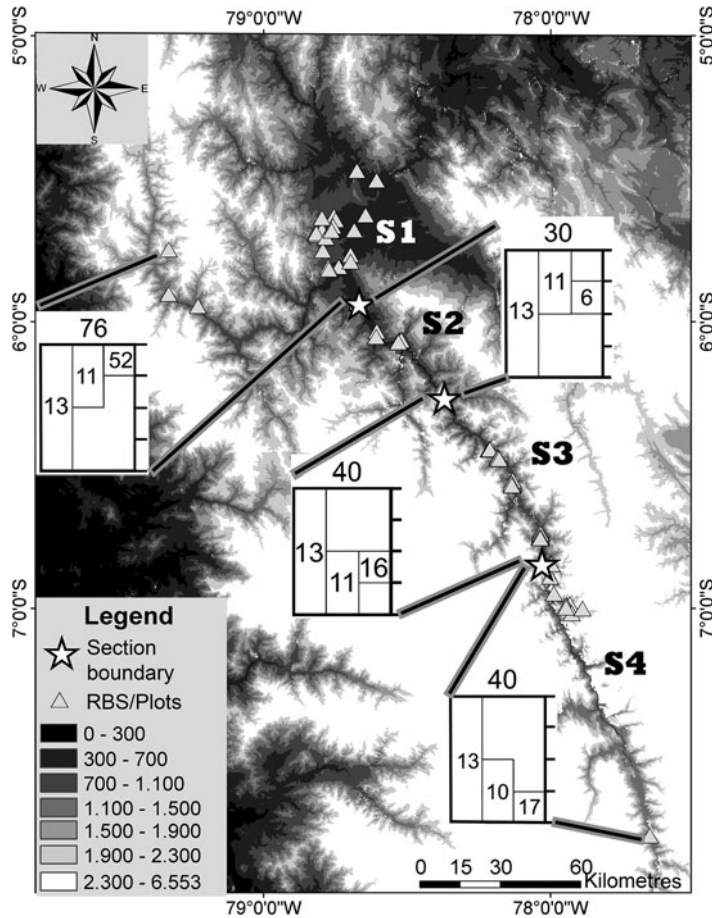


FIG. 5. Geographical distribution of endemic species across the Marañón. The subgraphs show the number of endemic species found in each geographical section separated by grey lines (S1–S4). The total number of endemic species found within each section is shown at the top of the subgraph, while the number of endemics restricted to or shared between sections is shown below. For example, 76 endemic species are found in Section 1 (S1), of which 52 are restricted to S1, 11 species overlap with S2, and 13 are ecologically and geographically widespread endemic species found across all sections. RBS = Rapid Botanical Survey.

2003; Giulietti *et al.*, 2004; Aguirre *et al.*, 2006; Oliveira-Filho *et al.*, 2006; Marcelo-Peña, 2008; Oliveira-Filho, 2010). Complete floristic checklists are still lacking in most areas but significant milestones have been reached in recent publications relating to particular areas, such as the checklist of vascular plants of the caatinga nucleus (Moro *et al.*, 2014).

Our study represents the first extensive study of the largest known inter-Andean SDTF fragments in the Marañón valley of northern Peru. Floristic composition, species richness and endemism of these forests reveal species diversity patterns that

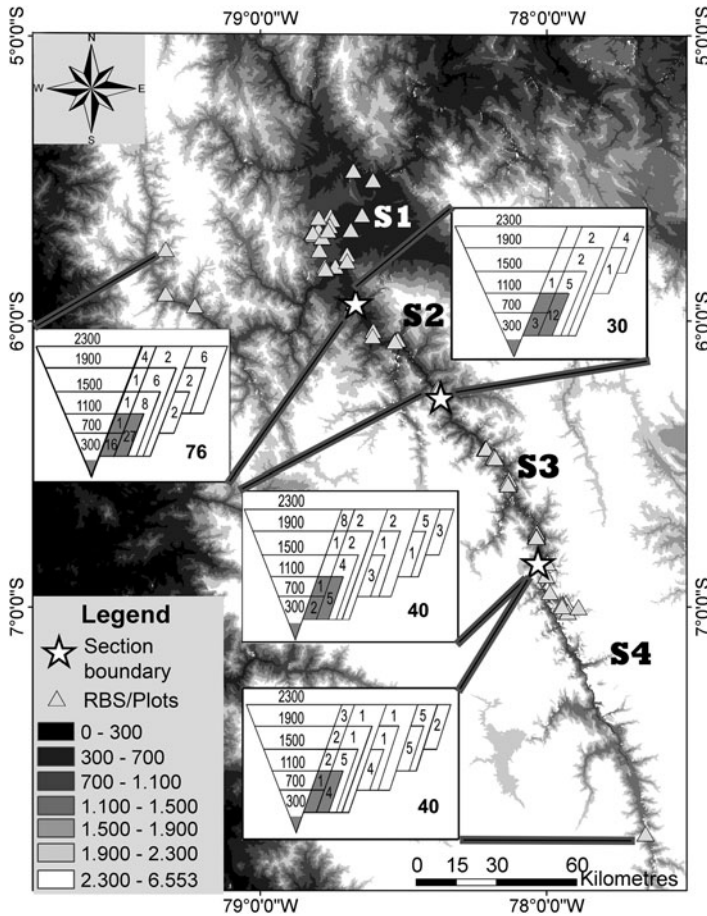


FIG. 6. Elevational distribution of endemic species in the Marañón within the four study sectors (S1–S4). The total number of endemic species is shown to the right of the subgraph. The right diagonal indicates the number of species strictly restricted to the elevational zone, with further right-hand side columns showing the overlap between different elevational zones. Only the data from the eastern slopes of the river survey were analysed for each geographical section within each altitudinal level. RBS = Rapid Botanical Survey.

should be considered in conservation planning and management at both national and international level.

Species diversity and floristic composition

The updated checklist of the Marañón presented here includes 440 species of woody vascular plants, of which 143 (33%) are endemic. At the local level, the Marañón forests appear species-poor, with 3–29 species ≥5 cm DBH recorded within a 0.1 ha study area, compared with other Peruvian and Neotropical SDTFs where an average of

25–30 and 50–70 species can be found, respectively (Gentry, 1982, 1988, 1995; Bridgewater *et al.*, 2003; Marcelo-Pena *et al.*, 2007). We emphasise, however, that plot-level species richness should be considered at a wider spatial scale, where species diversity is measured among plots rather than within plots. This is because studies focusing on beta-diversity have clearly shown that there is a large amount of species turnover across Andean SDTF nuclei over short geographical distances, implying high species diversity at regional rather than local scale. The high regional diversity only becomes apparent once species turnover between plots is analysed.

Floristically, the Marañón flora appears very similar to other Peruvian SDTFs and Neotropical SDTFs as a whole. For instance, the most species-rich plant families in the Marañón include Leguminosae, Euphorbiaceae, Cactaceae, Malvaceae and Compositae, as in Peruvian SDTFs generally (Linares-Palomino & Pennington, 2007). The Marañón SDTF is most closely related to Ecuadorian SDTFs based on floristic similarity, sharing 114 trees and 34 endemic species (Aguirre & Kvist, 2005; Linares-Palomino *et al.*, 2010; Marcelo-Peña *et al.*, 2010). As in all Neotropical SDTFs, Leguminosae is found to be the dominant family of the woody flora in terms of both species (77 species, 18%) and genera (30 genera, 14%) (Murphy & Lugo, 1986; Gentry, 1995; Trejo & Dirzo, 2002; Linares-Palomino *et al.*, 2010). Euphorbiaceae is the second most species-rich family, as in Mexican, Honduran and Antillean SDTFs (Trejo & Dirzo, 2002; Gordon *et al.*, 2004) and the Brazilian caatingas (Queiroz, 2006).

Our results support the prediction that the Marañón valley is a good representative of Peruvian SDTF diversity as a whole, and should be considered as a primary conservation target at national level in Peru. A total of 56% of the families and 78% of the genera present in Peruvian SDTFs are found in the Marañón valley. In terms of species, the Marañón represents the Peruvian SDTF flora equally well, with 47% of Leguminosae, 63% of Euphorbiaceae, 80% of Compositae, and 68% of Cactaceae species found in the valley. Furthermore, the Marañón SDTFs host all known SDTF species of *Verbesina*, *Espostoa*, *Acalypha*, *Buddleja*, *Caesalpinia*, *Ferreyranthus* and *Pappobolus*. Together, these results confirm that the Marañón flora is a good representative of the Peruvian SDTF flora as a whole, and should be considered as a conservation priority at the national level to establish the first conservation areas within SDTF in the country.

Patterns of endemism

Our results support previous findings that the woody flora of the Marañón is extremely rich in endemic species (33%) and genera (2%). These values are comparable to other biodiversity hotspots such as the native vascular flora of Galápagos, which comprises 560 species (including herbs) and 50 infraspecific taxa, of which 180 species (32% of the total) and all infraspecific taxa are endemic (Porte, 1983; Lawesson *et al.*, 1987; Tye, 2000). The highest levels of endemism in Neotropical SDTFs have been found in

the highly fragmented Mexican SDTFs with up to 60% endemism (Rzedowski, 1991), followed by the larger, more continuous Brazilian caatinga with 34% endemic species (Giulietti *et al.*, 2004). Our data therefore rank the Marañón close to both Mexican and Brazilian SDTFs. Although our study did not include herbaceous species, several endemic herbaceous species are known, including the monotypic *Rauhia* (Amaryllidaceae, 4 endemic spp.), *Matucana* (Amaryllidaceae, 8 endemic spp.), 18 endemic species of Bromeliaceae (León *et al.*, 2006) and 20 endemic species of *Peperomia* (Pino *et al.*, 2003, 2004, 2005, 2012; Pino, 2008). This highlights the importance of continuing floristic studies within the Marañón, where many more endemic species are likely to be found (Lewis *et al.*, 2010; Särkinen *et al.*, 2011b). Species accumulation curves from our study further confirm that more sampling is needed to record species diversity within the Marañón fully.

Our data indicate that Marañón SDTF is divided into two floristic subunits, the southern and northern forests, where much species turnover is focused in the narrow region between Ocalli (Amazonas) and Choropampa (Cajamarca) between 6°15'S and 6°18'S. For instance, 10 species restricted to the lowest elevational zones (e.g. *Browningia altissima*, *Armatocereus rauhii* subsp. *rauhii*, *Croton adipatus* Kunth, *Tetrasida chachapoyensis* and *Jatropha humboldtiana* McVaugh) show their distributional limits at Ocalli. Likewise, 17 species recorded between Chagual, Balsas and Ocalli (e.g. *Browningia pilleifera*, *Armatocereus rauhii* subsp. *balsasensis* (F.Ritter) Ostolaza, *Clusia rigida* M.Gustaffson and *Jatropha weberbaueri*) present their northern limits at Ocalli. The distributional patterns of plants observed in this study are similar to those observed for endemic birds and reptiles: three bird and four reptile species show their northern limits in Ocalli (birds – *Incaspiza ortizi* Zimmer, *Incaspiza laeta* Salvin and *Forpus xanthops* Salvin; reptiles – *Ameiva nodam* Koch, Venegas, Rödder, Flecks & Böhme, *Amphisbaena pericensis* Noble, *Phyllodactylus interandinus* Dixon & Huey and *Phyllodactylus johnwrighti* Dixon & Huey), whilst two birds and two reptiles have their southern limits in the same area (birds – *Incaspiza watkinsi* Chapman and *Melanopareia maranonica* Chapman: Statterfield *et al.*, 1998; Angulo *et al.*, 2007; reptiles – *Phyllodactylus delsolari* Venegas, Townsend, Koch & Böhme and *Phyllodactylus thompsoni* Venegas, Townsend, Koch & Böhme: Venegas *et al.*, 2008; Koch & Beraun, 2011; Koch *et al.*, 2013).

Within the northern and southern centres of endemism, elevational zonation of endemism is apparent. Our data show that, within the northern centre, most endemics are restricted to the lowest elevations (300–1100 m), whilst in the southern parts of the valley, most endemics are found at higher elevations (1500–2300 m). Many endemics are found to be restricted to relatively narrow elevational zones (500–800 m), indicating high beta-diversity even within the Marañón itself.

Although a large fraction of endemic species is locally restricted to specific geographical areas and elevational zones, a set of ecologically and geographically widespread endemic species can also be identified. For example, *Tecoma rosifolia* Kunth has the widest distribution pattern amongst the endemic species, occurring throughout the valley across the entire elevational range (600–2000 m). Five other endemic

species, namely *Diplopterys leiocarpa* (A.Juss.) W.R.Anderson & C.Davis, *Caesalpinia pluviosa* DC. var. *maraniona* G.P.Lewis & C.E.Hughes, *Mimosa incarum* Barneby, *Espostoa blossfeldiorum* and *Espostoa mirabilis*, are also relatively widely distributed along the valley at 1000–1500 m elevation. These species appear ecologically labile with high tolerance to different environmental conditions and should hence be considered as potential key species for SDTF restoration and conservation programmes.

Abundance of endemic species

Our plot data revealed interesting variation in the local abundance of endemic species. Results show that many of the dominating species found across the valley are in fact local endemics restricted to the Marañón. Such globally rare, but locally extremely abundant, species include *Browningia pilleifera* and *Armatocereus rauhii*. In terms of stem density, endemic species account for more than 50% of the standing diversity across the plots. These findings contrast with what has been found in neighbouring areas of SDTF, where most abundant species are widely distributed and do not include local endemics (Gentry, 1992; Prado & Gibbs, 1993; Fajardo *et al.*, 2005). For example, the most abundant species of the SDTFs of coastal Peru are widespread species such as *Libidibia glabrata* Kunth, *Handroanthus bilbergii* (Bureau & K.Schum.) S.O.Grose and *Terminalia valverdeae* A.H.Gentry. Similarly, the dominant species in the SDTFs of northeastern Peru include the relatively widespread *Alseis peruviana* Standl., *Eriotheca ruizii* (K.Schum.) A.Robyns, *Geoffroea spinosa* Jacq. and *Manilkara bidentata* (A.DC.) A.Chev. (Linares-Palomino, 2002; Bridgewater *et al.*, 2003).

The plot and survey data also show that a set of endemics has extremely low abundances, with 18% of the species found present only in a single plot, and a further 16% present in only two plots. This indicates that many species occur in low abundances in the Marañón. The distribution of these rare species may, however, also reflect modified distributions due to human activities, limitations by environmental factors, or simply sampling artefacts (Leal-Pinedo & Linares-Palomino, 2005). Although >15,400 surveyed individuals offer a solid dataset, more inventories are needed in sparsely explored areas of the valley to gather robust information on density, frequency and distribution of plants across the Marañón.

The distribution and abundance of endemic species in the Marañón fit recent predictions of species abundance patterns in highly isolated island-like communities (Rosindell & Phillimore, 2011; Rosindell & Harmon, 2013). These models predict that endemic species occurring on islands or island-like systems become relatively abundant over time given strong geographical isolation and dispersal limitation (Rosindell & Phillimore, 2011). Although not a true island, the Marañón has been identified as an island-like valley system based on evolutionary studies of endemic lineages, which show that the flora has evolved under strong isolation as on many oceanic islands over the past 10 million years (Pennington *et al.*, 2010; Särkinen *et al.*, 2012). Empirical studies from the similarly fragmented and island-like Mexican SDTFs support our

findings by showing that many locally abundant species have narrow geographical ranges (Williams *et al.*, 2010). This pattern of locally abundant but globally rare species is reflected in the fact that widespread and dominant species in Neotropical SDTFs are generally lacking due to the high beta-diversity across forest nuclei identified by previous studies (Pennington *et al.*, 2006; Linares-Palomino *et al.*, 2011). Although a set of common species for the complete biome has been identified for the entire Neotropics, no hyperdominant set of species exists for the SDTF similar to lowland rainforest communities identified as oligarchies or hyperdominants (Pitman *et al.*, 2013; ter Steege *et al.*, 2013). These patterns indicate that the Neotropical SDTFs have had an extremely different evolutionary history and suffer distinct current-day dynamics compared with other biomes. Further studies are needed to fully explore abundance differences in relation to range size across biomes, including their significance under future climate change scenarios.

Threats and the importance of SDTF conservation

Despite the accumulating data showing that the Marañón valley hosts a wealth of unique plant and animal species, there are no protected areas within the valley (Servicio Nacional de Áreas Protegidas, 2014, 2015). Accelerated landscape fragmentation due to agriculture, livestock, road construction, population growth and land invasions, as well as increasing demand for fuel, pose a serious threat to Marañón forests. Although no quantitative study of these threats has been published, the effect of anthropogenic disturbance on forest degradation and loss is evident in the field. A further threat is posed by the recent and ongoing plans to establish 15 dams in the area, flooding several kilometres of riverine SDTF along the Rio Marañón (Finer & Jenkins, 2012). The plans are now approved by the Ministry of Environment, and the new dams will flood 32.5 km² up to 850 m elevation around several sites at El Inca, El Mango, El Paraíso, Santa Rosa, Montegrande, Salazar, Nuevo Rioja, El Cura, Saquilillo, Tupén, San Lucas Chico, San Lucas Grande, Nueva Arica, Choropampa, La Mushca, Mapish, San Francisco, Libián, Tuén and Mendán (Chadin II dam site; AMEC, 2011; Finer & Jenkins, 2012).

Our analyses of endemism and species distribution patterns across the valley in terms of both geography and elevation can now be used to plan conservation areas in the lower elevation areas between 300 and 1100 m in the northern parts of the Marañón near Jaén and Utcubamba (Cumba and Pongo de Rentema), and in the higher elevation areas in the southern parts of the valley close to Balsas between 1500 and 2300 m elevation. As reflected in our data, protected areas are needed in both the northern and southern parts of the valley in order to preserve different types of SDTF community. The greatest priority should be given to the northern sections of the valley (S1–S2) between 300 and 1100 m, where the largest number of endemic species was recorded. These lower elevation zones are the most densely populated and farmed (e.g. towns of Jaén, Bagua and Balsas), however, and careful planning will be needed

to find locations for conservation areas. Areas with the greatest potential for conservation are steeply sloping and difficult to access, where the potential for farming is low. If conservation areas are established, fencing should be erected in order to keep grazing pressure to a minimum.

Our results reveal that the Marañón valley is an excellent representative of the woody flora of Peruvian SDTFs, and merits increased conservation efforts at both the national and global level. The importance of the Marañón valley lies not only in its endemic species but also in the fact that it is an arid region surrounded by tropical mesic biomes. Thus, the Marañón can be seen as an important natural laboratory for the study of how plants, invertebrates and vertebrates have adapted – and will adapt – to highly variable and stressful moisture regimes both in the past and as climate changes in the future (Giulietti *et al.*, 2004). The local endemic flora survived the upheaval of past climate changes during the Pleistocene several million years ago (Pennington *et al.*, 2010), and should hence be considered as a resource and opportunity in the face of the anthropogenic climate change predicted in the coming decades and centuries.

CONCLUSIONS

This study shows that the Marañón valley SDTFs from northern Peru are rich in terms of their woody flora, with high levels of endemism (33%) compared with their Neotropical counterparts. Our results reveal that the SDTFs of the Marañón valley are excellent representatives of the woody flora of the Peruvian SDTFs as a whole, including c.78% of generic diversity in only 3750 km². The Marañón valley requires greater attention in conservation agendas at both national and international level. Data presented here indicate that the valley consists of southern and northern centres of endemism, with wide variation in plant community composition across the valley. Within these centres, endemism and species diversity vary greatly across elevational zones. Interestingly, unlike in neighbouring SDTF areas, the Marañón flora is found to be dominated by endemic species at local level. The pattern of globally rare but locally abundant species appears a unique feature of the isolated island-like Marañón SDTFs, and requires further investigation. We strongly urge that governments at the national, regional and local levels, as well as NGOs, research institutes and universities, prioritise studies on the threats to the SDTF biome and its endemic species in the Marañón valley, and promote the creation of regional, municipal and private conservation areas. The valley is relatively small but substantial in terms of its biological heritage.

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