SYSTEMATIC AND ECOGEOGRAPHIC STUDIES ON CROP GENEPOOLS 10

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Atlas of Wild Potatoes

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ABSTRACT

This atlas describes the ecogeographic distribution of wild potatoes. They occur solely in the Americas, from the southwestern United States to central Argentina and Chile. To help the nonspecialist to understand the past and future changes in their classification, we first discuss the habitats, morphology, and taxonomy of wild potatoes. This is followed by a discussion of problems of data and information quality associated with the locality databases that were used for the maps in this atlas. Distribution maps are provided for all species and series (a taxonomic level that groups related species). Finally, statistics on ecogeographic distribution of wild potatoes, and analytical maps of species richness and series richness are provided.

Keywords: geographic distribution; geographic information systems; GIS; potato; sect. *Petota*; *Solanum*; Solanaceae; species distribution; species richness; wild potato.

1. INTRODUCTION

This atlas describes the ecogeographic distribution of wild potatoes. There are 196 currently accepted wild potato species (*Solanum* sect. *Petota*; Spooner and Hijmans, 2001). They occur solely in the Americas, from the southwestern United States to central Argentina and Chile. Wild potatoes are close relatives of cultivated potato (*Solanum tuberosum* L.), one of the world's principal food crops (Walker et al., 1999), and they have been used in programmes aimed at breeding for disease resistance, environmental tolerances, and other agronomic traits of interest (Ross, 1986; Hawkes, 1990; Spooner and Bamberg, 1994; Ochoa, 1999; Jansky, 2000). To date, at least 16 wild species have entered into the parentage of European and North American potato cultivars (Ross, 1986; Plaisted and Hoopes, 1989).

In this atlas we map and analyse the geographic distribution of wild potatoes. However, to put these maps and analyses in context we first discuss the habitats, morphology, and taxonomy of wild potatoes. Wild potato taxonomy is a complex and controversial topic, and it continues to be refined. Our goal is to provide the nonspecialist with some guidance to understand the past and future changes in the classification of wild potatoes. We also discuss the problems of data and information quality that are associated with the locality databases that were used for the maps in this atlas. We then provide distribution maps for all species and series (a taxonomic rank that groups related species). Finally, we provide statistics on ecogeographic distribution of wild potatoes, and map and discuss the geographic distribution of species richness.

The maps and analyses in this atlas are based on data from genebank databases and some additional data sources that were incorporated into a geographic information system (GIS). Geographic information systems can be used for many key activities related to the management of genetic resources, including planning of collecting missions, mapping areas of high diversity, and identifying areas where a trait of interest is present, but there are still few examples of such use (Guarino et al., 2001). Reasons for this may be the lack of access to data and software (Guarino et al., 2001), incomplete passport data (Greene and Hart, 1996), imprecise passport data (Hijmans et al., 1999), and a geographically biased sample (Hijmans et al., 2000).

In this atlas we explore the use of GIS to describe and analyse distribution data of wild potatoes. It provides basic information for use in further GIS-related research, including planning of collection missions and the assessment of relations between agronomic traits and the localities and ecologies where wild potato occur.

2. WILD POTATOES

Habitats

Wild potatoes are found from the southwestern United States to central Argentina and Chile. They occur from sea level to 4500 m, and in a wide variety of habitats including high-altitude Andean grasslands (puna and paramo vegetation), dry deciduous forests in Mexico, strand vegetation along Chilean beaches, and cool upland rain forests in the eastern Andes (Figure 1). In Mexico and the USA, wild potatoes are commonly found in such different environments as scrub and cactus vegetation, and pine, fir and oak forests (Hawkes, 1990). All species are terrestrial, except *Solanum morelliforme*[1] which is epiphytic and occurs in oak and pine forests from Central Mexico to Guatemala, and *S. clarum* which occurs in southern Mexico and Guatemala and grows on the ground in epiphytic-like conditions among mosses, or sometimes as an epiphyte.

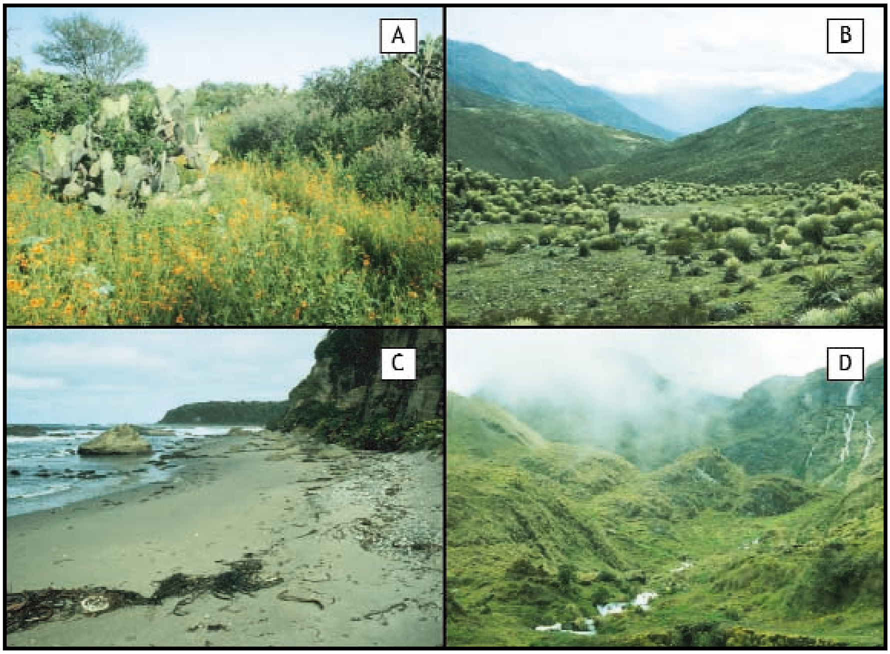

Figure 1. Wild potato habitats. A: dry deciduous forest in Jalisco, Mexico (2080 m); B: paramo in Mérida State, Venezuela (3050 m); C: seashore in the Chonos Archipelago, Región Aisén, Chile; D: humid highlands in La Paz Department, Bolivia (3900 m) (photos by David Spooner).

Some populations occur in relatively undisturbed habitats, but most thrive in recently disturbed areas in partial shade or in full sun, although they may or may not persist under constant disturbance. Ideal habitats for some species are in areas

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[1] See Table 1for full species names, including authors.

that have been recently logged or burned, along the sides of newly constructed roads, or on landfalls.

Hawkes (1994) suggested that because wild potatoes occur in this wide range of habitats, they have become tolerant to different environmental stresses and have developed strong resistance to a wide range of pests and diseases. He further suggested that cultivated potatoes evolved in cool temperate regions of the Andes and are often unable to resist the attacks of pests and diseases occurring over the broader range where they are now cultivated. Thus, a knowledge of the great ecogeographical range of wild potato species, contrasted with the narrower range of the cultivated ones, could be useful for appreciating the use of wild species in potato breeding.

Shapes and colours

Many wild potato species look similar to, and are easily confused with, cultivated potatoes. Figure 2 shows a variety of plant forms, ranging from *Solanum hougasii*, typical for a 'cultivated-like' form, to *S. agrimonifolium*, with somewhat parallel lanceolate leaflets seen in many members of series *Conicibaccata*; to *S. morelliforme*, with simple leaves and an epiphytic habit to *S. infundibuliforme*, with a diminutive stature and linear leaflets.

Flower shapes range from star-shaped (stellate), typical of many Mexican diploid species and some other species from South America, to highly wheel-shaped (rotate), and with intermediate shapes referred to as pentagonal or rotate-pentagonal (Spooner and Van den Berg, 2001) (Figure 3). Flower colours range from white, to cream white, to various shades of pink, purple and blue. Most species have round (globose) fruits but fruits can also be elongate, like chilli peppers (typical of ser. *Conicibaccata*), or have intermediate ovoid shapes (Figure 4).

Tubers grow on stolons (underground stems) that can attain a length of a meter or more. Tubers vary greatly in size from a few millimetres (e.g., *S. clarum*, *S. morelliforme*), to that of some of the cultivated species (e.g., *S. burtonii* or *S. candolleanum*). Their form varies from globose to tubular (straight to curved), with many intermediate shapes (Figure 5). Most species have tubers at the end of stolons, as in the cultivated species, but most species in ser. *Piurana* have tubers arranged along the stolons like beads on a string (Figure 5F) (Salas et al., 2001).

Various currently recognized wild potato species are so morphologically similar that they can be distinguished only by an overlapping series of character states, and their identification (and status as valid species) is problematical (Spooner and Van den Berg, 1992a; Spooner et al., 1995, 2001b; Van den Berg et al., 1998; Miller and Spooner, 1999). Some species are distinct and could never be confused with any others. For example, *S. bulbocastanum*, *S. infundibuliforme*, *S. lignicaule*, *S. morelliforme*, *S. olmosense*, *S. pinnatisectum*, *S. polyadenium*, *S. simplicissimum*, and some other species have distinctive features in leaves that are entire, or greatly dissected, or highly glandular, or possess other traits that allow for unambiguous identifications.

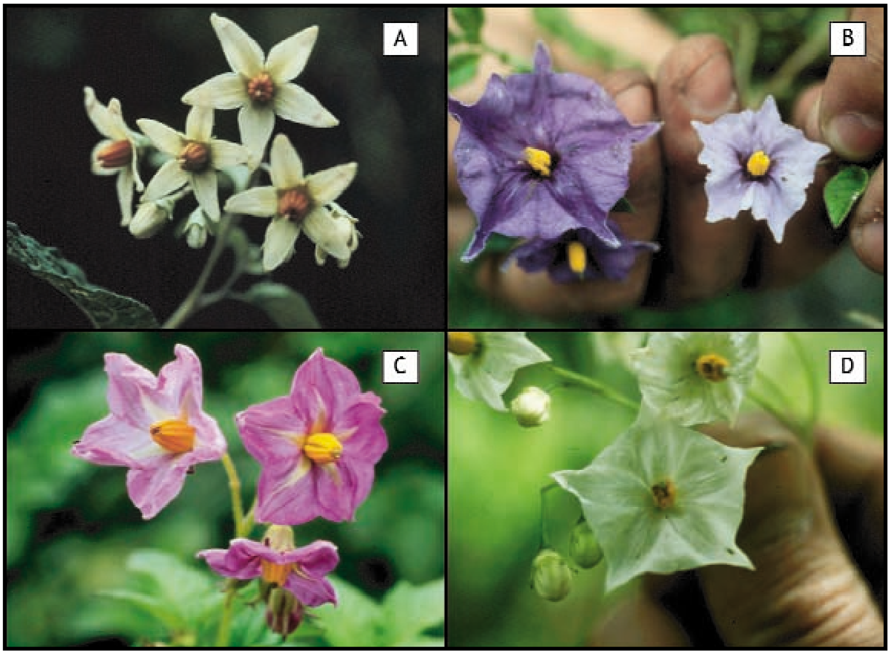

Figure 2. Wild potato plant forms. A: *Solanum hougasii*; B: *S. agrimonifolium*; C: *S. morelliforme;* D: *S. infundibuliforme* (photos by David Spooner).

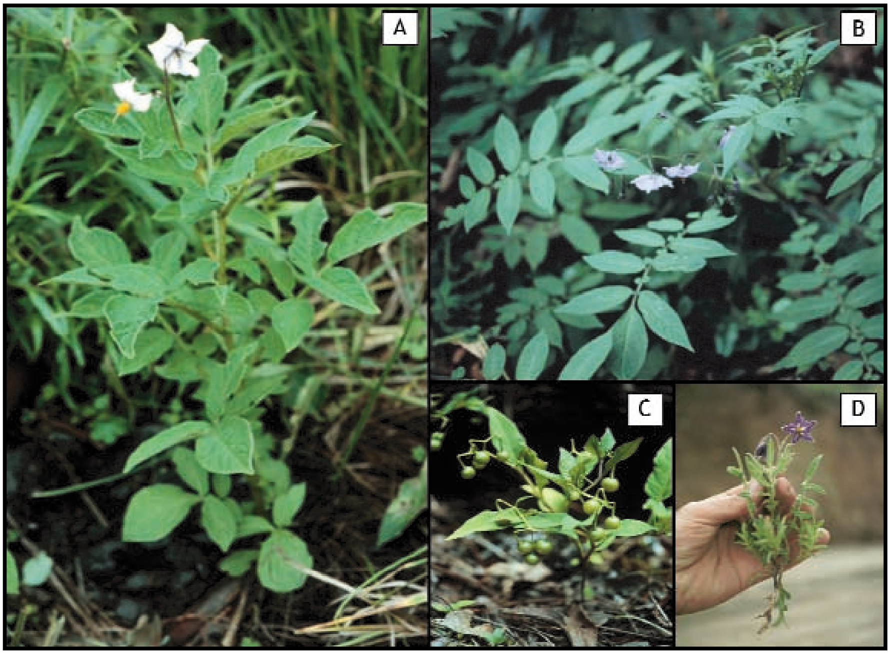

Figure 3. Wild and cultivated potato flowers. A: *Solanum bulbocastanum*; B: *S. paucijugum*; C: *S. tuberosum* (cultivated species); D: *S. colombianum* (photos by David Spooner).

Figure 4. Wild potato fruits. A: *Solanum verrucosum*; B: *S. andreanum*; C: *S. schenckii*; D: *S. moscopanum* (photos by David Spooner).

Figure 5. Wild potato tubers. A: *Solanum sparsipilum*; B: *S. polyadenium*; C: *S. acaule*; D: *S. chiquidenum*; E: *S. commersonii*; F: *S. piurae*. Scale across photos is comparable; the size of the largest tuber on panel E is approximately 3 cm (photos by Candelaria Atalaya).

3. POTATO TAXONOMY

A dynamic taxonomy

Linnaeus (1753) described the common cultivated potato species *Solanum tuberosum* L. but did not describe any wild potato species. The first valid published description of wild potato species was of *S. bulbocastanum* and *S. commersonii* by Dunal (1814). Walpers (1844) provided the first comprehensive treatment of wild potatoes and accepted 10 species. Subsequent comprehensive treatments were by Dunal (1852; 17 species), Baker (1884; 6), Wittmack (1909; 4), Hawkes (1956; 106), Correll (1962; 157), Hawkes (1963; 159), Hawkes (1990; 232), Spooner and Hijmans (2001; 196) (Figure 6).

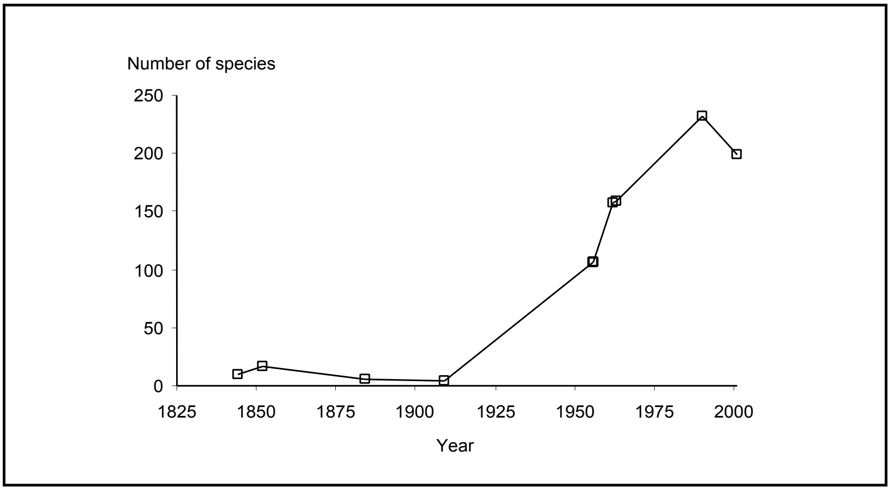

Figure 6. Number of accepted potato species over time.

Spooner and Hijmans (2001) listed 196 wild tuber-bearing potato species in *Solanum* sect. *Petota*, and three closely related non-tuber-bearing species in *Solanum* sect. *Etuberosum* (Bukasov and Kameraz) A. Child (Table 1). This list is an update of the comprehensive taxonomic treatment of Hawkes (1990), who recognized seven cultivated species and 225 wild species. This recent decrease in the number of accepted species, and despite the inclusion of 10 new species described during this period by Ochoa, is due to the exclusion of the non-tuber-bearing outgroup species that Hawkes (1990) placed in sect. *Petota* and synonymy of many species. In this atlas we follow the Spooner and Hijmans (2001) compilation of wild potatoes taxonomy with one exception: we changed *S. polytrichon* to *S. wightianum* because the former name was invalid (Nee, 1999).

The great morphological similarity of many wild and cultivated potatoes has always made it difficult to define species and infer their interrelationships. Different taxonomists have struggled with these issues, and conflicting taxonomic

Table 1. Wild potato species (*Solanum* sect. *Petota*) and three outgroup relatives in sect. *Etuberosum*, their standard three-letter codes, the number of the map in chapter 5 showing their distribution, series membership (or section membership for *Etuberosum*), and ploidy and Endosperm Balance Number (EBN) where known[1].

Species	**Code**	**Map**	**Series[2]**	**Ploidy (EBN)**
Solanum acaule Bitter	acl	45	*Acaulia*	4x (2EBN), 6x[3]
S. achacachense Cárdenas	ach	42	*Tuberosa*	2x
S. acroglossum Juz.	acg	23	*Piurana*	2x (2EBN)
S. acroscopicum Ochoa	acs	24	*Tuberosa*	2x
S. agrimonifolium Rydb.	agf	16	*Conicibaccata*	4x (2EBN)
S. alandiae Cárdenas	aln	41	*Tuberosa*	2x
S. albicans (Ochoa) Ochoa	alb	25	*Acaulia*	6x (4EBN)
S. albornozii Correll	abz	18	*Piurana*	2x (2EBN)
S. amayanum Ochoa	amy	26	*Tuberosa*	2x (2EBN)
S. ambosinum Ochoa	amb	24	*Tuberosa*	2x (2EBN)
S. anamatophilum Ochoa	amp	23	*Cuneoalata*	2x (2EBN)
S. ancophilum (Correll) Ochoa	acp	29	*Tuberosa*	2x (2EBN)
S. ancoripae Ochoa	anp	26	*Tuberosa*	2x
S. andreanum Baker	adr	20	*Tuberosa*	2x (2EBN)
S. ×arahuayum Ochoa	ara	26	*Tuberosa*	2x
S. ariduphilum Ochoa	adp	29	*Piurana*	2x (2EBN)
S. arnezii Cárdenas	arz	40	*Yungasensa*	
S. augustii Ochoa	agu	31	*Tuberosa*	2x (1EBN)
S. avilesii Hawkes and Hjert.	avl	39	*Tuberosa*	2x
S. ayacuchense Ochoa	ayc	24	*Conicibaccata*	2x (2EBN)
S. aymaraesense Ochoa	aym	24	*Tuberosa*	2x
S. berthaultii Hawkes	ber	43	*Tuberosa*	2x (2EBN)
S. bill-hookeri Ochoa	bhk	23	*Tuberosa*	2x
S. ×blanco-galdosii Ochoa	blg	31	*Cuneoalata*	2x (2EBN)
S. boliviense Dunal	blv	40	*Megistacroloba*	2x (2EBN)
S. bombycinum Ochoa	bmb	43	*Conicibaccata*	4x
S. brachistotrichum (Bitter) Rydb.	bst	5	*Pinnatisecta*	2x (1EBN)
S. brachycarpum Correll	bcp	13	*Demissa*	6x (4EBN)
S. brevicaule Bitter	brc	52	*Tuberosa*	2x (2EBN)
S. ×bruecheri Correll	bru	46	*Tuberosa*	
S. buesii Vargas	bue	25	*Conicibaccata*	2x (2EBN)
S. bukasovii Juz.	buk	37	*Tuberosa*	2x (2EBN)
S. bulbocastanum Dunal	blb	5	*Bulbocastana*	2x (1EBN)
S. burkartii Ochoa	brk	25	*Conicibaccata*	2x
S. burtonii Ochoa	brt	20	*Tuberosa*	3x
S. cajamarquense Ochoa	cjm	27	*Tuberosa*	2x (1EBN)
S. calacalinum Ochoa	cln	19	*Conicibaccata*	2x
S. calvescens Bitter	clv	57	*Commersoniana*	3x
S. candolleanum P. Berthault	cnd	49	*Tuberosa*	2x (2EBN)
S. cantense Ochoa	cnt	34	*Piurana*	2x (2EBN)

Species	**Code**	**Map**	**Series**[2]	**Ploidy (EBN)**
S. cardiophyllum Lindl.	cph	9	*Pinnatisecta*	2x (1EBN), 3x
S. chacoense Bitter	chc	57	*Yungasensa*	2x (2EBN)
S. chancayense Ochoa	chn	23	*Tuberosa*	2x (1EBN)
S. chilliasense Ochoa	chl	20	*Piurana*	2x (2EBN)
S. chillonanum Ochoa	*chi*	28	*Tuberosa*	2x
S. chiquidenum Ochoa	chq	24	*Piurana*	2x (2EBN)
S. chomatophilum Bitter	chm	23	*Conicibaccata*	2x (2EBN)
S. circaeifolium Bitter	crc	40	*Circaeifolia*	2x (1EBN)
S. clarum Correll	clr	15	*Bulbocastana*	2x
S. coelestipetalum Vargas	cop	27	*Tuberosa*	2x (2EBN)
S. colombianum Bitter	col	18	*Conicibaccata*	4x (2EBN)
S. commersonii Dunal	cmm	58	*Commersoniana*	2x (1EBN)
S. contumazaense Ochoa	ctz	34	*Conicibaccata*	2x (2EBN)
S. demissum Lindl.	dms	7	*Demissa*	6x (4EBN)
S. ×*doddsii* Correll	dds	42	*Tuberosa*	2x (2EBN)
S. dolichocremastrum Bitter	dcm	27	*Megistacroloba*	2x (1EBN)
S. donachui (Ochoa) Ochoa	dnc	20	*Conicibaccata*	
S. ×*edinense* P. Berthault	edn	11	*Demissa*	5x
S. etuberosum Lindl.	etb	59	Sect. *Etuberosum*	2x (1EBN)
S. fendleri A. Gray	fen	8	*Longipedicellata*	4x (2EBN)
S. fernandezianum Phil.	frn	58	Sect. *Etuberosum*	2x (1EBN)
S. flahaultii Bitter	flh	19	*Conicibaccata*	4x
S. flavoviridens Ochoa	flv	41	*Yungasensa*	3x[4]
S. gandarillasii Cárdenas	gnd	39	*Tuberosa*	2x (2EBN)
S. garcia-barrigae Ochoa	gab	20	*Conicibaccata*	
S. gracilifrons Bitter	grc	27	*Tuberosa*	2x
S. guerreroense Correll	grr	4	*Demissa*	6x (4EBN)
S. guzmanguense Whalen and Sagást.	gzm	23	*Simplicissima*	2x (1EBN)
S. hastiforme Correll	hsf	28	*Megistacroloba*	2x (2EBN)
S. hintonii Correll	hnt	8	*Pinnatisecta*	
S. hjertingii Hawkes	hjt	5	*Longipedicellata*	4x (2EBN)
S. hoopesii Hawkes and K.A. Okada	hps	41	*Tuberosa*	4x
S. hougasii Correll	hou	7	*Demissa*	6x (4EBN)
S. huancabambense Ochoa	hcb	29	*Tuberosa*	2x (2EBN)
S. huancavelicae Ochoa	hcv	32	*Tuberosa*	2x (2EBN)
S. huarochiriense Ochoa	hro	28	*Tuberosa*	2x (2EBN)
S. humectophilum Ochoa	hmp	29	*Piurana*	2x (1EBN)
S. hypacrarthrum Bitter	hcr	27	*Piurana*	2x (1EBN)
S. immite Dunal	imt	33	*Tuberosa*	2x (1EBN)[5]
S. incahuasinum Ochoa	inh	28	*Tuberosa*	2x (1EBN)
S. incamayoense K.A. Okada and A.M. Clausen	inm	59	*Tuberosa*	2x
S. incasicum Ochoa	ins	29	*Tuberosa*	2x (2EBN)

Species	**Code**	**Map**	**Series**[2]	**Ploidy (EBN)**
S. ×indunii K.A. Okada and A.M. Clausen	ind	59	*Acaulia*	3x
S. infundibuliforme Phil.	ifd	49	*Cuneoalata*	2x (2EBN)
S. ingifolium Ochoa	igf	28	*Ingifolia*	2x (1EBN)
S. iopetalum (Bitter) Hawkes	iop	12	*Demissa*	6x (4EBN)
S. irosinum Ochoa	irs	30	*Conicibaccata*	2x (2EBN)
S. jaenense Ochoa	jnn	30	*Conicibaccata*	6x (4EBN)
S. jalcae Ochoa	jlc	30	*Ingifolia*	2x (2EBN)
S. jamesii Torr.	jam	9	*Pinnatisecta*	2x (1EBN)
S. kurtzianum Bitter and Wittm.	ktz	59	*Tuberosa*	2x (2EBN)
S. laxissimum Bitter	lxs	30	*Conicibaccata*	2x (2EBN)
S. leptophyes Bitter	lph	55	*Tuberosa*	2x (2EBN), 4x (4EBN)
S. leptosepalum Correll	lps	6	*Tuberosa*	
S. lesteri Hawkes and Hjert.	les	10	*Polyadenia*	2x
S. lignicaule Vargas	lgl	34	*Lignicaulia*	2x (1EBN)
S. limbaniense Ochoa	lmb	31	*Conicibaccata*	2x (2EBN)
S. ×litusinum Ochoa	lit	40	*Yungasensa*	2x (2EBN)
S. lobbianum Bitter	lbb	20	*Tuberosa*	4x (2EBN)
S. longiconicum Bitter	lgc	15	*Conicibaccata*	4x
S. longiusculus Ochoa	lgs	30	*Tuberosa*	2x
S. lopez-camarenae Ochoa	lpc	31	*Tuberosa*	2x (1EBN)
S. macropilosum Correll	mcp	7	*Tuberosa*	
S. maglia Schltdl.	mag	57	*Maglia*	2x, 3x
S. marinasense Vargas	mrn	31	*Tuberosa*	2x (2EBN)
S. matehualae Hjert. and T.R. Tarn	mat	7	*Longipedicellata*	4x
S. medians Bitter	med	31	*Tuberosa*	2x (2EBN), 3x
S. megistacrolobum Bitter	mga	50	*Megistacroloba*	2x (2EBN)
S. ×michoacanum (Bitter) Rydb.	mch	8	*Pinnatisecta*	2x
S. microdontum Bitter	mcd	51	*Tuberosa*	2x (2EBN), 3x
S. minutifoliolum Correll	min	21	*Tuberosa*	2x (1EBN)
S. mochiquense Ochoa	mcq	32	*Tuberosa*	2x (1EBN)
S. morelliforme Bitter and G. Muench	mrl	12	*Morelliformia*	2x
S. moscopanum Hawkes	msp	20	*Conicibaccata*	6x (4EBN)
S. multiinterruptum Bitter	mtp	30	*Tuberosa*	2x (2EBN)
S. nayaritense (Bitter) Rydb.	nyr	12	*Pinnatisecta*	
S. nemorosum Ochoa	nmr	33	*Conicibaccata*	6x (4EBN)
S. neocardenasii Hawkes and Hjert.	ncd	39	*Tuberosa*	2x
S. neorossii Hawkes and Hjert.	nrs	54	*Tuberosa*	2x
S. neovalenzuelae L. López	nvz	21	*Conicibaccata*	4x
S. neovargasii Ochoa	nvg	33	*Conicibaccata*	2x
S. neovavilovii Ochoa	nvv	40	*Conicibaccata*	2x (2EBN)
S. ×neoweberbaueri Wittm.	nwb	32	*Tuberosa*	3x
S. nubicola Ochoa	nub	33	*Conicibaccata*	4x (2EBN)
S. okadae Hawkes and Hjert.	oka	46	*Tuberosa*	2x

Species	**Code**	**Map**	**Series**[2]	**Ploidy (EBN)**
S. olmosense Ochoa	olm	32	*Olmosiana*	2x (2EBN)
S. oplocense Hawkes	opl	53	*Tuberosa*	2x (2EBN), 4x (4EBN), 6x (4EBN)
S. orocense Ochoa	oro	21	*Conicibaccata*	
S. orophilum Correll	orp	35	*Tuberosa*	2x (2EBN)
S. ortegae Ochoa	ort	29	*Tuberosa*	2x
S. otites Dunal	oti	21	*Conicibaccata*	
S. oxycarpum Schiede	oxc	11	*Conicibaccata*	4x (2EBN)
S. palustre Poepp.	pls	57	Sect. *Etuberosum*	2x (1EBN)
S. pampasense Hawkes	pam	35	*Tuberosa*	2x (2EBN)
S. pamplonense L. López	ppl	19	*Conicibaccata*	4x
S. papita Rydb.	pta	13	*Longipedicellata*	4x (2EBN)
S. paucijugum Bitter	pcj	18	*Conicibaccata*	4x (2EBN)
S. paucissectum Ochoa	pcs	34	*Piurana*	2x (2EBN)
S. peloquinianum Ochoa	plq	34	*Cuneoalata*	2x (2EBN)
S. pillahuatense Vargas	pll	26	*Conicibaccata*	2x (2EBN)
S. pinnatisectum Dunal	pnt	10	*Pinnatisecta*	2x (1EBN)
S. piurae Bitter	pur	35	*Piurana*	2x (2EBN)
S. polyadenium Greenm.	pld	6	*Polyadenia*	2x
S. puchupuchense Ochoa	pch	35	*Tuberosa*	2x
S. raphanifolium Cárdenas and Hawkes	rap	33	*Megistacroloba*	2x (2EBN)
S. raquialatum Ochoa	raq	36	*Ingifolia*	2x (1EBN)
S. ×rechei Hawkes and Hjert.	rch	58	*Tuberosa*	2x, 3x
S. regularifolium Correll	rgf	19	*Tuberosa*	2x
S. rhomboideilanceolatum Ochoa	rhl	36	*Conicibaccata*	2x (2EBN)
S. ×ruiz-lealii Brücher	rzl	60	*Tuberosa*	
S. salasianum Ochoa	sls	36	*Conicibaccata*	2x
S. ×sambucinum Rydb.	smb	8	*Pinnatisecta*	2x
S. sanctae-rosae Hawkes	sct	58	*Megistacroloba*	2x (2EBN)
S. sandemanii Hawkes	snd	25	*Tuberosa*	2x (2EBN)
S. santolallae Vargas	san	34	*Conicibaccata*	2x (2EBN)
S. sarasarae Ochoa	srs	26	*Tuberosa*	2x (2EBN)
S. sawyeri Ochoa	swy	35	*Tuberosa*	2x (2EBN)
S. saxatilis Ochoa	*sax*	28	*Tuberosa*	2x (2EBN)
S. scabrifolium Ochoa	scb	36	*Tuberosa*	2x
S. schenckii Bitter	snk	10	*Demissa*	6x (4EBN)
S. ×semidemissum Juz.	sem	6	*Demissa*	6x
S. ×setulosistylum Bitter	stl	47	*Tuberosa*	2x
S. simplicissimum Ochoa	smp	32	*Simplicissima*	2x (1EBN)
S. soestii Hawkes and Hjert.	sst	39	*Circaeifolia*	2x
S. sogarandinum Ochoa	sgr	32	*Megistacroloba*	2x (2EBN), 3x
S. solisii Hawkes	sol	21	*Piurana*	
S. sparsipilum (Bitter) Juz. and Bukasov	spl	54	*Tuberosa*	2x (2EBN)

Species	Code	Map	Series[2]	Ploidy (EBN)
S. spegazzinii Bitter	spg	54	*Tuberosa*	2x (2EBN)
S. stenophyllidium Bitter	sph	6	*Pinnatisecta*	2x (1EBN)
S. stoloniferum Schltdl. and Bouchet	sto	4	*Longipedicellata*	4x (2EBN)
S. subpanduratum Ochoa	sup	19	*Conicibaccata*	4x
S. ×sucrense Hawkes	scr	41	*Tuberosa*	4x (4EBN)
S. sucubunense Ochoa	suc	21	*Conicibaccata*	
S. tacnaense Ochoa	tcn	26	*Tuberosa*	2x (2EBN)
S. tapojense Ochoa	tpj	25	*Tuberosa*	2x (2EBN)
S. tarapatanum Ochoa	trp	35	*Tuberosa*	2x
S. tarijense Hawkes	tar	48	*Yungasensa*	2x (2EBN)
S. tarnii Hawkes and Hjert.	trn	8	*Pinnatisecta*	2x
S. taulisense Ochoa	tau	26	*Tuberosa*	2x (2EBN)
S. trifidum Correll	trf	8	*Pinnatisecta*	2x (1EBN)
S. trinitense Ochoa	trt	25	*Tuberosa*	2x (1EBN)
S. tundalomense Ochoa	tnd	19	*Conicibaccata*	6x (4EBN)
S. tuquerrense Hawkes	tuq	21	*Piurana*	4x (2EBN)
S. ugentii Hawkes and K.A. Okada	ugt	39	*Tuberosa*	4x
S. urubambae Juz.	uru	36	*Conicibaccata*	2x (2EBN)
S. ×vallis-mexici Juz.	vll	9	*Longipedicellata*	3x
S. velardei Ochoa	vlr	23	*Tuberosa*	2x
S. venturii Hawkes and Hjert.	vnt	60	*Tuberosa*	2x (2EBN)
S. vernei Bitter and Wittm.	vrn	52	*Tuberosa*	2x (2EBN)
S. verrucosum Schltdl.	ver	10	*Tuberosa*	2x (2EBN)
S. vidaurrei Cárdenas	vid	47	*Tuberosa*	2x (2EBN)
S. ×viirsoii K.A. Okada and A.M. Clausen	vrs	58	*Acaulia*	3x
S. violaceimarmoratum Bitter	vio	42	*Conicibaccata*	2x (2EBN)
S. virgultorum (Bitter) Cárdenas and Hawkes	vrg	41	*Tuberosa*	2x
S. wightianum Rydb.[6]	wgt	11	*Longipedicellata*	4x (2EBN)
S. wittmackii Bitter	wtm	24	*Tuberosa*	2x (1EBN)
S. woodsonii Correll	wds	16	*Conicibaccata*	
S. yamobambense Ochoa	ymb	25	*Piurana*	2x
S. yungasense Hawkes	yun	49	*Yungasensa*	2x (2EBN)

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[1] Source: Spooner and Hijmans (2001, Table 4). That table also includes infraspecific taxa, hypotheses of hybrid origins, and references for ploidy and EBN.

[2] The series membership is from Hawkes (1990), but including subsequent changes for Peruvian species by Ochoa (1999). See Table 2 for series authors.

[3] Only *S. acaule* subsp. *palmirense* J. Kardolus is 6x.

[4] Source: Ochoa, 1991.

[5] Spooner and Hijmans (2001) also included 3x but the accession for which this was determined was later reidentified as S. ×*neoweberbaueri.*

[6] *Solanum wightianum* Rydb. is the proper substitute of the invalid name *S. polytrichon* Rydb. (Nee, 1999).

treatments of potatoes are the rule (Spooner and Van den Berg, 1992a). Ongoing research is continuing to refine the taxonomy of wild potatoes the latest figure of 196 wild species will surely be reduced with future studies. For example, Spooner et al. (2001b) suggest a need to reduce species in ser. *Longipedicellata*, and Van den Berg et al. (1998) and Miller and Spooner (1999) suggest reducing species in the *Solanum brevicaule* complex, but no formal taxonomic decisions have yet been made on these groups.

Many regional taxonomic treatments provide distribution maps of wild and cultivated species, species illustrations, data on crossing relationships, phylogenetic hypotheses, or nomenclature. These include treatments on Bolivia (Hawkes and Hjerting, 1989; Ochoa, 1990), Costa Rica (Spooner et al., 2001a), Guatemala (Spooner et al., 1998), Jalisco State, Mexico (Rodríguez and Vargas, 1994), Peru (Ochoa, 1999), sect. *Etuberosum*, occurring in Argentina and Chile (Contreras and Spooner, 1999), and series *Conicibaccata* for Mexico and Central America (Spooner et al., 2001c).

Ingroup and outgroup relationships

Potatoes belong to the large family Solanaceae (commonly known as the potato or nightshade family), of nearly worldwide distribution. Within this family, D'Arcy (1991) recognized 96 genera and 2300 species; Judd et al. (1999) 147 genera and 2930 species; and Hunziker (2001) 92 genera and 2300 species. Apart from potatoes, the Solanaceae contains several other economically important plants, including the eggplant, sweet and chilli peppers (*Capsicum* spp.), petunia, tobacco, and tomato; and lesser-known tropical fruits such as lulo (or naranjillo, *S. quitoense*), pepino (*S. muricatum*) and tree tomato (*Cyphomandra betacea*). Potatoes belong to the genus *Solanum*. The approximately 1100–1250 species of *Solanum* have been subdivided into sections, subsections, superseries, and series (D'Arcy, 1972; Nee, 1999; Hunziker, 2001).

Relationships of potato to its close relatives (outgroup relationships), and within the potato group (ingroup relationships) have always been controversial. Hawkes (1990) divided sect. *Petota* into subsection *Potatoe* Hawkes, with 19 tuber-bearing series, and subsection *Estolonifera* Hawkes with two non-tuber-bearing series: *Etuberosa* Juz. (containing *S. etuberosum*, *S. fernandezianum*, *S. palustre*) and *Juglandifolia* (Rydb.) Hawkes (containing *S. juglandifolium* Dunal, *S. lycopersicoides* Dunal, *S. ochranthum* Dunal, *S. sitiens* I.M. Johnst.). He considered the close relatives of sect. *Petota* to be members of *Solanum* sect. *Basarthrum* (Bitter) Bitter.

Spooner et al. (1993) used chloroplast DNA (cpDNA) restriction site data and morphological data to reinvestigate the relationships of all of these groups, along with the tomatoes (genus *Lycopersicon*), farther outgroups in *Solanum*, and other genera of the Solanaceae. Their results confirmed placement of all members of Hawkes' (1990) tuber-bearing species into sect. *Petota*, but the members of series *Etuberosa* and series *Juglandifolia* did not belong to sect. *Petota* and were supported as outgroups. Subsequent molecular studies are corroborating these outgroup relationships (Olmstead and Palmer, 1992, 1997; Bohs and Olmstead, 1997, 1999; Peralta and Spooner, 2001), and they will likely remain stable. Tomatoes are the sister taxon (the most closely related outgroup) of potatoes and are placed in the genus *Solanum* by taxonomists following a classification philosophy based on evolutionary relationships, or in the genus *Lycopersicon* by taxonomists following other classification philosophies (Spooner et al., in press).

Ingroup relationships remain controversial. The scheme of 19 tuber-bearing series of Hawkes (1990) is the latest comprehensive and widely used formal taxonomic treatment of ingroup relationships. Ochoa (1989) additionally described the new series *Simplicissima* to accommodate *S. simplicissimum*, and later he also placed *S. guzmanguense* in this series (Ochoa, 1999), and made additional changes in series membership of Peruvian species (Table 2).

Table 2. Names of series in *Solanum* sect. *Petota*, and number of species in each series.

Series	**Number of Species**
Acaulia Juz.	4
Bulbocastana (Rydb.) Hawkes	2
Circaeifolia Hawkes	2
Commersoniana Bukasov	2
Conicibaccata Bitter	38
Cuneoalata Hawkes	4
Demissa Bukasov	8
Ingifolia Ochoa	3
Lignicaulia Hawkes	1
Longipedicellata Bukasov	7
Maglia Bitter	1
Megistacroloba Cárdenas and Hawkes	7
Morelliformia Hawkes	1
Olmosiana Ochoa	1
Pinnatisecta (Rydb.) Hawkes	11
Piurana Hawkes	13
Polyadenia Bukasov ex Correll	2
Simplicissima Ochoa	2
Tuberosa (Rydb.) Hawkes	81
Yungasensa Correll	6

These 20 series are often poorly supported by molecular studies. Hosaka et al. (1984) provided the first molecular phylogenetic study of sect. *Petota* with chloroplast DNA restriction site data, and the series were little supported. Subsequent studies using cpDNA restriction site data (Spooner and Sytsma, 1992; Spooner and Castillo, 1997), nuclear restriction fragment length polymorphisms (nRFLP) (Bonierbale et al., 1990; Debener et al., 1990), and amplified fragment length polymorphisms (AFLP) (Kardolus, 1998) also failed to provide good support for series.

The most comprehensive phylogenetic studies to date regarding species coverage are the ones of Spooner and Sytsma (1992) and Spooner and Castillo (1997), who used chloroplast DNA restriction site data. These support only four clades, not 20 series. These four clades are: 1) the diploid species from the USA, Mexico, and Central America, exclusive of *S. bulbocastanum*, *S. cardiophyllum*, and *S. verrucosum*, 2) *S. bulbocastanum* and *S. cardiophyllum*, 3) all examined members of the South American series *Piurana* and some South American species classified in other series, and 4) all remaining South American species, and the polyploid species of the USA, Mexico, and Central America, and *S. verrucosum*. These results provide partial support for ideas of Hawkes (1990) and Hawkes and Jackson (1992) that the most primitive wild potatoes are Mexican and Central American diploid species with white stellate corollas (Figure 3A). These phylogenetic results are not definitive and await corroborative data from additional molecular markers. Clearly, however, the current series will be modified in the future.

Cultivated species

Cultivated species are not included in this atlas, but we mention them here to place them in the context of sect. *Petota*. Cultivated potatoes have been treated taxonomically in very different ways. For example, the Russian potato taxonomists Bukasov (1971) and Lechnovich (1971) recognized 21 cultivated species, Hawkes (1990) seven species with eight subspecies, and Ochoa (1990, 1999) nine species and 141 subspecies, varieties, and forms (including his unlisted autonyms) for the Bolivian cultivated species alone.

The above treatments classified the cultivated potatoes according to the taxonomic standards of the International Code of Botanical Nomenclature (ICBN; Greuter et al., 2000). Dodds (1962), in contrast, treated cultivated potatoes using the standards of the International Code of Nomenclature of Cultivated Plants (ICNCP; the latest version is Trehane et al., 1995). He recognized only three cultivated species with five ‘groups’ in one of them, *S. tuberosum*. Huamán and Spooner (in press) also used the ICNCP to recognize only a single cultivated species, *S. tuberosum*, with eight ‘cultivar-groups’ for the Andean and Chilean landrace populations (but not the modern varieties grown worldwide, which await further study). See Spooner et al. (in press) for a discussion of the relative merits of the ICBN or ICNCP for taxonomic treatment of the wild and cultivated species.

Complicating factors for a stable potato taxonomy

The goal of a stable taxonomy of wild potatoes is frustrated by introgressive hybridization between different species, hybrid speciation, morphological similarity of species, and phenotypic plasticity (Spooner and Van den Berg, 1992a). The problem of phenotypic plasticity was shown very effectively by Correll (1962) who illustrated three quite different morphological variants of the hexaploid wild species *Solanum demissum*, one collected from the field in Mexico, one grown from tubers of this collection in a greenhouse in Maryland, USA, and the third grown from tubers of the Maryland collection in a field plot in Wisconsin, USA.

Perhaps the greatest difficulty, however, is caused by introgression and hybridization. Many of the species at the same ploidy and EBN level, even some morphologically very distinct ones, can freely cross to form fertile hybrids, at least in early generations (Hawkes, 1958; Ugent, 1970). Approximately 13% (26) of the 196 tuber-bearing *Solanum* species have been hypothesized to have arisen by hybrid speciation (Table 1). In addition, hybridization not leading to widespread introgression or speciation is believed to be common (Hawkes and Hjerting, 1969, 1989). Recent molecular studies are supporting some hypotheses of introgressive hybridization or hybrid speciation (e.g., Rabinowitz et al., 1990; Clausen and Spooner, 1998), but others do not (e.g., Spooner et al., 1991; Miller and Spooner, 1996).

The extent and effect of hybridization and introgression in wild potatoes is still an open question that affects classification philosophies and practices. For example, Ugent (1970) postulated extensive gene flow within and between ploidy levels of cultigens and wild species (the crop-weed-complex concept, e.g., Harlan, 1992). Under this concept, extensive gene flow is thought to greatly homogenize cultigens and wild species at all ploidy levels to make division into species impractical.

Perhaps the most striking example of problematic species definition is the group of approximately 30 species in the *Solanum brevicaule* complex. They are putative progenitors of the indigenous cultivated species, but some could also be escapes from cultivation. The taxonomic difficulties of dealing with this group are dramatically illustrated by the fact that the experienced and careful taxonomists Hawkes and Hjerting (1989) and Ochoa (1990) provided different identifications for identical collection numbers of Bolivian members of the *Solanum brevicaule* complex 36% of the time (Spooner and Van den Berg, 1992a).

Morphological studies of the *Solanum brevicaule* complex by Van den Berg et al. (1998) and nRFLP and RAPD studies of the same accessions by Miller and Spooner (1999) were concordant in suggesting that 1) there were no species-specific morphological characters; 2) any species that may be valid would be distinguished only by using a complex of widely overlapping traits (polythetic morphological support); and 3) there was some support for the definition of two species with a north-south geographical partitioning: one species from Peru and northwestern Bolivia, and another from northwestern Bolivia to northern Argentina.

No formal taxonomic decisions have yet been made in the *Solanum brevicaule* complex, awaiting the results of ongoing replicated morphological studies in a more typical environment in Peru, and additional molecular data. However, if the previous results are confirmed, the number of wild potato species will be further reduced. Similar studies showing a need to reduce the number of wild potato species are Spooner and Van den Berg (1992b) for *S. berthaultii* and *S. tarijense*, Spooner et al. (1995) for the series *Demissa* and Spooner et al. (2001b) for the series *Longipedicellata*.

In addition to difficulty in distinguishing the wild species from each other, it is often difficult to distinguish wild from cultivated species. This is illustrated by taxonomic changes by Ochoa (1992), who reidentified the Venezuelan ‘wild’ species *S. paramonese* as *S. tuberosum* subsp. *andigena*, and by Hawkes (1990), who reidentified the Colombian ‘wild’ species *S. estradae* as the cultivated species

S. *phureja*, and the Peruvian 'wild' species *S*. *apurimacense* as *S*. *tuberosum* subsp. *andigena*. Spooner et al. (1999) encountered Quechua (an indigenous Andean language) terms for potatoes that illustrate well the difficulty of distinguishing wild from cultivated species. Apparent cultivars with large tubers that are weedy and persistent in cultivated fields are referred to by the name 'arakka'. Arakka potatoes are common throughout much of Bolivia and Peru. This is contrasted with 'siwwa' or 'sihua' potatoes, Quechua names of apparent cultivars that have escaped and persist naturally outside cultivated fields. There is another Quechua name, 'quita papa', for wild potatoes, not cultigens. Often, the only feature useful to distinguish cultivated from wild potatoes are large tubers, short stolons, and the fact that they are cultivated.

Breeding barriers

Not all wild potato species can cross with each other and produce fertile offspring. The degree to which two species are interfertile must be tested experimentally but can be predicted to a great extent from their ploidy and Endosperm Balance Number (EBN). These are of interest for taxonomic and phylogenetic considerations, but are also of practical importance for breeders.

Ploidy refers to the number of chromosome sets present, and the lowest number of sets is 2, referred to as diploid or 2x. Potatoes have 12 distinct chromosomes so diploid potatoes have 12 x 2 = 24 chromosomes. The ploidy level of 14 of the 196 wild potatoes is not known (Table 1), leaving 182 with known ploidy. Of these, 139 are diploid, and six of these diploids have additional triploid populations with 36 chromosomes (3x). Seven species are exclusively triploid, 22 exclusively tetraploid (48 chromosomes, 4x), one exclusively pentaploid (60 chromosomes, 5x), and 12 exclusively hexaploid (72 chromosomes, 6x). Three species have populations with more than one even ploidy level (*S. acaule* 4x, 6x; *S. leptophyes* 2x, 4x; *S. oplocense* 2x, 4x, 6x). The triploid and pentaploid populations are generally highly sterile. They are less likely to be discovered as most germplasm collecting expeditions collect seed rather than tubers because tubers contain less genetic diversity and more diseases. It is likely, therefore, that the number of species with additional triploid or pentaploid populations is greater than currently known.

The EBN system forms a strong isolating mechanism in sect. *Petota*. The EBN hypothesis was first published by Johnston et al. (1980) to explain success or failure of intra- and interspecific crosses, due to the functioning or breakdown of the endosperm after fertilization. The EBNs are hypothetical genetic factors independent of ploidy and empirically determined relative to other EBNs. They are based on crossability with standard EBN test crossers or other species of known EBN, and are published with the actual ploidy of the species. In potato, these are 2x (1EBN), 2x (2EBN), 4x (2EBN), 4x (4EBN), and 6x (4EBN). Table 1 provides all currently known ploidy and EBN numbers. Differences in EBN are important barriers in nature, but ploidy manipulations to bridge EBN barriers, and general lack of strong crossability barriers within species sharing EBN, have allowed relatively easy access of these wild species by breeding programmes (Hermundstad and Peloquin, 1985; Peloquin et al., 1989).

4. DATA AND SOFTWARE

Collecting expeditions

Most of the data used in the remainder of this atlas are derived from databases of wild potato collection expeditions. Collection of live samples (typically seeds or tubers) to contribute to potato breeding programmes started in the 19th century when Mexican wild potatoes were collected for use as a source of resistance against *Phytophthora infestans*, the pathogen that had caused the Irish potato famine (Hawkes, 1994). The first large-scale germplasm collections of potatoes were by the Russian workers Bukasov, Juzepczuk, and Kameraz, who collected in Mexico, Central America, and South America in the 1920s and 1930s. There were major British expeditions to Mexico and South America in the 1930s, conducted by Balls, Balls, and Hawkes. Hawkes later collected in many more countries. It is impossible to mention all other later collectors of wild potatoes, but significant collectors in addition to those mentioned above are Ochoa and Salas for South America, Okada for Argentina, and Tarn and colleagues for Mexico. Summaries of collectors and their expeditions can be found in Correll (1962), Hawkes and Hjerting (1969, 1989), Huamán (1986), Ochoa (1990, 1999), Bamberg et al. (1996), Hawkes (1997), Huamán et al. (1997), and Spooner and Hijmans (2001). The availability of germplasm of these collections is detailed in Kehoe (1986), Hoekstra and Seidewitz (1987), Spooner and Bamberg (1994), Wilkinson et al. (1994), Bamberg et al. (1996), Angeli et al. (2000a,b), and Huamán et al. (2000).

Data sources

In the following chapters we employ a large database of localities where wild potatoes were observed (whether collected or not). This database is a slightly updated version of the one used by Hijmans and Spooner (2001). Some new records were added and some existing records with erroneous coordinates or species identifications were corrected or deleted.

Most records were taken from genebank databases. Genebank databases typically have four types of data: passport (taxonomic name, collector and collector number, place of collection), management (where and how germplasm collections are maintained), characterization (morphological descriptors) and evaluation (presence of useful traits such as resistance). Passport data include a description of the sites where accessions were collected, both as a narrative and as geographic coordinates. Through these geographic coordinates, genebank data can be incorporated into GIS and used to map the localities as well as the distribution of variables (e.g. species, flower colour, heat tolerance) associated with the accessions/localities.

The following sources were used:

1) The Inter-genebank Potato Database, which has data from seven genebanks in the USA, Peru, The Netherlands, Germany, Argentina, the UK, and Russia (in order of size of contribution) (Huamán et al., 2000).
2) Data from 16 collecting expeditions in 12 countries by D.M. Spooner and co-workers (Spooner and Hijmans, 2001). These include records of accessions that

are not in genebanks because they were collected as herbarium species or were lost as living specimens after collection.

3) A database of herbarium records developed by J.G. Hawkes (Hawkes, 1997).
4) Hawkes and Hjerting (1969); Argentina, Brazil, Paraguay and Uruguay.
5) Hawkes and Hjerting (1989); Bolivia.
6) Ochoa (1990); Bolivia.
7) Ochoa (1999); Peru.
8) Spooner et al. (1998); Guatemala.
9) Spooner et al. (1999); Peru.
10) Spooner et al. (2001a); Costa Rica.
11) Spooner et al. (2001c); Mexico.

We used all records from sources 1–3 that included a species name and passport data. Geographic coordinate data were absent for many records. For the genebank databases, coordinates were assigned using the locality description where possible. For Hawkes' (1997) database, this was only attempted for species for which there were fewer than five observations with coordinate data. Sources 5–7 were used to verify and improve the geographic coverage of the species distribution data. Additional herbarium records were taken from sources 8–11.

Data quality

Coordinate data in genebank databases often lack precision, and were checked and sometimes modified following procedures described by Hijmans et al. (1999). First, we checked for gross errors, such as accessions located in the oceans. Then, we made overlays (simultaneous spatial queries) of the collection sites and administrative boundary databases (first level subdivision for Mexico and Central America; first and second levels for the United States and South America; and first, second and third levels for Peru). We compared the names of the administrative units according to the wild potato distribution database with those of the administrative boundary database. In case of discrepancies between the two databases, the coordinates were checked against the locality description and new coordinates were assigned where needed.

Dot maps of the distribution of all species were compared with published species distribution maps from the floristic sources 5–7. When general areas of occurrence were already represented on our maps, we did not include additional points, because of a possible lack of precision of many of these maps, and the risk of duplicating records. However, if it appeared that our distribution maps did not include all major areas where a species was reported to occur, we did include additional observations for these areas.

Making these maps with all separate species was also useful in spotting errors in the taxonomic labels of the collections. With so many taxa and taxonomic changes, there are bound to be some labelling errors in this database. Some of these errors were easy to spot because they were outliers. If, after consultation of the herbarium specimen or the literature, the labels of these outliers were considered incorrect, they were relabelled were possible, or were removed. Less conspicuous labelling errors may still be present, but fortunately these are also less likely to have a strong effect on the results presented here.

In some cases wild potato species are known from only one site whereas our maps indicated that they are from more (nearby) sites. We have only corrected this in a few extreme cases, where points were very far apart. Given the precision of the coordinate data and our mapping approach, there are likely to be a number of cases where the same site is represented by more than one nearby dot, but where it is often impossible to know which of these dots is correct. An alternative would have been to use grid based distribution maps in which nearby observations, that in fact represent the same location, would likely fall in the same grid.

Information quality

Plant distribution data are sometimes collected by systematic sampling of a fixed number of populations for a given area. This method yields representative samples that allow, for example, comparison of diversity indices (typically a measure of the number of species and their relative abundances) for these different areas. Unfortunately, this type of ideal data rarely exists for large areas. This is because databases are often assembled from different sources and, in the case of germplasm databases, because collecting was not aimed at geographic representativeness per se, but rather at maximizing diversity. Obtaining a large and representative sample is limited by time and other practical limitations, particularly for expeditions in vast, rugged areas like the Andes with few roads. Wide coverage of such areas precludes roaming far from main roads. Therefore, in practice, explorers cannot sample randomly, particularly for narrowly endemic species.

Due to these spatial differences in recorder (a person who takes data) effort (Rich and Woodruff, 1992; Prendergast et al., 1993; Gaston, 1996; Hijmans et al., 2000), data on plant distributions are typically biased. In extreme cases, differences in the number of species between areas would reflect the amount of time spent there by recorders, and not actual differences in distribution.

Hijmans et al. (2000) evaluated the representativeness of a collection of wild potatoes from Bolivia, and defined and assessed four types of biases: *species, species-area*, *hotspot*, and *infrastructure*. Species bias is the sampling of some species more often than others. Species-area bias is defined as sampling that is disproportionate to the total area in which a species is found. A species bias can arise when a species is more widespread and/or abundant than others. But it can also arise when collectors have a preference for a particular species or when a species is common in easily accessible areas such as roadsides, and is therefore more likely to be spotted and collected. The latter would likely also lead to a species-area bias, when a species is collected more often given its range size as compared to other species.

On the other hand, collection expeditions are sometimes justified by the absence of certain species in genebanks (e.g., Spooner et al. 1999), and much effort may be expended to obtain samples of these species, which may be difficult to collect. Although such strategies may decrease the species bias, they may at the same time increase the species-area bias. If a species-area bias is a reflection of the actual abundance of the different species, this is in fact a desired situation from a geographic analysis perspective. However, this may decrease the overall diversity of the collection, which is not desirable from the perspective of the curator of a collection.

Hotspot bias is the disproportionate sampling of areas with high levels of diversity. This would occur when collectors tend to collect in areas where previous expedition reports indicate the presence of many taxa. A problem in assessing this type of bias is that it is not known if and how many unsuccessful attempts were made to collect wild potatoes in areas of low diversity, and the bias might not reflect differences in effort, but in actual abundance. Locations where there was considerable and unsuccessful searching effort for a particular group of plants are not recorded in genebank databases. Few collectors systematically include observations on the absence of certain species in given areas in their records. It would be useful if collectors would develop a more systematic approach to documentation that includes absence/presence and abundance data for all sites they explore, whether germplasm was collected or not.

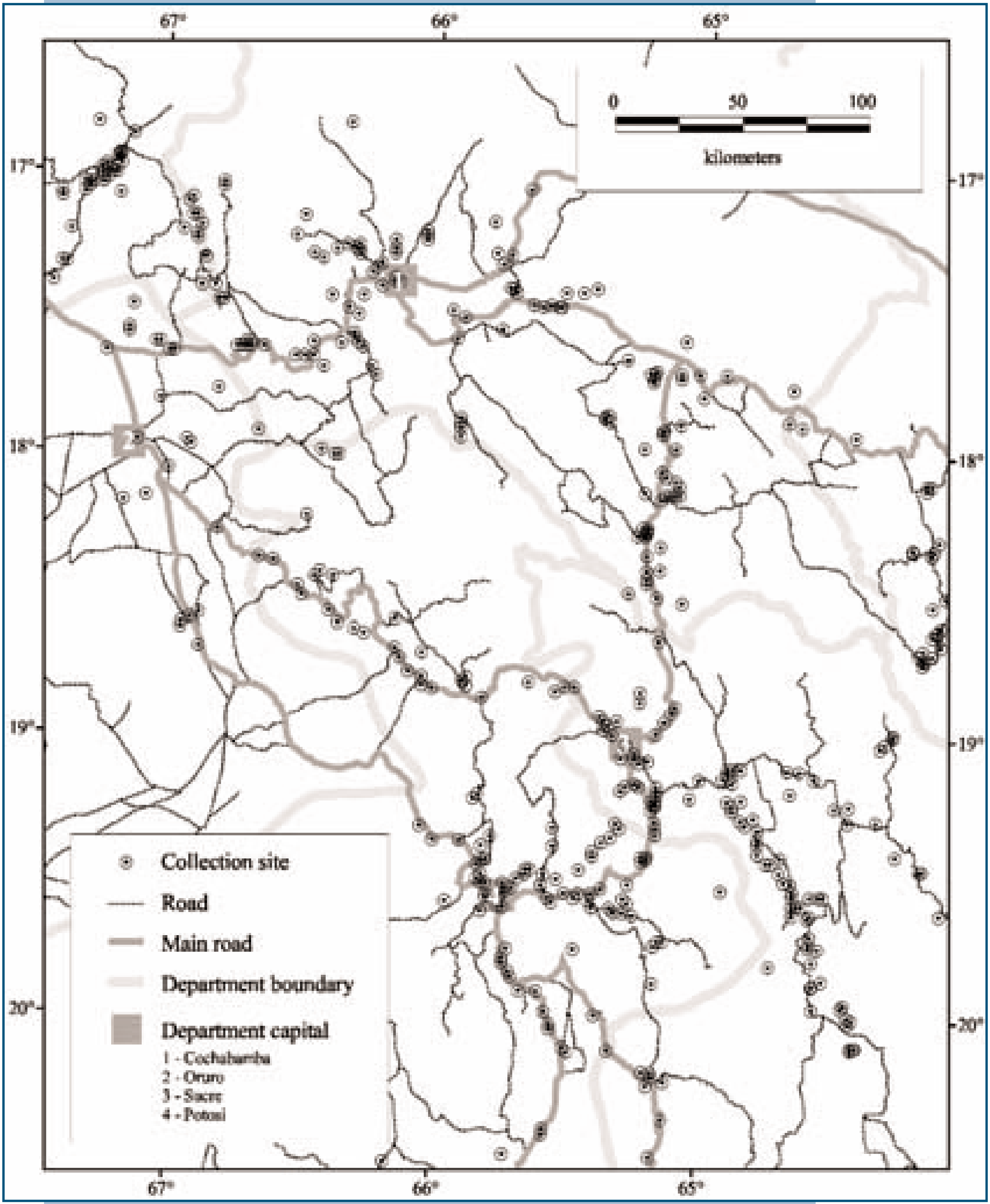
Because our data were gathered from several sources this may have led to the presence of some duplicate collections made at the same locality. Particularly type localities of rare species were visited by different expeditions, as these species may not be found elsewhere. Overall, however, it may make our data more reliable given the timing dependency of the results of wild potato exploration: there are differences within and among years in the likelihood of finding certain species in certain locations.

Some of our records are recent, but many date back many years. In some cases, the habitat in which the species occurred has now disappeared. For example, Spooner et al. (1998) describe a rapid rate of loss of wild potato habitat in upland forests in Guatemala. However, our recent experience in Peru, and elsewhere, indicates that populations often persist for many years. For example, Spooner et al. (1999) and Salas et al. (2001) collected many wild potato species in Peru in the exact location, often at the type locality, where they had been collected many years before. In some cases, it was not possible to collect at documented localities, but this was often attributed to phenology, as wild potatoes often have a short growing period. In other cases, incomplete locality data hindered collections.

Infrastructure bias is the disproportionate sampling of areas near roads and towns. In the case of the Bolivian wild potato collection (Map 1; Figure 7), the infrastructure bias was strong: 60% of all wild potato accessions were collected within 2 km of a road, the expected value, if collections had been made randomly, and assuming a random distribution of wild potatoes over the landscape, was 22%. An example of a road bias in the data for a specific species is our data for *S. yungasense*, which is known from three areas (Map 1), in Puno department in Peru and from La Paz and Cochabamba departments in Bolivia. It is likely that it occurs in the areas in between as well, but there have been no collections there as access to these areas is very difficult.

The fact that wild potatoes have been over-sampled near roads and cities may render the genebank collections less geographically representative, but there may

Map 1. Collecting sites and roads in central Bolivia (source: Hijmans et al., 2000).



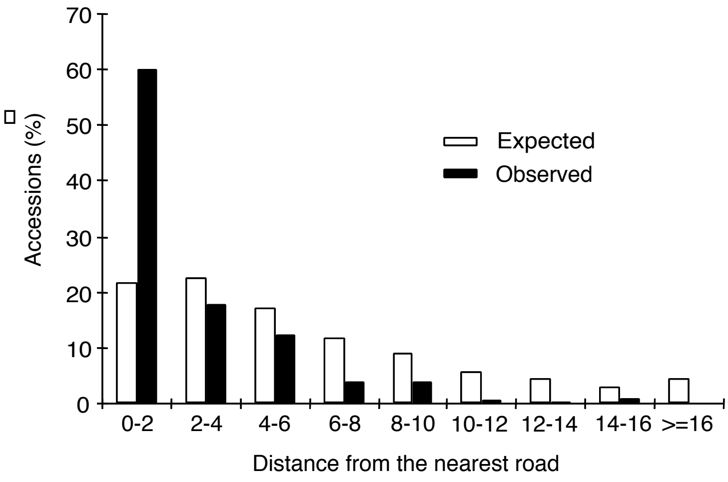


Figure 7. Expected and observed distance from the road of locations where wild potatoes were observed in central Bolivia (source: Hijmans et al., 2000).

be a positive side to this. Genetic erosion is often due to increased human activity such as building and agriculture, which mostly occurs near roads and cities. Therefore, it may be that the infrastructure bias has inadvertently led to a collection bias toward genepools that are most endangered. However, the opposite might also be true: infrastructure bias may have favoured collection of common weedy species that tend to grow near roads. For these species, an apparent infrastructure bias would be expected even if collections were made randomly throughout an area. Other species may be reduced near roads and cities because of land-use patterns such as grazing. For these species, an infrastructure bias would lead to under-collecting.

Assessing the presence of these biases, however, can help in understanding the information quality of the data. Decision on how much deviation from the expected is needed to consider a bias important is a matter of judgment, based on how the information will be used. If there is evidence for an infrastructure bias, care should be taken that species diversity maps that are derived from these data are not strongly influenced by this bias. This can be done by using large grid cells ('averaging over areas with and without roads'), or by using spatial extrapolation techniques (e.g., Jones et al., 1997; Skov, 2000). Some biases are inevitable; in normal cases, with some species more abundant than others, a dataset will have either a species or a species-area bias, and in most cases it will have both. Neither bias is thus necessarily a bad thing, depending on how the data will be used.

Software

We used ArcInfo, ArcView, and DIVA-GIS to analyse and visualize the data. ArcInfo and ArcView are generic GIS programmes of the Environmental Systems Research Institute (ESRI, Redlands, CA, USA). ArcInfo was used for some more complex operations (projecting grids; calculation of circular areas). ArcView was used for a number of operations, including data map projection, extracting altitude data, and final map production. All coordinate data were transformed to the Lambert equal-area azimuthal projection, with 80°W as the central meridian and the equator as the reference latitude.

The DIVA-GIS software is a free programme specifically aimed at the analysis of biodiversity data (Hijmans et al., 2001). It was used for mapping of species and series richness, to calculate a species distribution statistic, and to extract climate data for collecting sites.

5. DISTRIBUTION MAPS

Methods

This chapter contains distribution maps of all 196 currently accepted wild potato species (Table 1), and of the 20 wild potato series. Maps of the three species in sect. *Etuberosum* are also provided because these species are closely related to potato, are useful for potato breeding, and are maintained in potato genebanks.

Map 2 shows where wild potatoes grow. This single map of the whole region was not to depict species distributions because that would not have allowed for good detail. At the same time, many different maps of small and different areas would complicate comparison of the distributions. As a compromise, we used seven base maps of different areas that partly overlap. For example, parts of Peru and Bolivia can be found on three maps. In most cases we used the largest scale map (i.e., the map with the smallest area, or highest resolution) possible to map the distribution of a species. Thus a species that only occurs in southern Peru can be found on a map of Peru, and not on one for the Southern Andes. Only the map for *S. acaule* (Map 45) is different from its base map; it covers a larger area to accommodate all points.

In addition to the species distribution maps we also made distribution maps for series. As most taxonomic series cover a large area, these were all mapped on a single base map for the whole region.

There are species distribution maps for the following areas (from North to South):

1) Guatemala, Mexico and USA; Maps 4–13.
2) Central America (Costa Rica, Guatemala, Honduras, and Panama); Maps 15–16.
3) Northern Andes (Colombia, Ecuador, and Venezuela); Maps 18–21.
4) Peru; Maps 23–37.
5) Bolivia; Maps 39–43.
6) Southern Andes (Argentina, Bolivia, and Peru); Maps 45–55.
7) Southern cone (Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay); Maps 57–60.

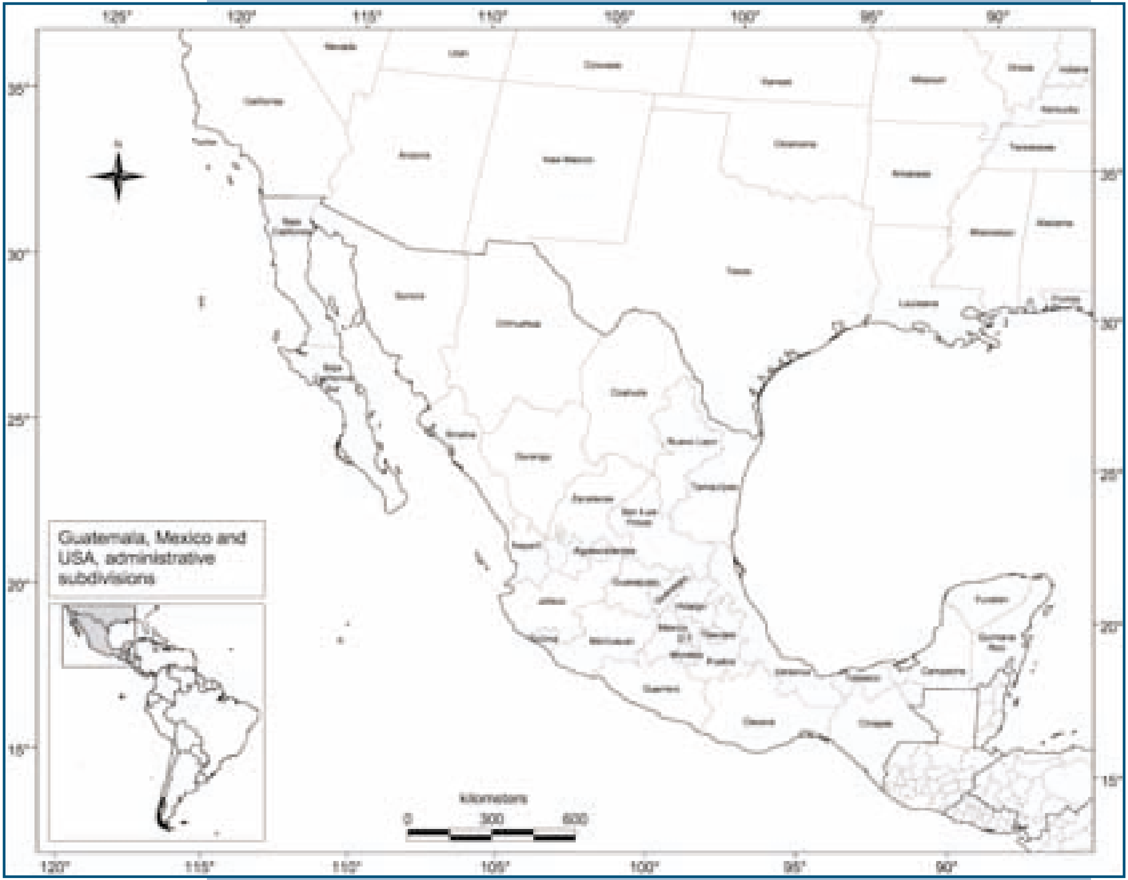
Each map shows the distribution of up to eight species. Putting more than one species on a map could lead to confusion because of overlapping symbols, but we have grouped the species in such a way that this is avoided. When there are overlapping symbols on a map, these are always for one species only, avoiding ambiguity.

All maps show country boundaries and first level internal administrative subdivisions (Departments for Bolivia, Colombia, Guatemala, Honduras, Paraguay, Peru, and Uruguay; Provinces for Argentina, Costa Rica, Ecuador, and Panama; Regions for Chile; and States for Brazil, Mexico, USA, and Venezuela). The names of the first-level administrative subdivisions are shown only on the base maps that precede the species maps.

Map 2. Area of known distribution of wild potatoes (gray shade).

Guatemala, Mexico, and USA

Map 3. First-level administrative subdivisions in Guatemala, Mexico, and the USA.

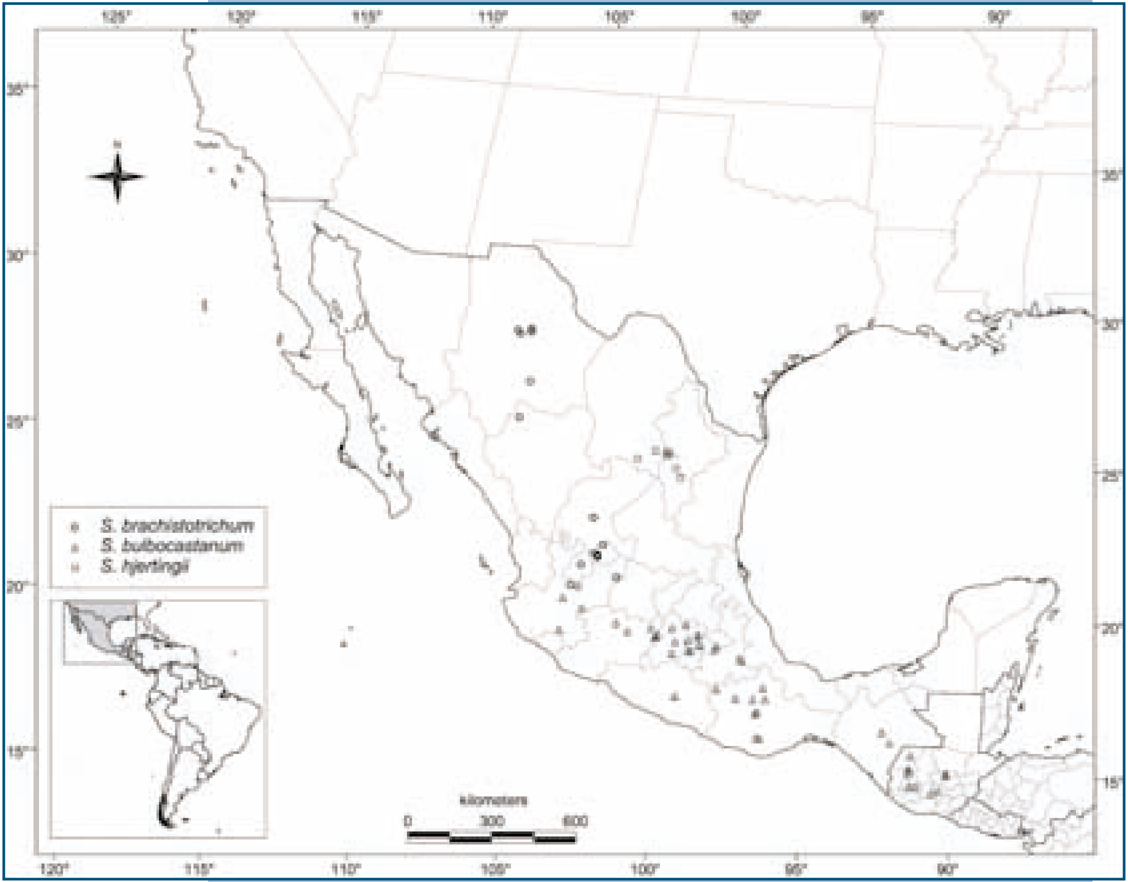


Guatemala, Mexico, and USA

Map 4. Distribution of *S. guerreroense* and *S. stoloniferum.*

Guatemala, Mexico, and USA

Map 5. Distribution of *S. brachistotrichum, S. bulbocastanum,* and *S. hjertingii.*

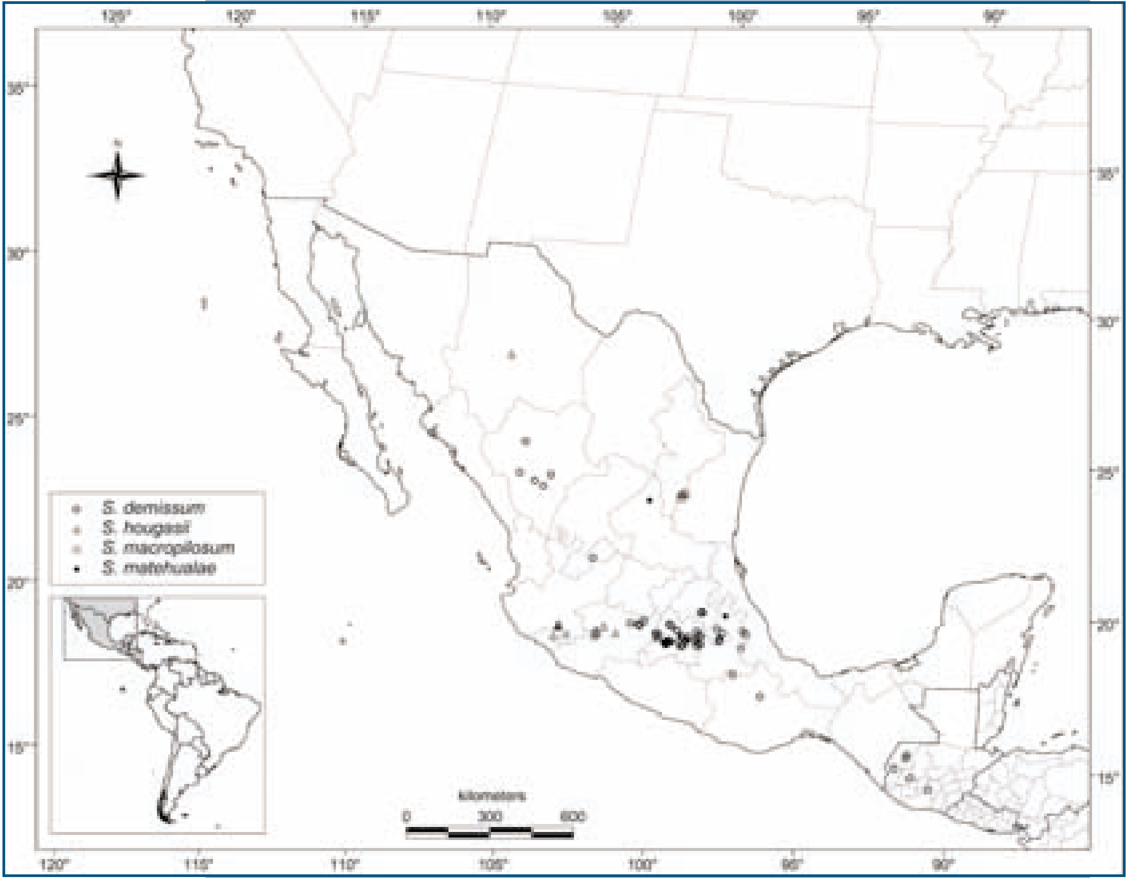


Guatemala, Mexico, and USA

Map 6. Distribution of *S. leptosepalum, S. polyadenium, S. stenophyllidium,* and *S. ×semidemissum.*

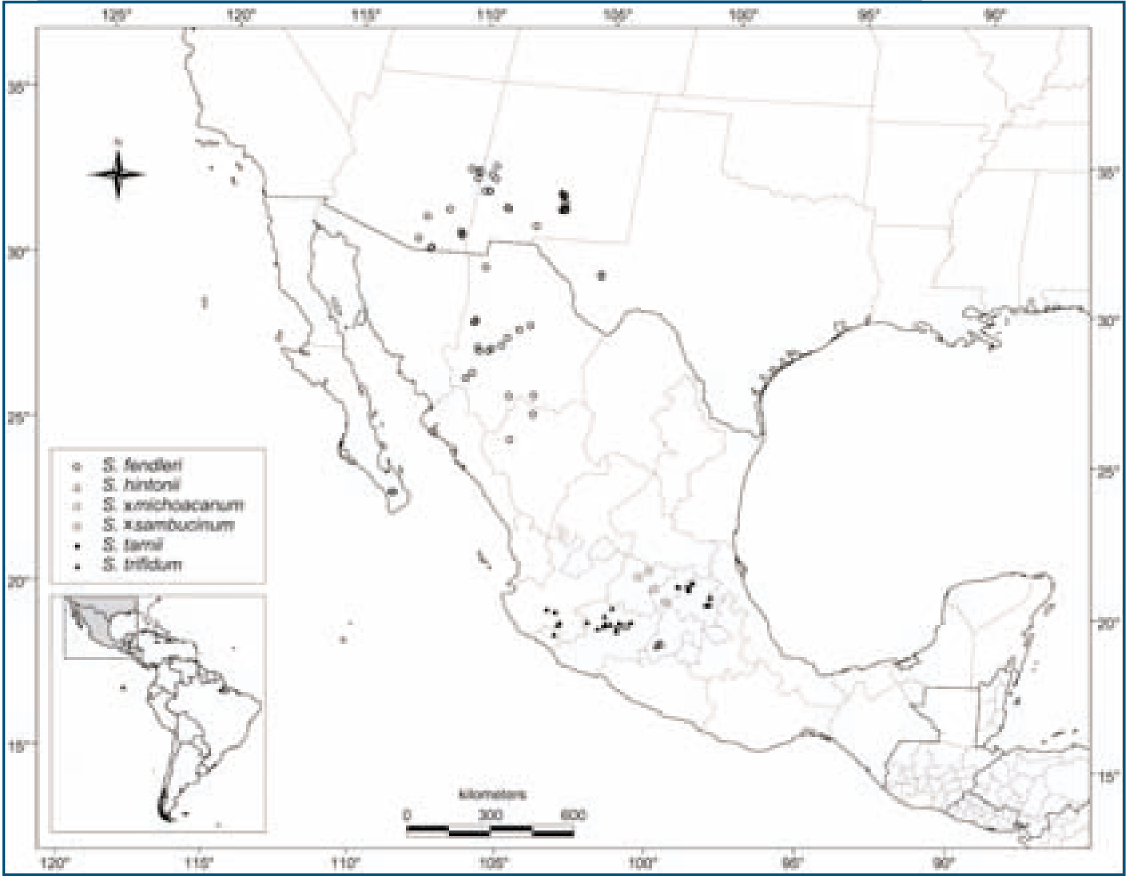
Guatemala, Mexico, and USA

Map 7. Distribution of *S. demissum, S. hougasii, S. macropilosum,* and *S. matehualae.*



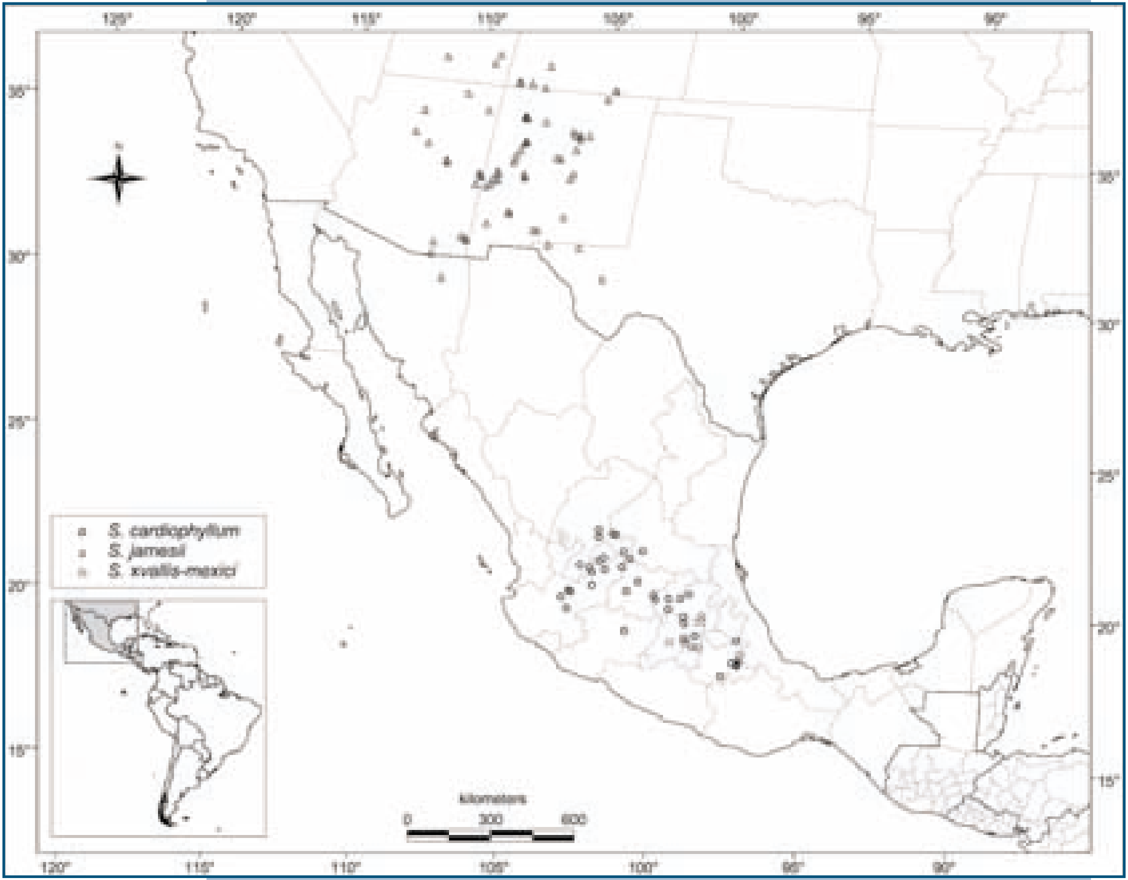
Guatemala, Mexico, and USA

Map 8. Distribution of *S. fendleri, S. hintonii, S. ×michoacanum* , *S. ×sambucinum, S. tarnii,* and *S. trifidum.*



Guatemala, Mexico, and USA

Map 9. Distribution of *S. cardiophyllum, S. jamesii,* and *S. ×vallis-mexici.*

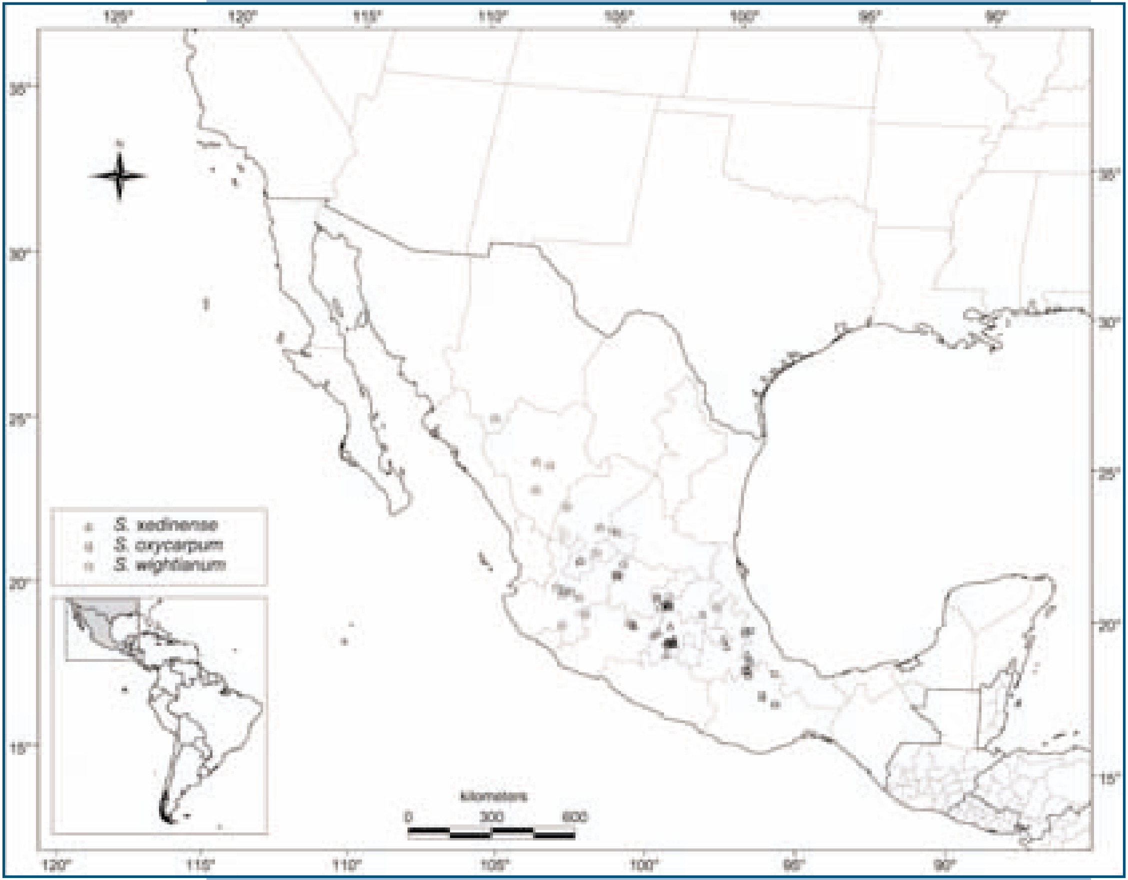


Guatemala, Mexico, and USA

Map 10. Distribution of *S. lesteri*, *S. pinnatisectum*, *S. schenckii*, and *S. verrucosum*.

Guatemala, Mexico, and USA

Map 11. Distribution of *S. ×edinense*, *S. oxycarpum*, and *S. wightianum*.

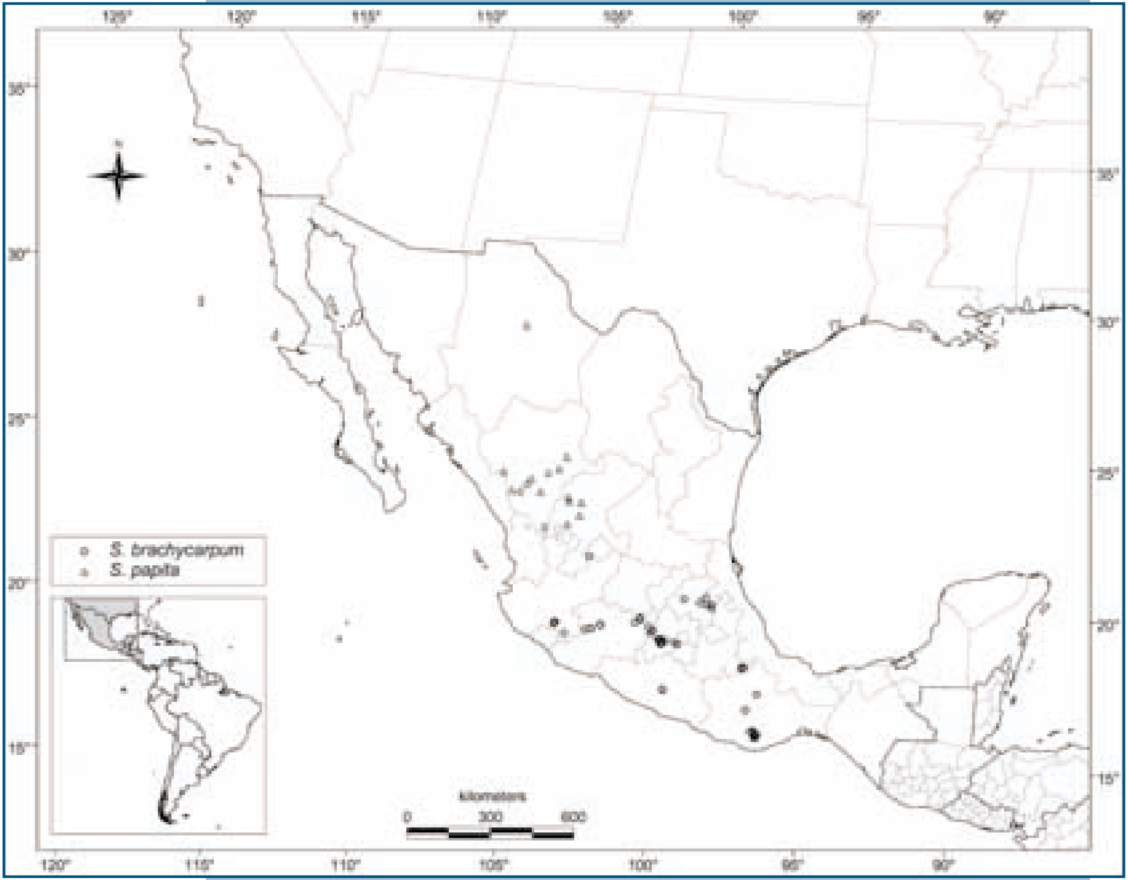


Guatemala, Mexico, and USA

Map 12. Distribution of *S. iopetalum*, *S. morelliforme*, and *S. nayaritense*.

Guatemala, Mexico, and USA

Map 13. Distribution of *S. brachycarpum* and *S. papita*.

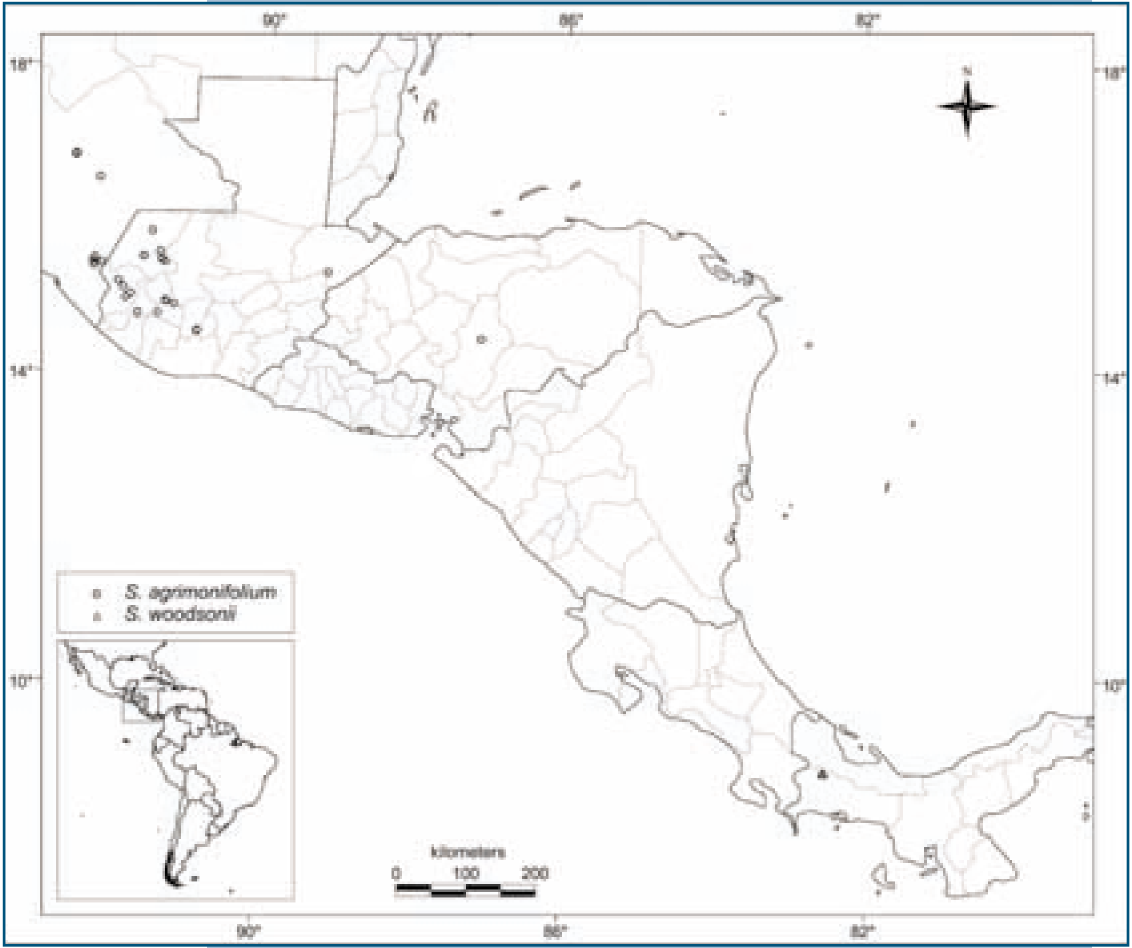


Central America

Map 14. First-level administrative subdivisions in Central America.

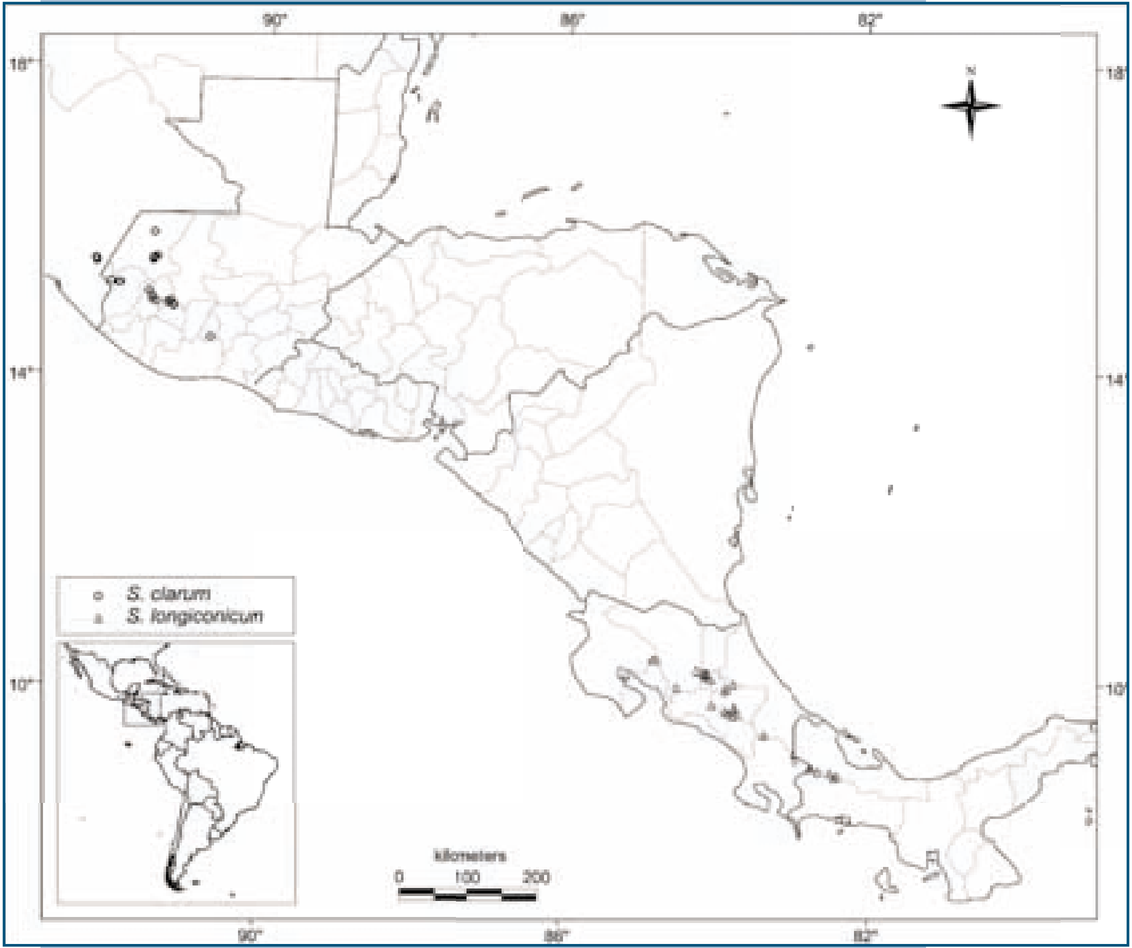
Central America

Map 15. Distribution of *S. agrimonifolium* and *S. woodsonii*.



Central America

Map 16. Distribution of *S. clarum* and *S. longiconicum*.

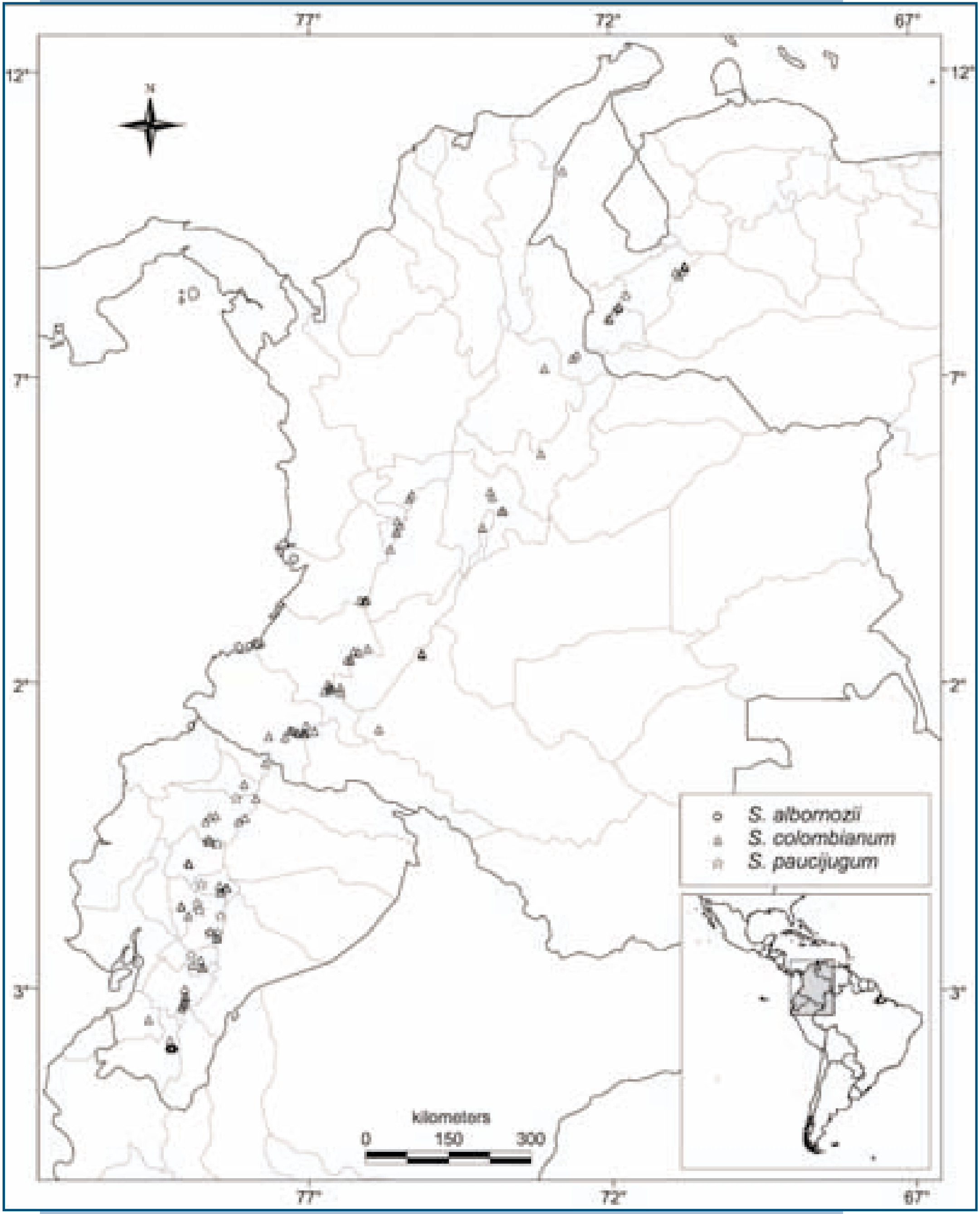


Northern Andes

Map 17. First-level administrative subdivisions in the northern Andes.

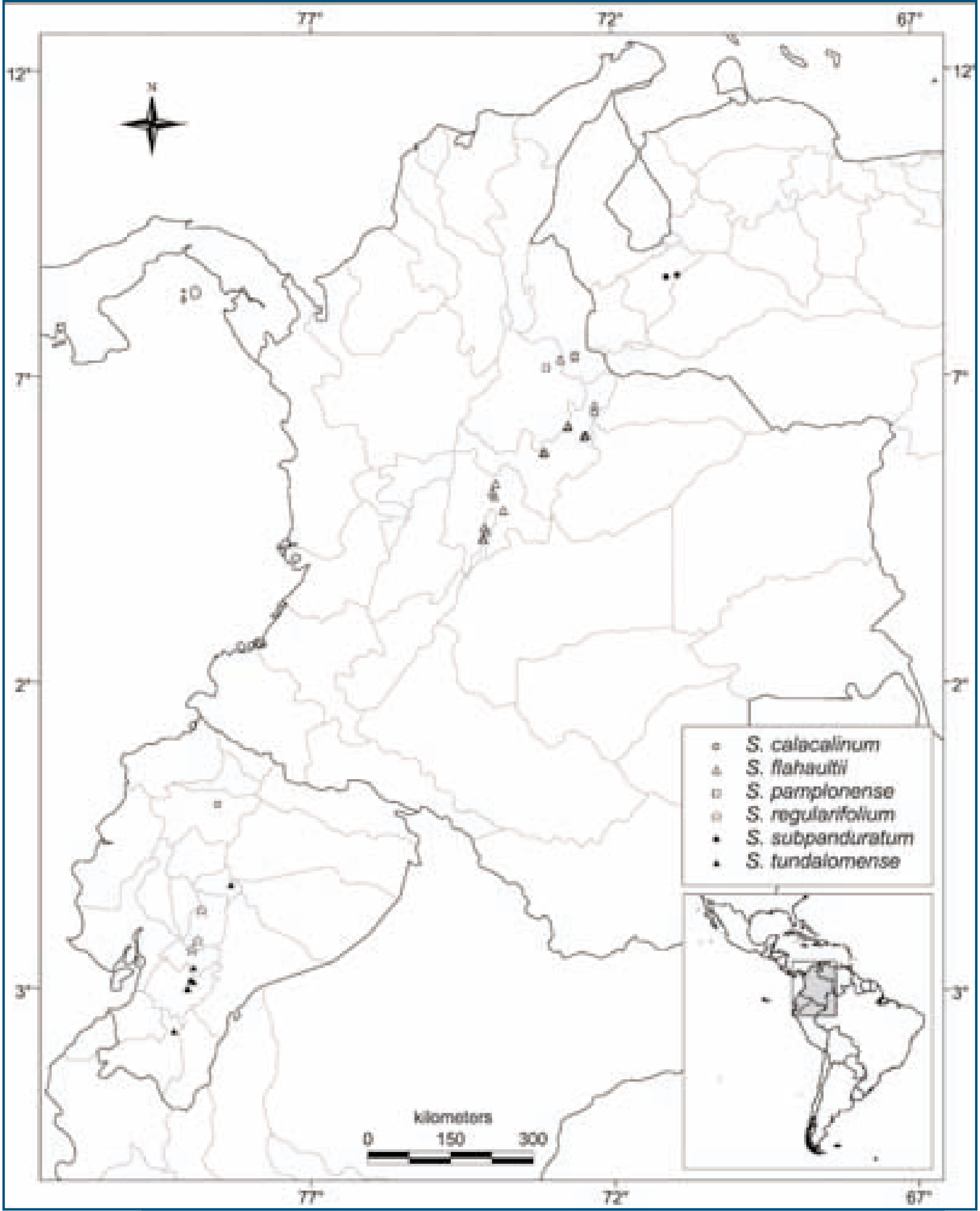
Northern Andes

Map 18. Distribution of *S. albornozii*, *S. colombianum*, and *S. paucijugum.*



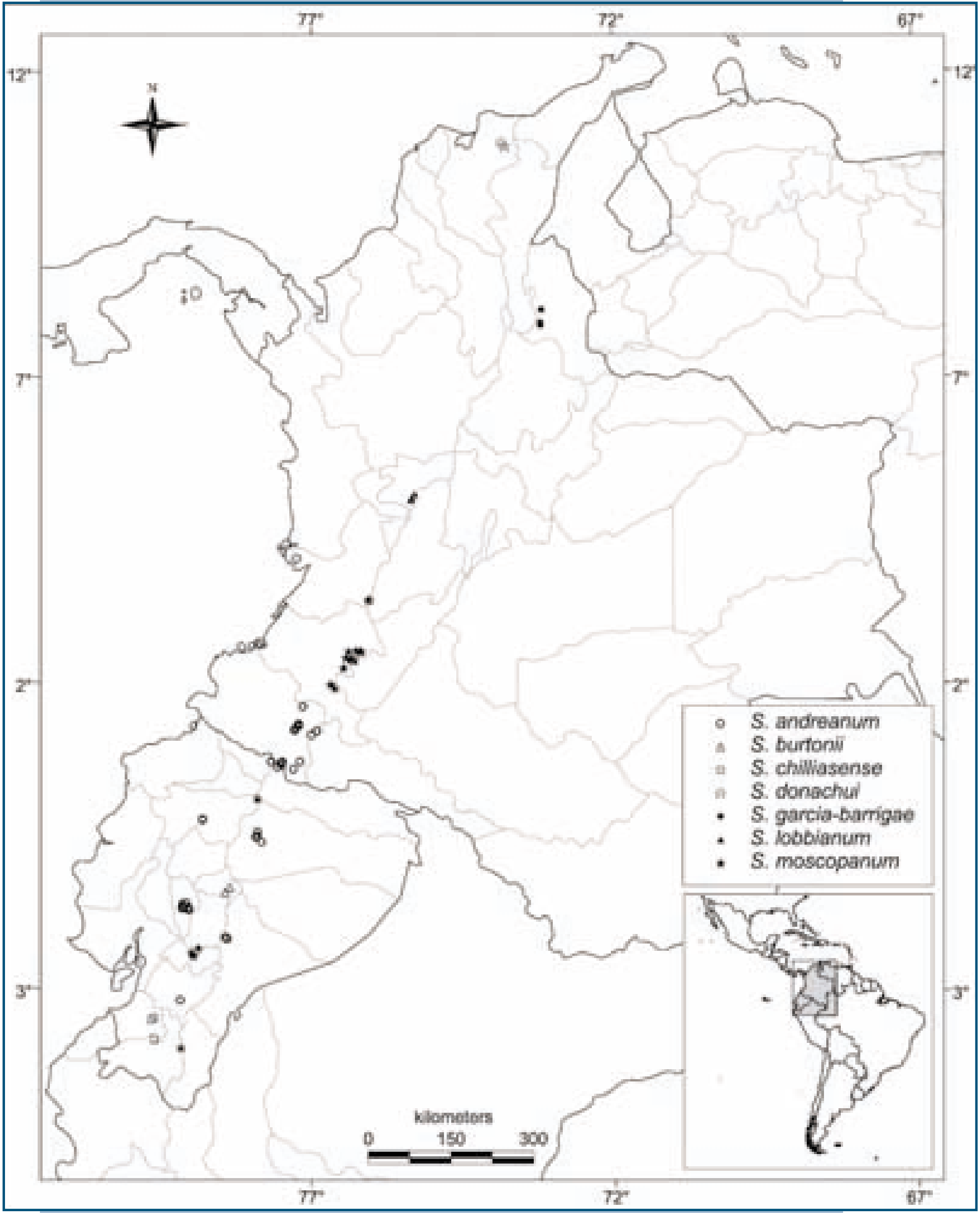
Northern Andes

Map 19. Distribution of *S. calacalinum*, *S. flahaultii*, *S. pamplonense*, *S. regularifolium*, *S. subpanduratum*, and *S. tundalomense*.



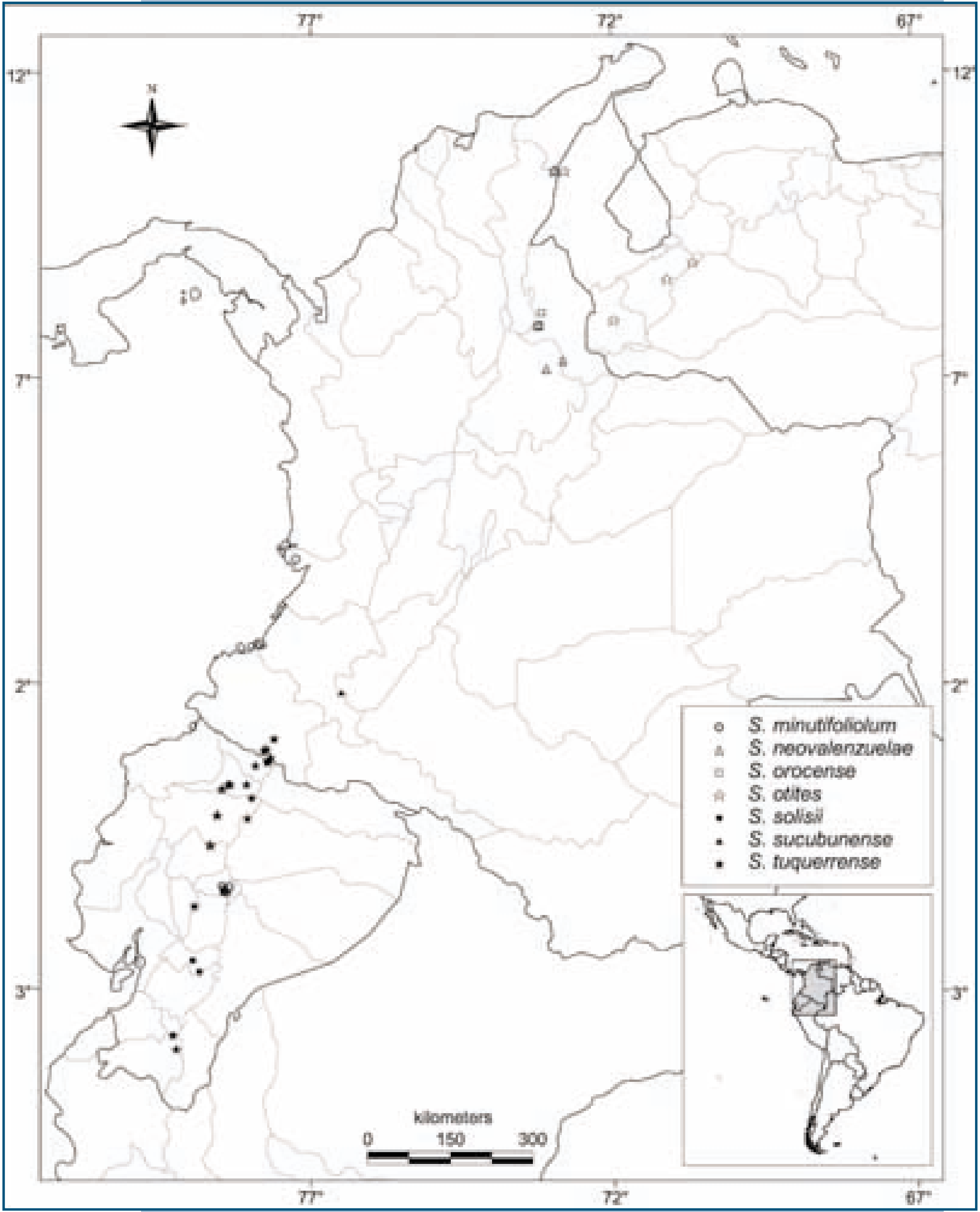
Northern Andes

Map 20. Distribution of *S. andreanum*, *S. burtonii*, *S. chilliasense*, *S. donachui*, *S. garcia-barrigae*, *S. lobbianum*, and *S. moscopanum*.



Northern Andes

Map 21. Distribution of *S. minutifoliolum*, *S. neovalenzuelae*, *S. orocense*, *S. otites*, *S. solisii*, *S. sucubunense*, and *S. tuquerrense*.

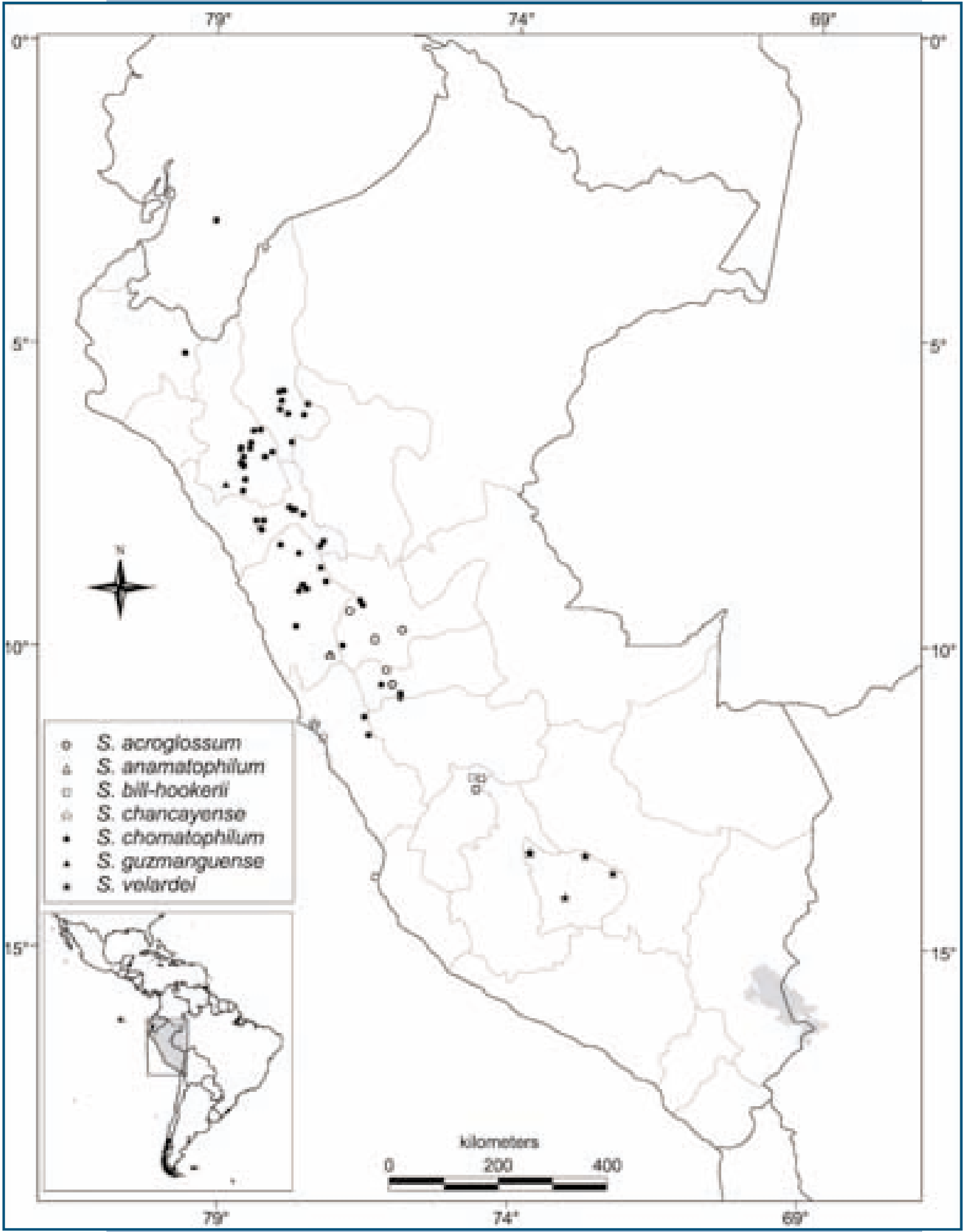


Peru

Map 22. First-level administrative subdivisions in Peru.

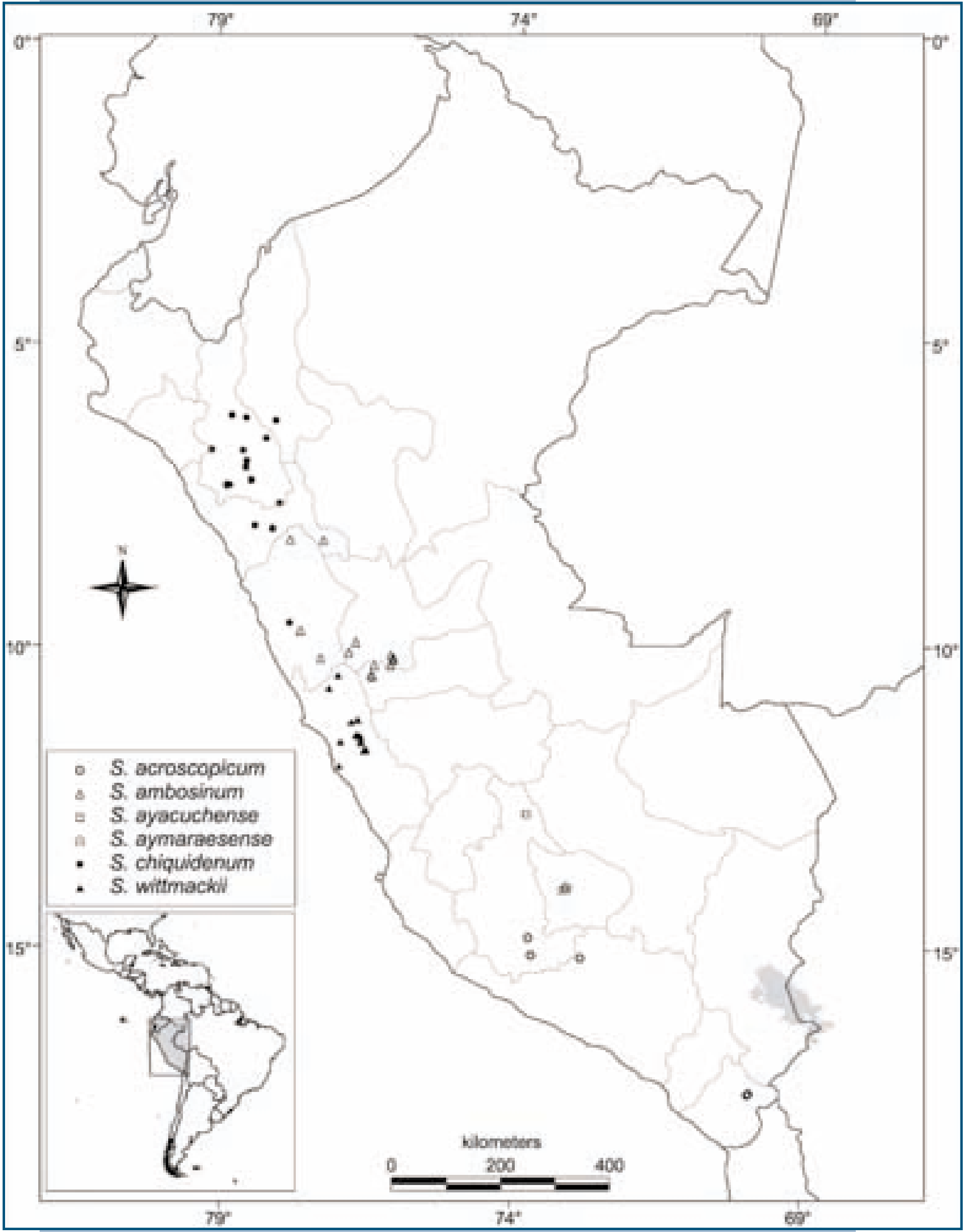
Peru

Map 23. Distribution of *S. acroglossum*, *S. anamatophilum*, *S. bill-hookeri*, *S. chancayense*, *S. chomatophilum*, *S. guzmanguense*, and *S. velardei*.



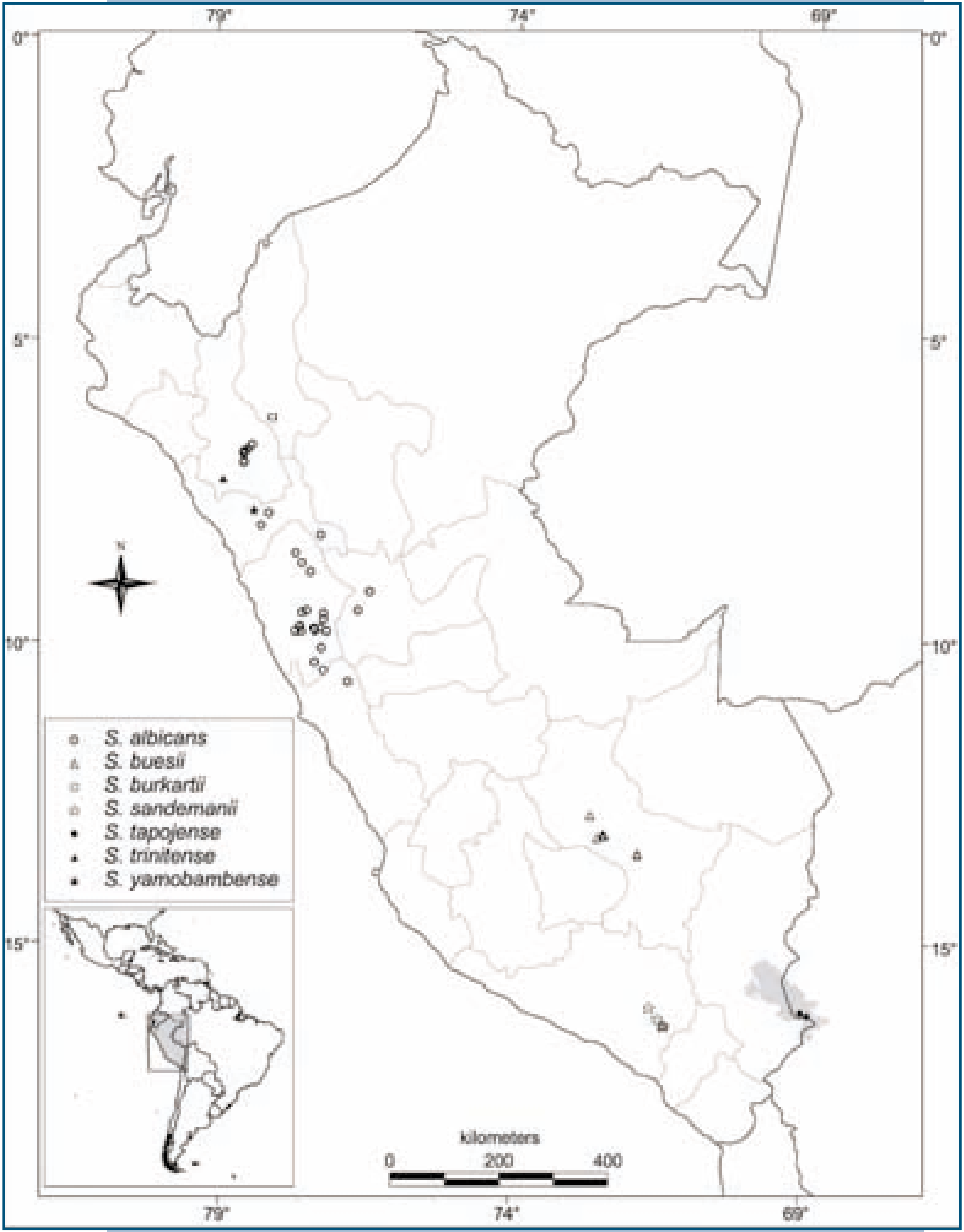
Peru

Map 24. Distribution of *S. acroscopicum*, *S. ambosinum*, *S. ayacuchense*, *S. aymaraesense*, *S. chiquidenum*, and *S. wittmackii*.



Peru

Map 25. Distribution of *S. albicans*, *S. buesii*, *S. burkartii*, *S. sandemanii*, *S. tapojense*, *S. trinitense*, and *S. yamobambense*.

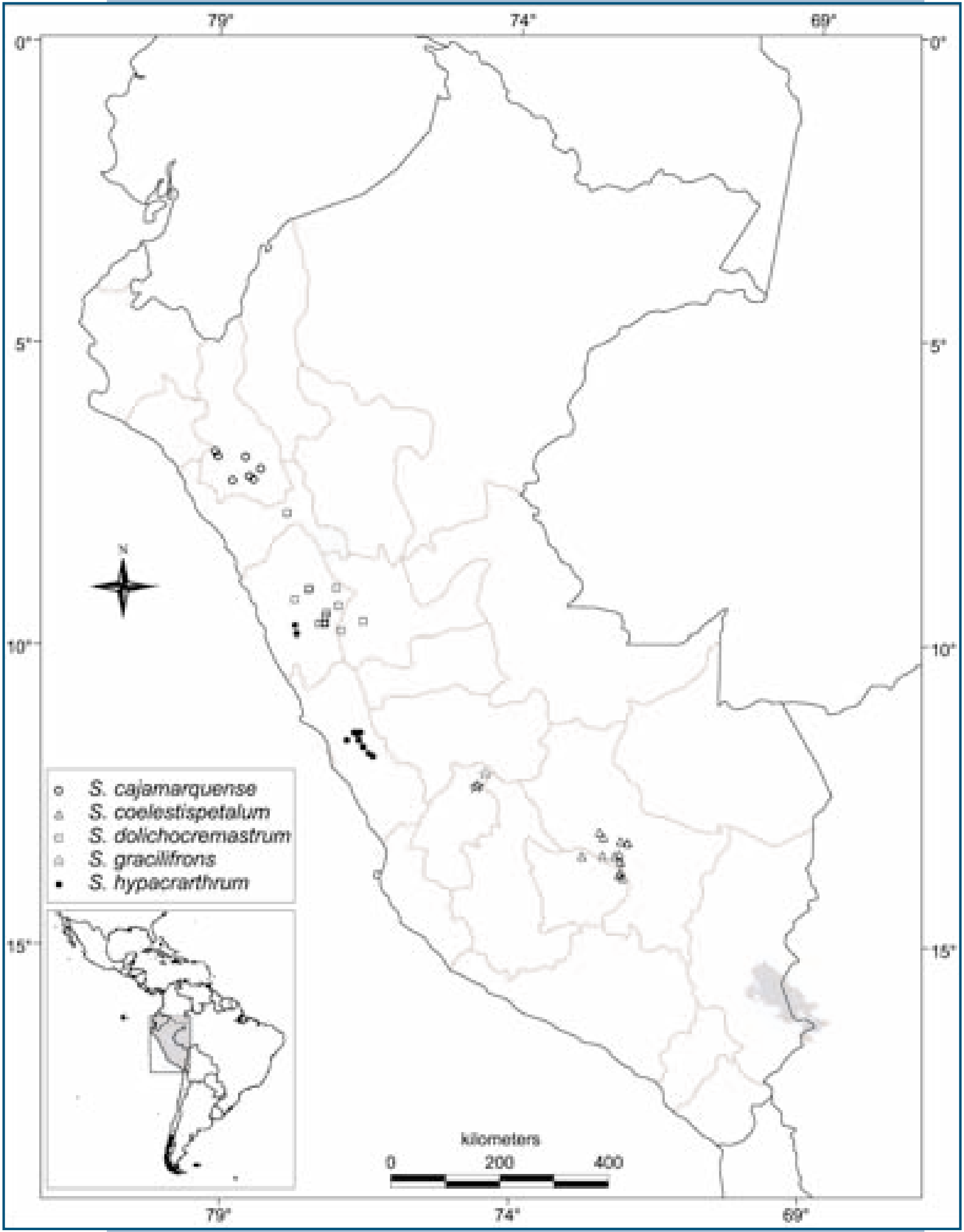


Peru

Map 26. Distribution of *S. amayanum*, *S. ancoripae*, *S. ×arahuayum*, *S. sarasarae*, *S. tacnaense*, *S. taulisense,* and *S. pillahuatense*.

Peru

Map 27. Distribution of *S. cajamarquense*, *S. coelestipetalum*, *S. dolichocremastrum*, *S. gracilifrons*, and *S. hypacrarthrum*.



Peru

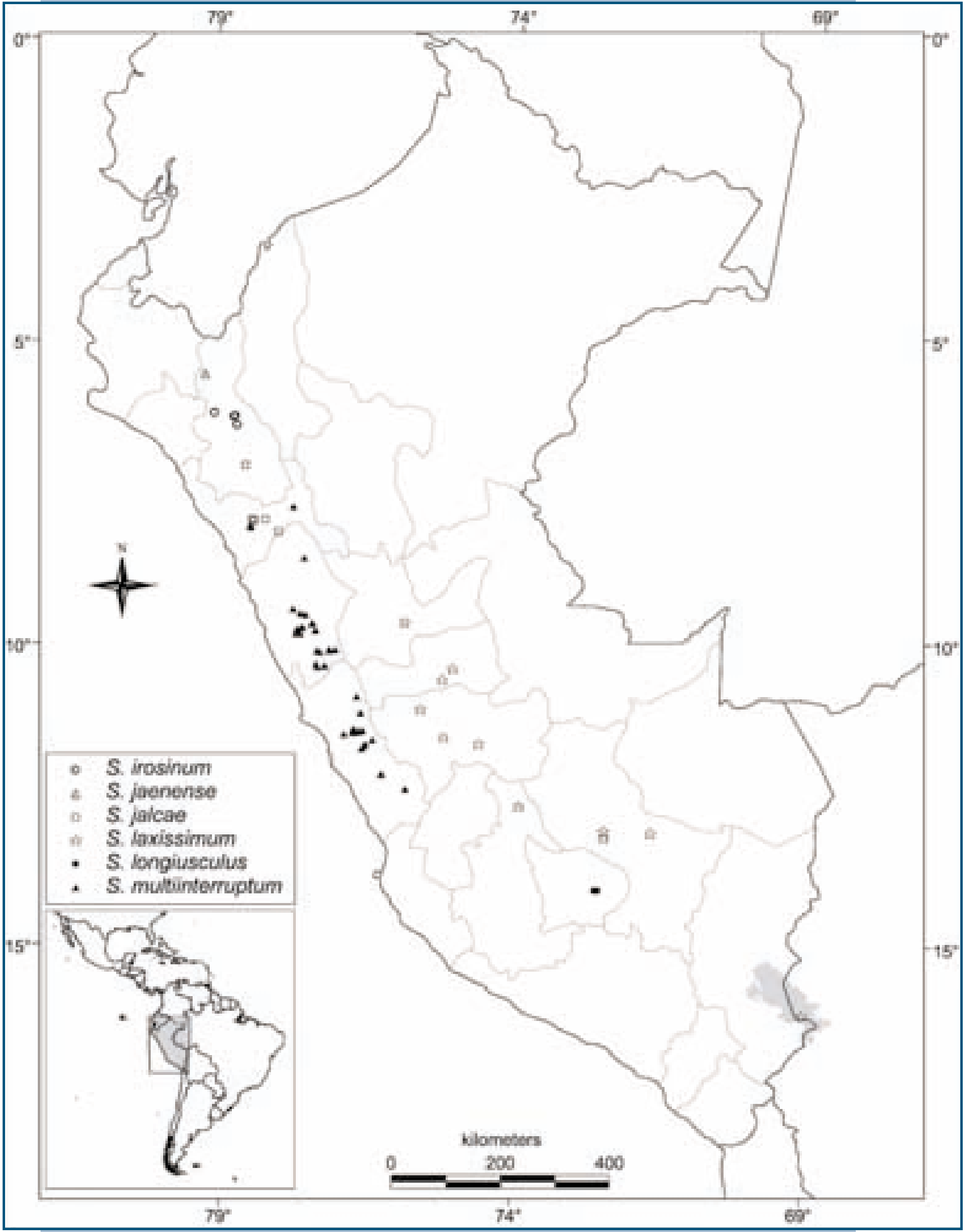
Map 28. Distribution of *S. chillonanum*, *S. hastiforme*, *S. huarochiriense*, *S. incahuasinum*, *S. ingifolium*, and *S. saxatilis*.

Peru

Map 29. Distribution of *S. ancophilum*, *S. ariduphilum*, *S. huancabambense*, *S. humectophilum*, *S. incasinum*, and *S. ortegae*.

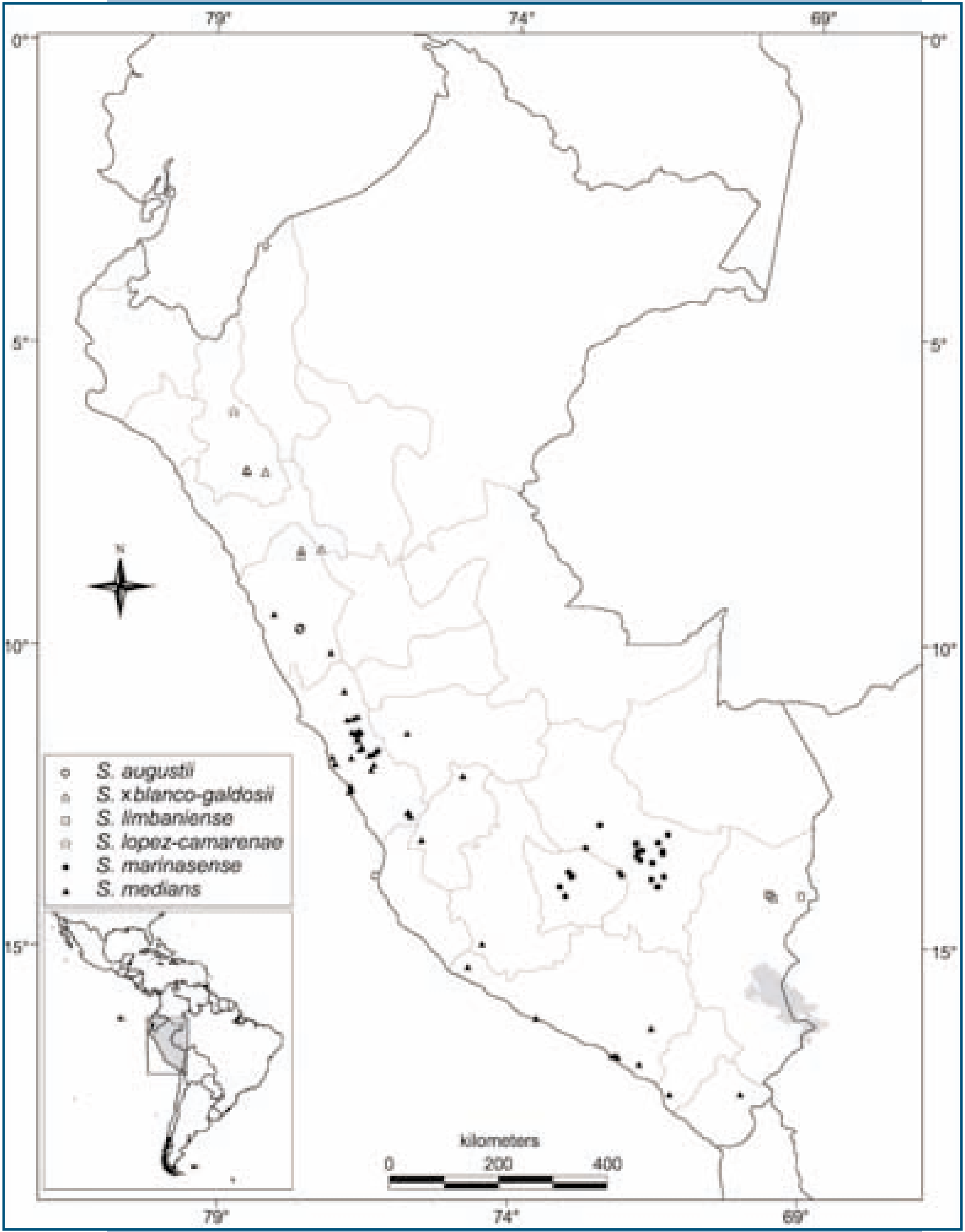
Peru

Map 30. Distribution of *S. irosinum*, *S. jaenense*, *S. jalcae*, *S. laxissimum*, *S. longiusculus*, and *S. multiinterruptum*.



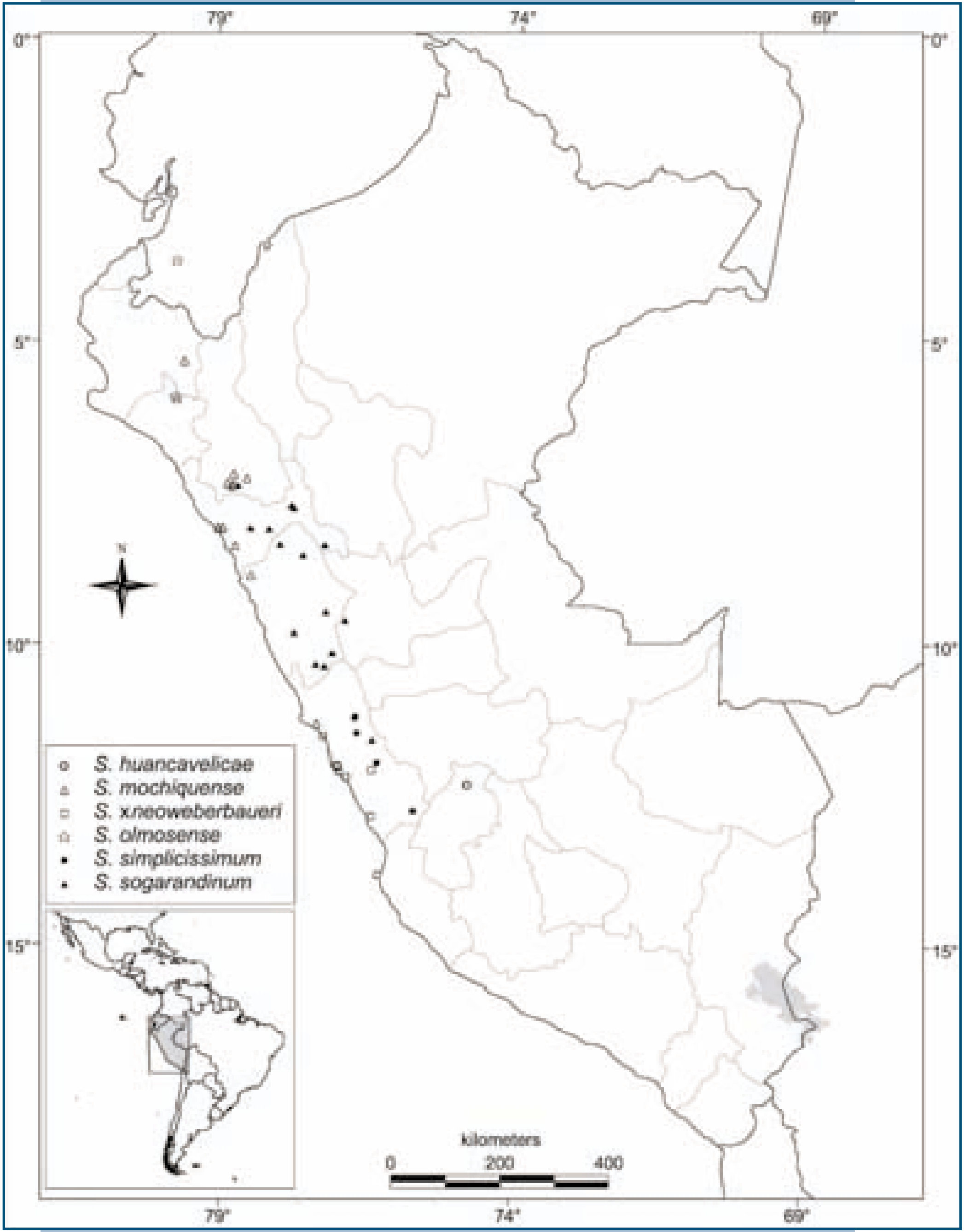
Peru

Map 31. Distribution of *S. augustii*, *S. limbaniense*, *S. lopez-camarenae*, *S. marinasense*, *S. medians*, and *S. ×blanco-galdosii*.



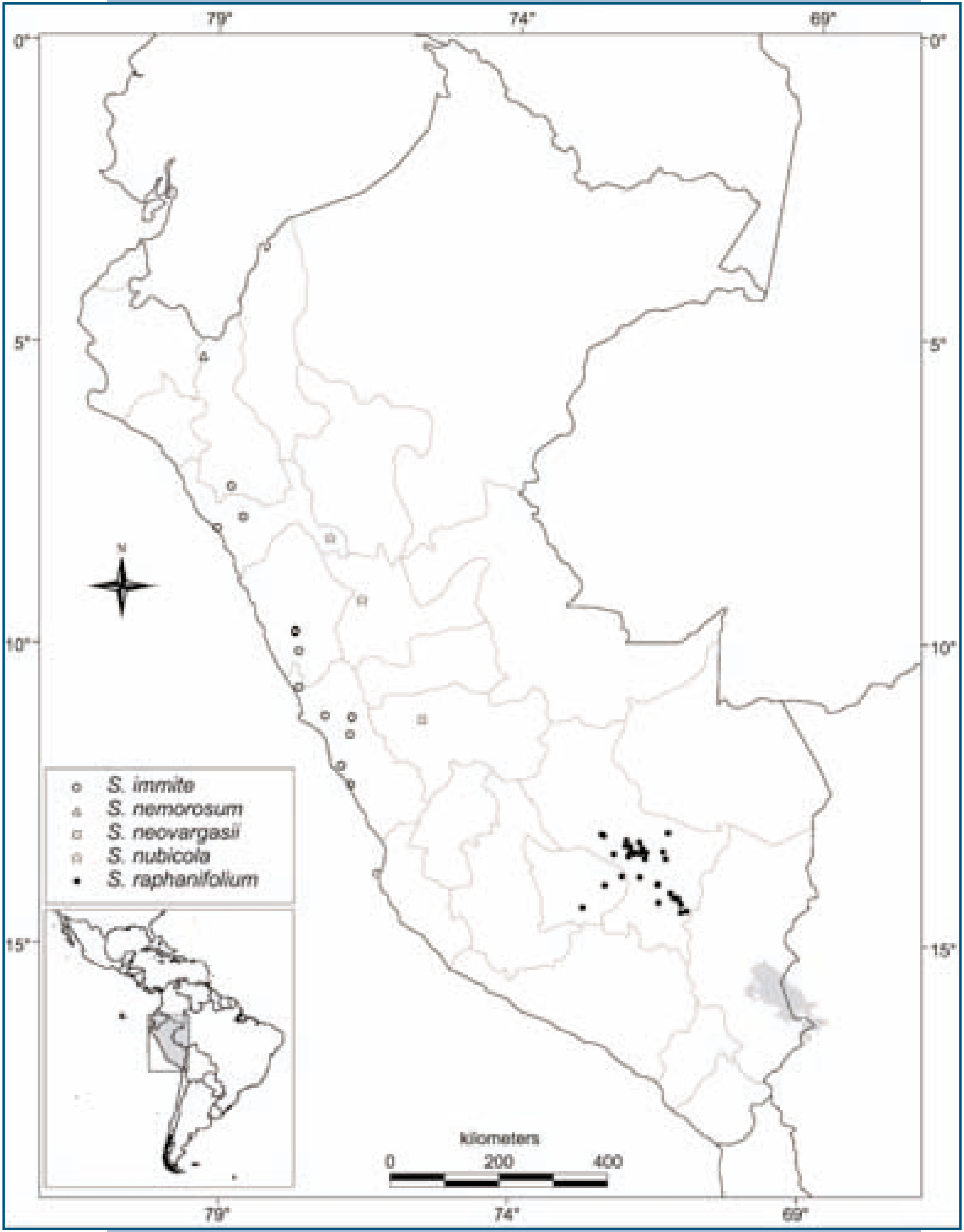
Peru

Map 32. Distribution of *S. huancavelicae*, *S. mochiquense*, *S. olmosense*, *S. simplicissimum*, *S. sogarandinum*, and *S. ×neoweberbaueri*.



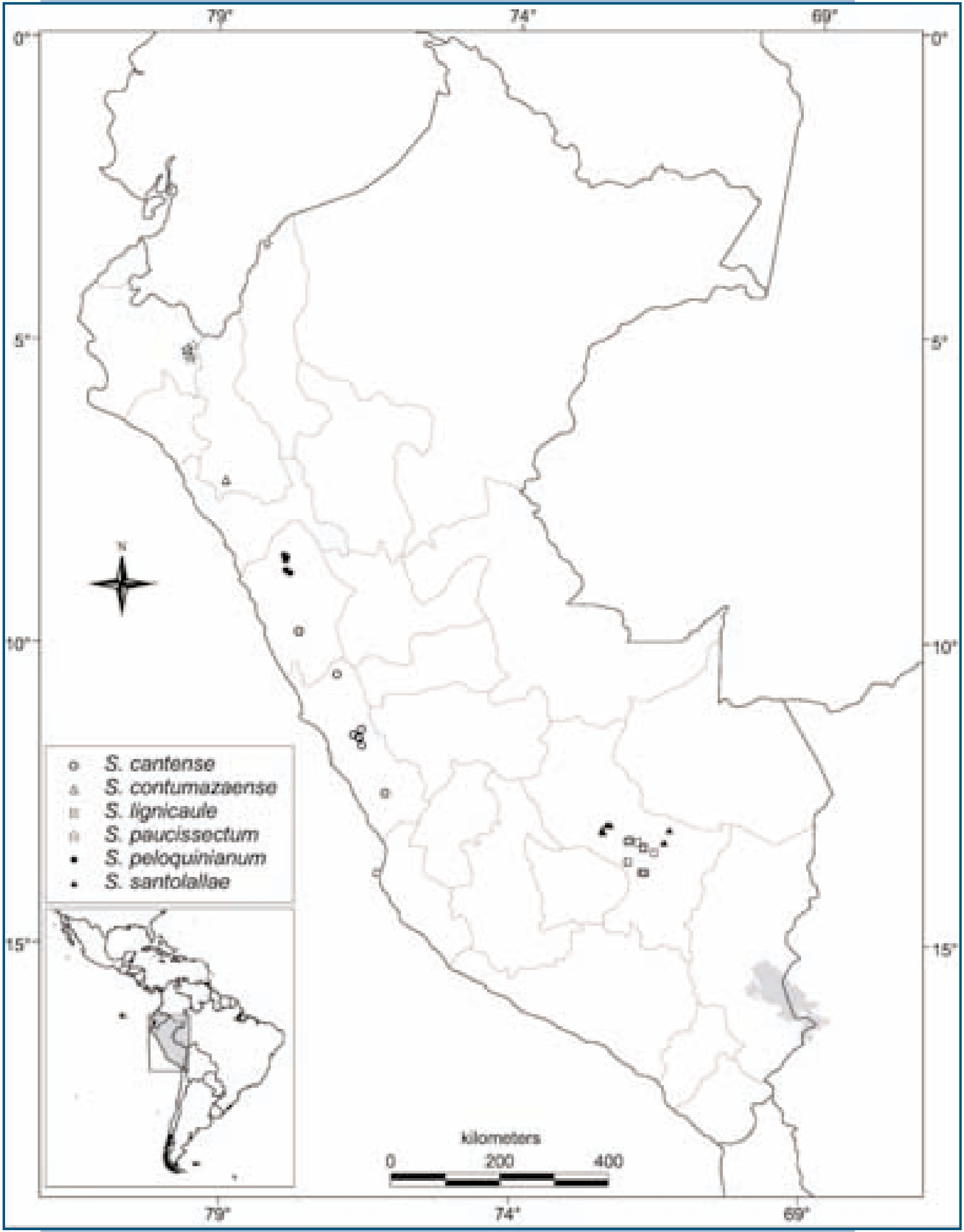
Peru

Map 33. Distribution of *S. immite*, *S. nemorosum*, *S. neovargasii*, *S. nubicola*, and *S. raphanifolium*.



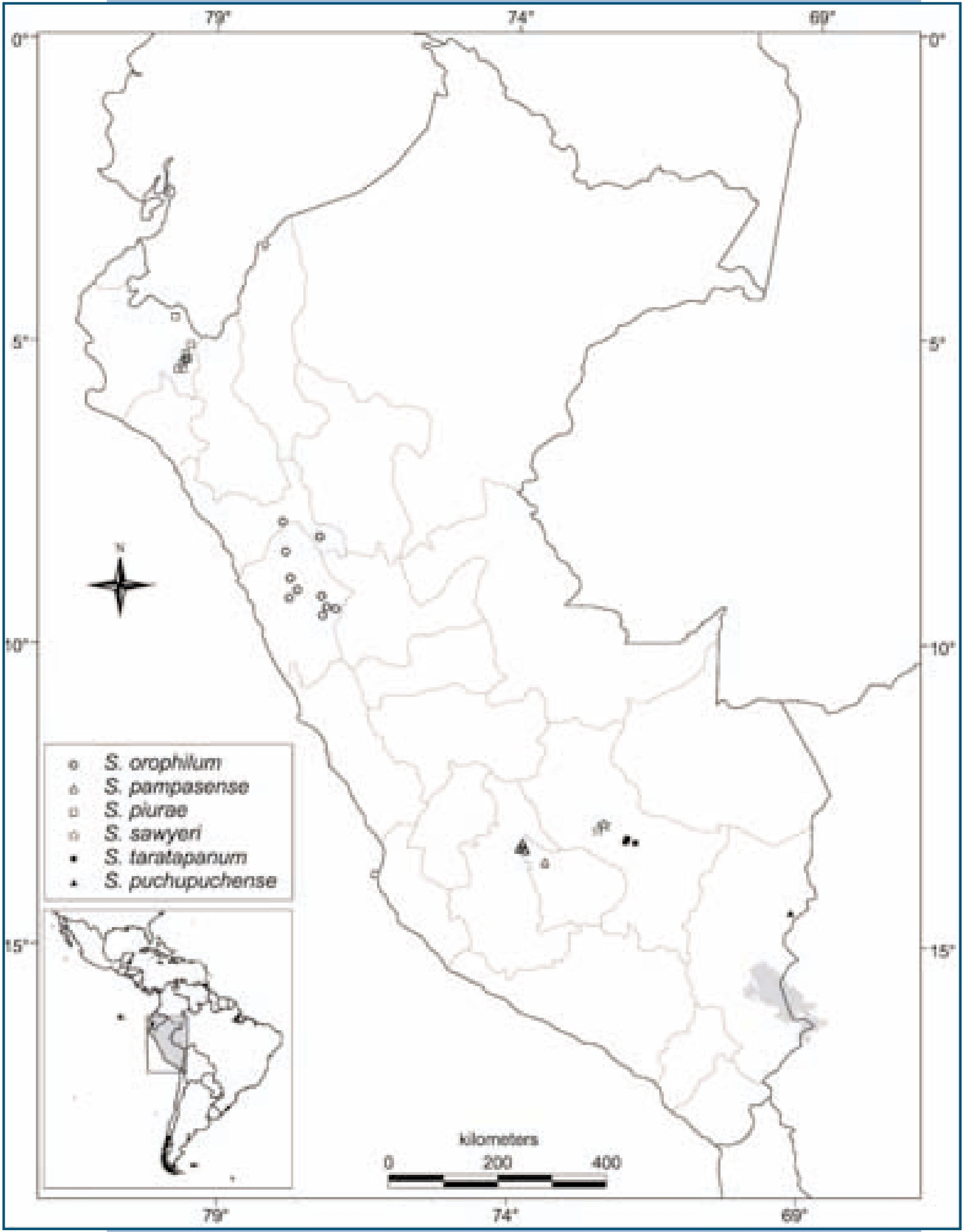
Peru

Map 34. Distribution of *S. cantense*, *S. contumazaense*, *S. lignicaule*, *S. paucissectum*, *S. peloquinianum*, and *S. santolallae*.



Peru

Map 35. Distribution of *S. orophilum*, *S. pampasense*, *S. piurae*, *S. puchupuchense*, *S. sawyeri*, and *S. taratapanum*.

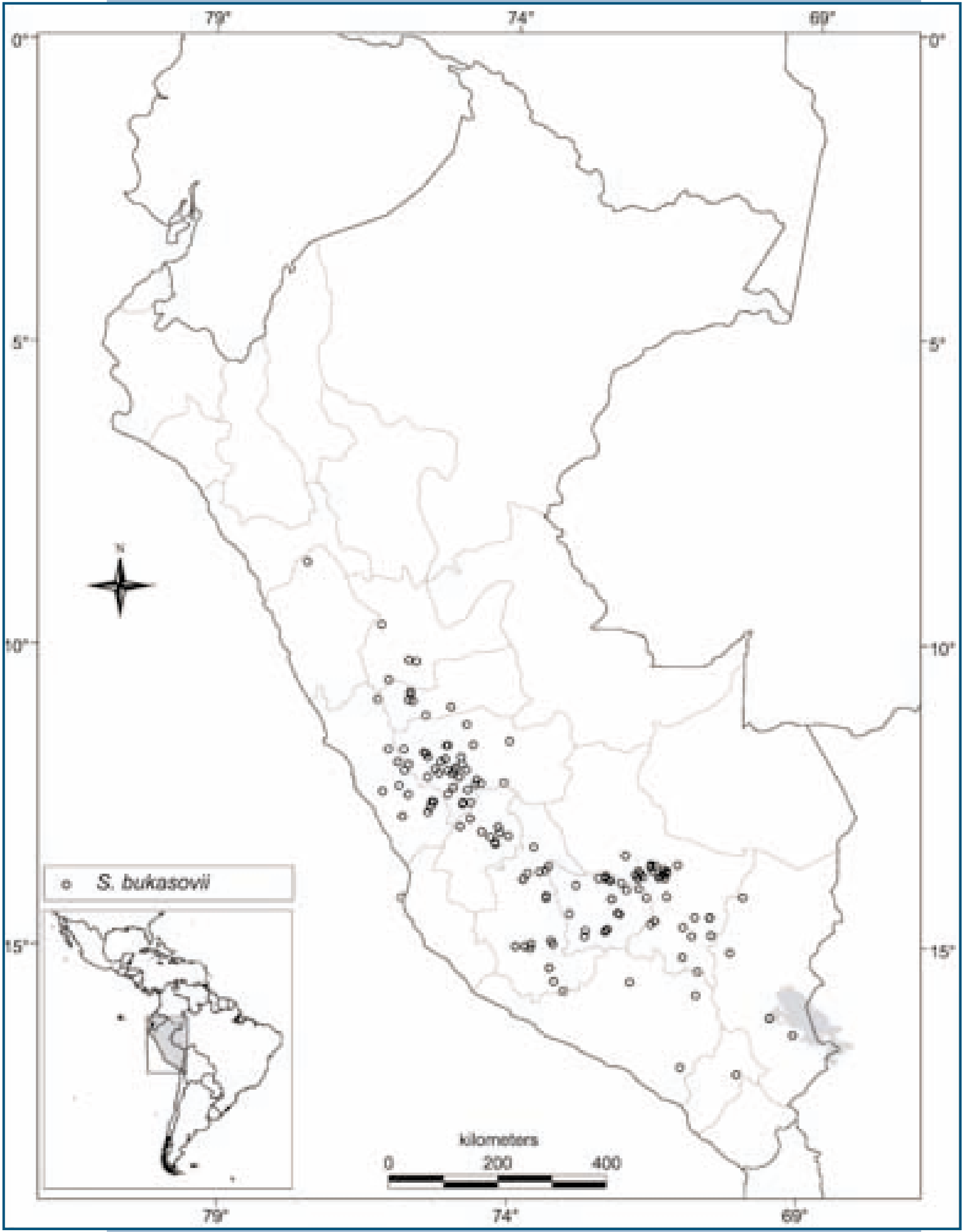


Peru

Map 36. Distribution of *S. raquialatum*, *S. rhomboideilanceolatum*, *S. salasianum*, *S. scabrifolium*, and *S. urubambae*.

Peru

Map 37. Distribution of *S. bukasovii*.

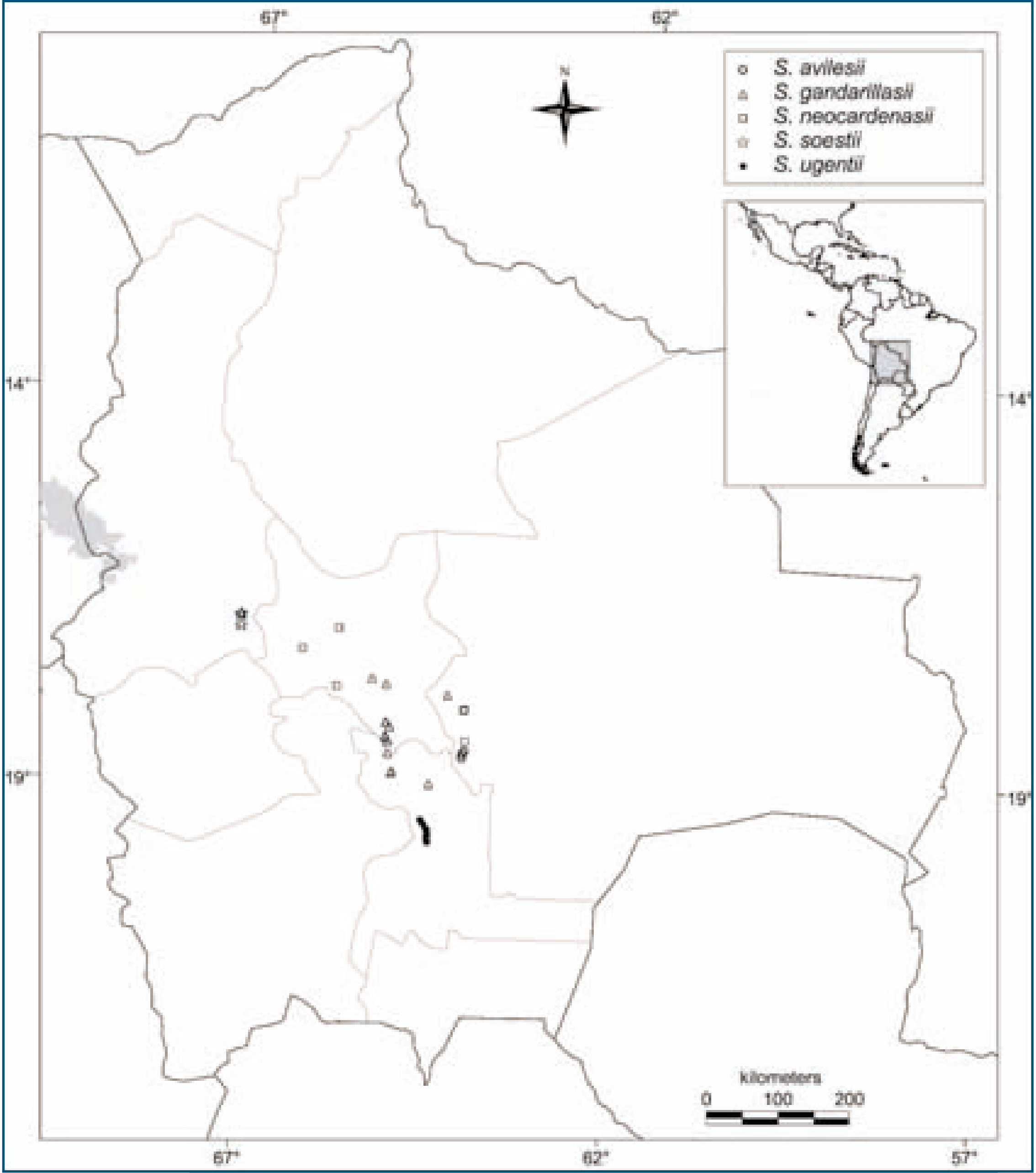


Bolivia

Map 38. First-level administrative subdivisions in Bolivia.

Bolivia

Map 39. Distribution of *S. avilesii*, *S. gandarillasii*, *S. neocardenasii*, *S. soestii*, and *S. ugentii*.

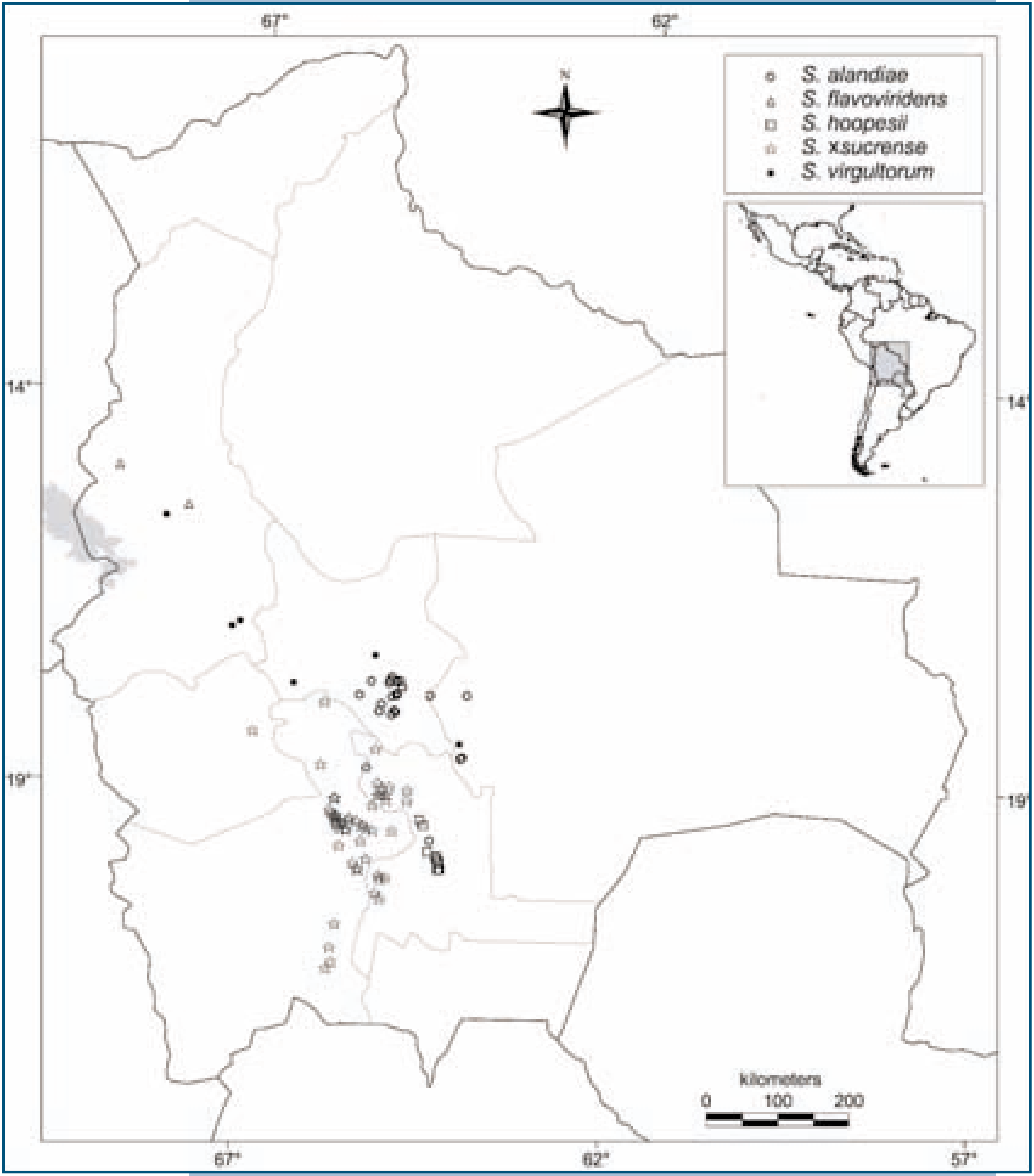


Bolivia

Map 40. Distribution of *S. arnezii*, *S. boliviense*, *S. circaeifolium*, *S. neovavilovii*, and *S. ×litusinum*.

Bolivia

Map 41. Distribution of *S. alandiae*, *S. flavoviridens*, *S. hoopesii*, *S. virgultorum*, and *S. ×sucrense*.



Bolivia

Map 42. Distribution of *S. achacachense*, *S. ×doddsii*, and *S. violaceimarmoratum*.

Bolivia

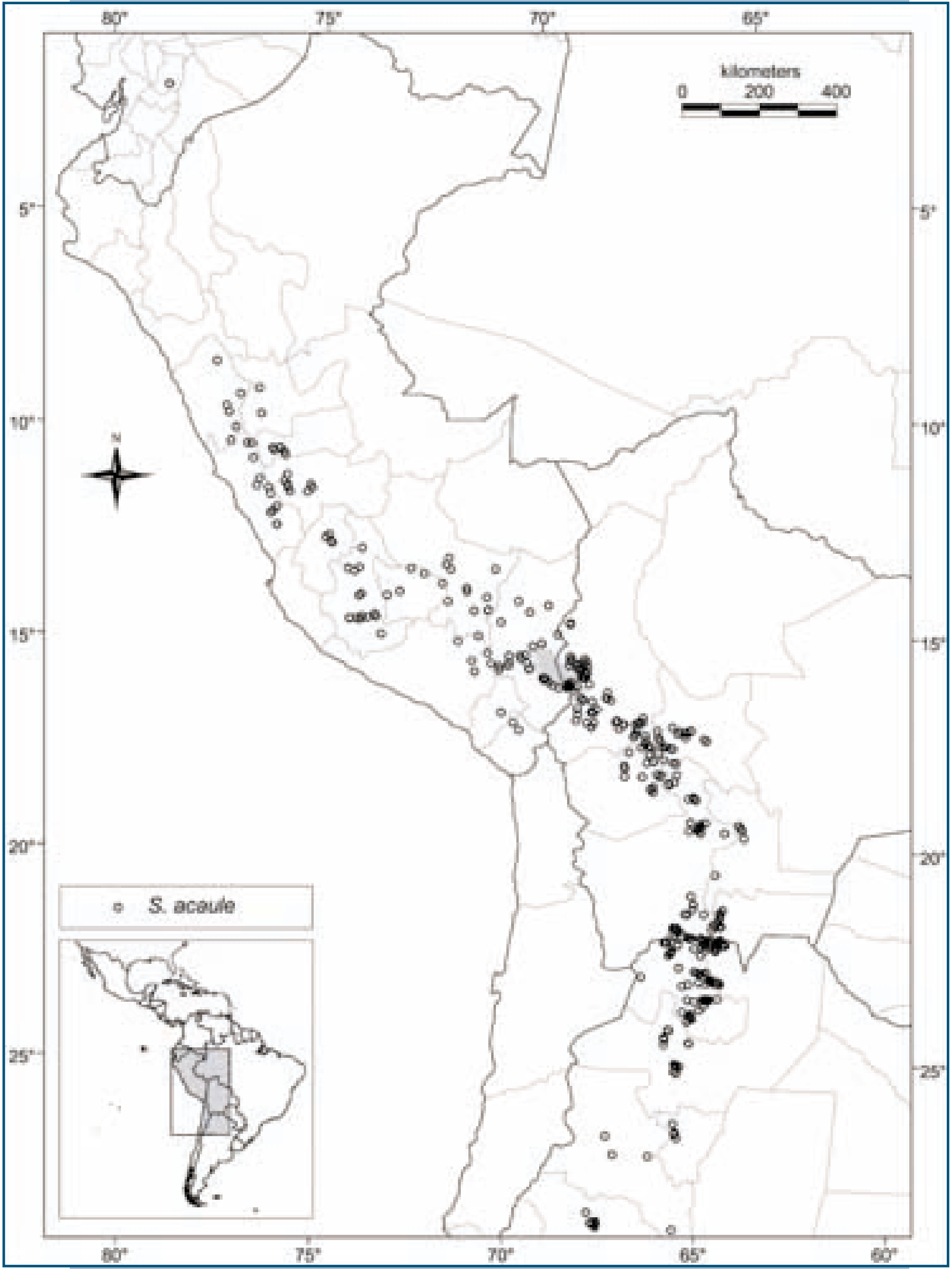
Map 43. Distribution of *S. berthaultii* and *S. bombycinum*.

Southern Andes

Map 44. First-level administrative subdivisions in the southern Andes.

Southern Andes

Map 45. Distribution of *S. acaule*.



Southern Andes

Map 46. Distribution of *S.* ×*bruecheri* and *S. okadae*.

Southern Andes

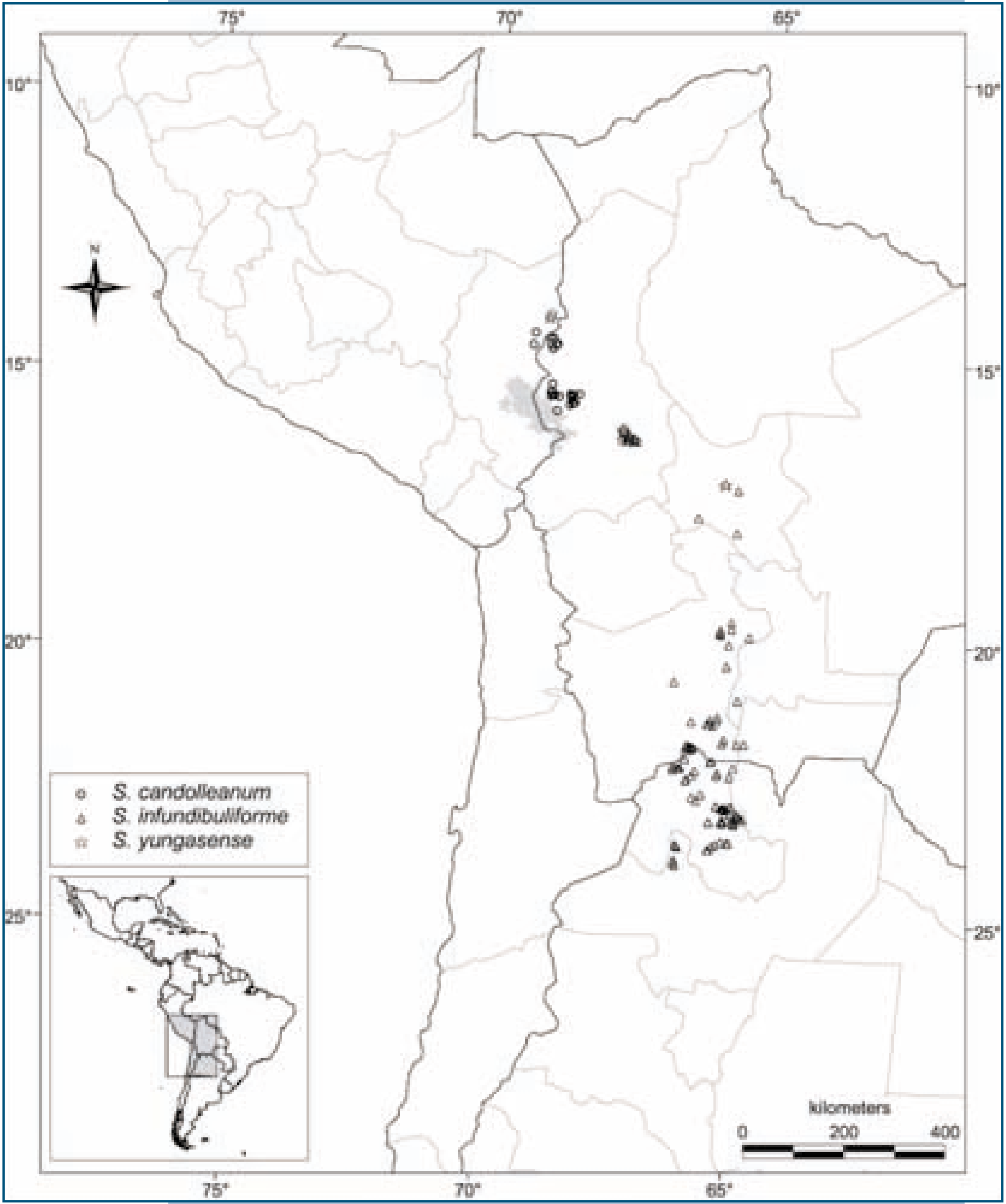
Map 47. Distribution of *S. ×setulosistylum* and *S. vidaurrei*.

Southern Andes

Map 48. Distribution of *S. tarijense*.

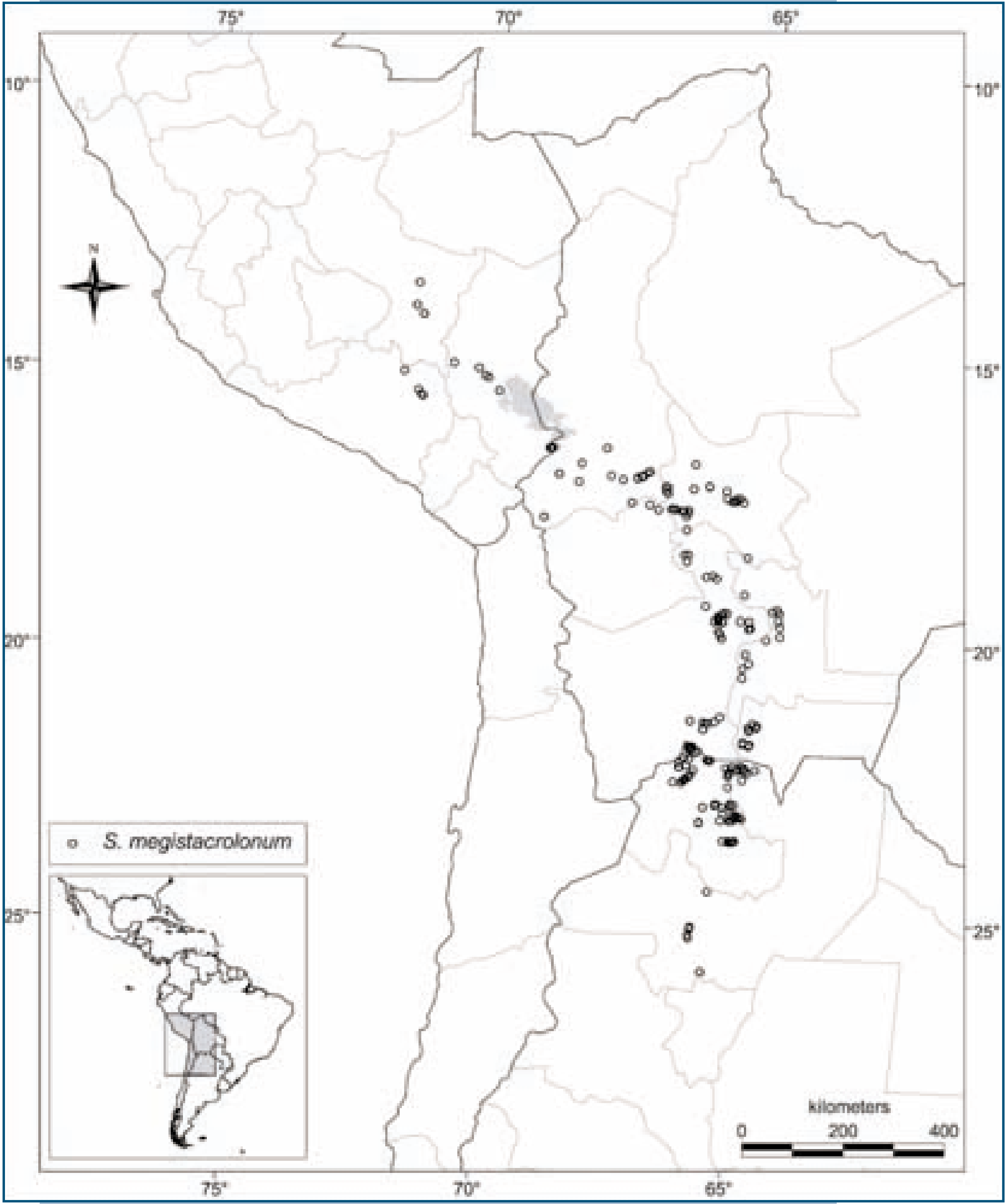
Southern Andes

Map 49. Distribution of *S. candolleanum*, *S. infundibuliforme*, and *S. yungasense*.



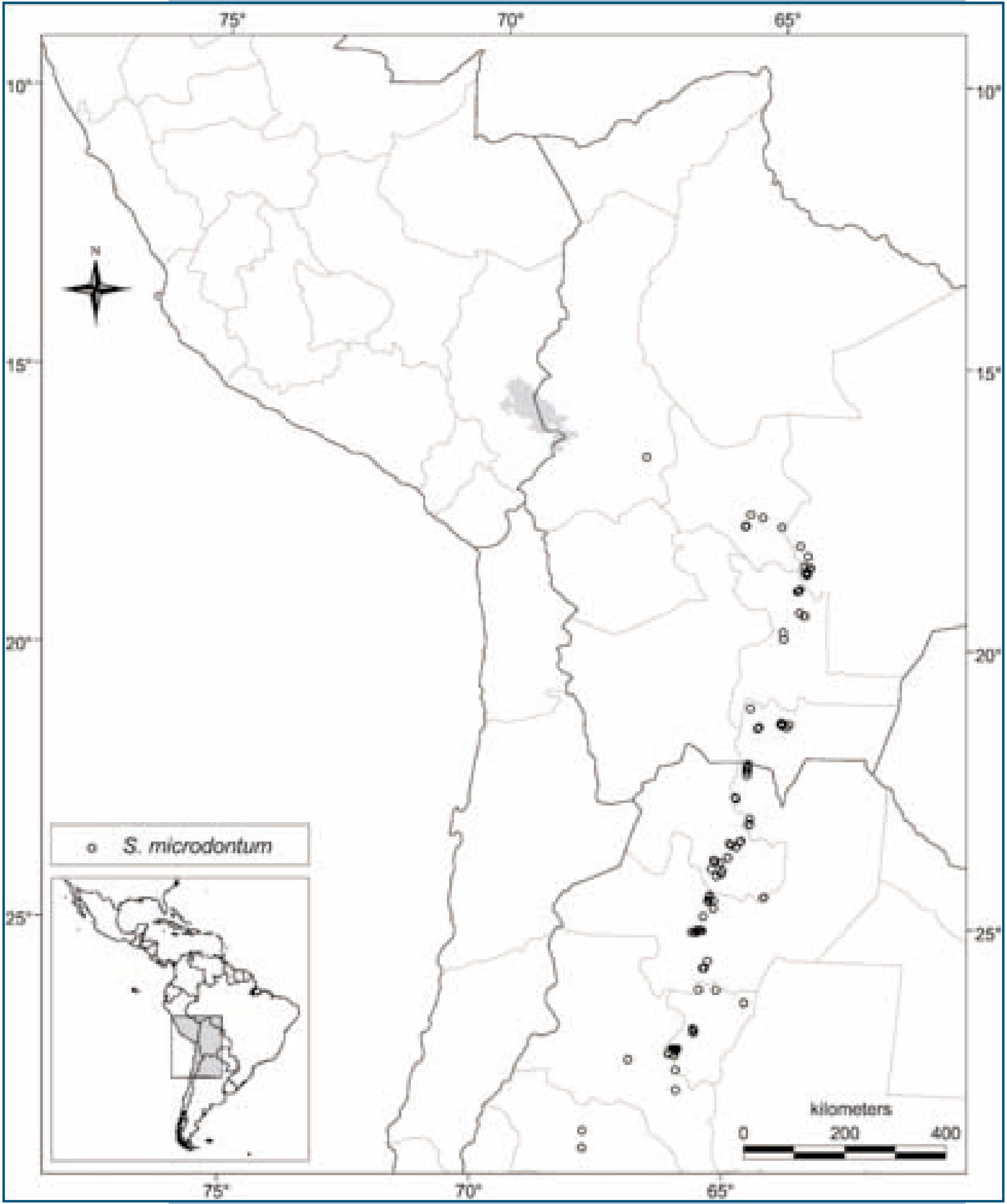
Southern Andes

Map 50. Distribution of *S. megistacrolonum*.



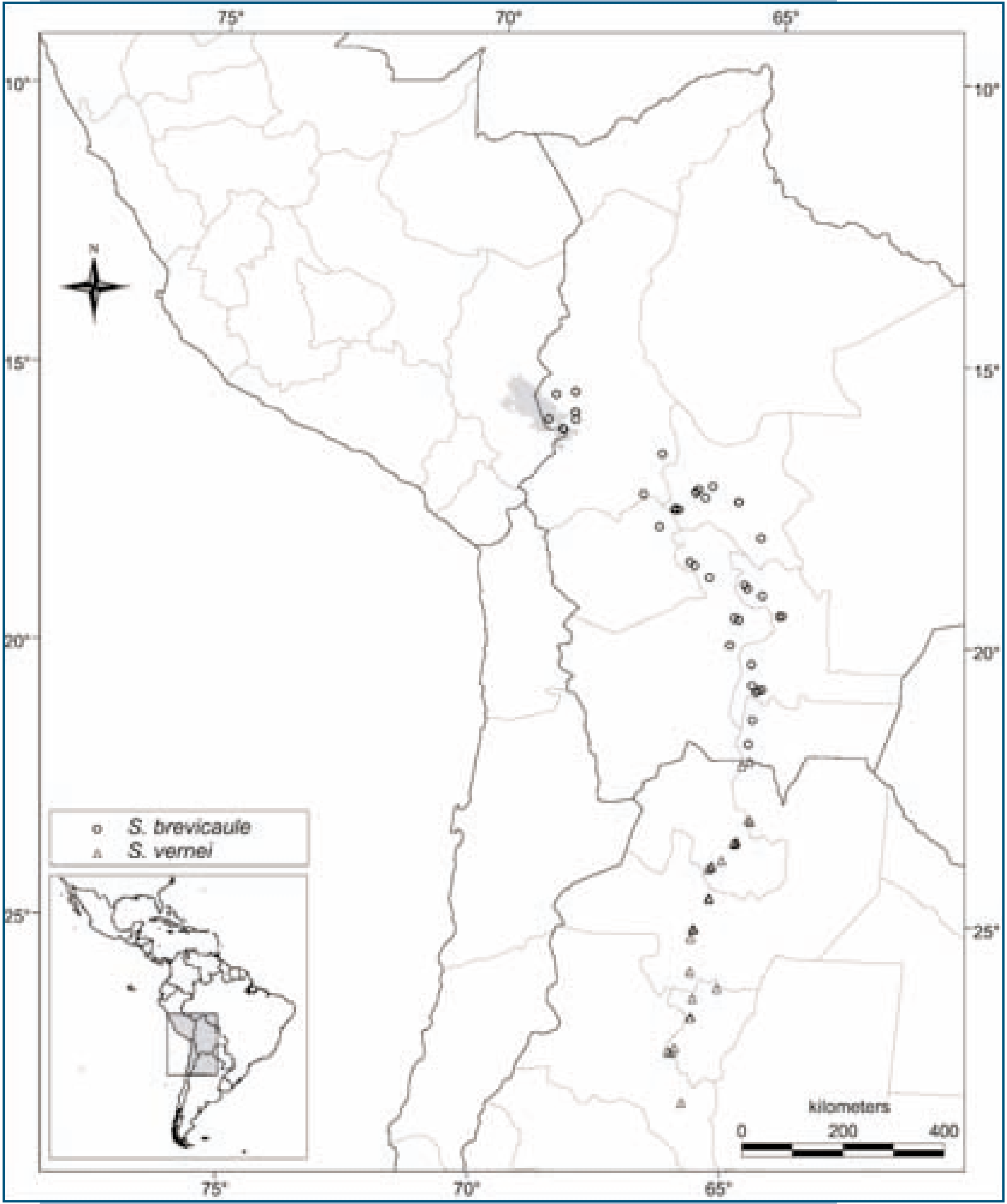
Southern Andes

Map 51. Distribution of *S. microdontum*.



Southern Andes

Map 52. Distribution of *S. brevicaule* and *S. vernei*.

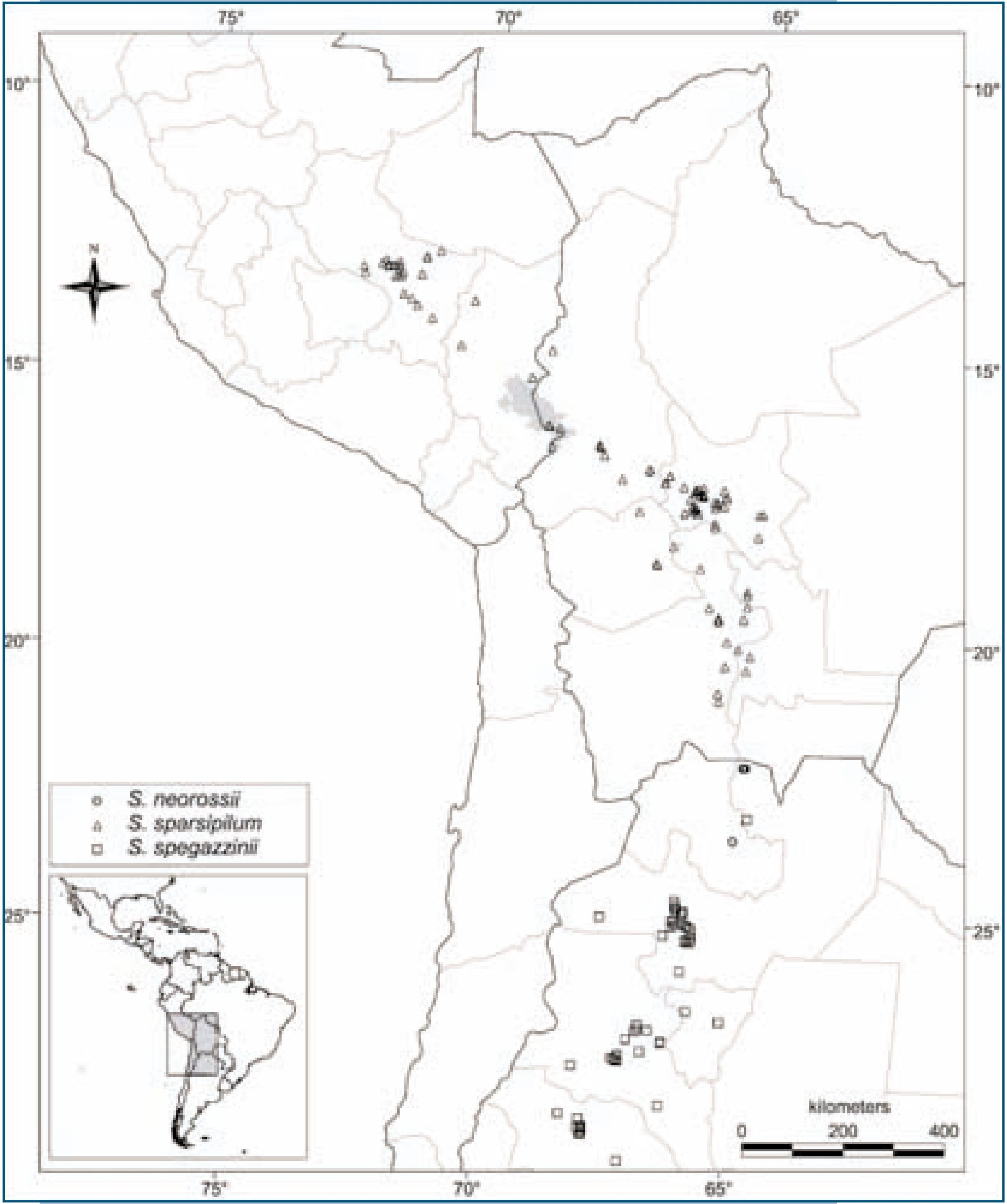


Southern Andes

Map 53. Distribution of *S. oplocense*.

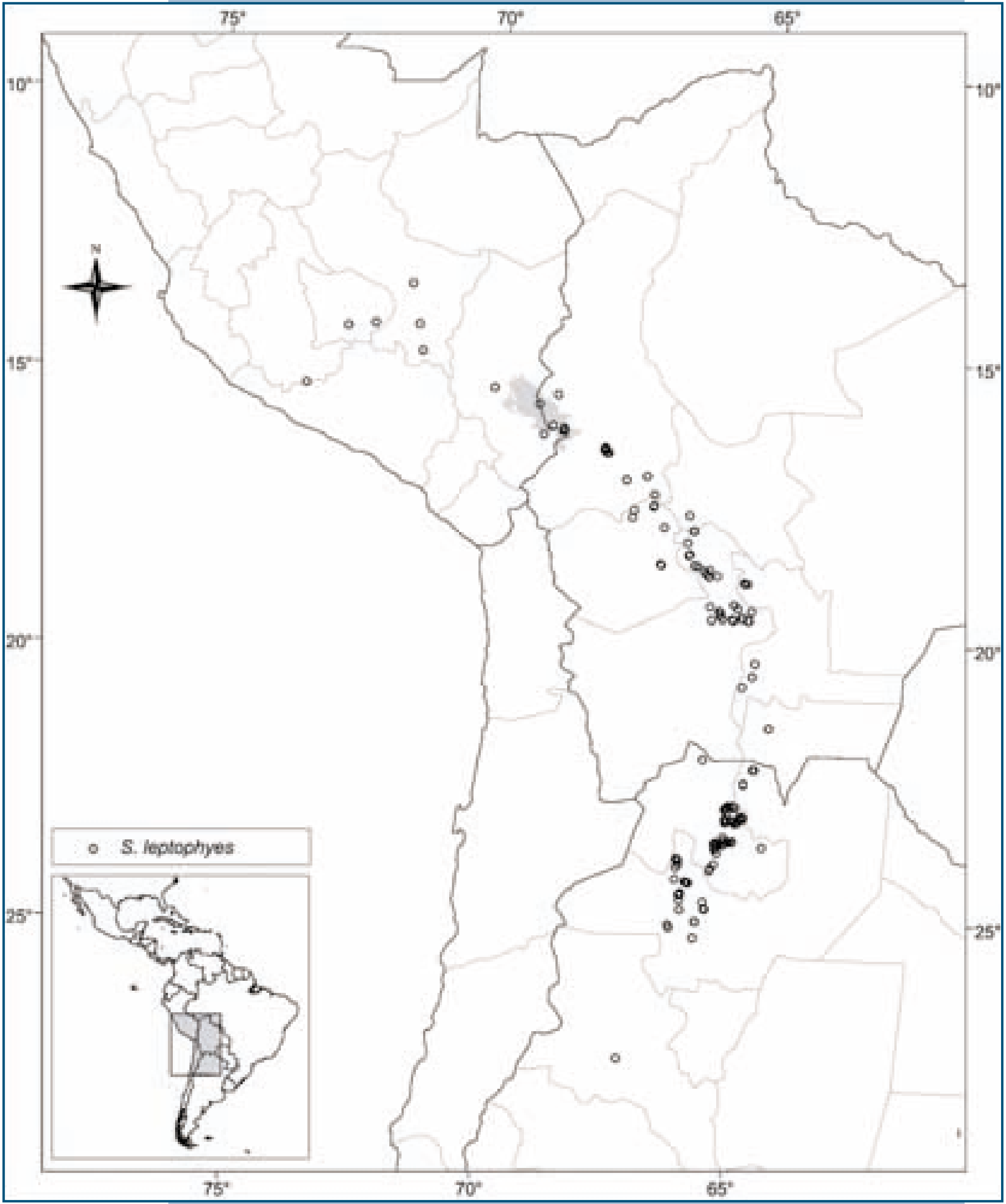
Southern Andes

Map 54. Distribution of *S. neorossii*, *S. sparsipilum*, and *S. spegazzinii*.



Southern Andes

Map 55. Distribution of *S. leptophyes*.

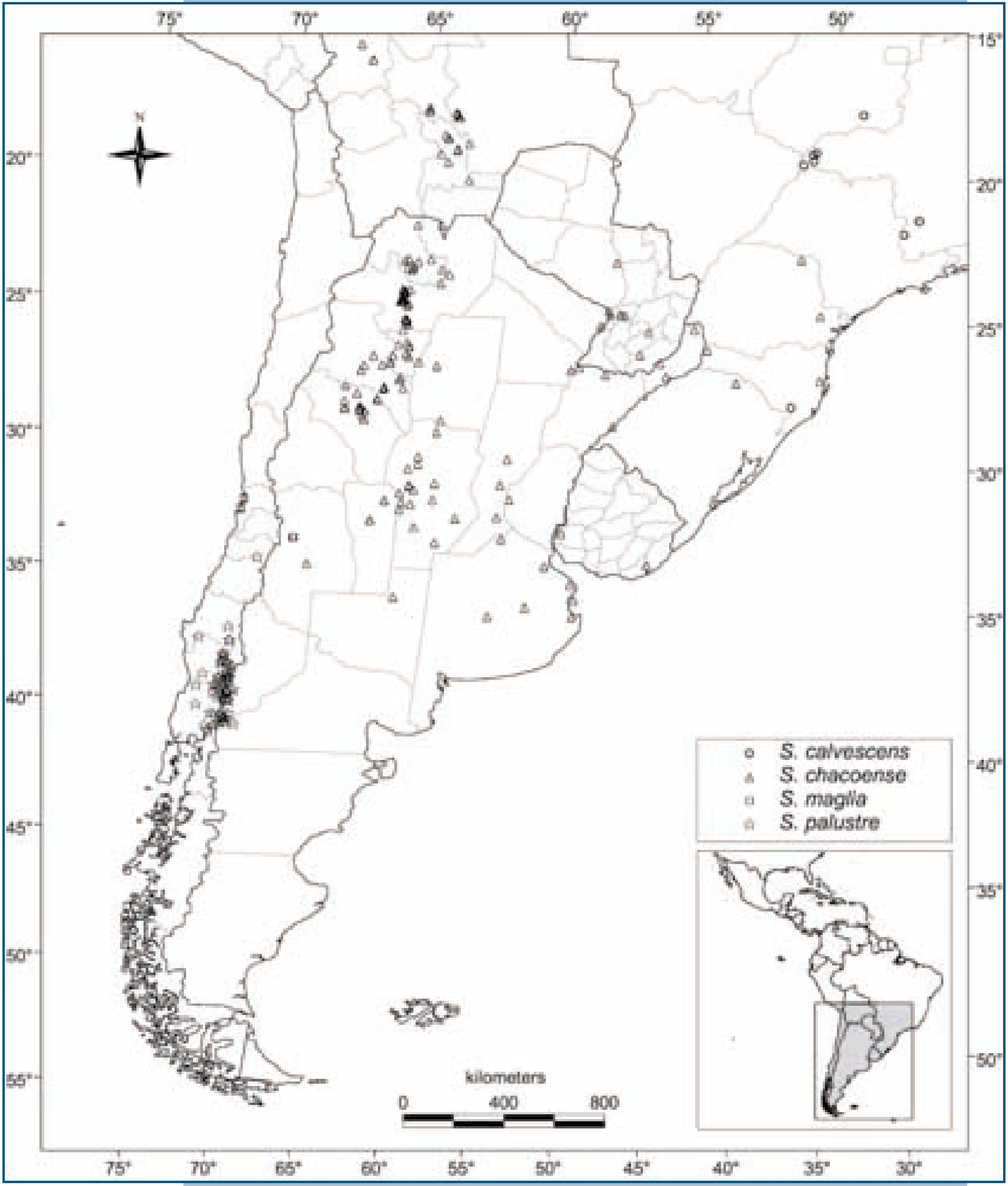


Southern cone

Map 56. First-level administrative subdivisions in the Southern cone.

Southern cone

Map 57. Distribution of *S. calvescens*, *S. chacoense*, *S. maglia*, and *S. palustre*.



Southern cone

Map 58. Distribution of *S. commersonii*, *S. fernandezianum*, *S. sanctae-rosae*, *S. ×rechei*, and *S. ×viirsoii*.

Southern cone

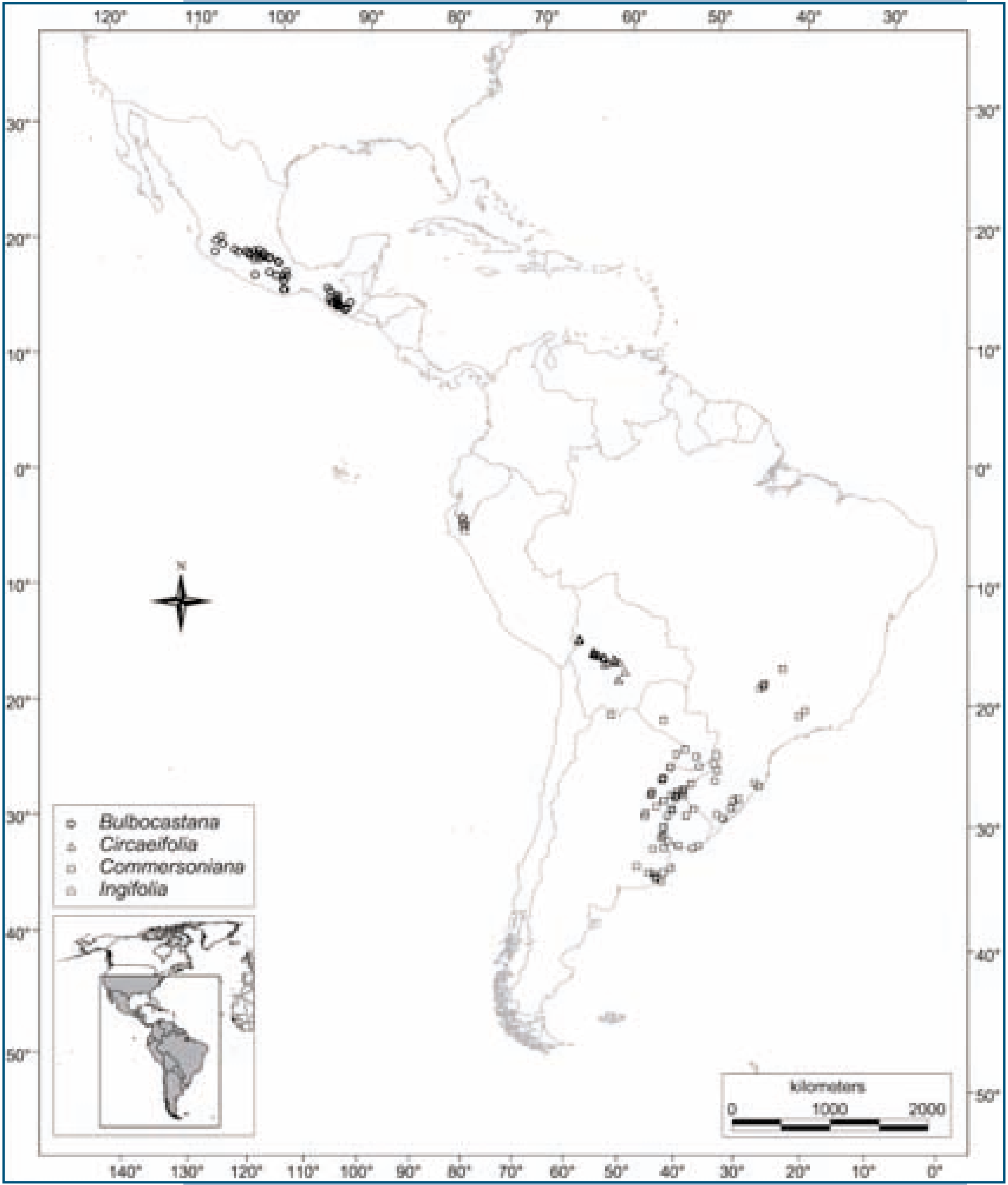
Map 59. Distribution of *S. etuberosum*, *S. incamayoense*, *S. kurtzianum*, and *S. ×indunii*.

Southern cone

Map 60. Distribution of *S. venturii* and *S. ×ruiz-lealii*.

Distribution of series

Map 61. Distribution of series *Bulbocastana*, *Circaeifolia*, *Commersoniana*, and *Ingifolia*.

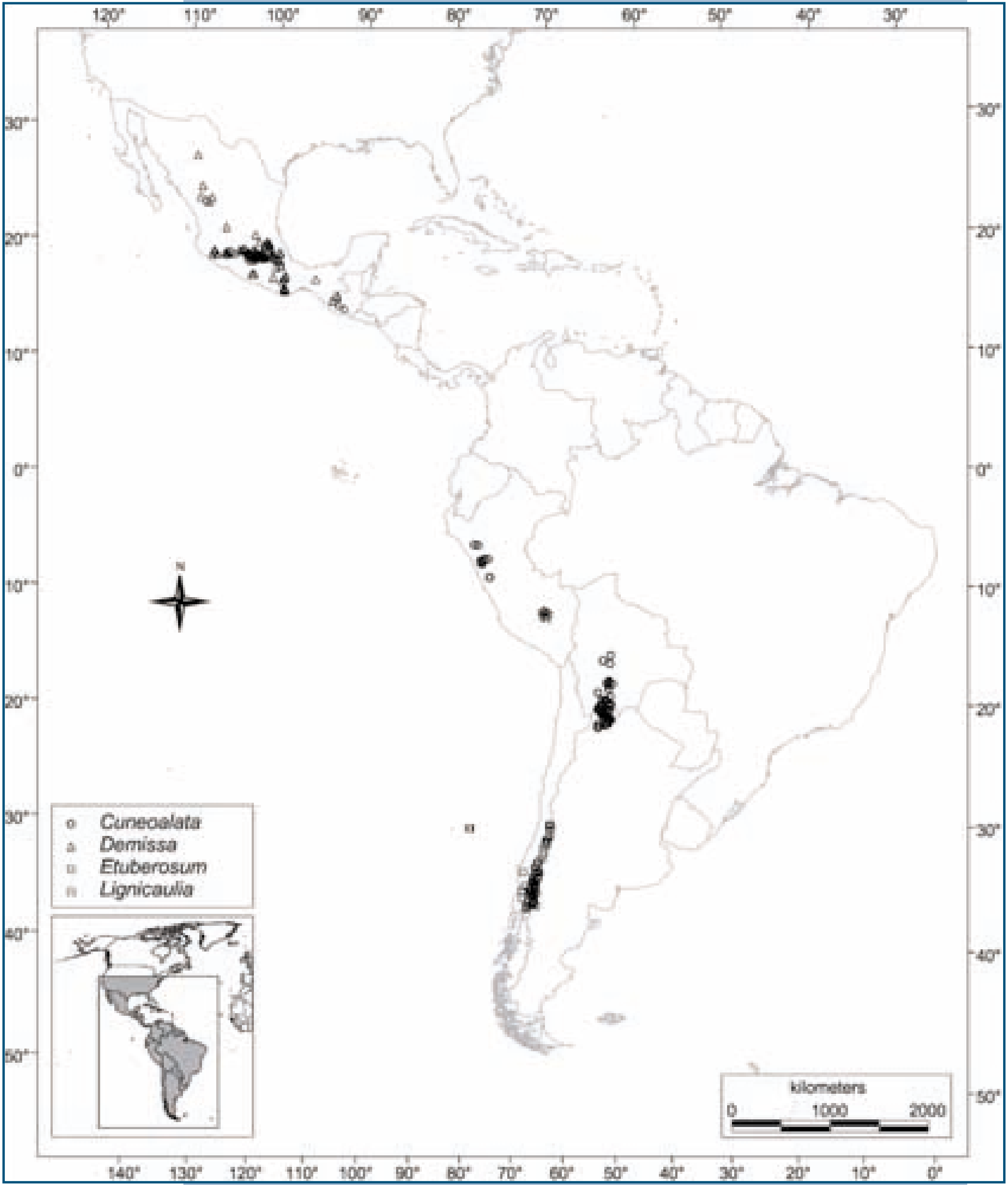


Distribution of series

Map 62. Distribution of series *Megistacroloba*, *Morelliformia*, and *Olmosiana*.

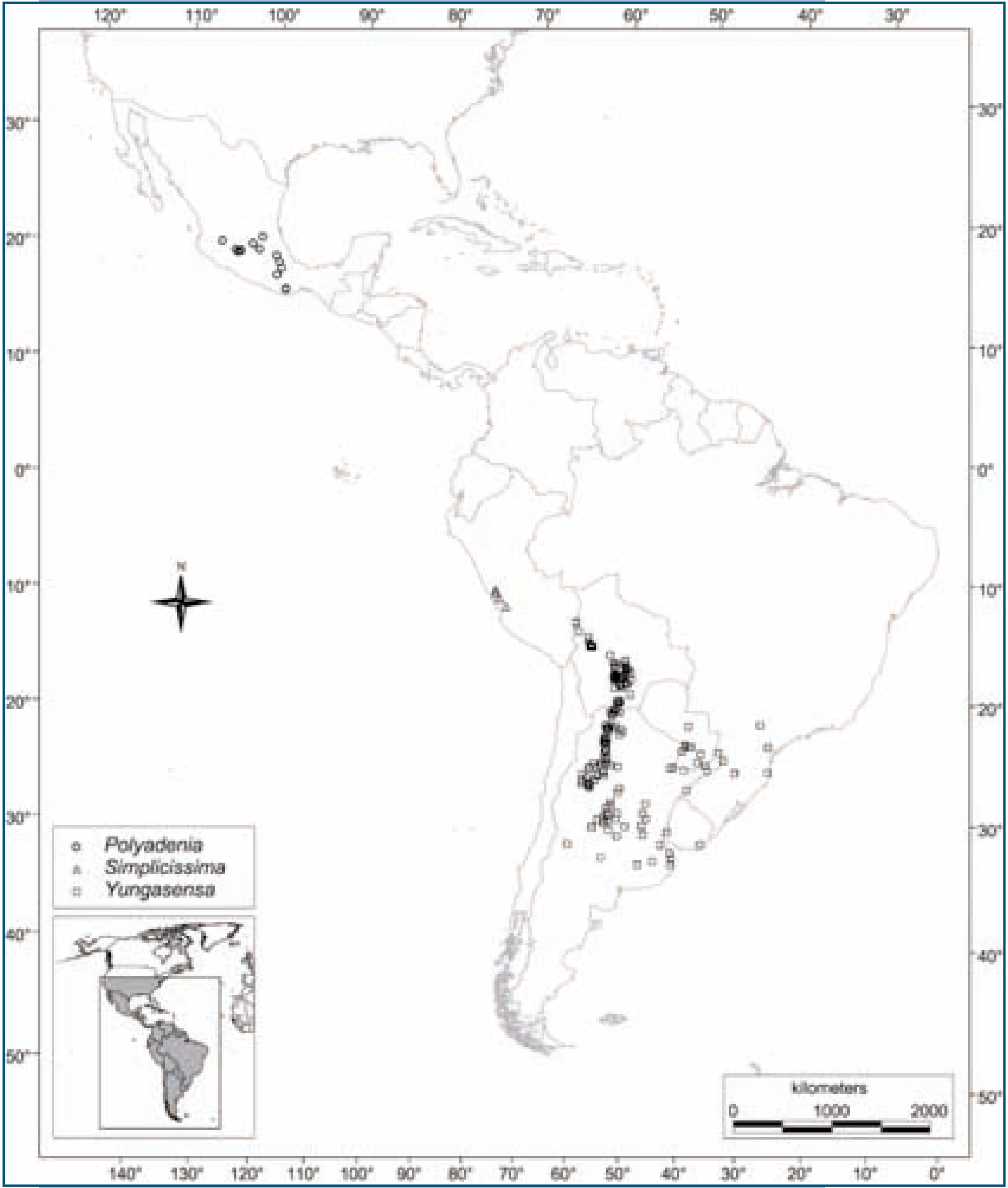
Distribution of series

Map 63. Distribution of series *Cuneoalata*, *Demissa*, and *Lignicaulia*, and of section *Etuberosum*.



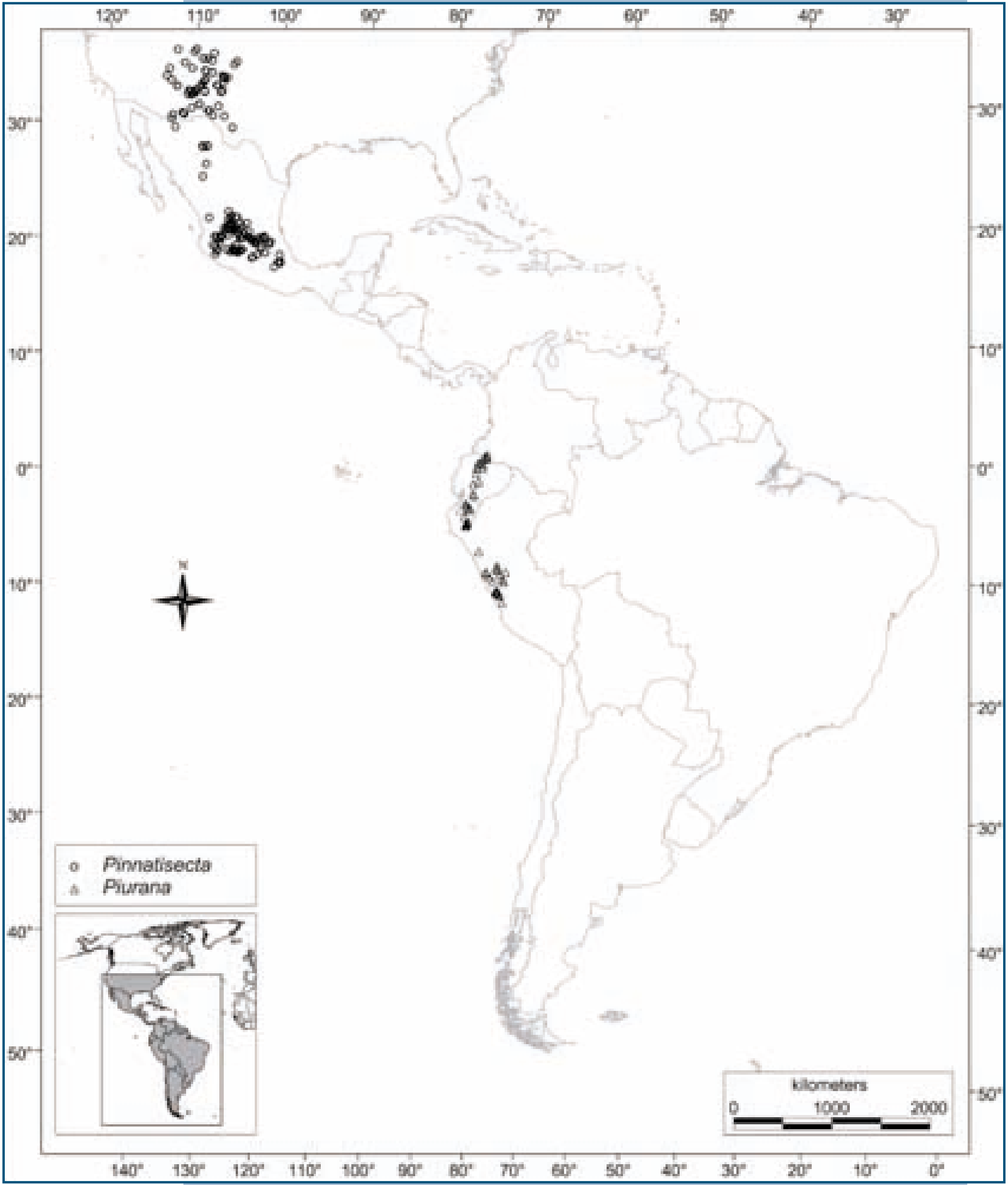
Distribution of series

Map 64. Distribution of series *Polyadenia*, *Simplicissima*, and *Yungasensa*.



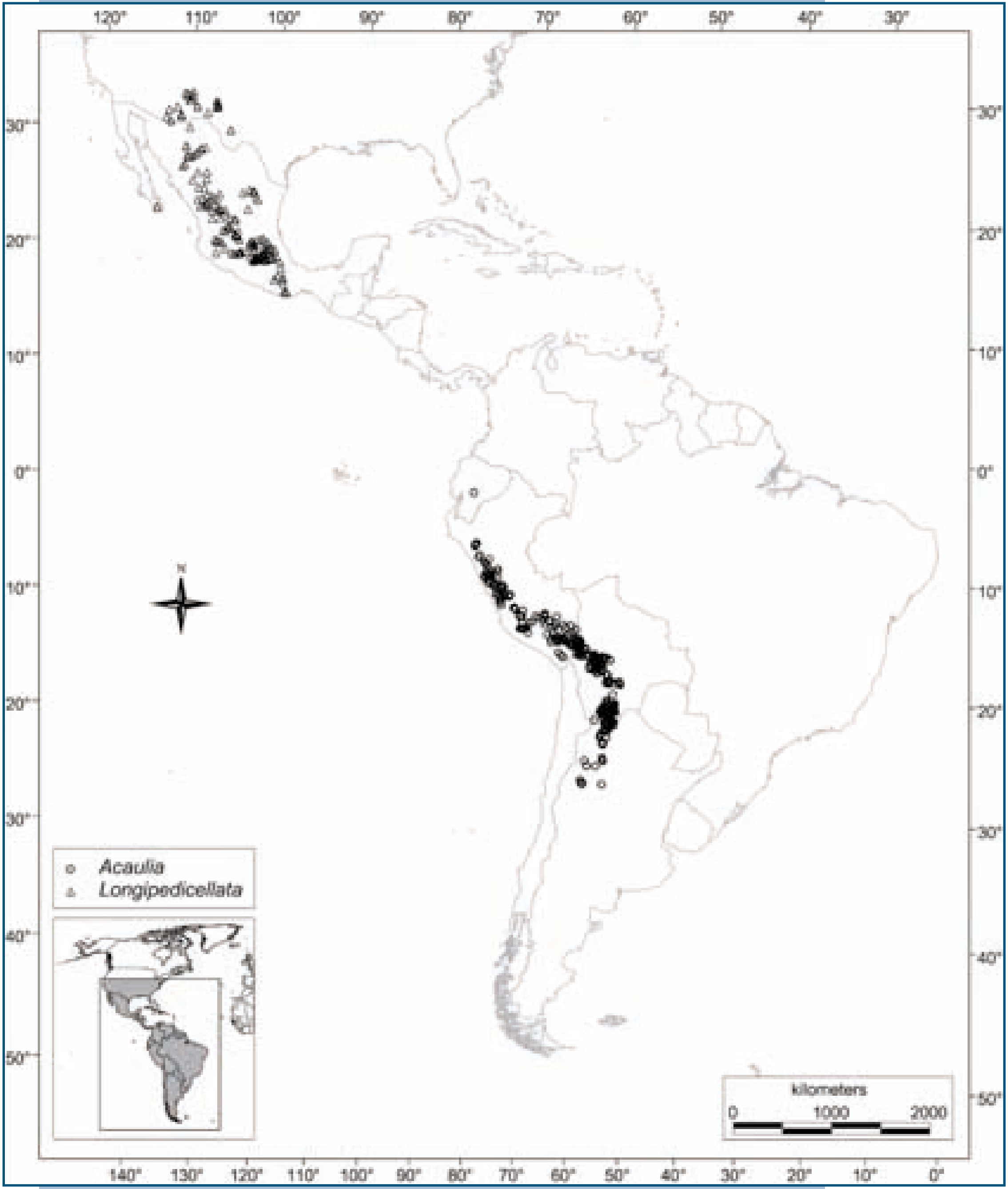
Distribution of series

Map 65. Distribution of series *Pinnatisecta* and *Piurana*.



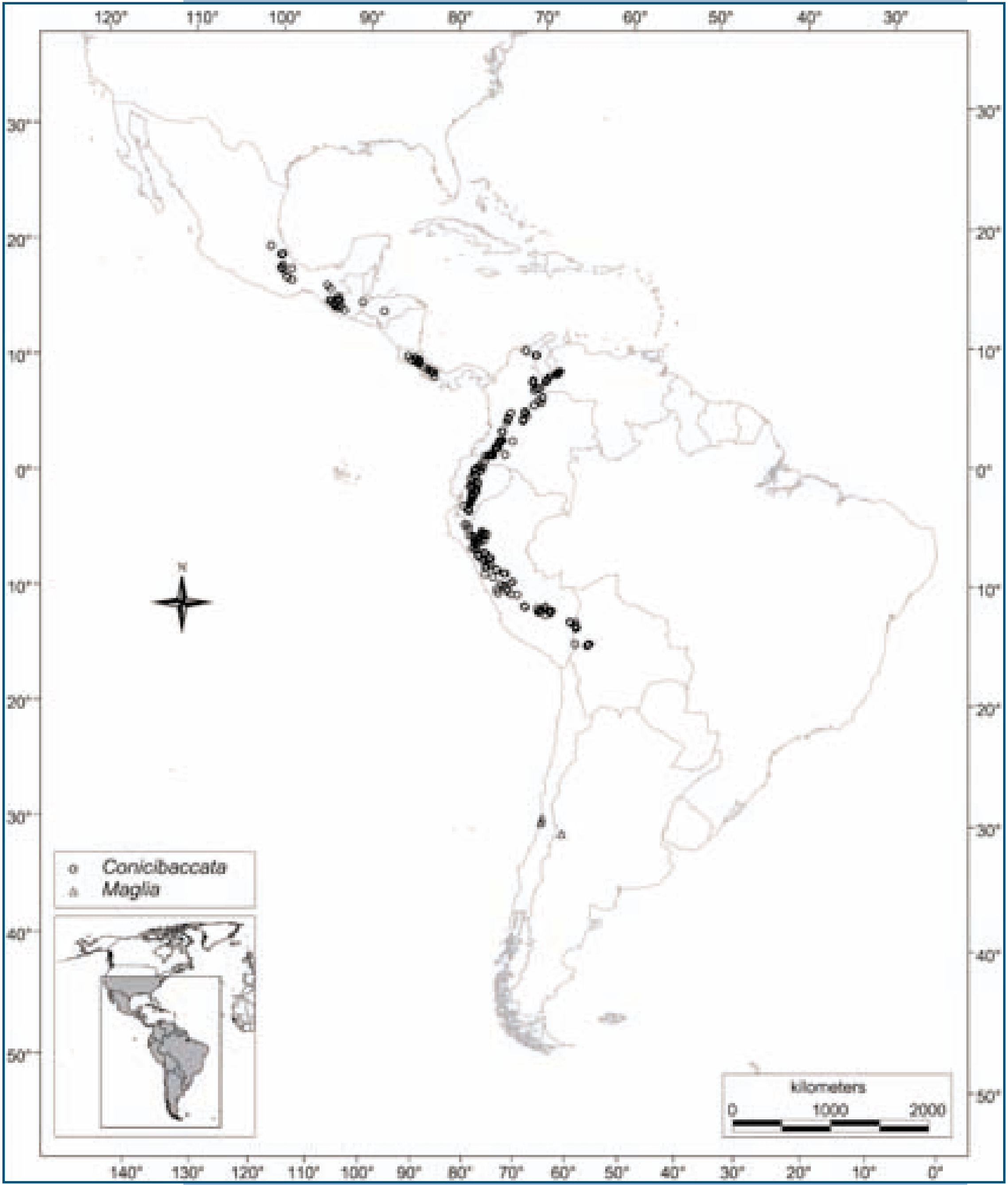
Distribution of series

Map 66. Distribution of series *Acaulia* and *Longipedicellata*.



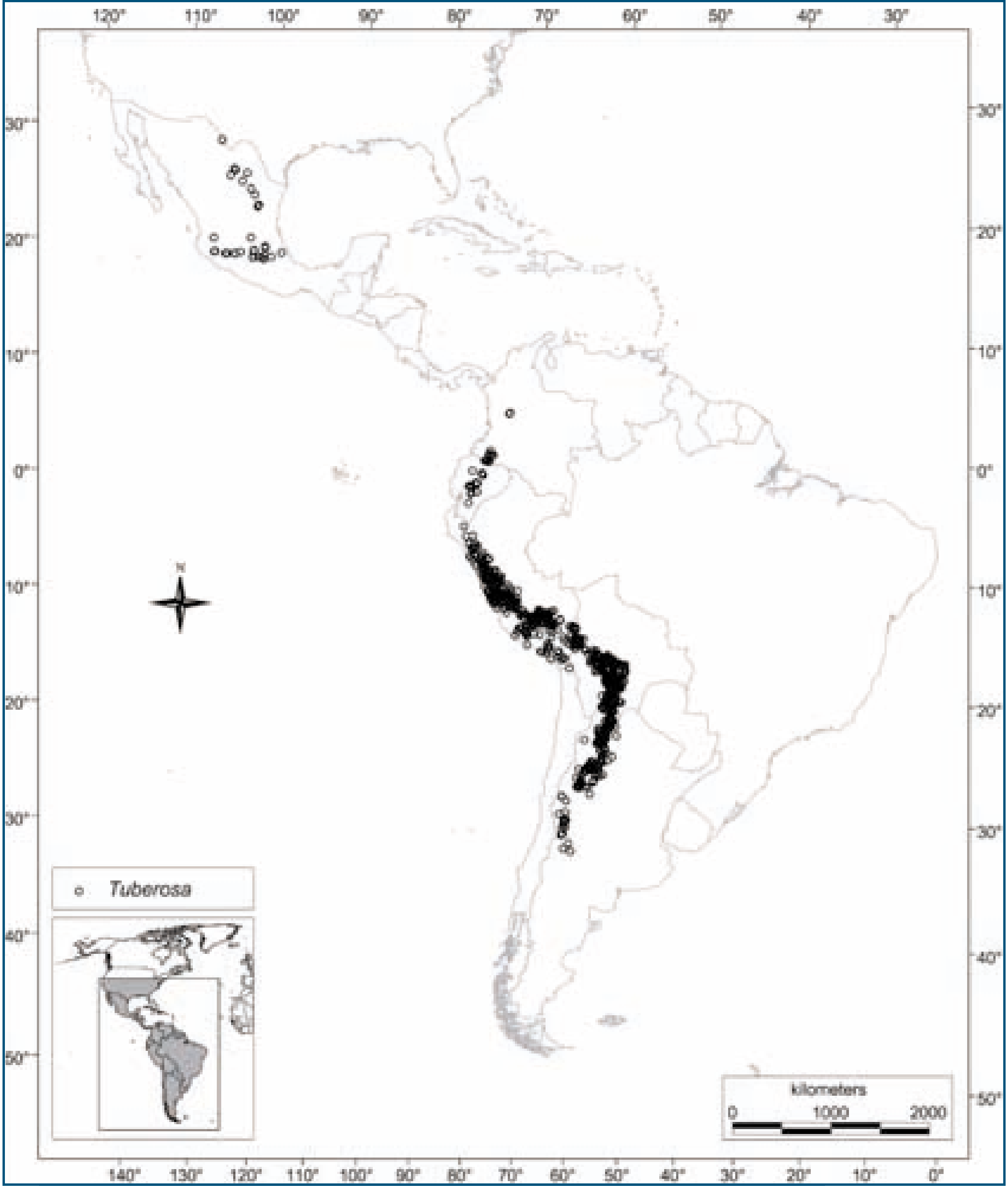
Distribution of series

Map 67. Distribution of series *Conicibaccata* and *Maglia*.



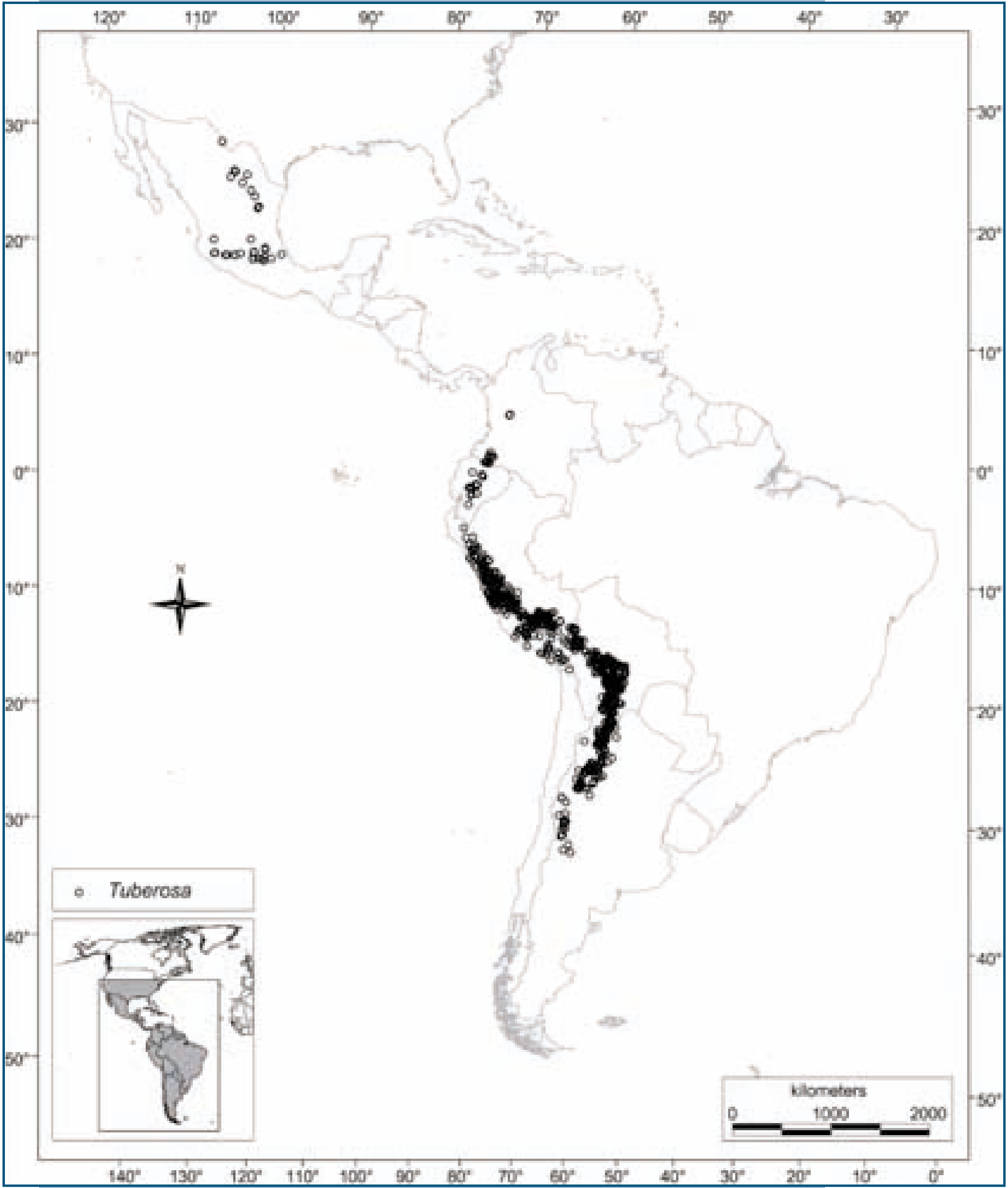
Distribution of series

Map 68. Distribution of series *Tuberosa*.



Distribution of series

Map 68. Distribution of series *Tuberosa*.



6. ECOGEOGRAPHIC STATISTICS

In this chapter we describe the distribution of wild potato species by country, we estimate their range sizes and abundance, and analyse species level ecogeographic statistics (altitude, temperature and rainfall). The material presented in this and the next chapter updates and expands the results of Hijmans and Spooner (2001), but includes only members of sect. *Petota* (unlike Hijmans and Spooner (2001) who also included the three species of sect. *Etuberosum*).

Distribution by country

Wild potatoes occur in 16 countries (Table 3), but four of these (Argentina, Peru, Bolivia, and Mexico) account for 89% of the records in the database, and they harbour 87% (171) of all species. There is a huge gap between the number of observations from each of these four countries (>926) and from the other countries (< 158).

Peru has by far most species (91 species; 46% of the total), followed by Bolivia and Mexico (36 species each). Peru also has the highest number of rare species (47; here defined as species with five or fewer observations), and 15 Peruvian species occur only once in our database (out of 17 species that occur once). The relative number (over all species in a country) of rare species is highest in Columbia (54%), Ecuador, Peru, and Venezuela.

Table 3. Wild potato distribution by country.

Country	Observations (Obs)	Species	Obs/species	Rare species (Obs ≤ 5)
Bolivia	1296	36	36	5
Brazil	24	3	8	0
Chile	6	2	3	0
Colombia	144	13	11	7
Costa Rica	24	1	24	0
Ecuador	143	16	9	8
Guatemala	69	5	14	0
Honduras	2	2	1	0
Mexico	926	36	26	6
Panama	15	2	8	0
Paraguay	22	2	11	0
Peru	1397	91	15	43
Uruguay	13	2	7	0
USA	158	3	53	0
Venezuela	24	3	8	1
Total	**5921**	**196**	**30**	**72**

The ratio between the number of observations and the number of species was calculated to assess intensity of collection by country, given the species richness it harbours. The ratio varies strongly across countries and is very high in species-poor USA as well as in species-rich Argentina, indicating that these two countries have been explored more intensively for wild potatoes than have other countries, relative to their species richness. The ratio is low in many countries, some of which have low known wild potato species richness. However, other countries in this group have an intermediate level of species richness, such as Ecuador (16 species) and Colombia (13 species). Because the number of species tends to increase with collector effort, the countries with a low ratio between species and observations would be the most likely places to find species that have not yet been discovered. Ecuador and Colombia have an intermediate number of species, but are second and third in the ranking of rare species. This might be an artefact of the low number of observations from these countries with intermediate species richness.

Although Peru seems to be reasonably well explored (number of species over observations), it has an extraordinarily high number of apparently rare species. This indicates that Peru may still harbour unknown species, as illustrated by the 10 new Peruvian wild potato species described by Ochoa between 1990 and 1999 (Spooner and Hijmans, 2001). Peruvian species are also underrepresented in genebanks, although recent collecting efforts have partly filled this important gap (Spooner et al., 1999; Salas et al., 2001).

Only 35 species occur in two or more countries. Most of these country co-occurrences are from Bolivia and Argentina (11 species in common), from Bolivia and Peru (eight species in common) and Guatemala and Mexico (5 species). There are no species that occur in both North and South America.

Solanum chacoense (Map 57) is the only species that occurs in five countries, and *S. acaule* (Map 45) and *S. commersonii* (Map 58) are the only ones that occur in four countries. *Solanum chacoense* actually occurs in some additional countries as introduced ornamental plants, or wild escapes, that we do not consider here: it occurs in Lima, Peru (where it was described as *S. limense* Correll), near Adelaide, Australia (observed by Spooner), and in the wild near Simla, India (Surinder K. Kaushik, personal communication).

Distribution by species

The distribution of the number of observations by species is far from uniform (Figure 8). The most frequently observed species are *S. acaule* (627 observations), *S. leptophyes* (335), *S. megistacrolobum* (319), *S. bukasovii* (258), and *S. chacoense* (205). These five species account for 29% of the records and *S. acaule* alone accounts for 11%. The 72 species (37% of all species) with the least number of observations (five or fewer each) make up only 3% of the records. There are 21 species for which we have two observations, and 17 species for which we have only one observation. This ‘reverse J-shaped’ pattern is commonly found and a similarly skewed distribution has been described for Bolivian genebank accessions by Hijmans et al. (2000), and for the Interpotato Genebank by Huamán et al. (2000).

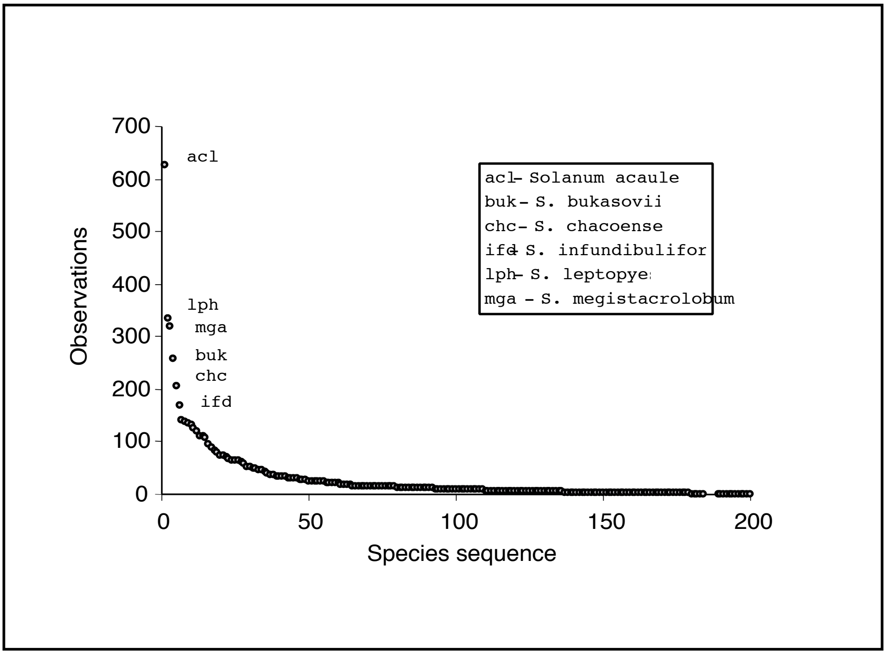


Figure 8. Number of observations by species in our database.

Range size statistics

It is not obvious how to estimate range sizes from distribution data. It can be done by drawing polygons around the dots of the localities of a species, and measuring the area of the polygons. However, this is subjective, particularly in the case of dots that are far apart, or with species with disjunct distributions.

Instead, we used two statistics that can be objectively measured (1) maximum distance (MaxD) between two observations of a single species and (2) circular area (CA_r). MaxD is defined as the maximum distance (in meters) between all possible pairs of observations of one species. It was calculated with DIVA-GIS. CA_r was calculated with ArcInfo by assigning a circular area with a radius *r* to each observation, and calculating the total area of all circles per species. Areas where circles of a species overlap are included only once. Figure 9 illustrates how these two statistics are calculated.

CA_r is expressed as the area relative to the area of one circle, i.e., as the number of circular areas covered. The assumption is that each point observation represents a group of plants that covers a circular area with the selected radius. We used a radius of 50 km (i.e., CA_{50}). Expressing CA_r as the number of circles instead of the absolute area makes it unitless and more easily comparable across different studies and scales (when a radius other than 50 km is chosen).

Although the distribution statistics would be of most value when the assumption of equal collecting effort would has been met, we believe it is still worthwhile to describe species distributions in this way because major trends and differences are still likely to be valid.

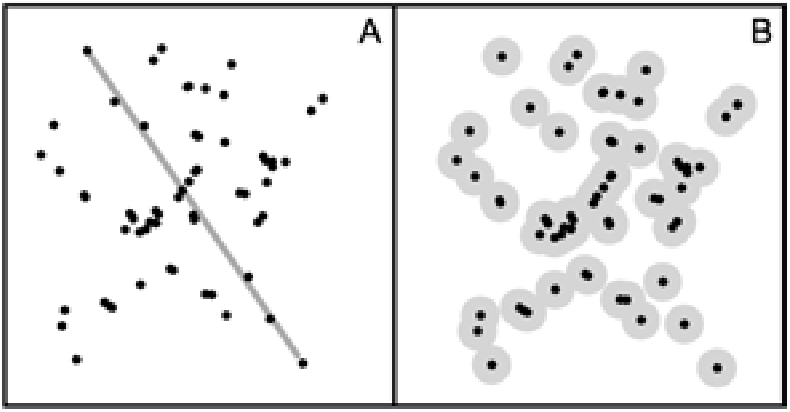


Figure 9. Illustration of the calculation procedure of MaxD (A) and CA_{50} (B) for *S. jamesii* in the USA and Mexico. The dots on panel A are the observations, the line represents the MaxD. The shaded area on panel B represents the CA_{50}.

The results are tabulated by species in Table 4. The average MaxD over species is 362 km. For 68 species (over one-third of all species) MaxD is less than 50 km, and for 104 species (53% of the total) it is less than 200 km (Figure 10). The largest MaxD observed was for *S. acaule*. At the time of this research, this number had recently increased by 732 km to a total of 3253 km, due to the recent discovery of the species in Ecuador (Spooner et al. [1992] identified it as *S. albicans*, but Kardolus [1998], recognized it an anomalous new hexaploid variety of *S. acaule*). This 'geographic outlier' can clearly be observed on Map 45. MaxD is a straightforward and easy to understand statistic, but one of its shortcomings is that it does not capture the distribution of a species that occurs in two relatively far away (disjunct) areas. This is uncommon in wild potato, but *S. okadae* (Map 46) is an example.

Average circular area (CA_{50}) over all species is 6.5, but its distribution is strongly skewed (Figure 10). Eighty-one species have a CA_{50} of less than 2, and 127 have a CA_{50} of equal to or less than 5 (many more than the 72 species with five or fewer observations).

Although MaxD and CA_{50} are strongly related (Figure 11), there are some species that deviate from the general trend. *Solanum calvescens*, *S. morelliforme*, *S. demissum*, *S. hougasii*, and *S. okadae* are among the species that have a much lower CA_{50} than expected on basis of their MaxD (Figure 11; Table 4). This deviation is related to having a very elongated and/or disjunct area of distribution, and a relatively low number of observations. In contrast, *S. acaule*, *S. bukasovii*, *S.*

Table 4 Ecogeographic distribution statistics for wild potato species. Order and three-letter species codes follow Table 1. Number of observations (Obs); Range size: MaxD and CA$_{50}$; Mean and standard deviation (SD) of altitude (Alt), annual average temperature (Temp) and annual precipitation (Rain). See text for procedures and data sources.

		Range size		**Alt**		**Temp**		**Rain**	
Code	**Obs**	**MaxD**	**CA$_{50}$**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
acl	627	3253	73.0	3796	390	9.2	2.3	524	185
ach	8	23	1.4	4060	158	8.9	0.5	695	15
acg	6	154	3.5	3069	951	11.1	3.6	748	53
acs	7	495	3.4	3485	351	7.4	1.7	254	30
agf	31	641	8.4	2595	665	19.0	2.0	2376	610
aln	32	239	6.3	2679	360	15.8	1.3	634	58
alb	66	468	9.6	3737	322	12.0	2.3	625	83
abz	5	7	1.1	2482	242	15.1	0.0	926	0
amy	2	8	1.1	3124	865	14.6	0.7	690	233
amb	17	293	5.7	2966	581	9.9	2.3	711	92
amp	2	2	1.0	2750	71	10.9	4.9	505	229
acp	15	218	4.0	3722	333	9.6	1.7	717	82
anp	1	0	1.0	3864		5.6		412	
adr	41	578	8.8	2495	358	16.0	2.1	1609	343
ara	1	0	1.0	2820		10.9		371	
adp	3	139	2.5	3152	643	12.4	1.5	670	163
arz	15	146	3.2	2378	327	17.4	1.1	702	85
agu	2	3	1.0	3333	53	11.3	0.0	615	0
avl	5	10	1.1	2810	108	19.1	0.2	793	22
ayc	1	0	1.0	3000		16.0		776	
aym	3	7	1.1	2589	185	7.7	0.0	415	0
ber	75	288	8.5	2578	355	14.7	1.6	624	53
bhk	4	23	1.4	3120	172	15.2	1.2	846	38
blg	6	201	3.0	3138	431	12.7	1.5	707	91
blv	46	528	7.5	3254	236	13.9	1.6	546	65
bmb	2	8	1.1	3356	499	9.5	0.0	971	0
bst	26	952	9.1	2091	321	17.9	1.3	491	157
bcp	64	883	15.7	2603	349	18.0	2.2	1086	274
brc	52	790	17.2	3487	513	12.2	2.7	597	141
bru	3	97	2.0	2395	1596	11.9	6.1	572	242
bue	11	113	2.5	3232	788	9.7	1.9	662	80
buk	258	1245	34.5	3665	509	8.5	2.5	635	182
blb	65	1510	24.5	2086	484	16.9	2.7	1247	680
brk	2	1	1.0	3001	1	15.3	0.0	723	0
brt	2	12	1.1	3000	0	13.4	0.0	1205	0
cjm	12	89	2.7	2768	104	14.7	1.6	558	124
cln	1	0	1.0	3000		16.1		1749	
clv	8	1200	5.9	872	330	22.1	3.7	1528	63

		Range size		Alt		Temp		Rain	
Code	**Obs**	**MaxD**	**CA_{50}**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
cnd	36	161	4.0	3702	404	10.2	1.4	878	178
cnt	8	335	4.5	3005	374	10.1	2.5	443	84
cph	48	695	19.0	2038	236	17.5	1.4	637	163
chc	205	2426	74.2	1232	863	16.3	3.6	743	369
chn	7	32	1.4	430	178	18.2	0.1	117	17
chl	3	40	1.5	2512	1258	18.6	0.5	825	84
chi	2	8	1.1	4075	35	8.3	0.0	558	0
chq	21	397	7.2	2975	419	14.6	1.6	552	118
chm	79	985	17.0	3456	608	13.0	2.7	711	128
crc	38	586	9.2	3112	453	12.7	2.4	699	59
clr	27	198	4.5	3160	232	18.0	2.0	2504	402
cop	21	96	3.1	3340	498	9.0	0.7	618	71
col	109	1734	28.8	3045	479	15.9	2.9	1432	368
cmm	82	1778	45.2	138	379	18.0	2.9	1204	315
ctz	2	1	1.0	2915	106	17.0	0.0	357	0
dms	134	1912	19.7	3007	481	15.1	1.5	1046	381
dds	24	230	5.5	2359	205	16.8	1.1	628	65
dcm	15	244	4.6	3985	275	9.2	2.1	749	35
dnc	2	9	1.1	3165	219	16.3	5.0	1627	95
edn	35	427	7.3	2997	370	15.2	2.1	993	140
fen	94	1236	25.1	2264	363	13.3	3.4	441	111
flh	21	356	6.4	3344	424	13.9	1.2	1216	290
flv	2	111	2.0	1958	2039	16.6	5.2	1163	212
gnd	16	168	4.4	2140	238	16.7	0.9	616	38
gab	4	28	1.3	2751	899	21.0	0.0	1556	129
grc	4	2	1.0	2587	482	14.6	1.5	837	49
grr	2	476	2.0	2380	1541	22.0	1.5	923	56
gzm	4	1	1.0	2273	285	17.0	0.0	357	0
hsf	6	244	3.4	3196	615	13.9	1.4	736	60
hnt	6	17	1.2	1711	237	18.4	0.6	1191	57
hjt	13	168	3.7	2193	195	18.5	0.5	397	49
hps	14	74	2.0	2861	417	17.7	0.8	663	19
hou	16	1069	5.2	2722	485	20.3	1.9	980	190
hcb	9	104	2.4	2379	887	18.0	1.9	429	102
hcv	1	0	1.0	3926		10.8		759	
hro	17	345	4.8	3483	614	9.6	3.3	475	108
hmp	3	48	1.6	2892	101	17.2	0.5	832	54
hcr	15	279	3.1	2906	622	10.8	2.0	404	73
imt	13	591	7.5	1442	944	14.5	3.8	325	184
inh	1	0	1.0	2875		17.6		305	
inm	10	38	1.5	2260	232	9.8	0.9	587	32

		Range size		Alt		Temp		Rain	
Code	**Obs**	**MaxD**	**CA_{50}**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
ins	1	0	1.0	3900		8.9		612	
ind	2	51	1.6	3947	1343	8.9	1.5	470	96
ifd	170	751	15.7	3627	333	8.8	1.9	363	113
igf	5	16	1.2	2985	339	18.0	0.0	548	42
iop	6	459	3.3	2145	206	15.8	1.5	1399	365
irs	9	47	1.7	2905	323	15.5	0.5	532	34
jnn	1	0	1.0	2700		15.7		450	
jlc	6	137	2.7	3499	297	13.4	1.0	581	54
jam	89	972	35.2	2105	312	10.2	3.1	370	60
ktz	132	928	18.0	1562	512	13.0	2.5	314	109
lxs	11	1025	8.7	2689	1104	14.7	4.5	1041	490
lph	335	1587	31.4	3458	391	9.0	2.2	474	87
lps	6	471	5.1	1790	400	19.8	0.7	267	42
les	4	173	2.1	2281	86	17.0	0.7	862	171
lgl	14	67	2.3	3094	337	9.6	0.4	703	37
lmb	4	59	1.8	3071	814	13.2	2.9	1536	268
lit	3	15	1.2	2063	56	18.0	0.0	634	0
lbb	5	13	1.2	3541	139	15.0	0.7	1993	59
lgc	33	341	6.1	2265	542	21.7	1.8	3601	480
lgs	2	6	1.1	3550	212	7.2	0.1	483	15
lpc	1	0	1.0	2700		15.8		542	
mcp	6	23	1.3	2707	393	16.4	0.4	496	25
mag	10	254	2.6	903	910	11.8	1.3	409	44
mrn	31	221	6.1	3058	656	9.4	1.8	706	234
mat	3	497	2.0	2247	737	17.7	0.3	845	808
med	61	1227	16.6	2135	1077	10.8	4.3	364	206
mga	319	1475	35.0	3732	354	10.1	2.6	462	147
mch	4	7	1.1	2038	49	18.2	0.1	921	26
mcd	139	1373	23.3	2441	584	14.5	3.1	639	119
min	5	13	1.3	2688	891	13.7	0.5	1263	131
mcq	12	707	5.8	1180	1060	17.3	1.7	299	200
mrl	34	1647	14.7	2426	340	18.3	1.9	1786	760
msp	24	884	6.5	3186	274	14.1	1.4	1576	261
mtp	69	560	9.9	3430	327	10.6	2.5	537	129
nyr	5	215	2.4	2280	139	19.9	1.7	914	208
nmr	2	0	1.0	2786	21	15.3	0.0	529	0
ncd	6	262	4.0	2357	783	16.5	2.8	737	115
nrs	5	147	2.1	2992	304	11.0	0.1	487	62
nvz	2	33	1.4	2330	1867	17.6	2.6	1293	333
nvg	1	0	1.0	2800		11.1		830	
nvv	9	23	1.3	3292	349	10.6	1.3	1076	125

		Range size		Alt		Temp		Rain	
Code	**Obs**	**MaxD**	**CA_{50}**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
nwb	16	173	3.5	303	550	17.2	2.1	96	81
nub	2	128	2.0	3752	200	15.8	0.5	863	58
oka	44	918	6.0	2991	316	12.1	1.3	664	47
olm	4	254	2.1	1687	146	21.7	1.3	231	23
opl	121	733	13.7	3243	425	11.2	3.0	392	152
oro	5	26	1.3	3388	427	21.0	0.0	1618	141
orp	13	188	4.7	3503	337	9.4	1.7	756	53
ort	1	0	1.0	2600		8.8		528	
oti	8	302	3.9	2721	542	19.8	2.2	1274	284
oxc	24	855	6.6	2324	334	18.0	2.2	1651	400
pam	8	54	1.8	2521	443	12.7	0.9	508	20
ppl	4	56	1.7	2774	1205	15.4	4.7	1145	443
pta	28	731	10.1	2564	239	16.7	1.7	618	179
pcj	15	297	5.2	3561	130	12.2	1.0	1040	185
pcs	7	24	1.4	3156	94	18.2	0.8	423	52
plq	6	35	1.5	2272	305	11.0	1.1	640	61
pll	2	13	1.2	2800	0	12.4	0.0	1077	0
pnt	22	467	8.1	1983	413	17.4	1.7	692	142
pur	14	97	2.4	2558	618	18.7	1.1	434	103
pld	21	666	8.3	2172	152	17.0	1.1	872	140
pch	1	0	1.0	3106		12.3		1317	
rap	74	210	6.4	3555	352	8.7	1.4	697	103
raq	5	61	1.8	2051	553	19.0	0.7	370	44
rch	13	13	1.2	1828	134	12.8	0.8	242	5
rgf	4	74	1.9	2667	299	13.5	1.6	1059	320
rhl	5	79	1.9	2814	516	14.5	2.4	875	103
rzl	9	878	6.0	1133	506	13.4	1.6	339	68
sls	1	0	1.0	3000		18.3		674	
smb	4	134	3.0	2093	50	17.0	0.6	567	90
sct	19	312	5.2	2852	428	11.9	2.1	662	140
snd	6	43	1.6	2890	211	10.4	0.2	221	12
san	8	123	2.6	2713	606	11.4	2.1	905	420
srs	2	23	1.3	3084	118	7.3	0.1	212	9
swy	3	15	1.2	2080	203	11.4	0.4	764	5
sax	1	0	1.0	4697		9.0		1013	
scb	2	15	1.2	2970	42	12.8	0.0	764	0
snk	14	761	6.7	2696	131	18.3	2.2	858	301
sem	28	253	5.3	2968	431	15.0	1.9	1027	107
stl	13	272	3.6	1780	319	13.6	1.7	402	114
smp	5	203	3.1	2958	987	8.3	1.8	475	85
sst	10	17	1.2	3013	315	11.8	0.9	661	48

		Range size		Alt		Temp		Rain	
Code	**Obs**	**MaxD**	**CA_{50}**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
sgr	17	527	8.9	3500	487	11.8	2.9	630	132
sol	4	150	2.3	3885	706	13.0	0.6	1139	81
spl	140	1112	25.3	3101	508	11.5	2.5	677	249
spg	107	724	14.5	2617	636	9.5	2.8	431	136
sph	10	261	4.7	1599	331	19.9	1.2	846	162
sto	125	1709	28.2	2457	376	16.4	1.7	917	227
sup	2	21	1.3	2587	1575	17.7	0.1	1121	11
scr	71	374	9.5	3338	384	11.7	2.3	433	102
suc	1	0	1.0	2950		15.4		1702	
tcn	9	205	3.6	3042	426	9.8	1.9	223	50
tpj	2	14	1.2	3904	76	8.8	0.1	714	26
trp	5	19	1.3	3235	571	9.4	0.5	721	25
tar	112	858	14.9	2348	408	14.9	2.5	602	88
trn	11	130	3.1	2401	98	17.3	1.5	1107	359
tau	3	10	1.1	3700	295	13.3	0.0	816	5
trf	33	306	6.4	2363	570	18.6	1.9	962	114
trt	1	0	1.0	3450		17.0		357	
tnd	14	285	3.4	3134	271	13.9	0.7	1114	118
tuq	25	593	7.1	3390	432	13.3	1.7	1173	228
ugt	11	33	1.4	3443	252	16.8	0.3	644	15
uru	16	90	3.0	2884	424	10.0	2.1	732	209
vll	14	258	4.6	2708	171	14.2	1.0	976	124
vlr	12	157	3.7	3785	634	11.9	2.7	505	35
vnt	12	436	5.3	3015	472	11.1	1.2	604	47
vrn	46	689	10.1	2962	597	11.8	1.8	615	80
ver	50	739	15.4	2994	410	18.0	2.6	865	256
vid	58	744	10.7	3354	314	9.5	2.2	451	64
vrs	2	9	1.1	3550	71	8.4	0.0	417	0
vio	10	31	1.4	2824	696	12.7	1.8	788	86
vrg	8	522	5.1	3025	862	13.6	3.2	697	158
wgt	53	922	17.0	2069	360	17.1	1.5	645	155
wtm	25	167	3.8	2529	1040	11.2	3.3	359	138
wds	6	2	1.0	2945	631	21.9	0.0	3372	0
ymb	1	0	1.0	3160		14.1		513	
yun	31	484	3.7	1691	307	15.5	1.2	995	378

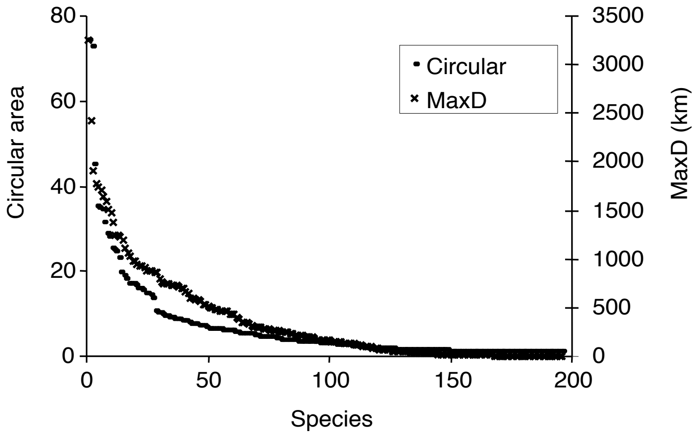


Figure 10. Two measures of range size of wild potato species. Maximum distance between two observations of one species (MaxD) and circular area (CA_{50}, see text). Species sequence is not necessarily the same for MaxD and CA_{50}.

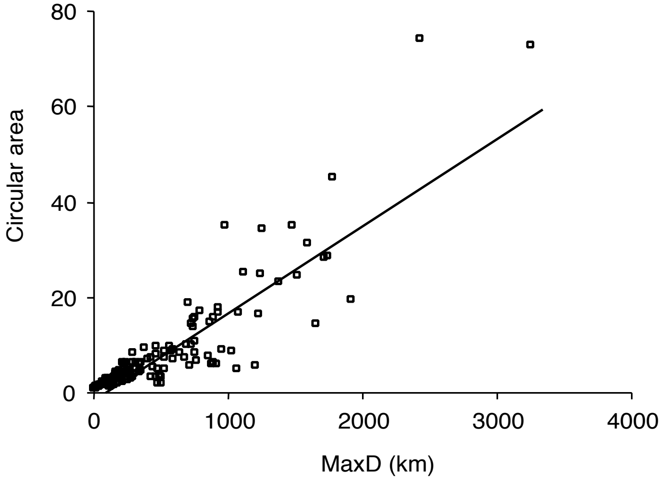


Figure 11. Maximum distance (MaxD) versus circular area (CA_{50}, see text) for all wild potato species. Regression line: $y = 0.0183x - 0.1334$; $R^2 = 0.803$.

chacoense, *S. commersonii*, and *S. jamesii* have a CA_{50} that is much greater than predicted. This is related to a relatively round area of distribution and a high number of observations.

On average, a species has a CA_{50} of 0.15 times its number of observations (Figure 12, regression line). As expected, both maximum distance and circular area go up with the number of observations. Nevertheless, important differences among species can be observed from Figure 11. For example, *S. acaule* and *S. chacoense* occur in an area of comparable size (CA_{50} = 73 for *S. acaule* and 74 for *S. chacoense*), but *S. acaule* has been observed about three times more often, suggesting that it is more abundant. *Solanum commersonii* is third in terms of CA_{50}, but is only 17th in terms of number of observations. The CA_{50} of *S. commersonii* is 0.36 times its number of observations while for *S. acaule* it is 0.12 times its number of observations. This suggests that *S. commersonii* is less abundant within its area of distribution than *S. acaule*.

The CA_{50} statistic was plotted against the number of observations to explore differences in abundance among species (Figure 12). A species with a high number of observations per CA_{50} would be abundant within its area of distribution, whereas a low number would indicate that a species has a more scattered distribution within the range in which it occurs.

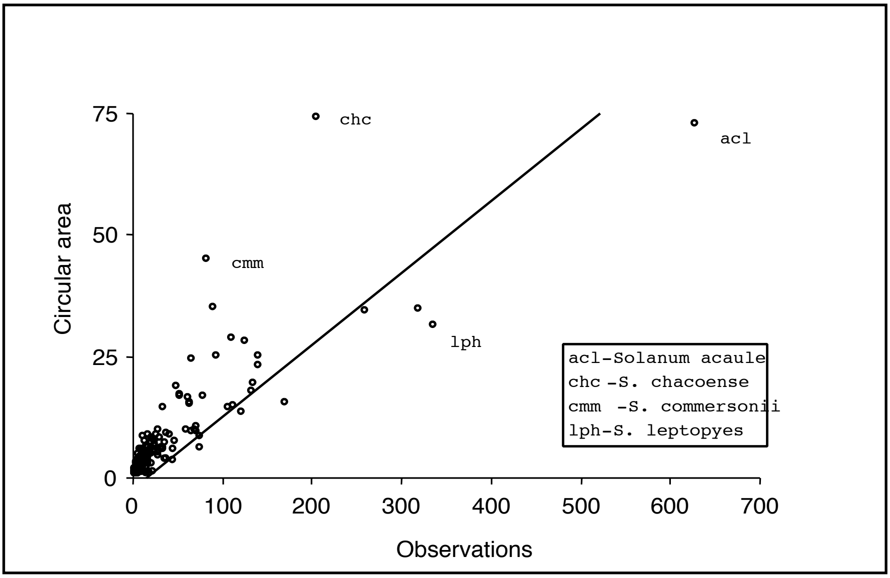


Figure 12. Circular area (CA_{50}) versus number of observations of wild potato species. Each dot refers to one species. Regression line: y = 0.15x, R^2 = 0.68.

Altitude and climate

Maps 69–71 show altitude, annual average temperature, and annual precipitation for the Americas, excluding the northern USA and Canada, where no wild potatoes occur. Altitude data were taken from a global 30 arc-second (each cell is approximately 0.8 km^2) grid with altitude data (GTOPO30; United States Geological Survey, 1998). Climate data are from 10 arc-minute resolution interpolated climate grids by Jones (1991) for Latin America and a 0.5-degree grid by New et al. (1999) for the USA.

These grids were used to assign altitude, annual average temperature, and total precipitation to all accessions. The estimate of altitude was only used for the records for which the passport data did not include altitude. We calculated averages over species (Table 4), and observations, and graphed their distribution and their distribution over latitude (Figures 13 to 18).

We grouped the altitude distribution data (over all observations, and over the average by species) in classes of 250 m and plotted the number of observations per class. Most wild potatoes occur in the highlands, particularly between 2000 and 4000 m. (Figure 13). The altitude distribution by species peaks around 3000 m. The altitude distribution by number of observations is flatter, peaks at 3500 m, and remains high until 4000 m. This implies that the species that occur at higher altitudes are generally among the more common species, such as *S. acaule*.

The average altitude for all species is 2788 m when weighted by species, and 2919 m when giving equal weight to all observations in the database. Ninety-five percent of the wild potato species occur, on average, above 1500 m. Of all observations, 51% appear in areas above 3000 m. Most of the lower altitude

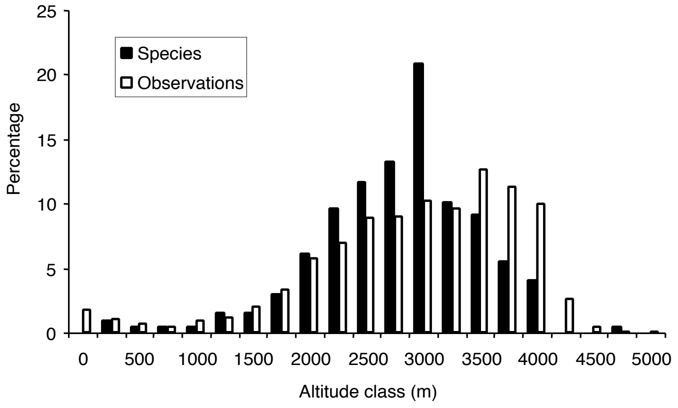
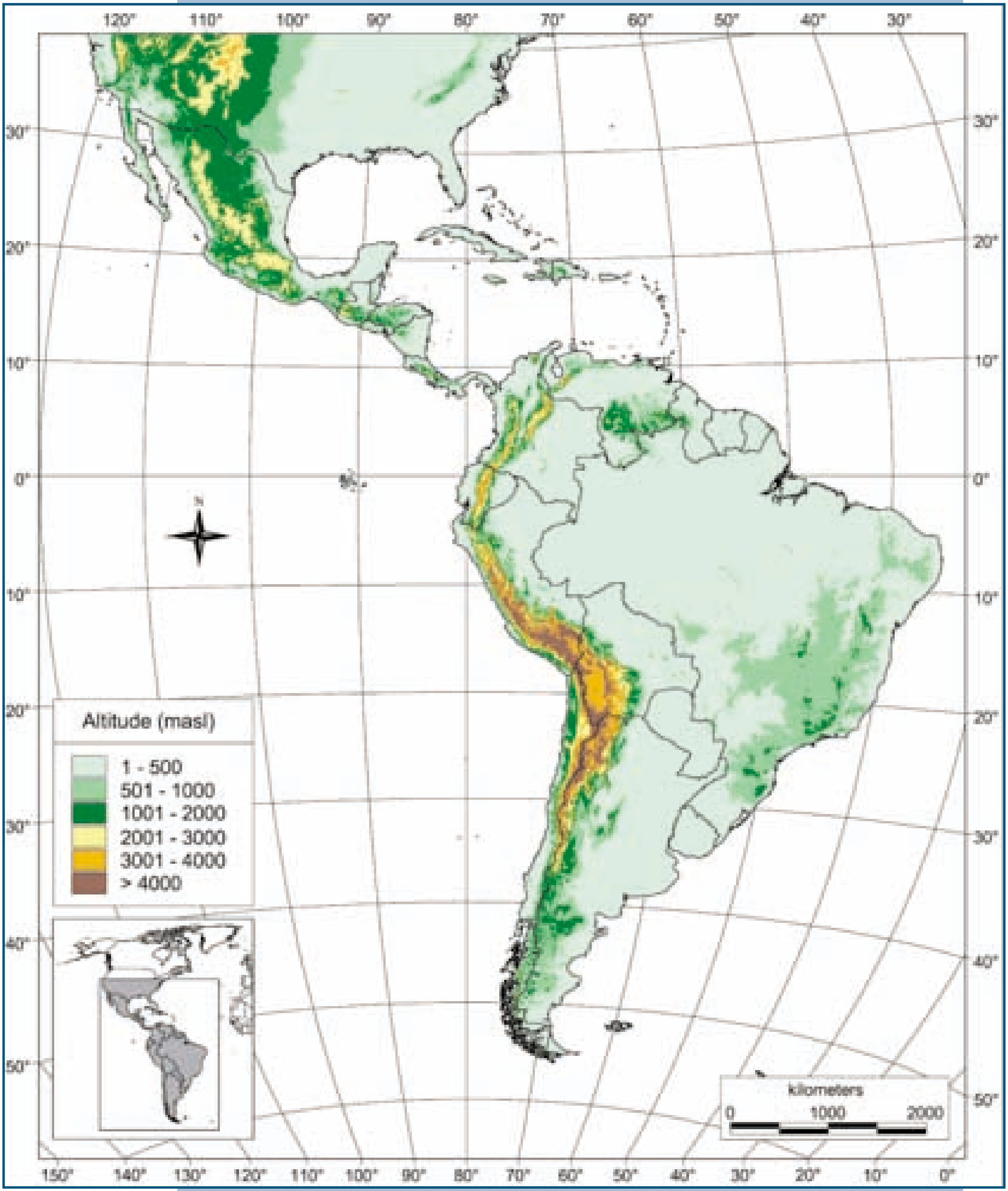
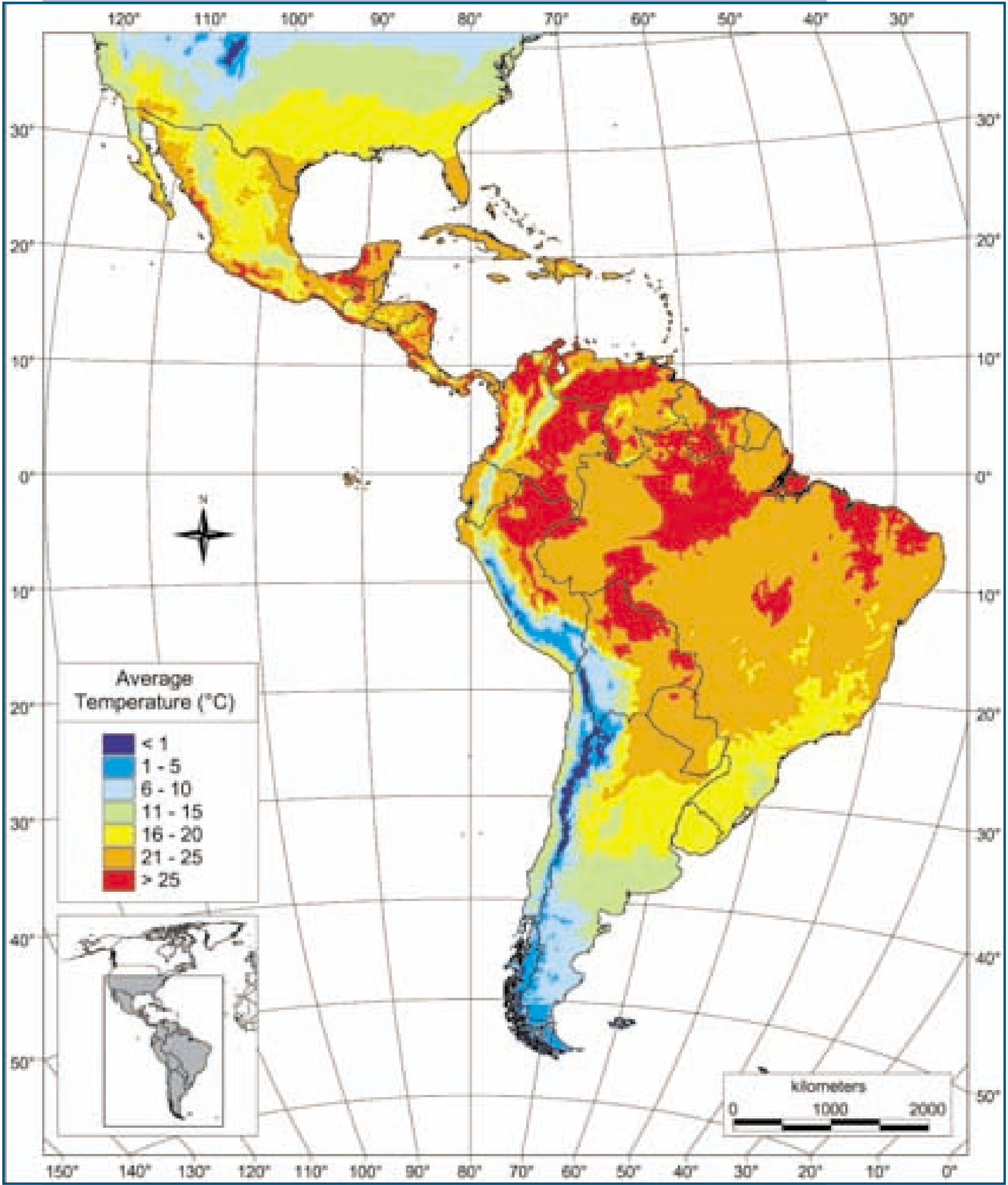


Figure 13. Altitude distribution of wild potatoes, for observations and species. The values on the horizontal axis are the mid-values of each 250-m-wide altitude class.

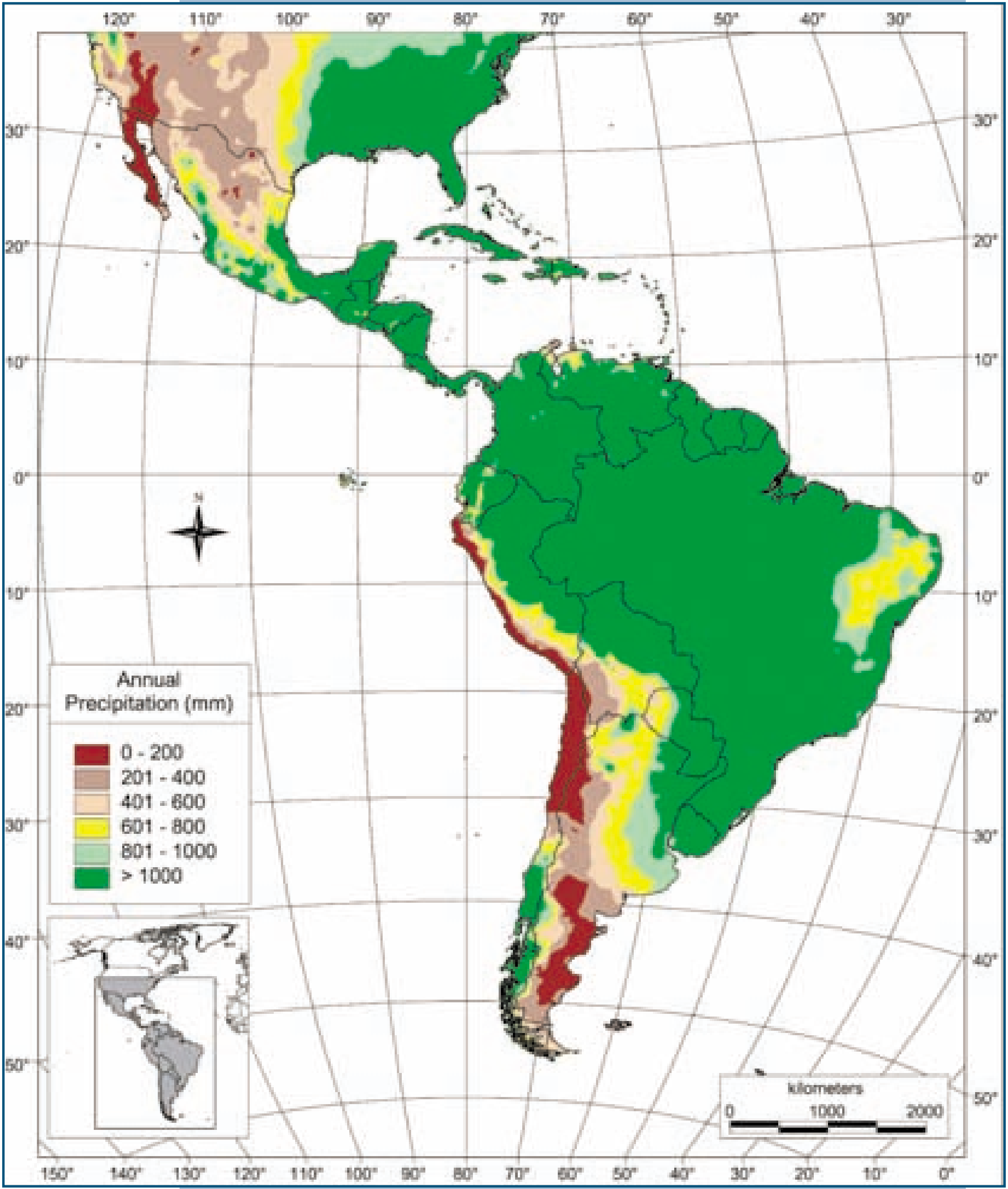
Map 69. Altitude.



Map 70. Annual average temperature.



Map 71. Annual total precipitation.



species and observations are from the plains and hills in Argentina, Brazil, Paraguay, and Uruguay, i.e., from high latitudes in the southern hemisphere.

At low latitudes in the southern hemisphere, the average altitude of wild potatoes habitats is below 1000 m (Figure 14). In most of the southern tropics, from 7°S to 24°S, wild potatoes occur at very high altitudes, on average at 3000 m or higher. Going north, the average altitude of wild potatoes gently decreases to 2000 m around 38°N. At the latitudinal extremes, wild potatoes occur in the lowlands in the southern hemisphere, but at around 2000 m in the northern hemisphere

Estimated average annual temperature in wild potato habitats ranges between –1 and 26°C; and between 5.6 and 22.1°C when averaged over species (Figure 15). The average temperature over observations is 12.7°C and 14.1°C over species. Annual temperature is lowest at highest latitudes between 9°S and 25°S, where wild potato habitats occur at high altitudes and north of 33°N, where they grow at mid-altitudes at a high latitude (Figure 16).

Precipitation in wild potato habitats ranges from less than 250 mm in the coastal desert of Peru (loma vegetation), where *S. chancayense* and *S. neoweberbauerii* occur, to more than 3000 mm for the Mesoamerican species *S. longiconicum* and *S. woodsonii* (Table 4). Average precipitation is 793 mm over species and 702 mm over observations. The species in the drier areas are more abundant than those in the wetter areas (Figure 17). There is a clear peak in precipitation between 19°N and 3°S, representing the northern Andes and Mesoamerica, where annual precipitation is more than 1000 mm. Precipitation is also higher in some areas south of 25°S (Figure 18).

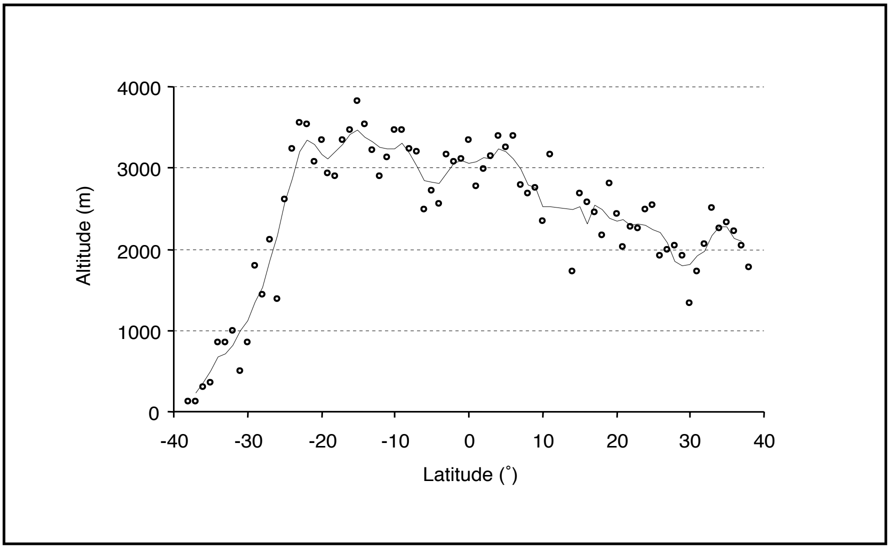


Figure 14. Altitude distribution by latitude of wild potato observations. Each dot represents one degree of latitude. The southern hemisphere is indicated with a minus sign.

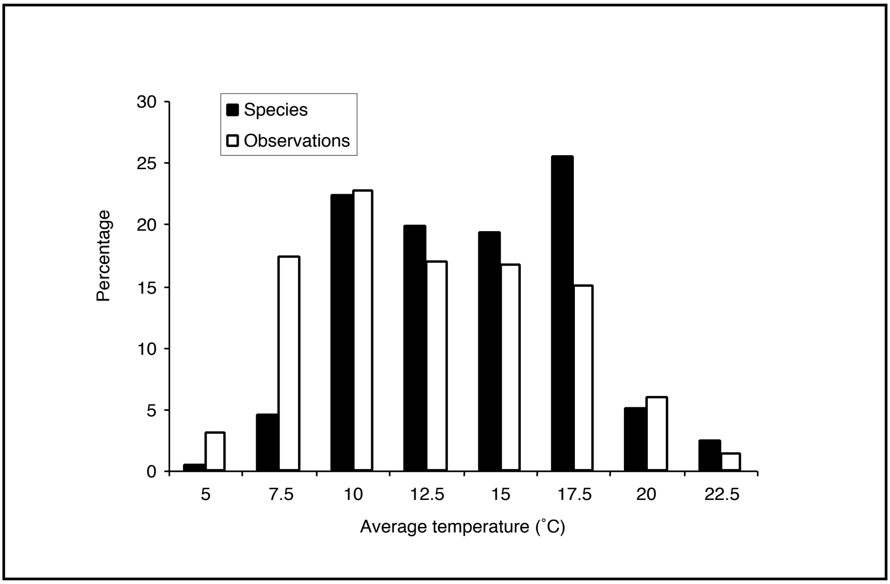


Figure 15. Temperature distribution of wild potatoes, for observations and species. The values on the horizontal axis are the mid values of each 2.5°C-wide temperature class.

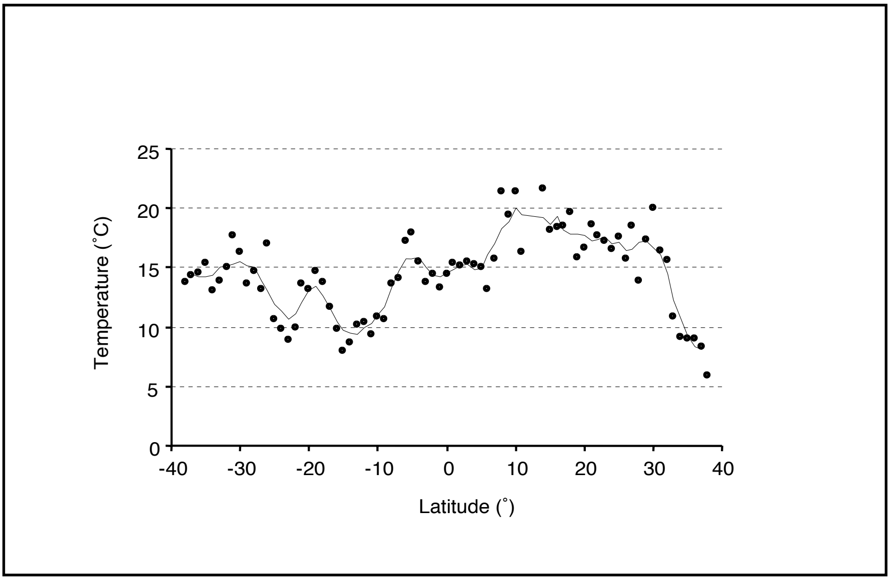


Figure 16. Temperature distribution of wild potato (over observations) by latitude. Each dot represents one degree of latitude. The Southern hemisphere is indicated with a minus sign.

Species distribution by latitude

We tabulated the number of species by latitude. First, the number of species that occur in strips of 1° latitude was determined. Then, to obtain a smoothed line, for each 1° latitude zone the moving average was calculated, using five adjacent zones (the point itself and two on each side).

Wild potatoes occur between 38°N and 41°S. The highest number of species per degree latitude (>20) occurs between 8°S and 20°S, i.e., from north-central Peru to central Bolivia, and at around 20°N, in the central Mexican highlands (Figure 19). The distribution of the number of species by latitude follows a bimodal distribution. There is a remarkably similar pattern between 20° and 40° in both hemispheres. However, in the zone between 20°N and 20°S, and particularly the zones between 8°N and 15°N and 8°S and 15°S, the number of species is rather different, with a conspicuously higher number of species in the southern hemisphere.

The lower species richness around the equator, particularly in the northern hemisphere, as compared with higher tropical latitudes, contrasts with the general pattern of increasing species richness (of all flora and fauna) towards the equator (e.g., Blackburn and Gaston, 1996; Gaston and Williams, 1996). The absence of cool tropical highlands appears to be an important factor that explains the paucity of wild potato species around the equator, particularly in the northern hemisphere. The climate in these equatorial areas is also more humid and less seasonal. The absence of a clear dry (or cold) season could diminish the relative fitness of tuber-bearing perennials such as wild potatoes. At higher latitudes, where the data are similar for both hemispheres, there is a considerable stretch of high mountains in central Mexico (the Mexican transvolcanic belt) and in South America (the Andes).

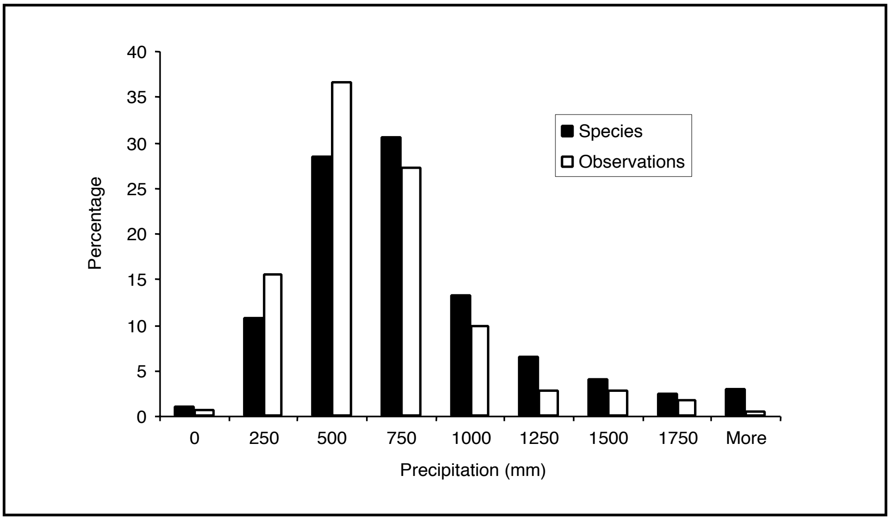


Figure 17. Precipitation distribution of wild potatoes, for observations and species. The values on the horizontal axis are the mid values of each 250-mm-wide precipitation class.

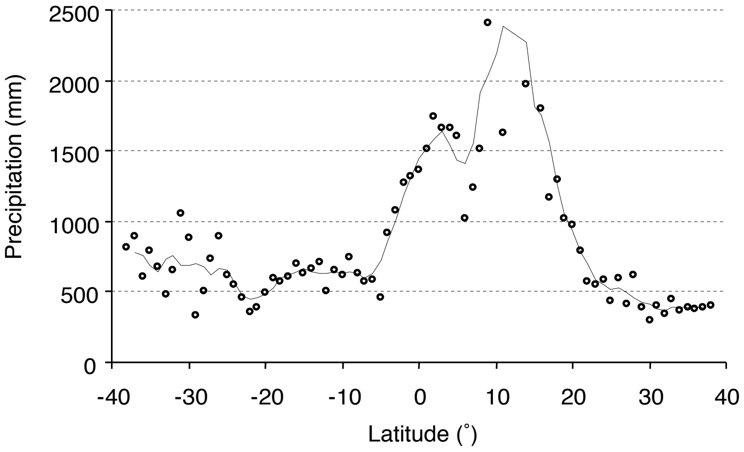


Figure 18. Precipitation distribution of wild potato (over observations) by latitude. Each dot represents one degree of latitude. The Southern hemisphere is indicated with a minus sign.

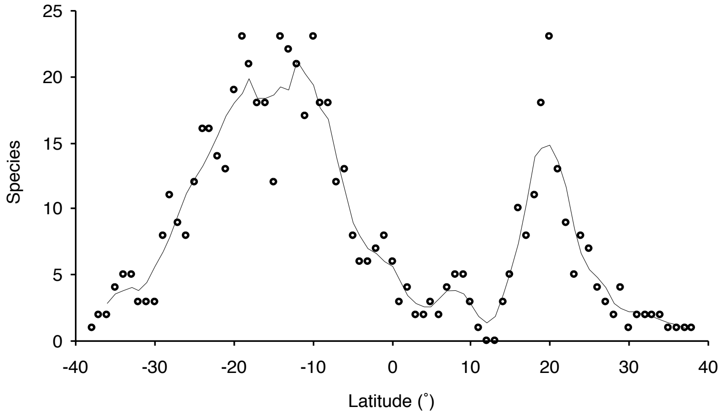


Figure 19. Number of wild potato species by latitude. The southern hemisphere is indicated with a minus sign. The line is the five-observations moving average.

7. DIVERSITY

Species richness

We determined the geographic distribution of species richness using 50 x 50 km grid cells. We used species richness as our measure of diversity because it is a simple, widely used, well-understood, and useful measure of taxonomic diversity (Gaston, 1996), and because it is less sensitive than diversity indices to the problems of unsystematic sampling intensities and procedures (Chapter 4). On the other hand, species richness is highly sensitive to labelling errors, and minor differences between the results presented here and in Hijmans and Spooner (2001) are largely due to removing this type of error, after further inspection of the species distribution maps of Chapter 5. Another reason for discrepancies with the previous study is that here we did not include the members of sect. *Etuberosum* in our analysis.

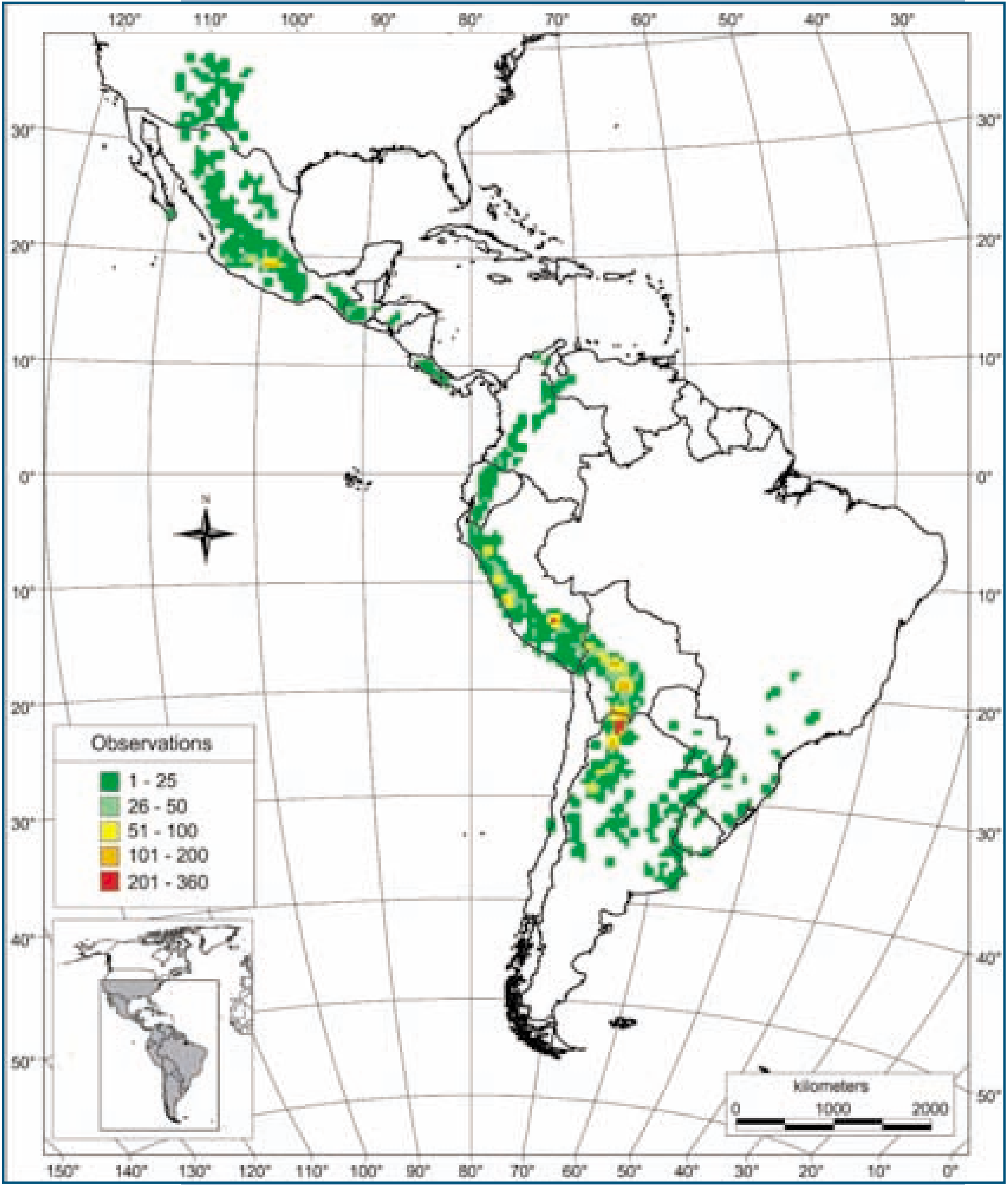
Because the origin of a grid is arbitrary but can influence the results, it may not be accurate to assign a point to one cell only, if the point is located near one or three other cells. Therefore, the data were assigned to grid cells using a circular neighbourhood (Cressie, 1991; Bonham-Carter, 1994) with a radius of 50 km, using the DIVA-GIS software. All the observations within that neighbourhood were assigned to its respective grid cell, and an observation can, therefore, be assigned more than once. The result is a smoother grid, which is less biased by the origin of the grid and also less sensitive to small changes (errors) in the coordinate data. In this paper, grid cells refer to circles with an area of pr^2 = 7854 km^2 with their centre in the middle of a grid cell with an area of 2500 km^2.

The grid based maps showing the number of observations (Map 72) and species richness (Map 73) give a much more refined picture than the country summaries presented in Table 3. Species richness is clearly not homogeneously distributed within countries.

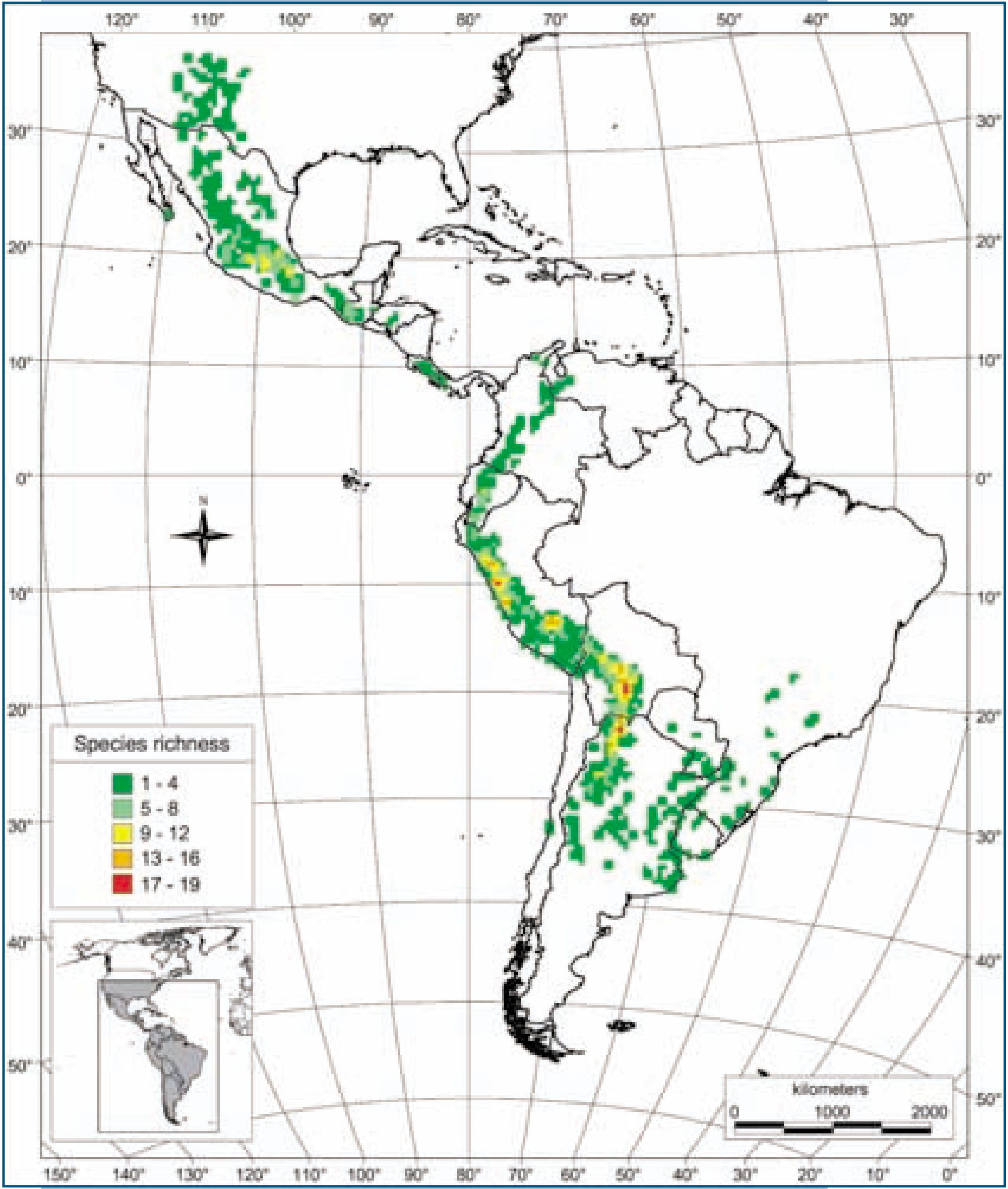
Species richness is particularly high in the southern and central Andes, and in central Mexico. Going from north to south, the principal areas with high species richness are:

1) The central Mexican highlands (México and Michoacán states).
2) A small area in central Ecuador (Chimborazo province).
3) A stretch from northern to central Peru (in Ancash, southern Cajamarca, La Libertad, and Lima departments).
4) Southern Peru (in Cusco department).
5) Central Bolivia (in Cochabamba, Chuquisaca, and Potosí and to a lesser extent La Paz and Tarija departments)
6) Northern Argentina (Jujuy and Salta provinces).

Map 72. Number of observations of wild potato species per 50 x 50 km grid cell.



Map 73. Number of wild potato species per 50 x 50 km grid cell.



On Map 73 there are few cells with many species and many cells with few species (Figure 20). Cells with more than 12 species are only found in Peru, Bolivia, and Argentina; Ecuador and Mexico are the only two additional countries that have cells with nine or more species (Table 5). Only 6% of the cells have ten or more species, while 46% of the cells only have one species (Figure 20).

The highest number of species in a single grid cell is 19, and occurs in the department of Potosí in Bolivia (Table 5). A grid cell adjacent to this cell has 17 species. There are two additional cells with 17 species: in the Peruvian department of Ancash, and in northern Argentina (in Jujuy province). Although Peru has more species overall, its most species-rich areas are comparable in species richness to those of Bolivia. However, Peru has more cells with a high number of species, and its most species-rich cell only has 19% of all species present in the country. This again illustrates the high number of endemic species in Peru. In Bolivia, in contrast, the most species-rich grid cell has 53% of all Bolivian species. There are also occurrences of relatively species-rich areas in Argentina (65% of all species in that country), Ecuador (56%), and in all countries with only a few species, but to a lesser extent in Colombia (31%) and Mexico (33%).

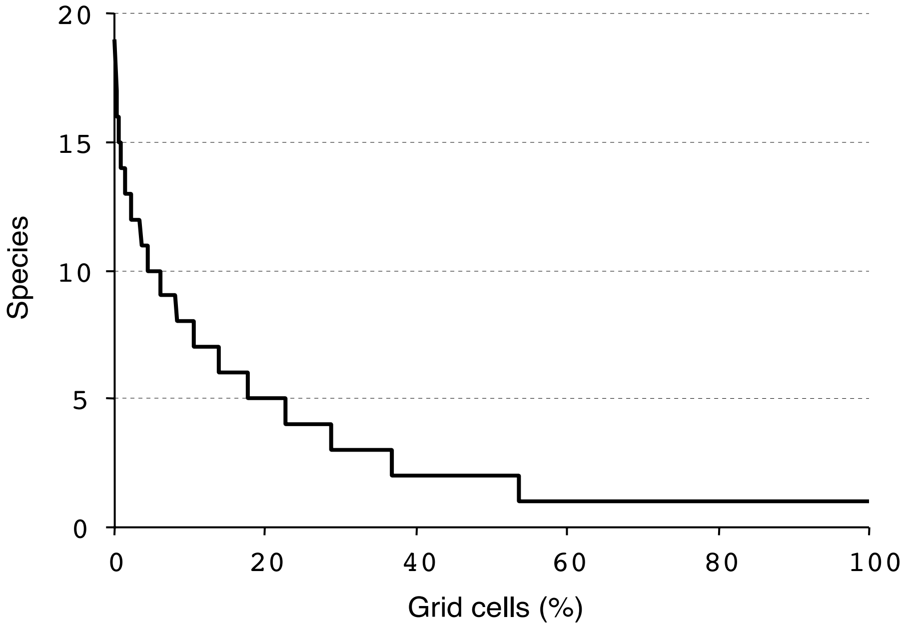


Figure 20. Frequency distribution of the number of wild potato species per 50 x 50 km grid cell.

We assessed the extent to which the number of observations predicts the number of species by plotting the number of species vs. the number of observations per grid cell. The number of species follows a similar pattern to that of the number of observations. There is a strong positive correlation between the number of observations and species richness per grid cell (Figure 21; compare Maps 72 and 73). On average over all grid cells, there are 4.7 observations per species. Important deviations from this average are some areas in the USA and Argentina. As mentioned above, the number of observations in these two countries is high in comparison to the number of species. There is a relatively high number of samples in Argentina, particularly in the areas with high diversity. For example, there are 311 observations in the cell in Argentina with the highest number of species (17), a much higher ratio than for Peru (90 observations:17 species) or Bolivia (101 observations:19 species). However, in Argentina wild potatoes occur over a larger area than in any other country (289 grid cells) and the number of observations averaged out over that area has an intermediate value (16.4 per grid cell), lower than that of Peru (19.4) and of Bolivia (40.3).

Table 5. Grid-based species richness statistics by country.

Country	**No. of grid cells with one or more obs.**	**Mean no. of spp. per grid cell**	**Mean no. of obs. per grid cell**[1]	**Highest no. of spp. in one cell**[1]	**Concentration of species richness**[2]
Argentina	288	2.4	16.4	17	65
Bolivia	114	6.4	40.3	19	53
Brazil	60	1.0	1.4	2	67
Chile	11	1.1	2.3	2	100
Colombia	65	1.9	7.3	4	31
Costa Rica	12	1.0	6.5	1	100
Ecuador	36	4.1	12.4	9	56
Guatemala	18	3.4	12.4	6	120
Honduras	5	1.2	1.2	2	100
Mexico	275	3.2	10.7	12	33
Panama	5	1.6	8.2	2	100
Paraguay	24	1.3	2.6	2	100
Peru	230	4.6	19.3	17	19
Uruguay	24	1.2	1.8	2	100
USA	118	1.2	3.9	2	67
Venezuela	11	2.2	7.0	3	100

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[1] Because of the use of circular neighbourhoods, the number of observations added over grid cells is higher than the actual total number of observations, and the number of species in a country can be higher than that in Table 3 because of cells that are in more than one country

[2] The percentage of the total number of species in a country in the cell with highest number of species in that country. In on case this is higher than 100% because of cells that are in more than one country.

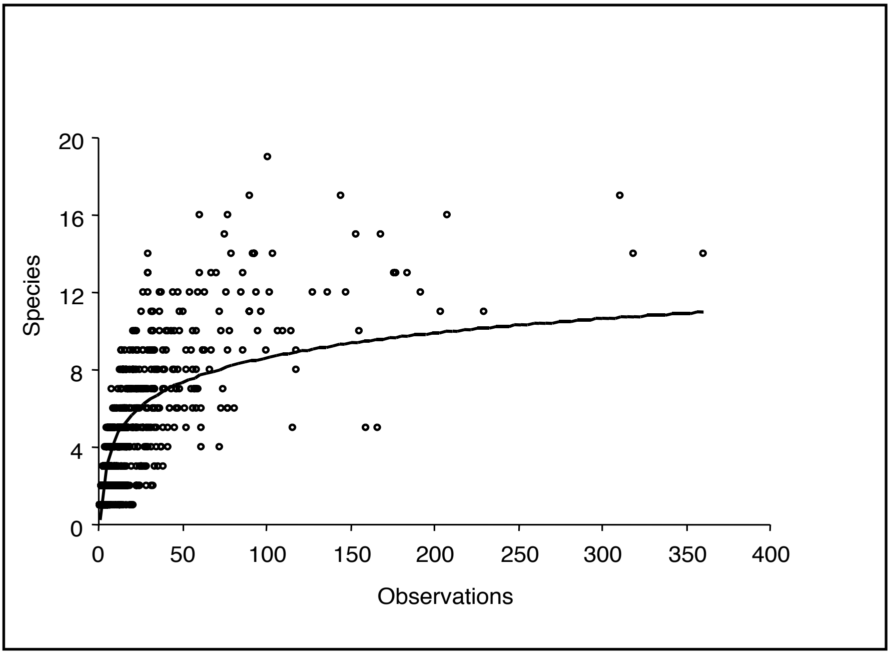


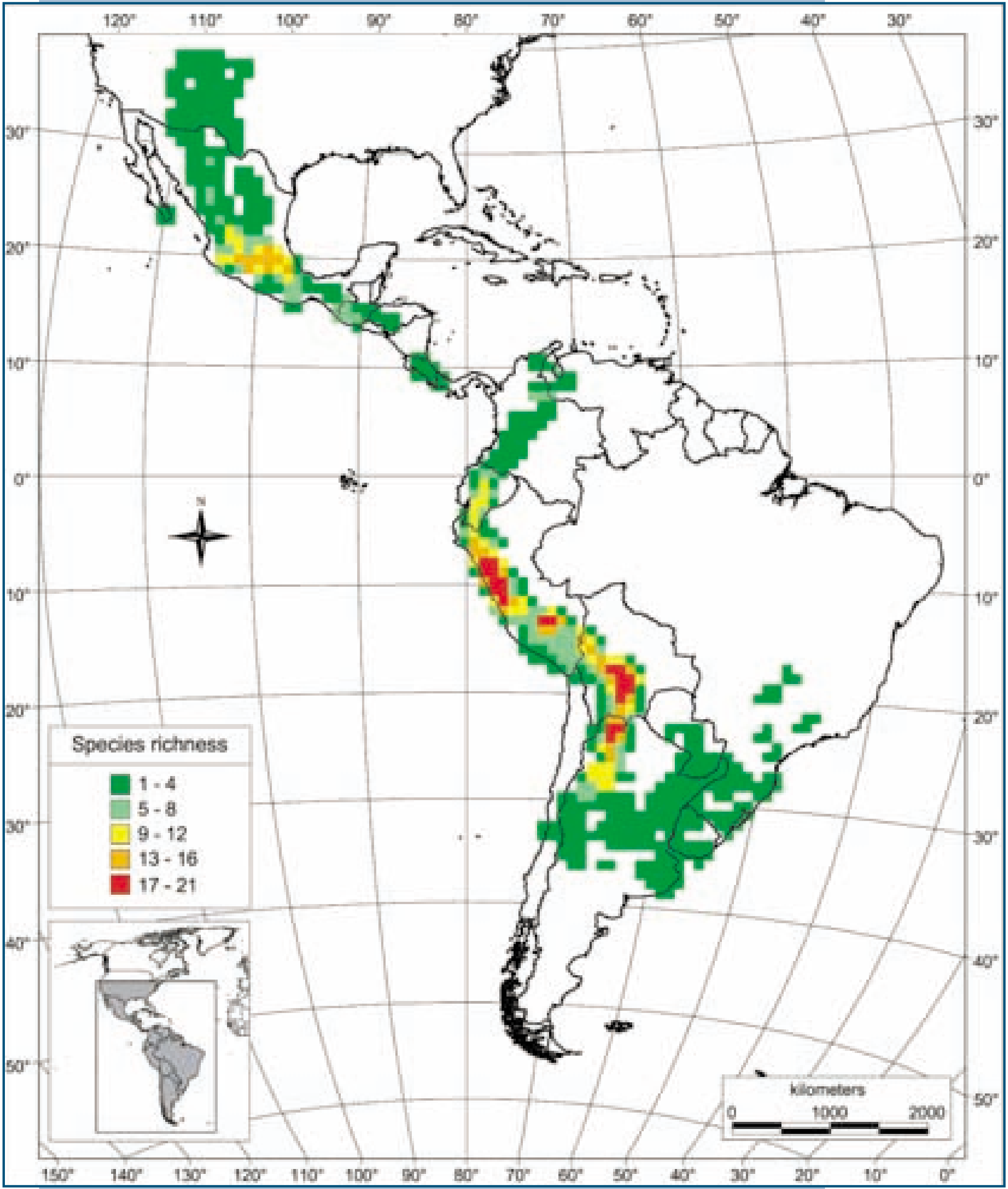
Figure 21. Ratio of the number of wild potato species to number of observations for each grid cell (obs. = 1247). Correlation coefficient = 0.74. Regression line: y = 0.22 + 1.84ln(x), R^2 = 0.68.

Scale effect

The grid/neighbourhood procedure leads to smoother, and hopefully more representative maps. However, there are yet other factors that influence the results (such as size, shape, and method used to define the neighbourhood). In addition, the scale effect (i.e., the effect of grid cell size) can be important. When larger grid cells are used the number of species per grid cell will generally increases, depending on the degree of species turnover (or 'beta-diversity') between grid cells.

An exhaustive study of the effects of gridding methods and scale effects is not provided here. We only compare the results of the species richness mapping in the previous section, with a species richness map that was made using the same method, but at a different scale (100 x 100 km grid cells) (Map 74). Among the difference between this map and the map at the higher resolution (50 x 50 km; Map 73) that the average number of species per grid cell goes up from 3.1 to 4.1 species per grid cell and that the highest number of species per grid cell goes up from 19 to 22 species. More importantly, there is also a shift in relative levels of species richness between areas. At higher resolution, grid cells in Peru have a relatively strong gain of species richness. This clearly reflects the high number of Peruvian endemic species (here defined as a narrow range size [Rabinowitz, 1981]), which leads to a high species turnover between nearby grid cells (see also the discussion about 'complementarity' in Hijmans and Spooner [2001]).

Map 74. Number of wild potato species per 100 x 100 km grid cell.



Series

The composition of series is often not supported by molecular data (Chapter 3), and is likely to undergo considerable change. However, series are commonly used and provide the only formal taxonomic grouping of species. In Chapter 5 we presented maps of their distribution, based on the species distribution maps, here we analyse the distribution of species richness. There are many small series: four have only one component species and half have three species or fewer (Table 6). There are two very large series: *Tuberosa* with 81 species and *Conicibaccata* with 38.

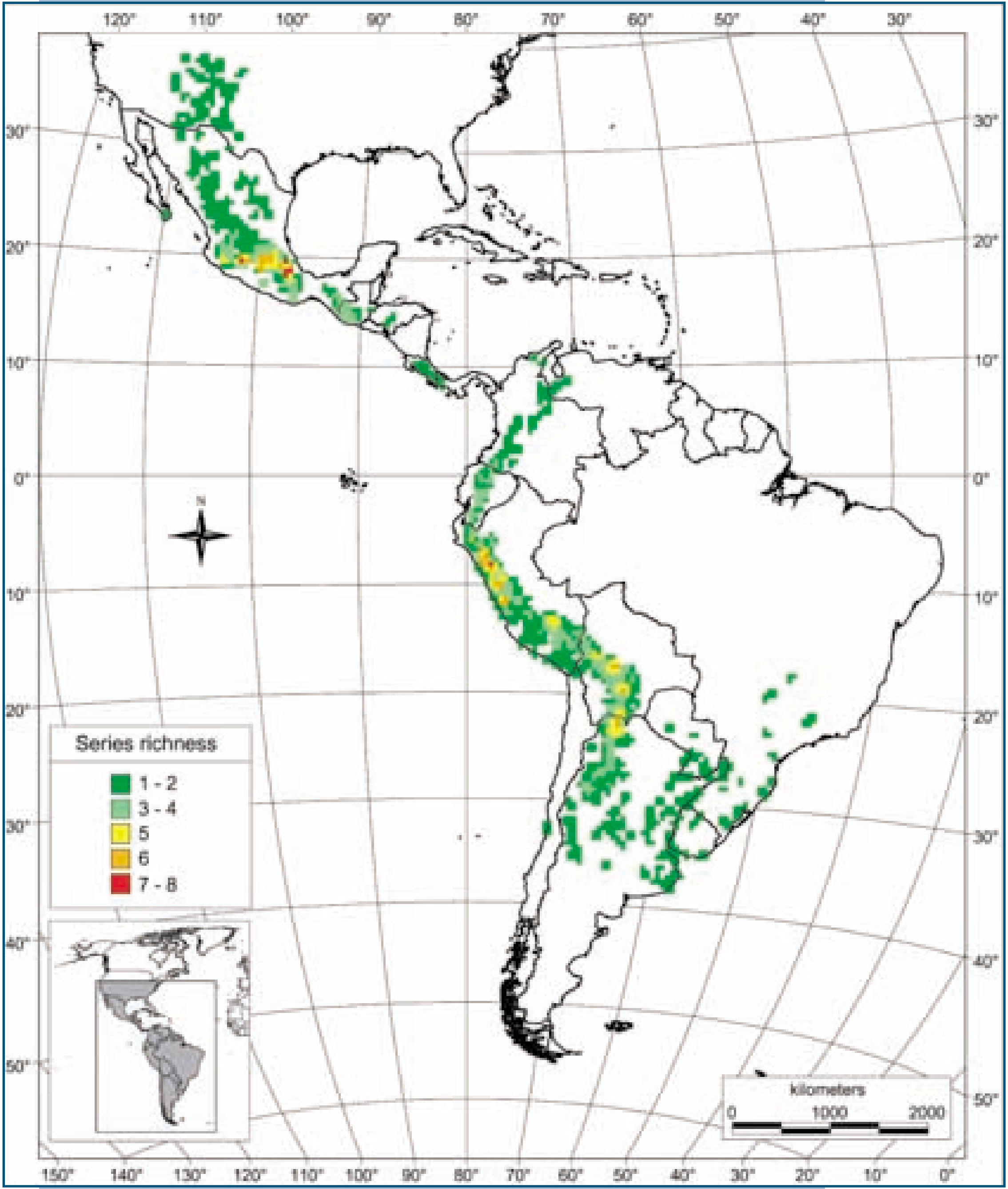
Table 6. Number of species and number of observations (Obs) in our database, and average number of observations over species for each series.

Series	**Species**	**Obs**	**Obs/Species**
Acaulia Juz.	4	697	174.3
Bulbocastana (Rydb.) Hawkes	2	92	46.0
Circaeifolia Hawkes	2	48	24.0
Commersoniana Bukasov	2	90	45.0
Conicibaccata Bitter	38	484	12.7
Cuneoalata Hawkes	4	184	46.0
Demissa Bukasov	8	299	37.4
Ingifolia Ochoa	3	16	5.3
Lignicaulia Hawkes	1	14	14.0
Longipedicellata Bukasov	7	330	47.1
Maglia Bitter	1	10	10.0
Megistacroloba Cárdenas and Hawkes	7	496	70.9
Morelliformia Hawkes	1	34	34.0
Olmosiana Ochoa	1	4	4.0
Pinnatisecta (Rydb.) Hawkes	11	258	23.5
Piurana Hawkes	13	115	8.8
Polyadenia Bukasov ex Correll	2	25	12.5
Simplicissima Ochoa	2	9	4.5
Tuberosa (Rydb.) Hawkes	81	2348	29.0
Yungasensa Correll	6	368	61.3

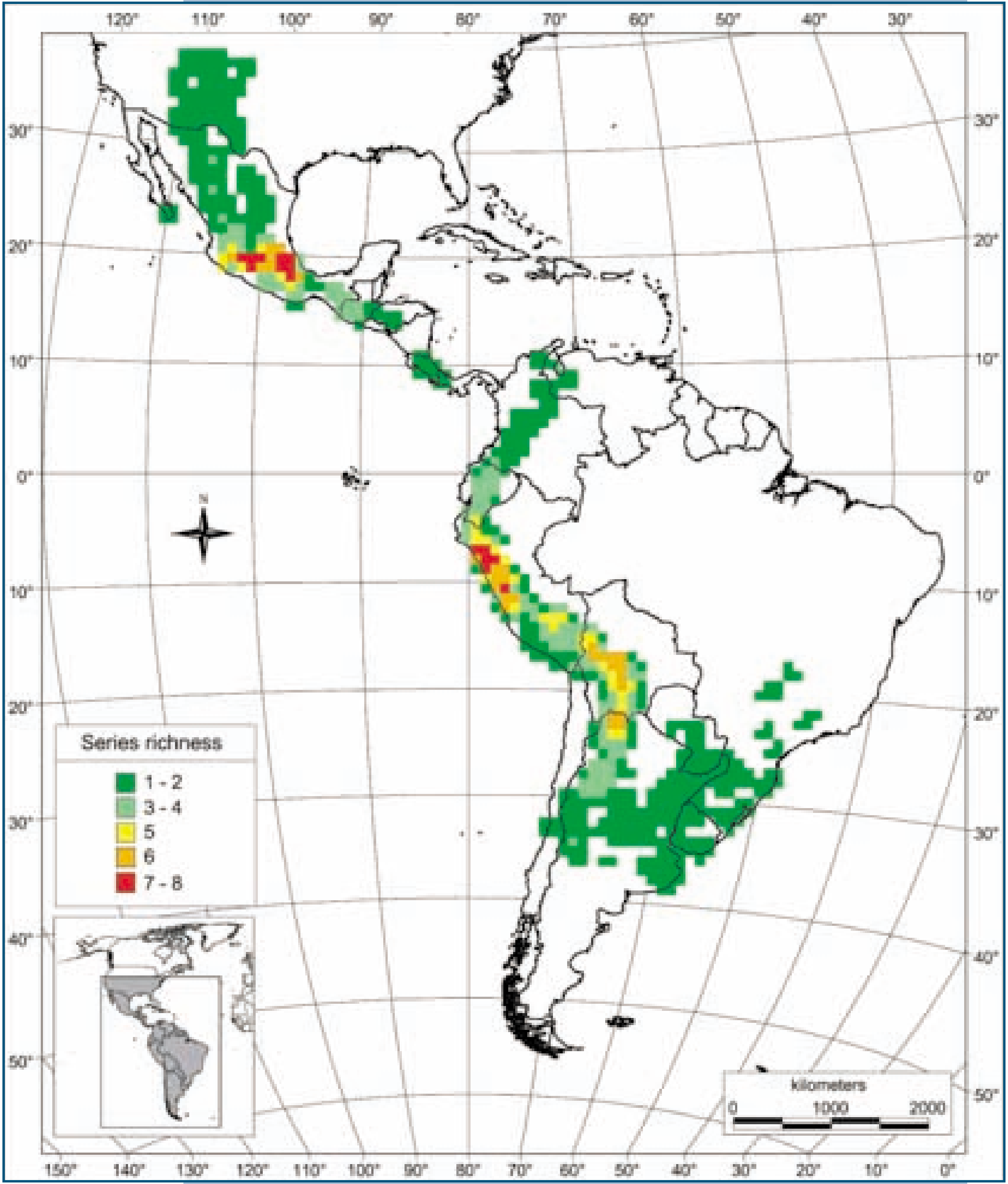
Many series have overlap in their distribution. Central Mexico, and central to north Peru stand out for series richness (Map 75). There are three small areas with high series richness between central Bolivia and north Argentina. Both at the 50 x 50 km and 100 x 100 km scale (Map 76), there are no areas with more than eight series.

Although the pattern of series richness is different from that of species richness, there is a weak relationship between the number of species and series in a grid cell (Figure 22). The most common observation is of one species, and hence one series, followed by two species and two series. There is one case of six species and six series, and one of five species and five series in one grid cell. The extreme on the other end is two grid cells with seven species from one series.

Map 75. Number of wild potato series per 50 x 50 km grid cell.



Map 76. Number of wild potato series per 100 x 100 km grid cell.



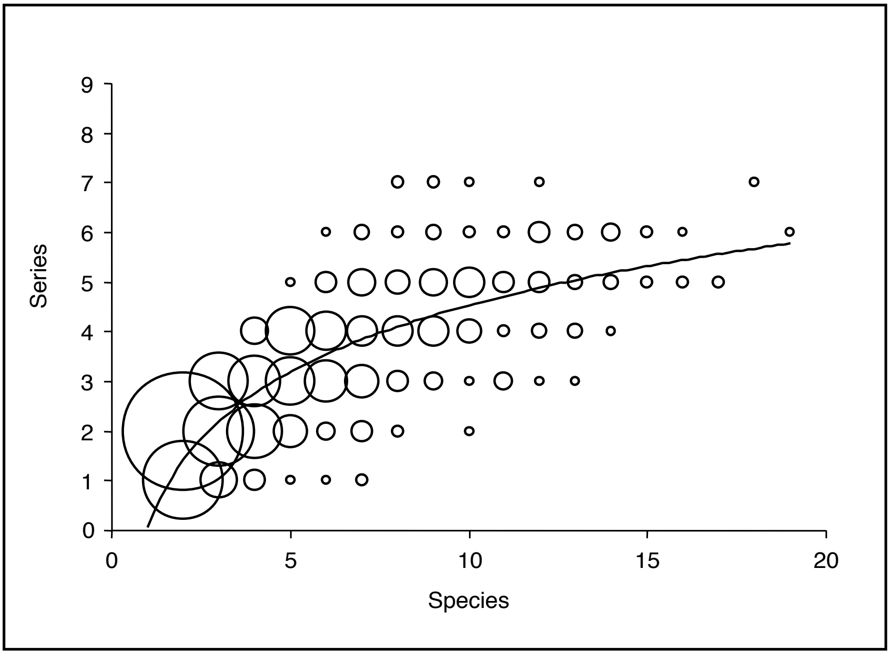


Figure 22. Number of series versus number of species by grid cell. The size of the bubble is relative to the number of grid cells (the largest bubble represents 150 cells, and the smallest 1 grid cell). The point for 1 species and 1 observation (601 grid cells) is not drawn. Regression line: $y = 0.072 + 1.94\text{Ln}(x)$; $R^2 = 0.388$.

8. CONCLUSION

Although distribution maps of wild crop relatives are common (e.g., Zeven and Zhukovsky, 1975), this is one of the first studies in which a group of closely related wild crop relatives is systematically described, mapped and then analysed using GIS. For this type of activity, it is vital to have good passport (locality) data. Typically, the quality genebank and other databases leaves much to be desired, and this may hamper analysis. Nevertheless, much can be done to improve the data quality, and to assess the information quality.

In this study, the ecogeographic distribution of wild potatoes was analysed quantitatively. Wild potatoes occur over a large range of climates both in terms of temperature and precipitation. However, they typically occur in cool climates, and not in very (seasonally) cold areas, or in the tropical lowland areas (annual average temperature >20°C). Although a few species occur in very wet areas, they are more common in semi-arid and subhumid areas with less than 800 mm of precipitation. Areas of high species and series richness were identified, expanding on the study of Hijmans and Spooner (2001).

A complication for this type of study is the existence of conflicting taxonomic classifications (Gaston, 1996) and wild potatoes are a classic case in this respect (Chapter 3; Harlan and De Wet, 1971; Spooner and Van den Berg, 1992a). Because of the complexity and dynamic nature of wild potato taxonomy, databases contain many names that are no longer accepted taxa, and others that are simply wrong. The comprehensive wild potato taxonomy of Hawkes (1990) and the review of subsequent changes by Spooner and Hijmans (2001), were crucial for this study, and basic taxonomic groundwork will be important in all other studies in which the distribution of species and diversity of a taxonomically complex group is analysed.

This atlas thus provides a snapshot of the taxonomy and species distribution at this point in time. There will certainly be future changes in wild potato taxonomy, as well as increased knowledge about the distribution of different species.

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