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Endemic wild potato (*Solanum* spp.) biodiversity status in Bolivia: reasons for conservation concerns

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Running head: Conservation status of Bolivian wild potato diversity

Abstract

Crop wild relatives possess important traits, therefore *ex situ* and *in situ* conservation efforts are essential to maintain sufficient options for future crop improvement. Bolivia is a centre of wild relative diversity for several crops, among them potato, which is an important staple worldwide and the principle food crop in this country. Despite their relevance for plant breeding, limited knowledge exists about their *in situ* conservation status. We used Geographic Information Systems (GIS) and distribution modelling with the software Maxent to better understand geographic patterns of endemic wild potato diversity in Bolivia. In combination with threat layers, we assessed the conservation status of all endemic species, 21 in total. We carried out a complementary reserve selection to prioritize areas for *in situ* conservation and excluded 25% of the most-threatened collection sites because costs to implement conservation measures at those locations may be too high compared to other areas. At least 71% (15 of 21 species) has a preliminary vulnerable status or worse according to IUCN red list distribution criteria. Our results show that four of these species would require special conservation attention because they have only been observed in < 15 locations and are highly threatened by human accessibility, fires and livestock pressure. Although highest species richness occurs in south-central Bolivia, i.e. in the departments Santa Cruz and Chuquisaca, the first priority area for *in situ* conservation according to our reserve selection exercise is central Bolivia, Cochabamba, which is less threatened than the potato wild relatives' hotspot in south-central Bolivia. Only seven of the 21 species have been observed in protected areas. To improve coverage of potato wild relatives' distribution by protected areas, we recommend to start inventories in parks and reserves with high modelled diversity. Finally, to improve *ex situ* conservation, we targeted areas for germplasm collection of species with not any or less than five accessions conserved in genebanks.

Key words: Crop wild relatives; *Ex situ* conservation; *In situ* conservation; IUCN red listing; Potato breeding material; Reserve selection; Species distribution modelling; Threat assessment

Introduction

Crop wild relatives (CWRs) include crop progenitors and their closely related species. Many of the latter species possess traits of interest for crop improvement, providing plant breeders with genes coding for biotic and abiotic stress resistance (e.g. resistance against pests and diseases, temperature, drought or salinity stress) or higher values for nutritional traits compared to varieties of their crop relatives, to name but a few (Tanksley and McCouch, 1997). Besides their role in providing genes for crop breeding, many CWRs are already exploited by local communities as they directly contribute to food security through provision of fruits, leaves, tubers and/or or seeds.

Most CWRs are maintained *in situ* and their conservation status is therefore often still largely unknown. Many CWRs are increasingly menaced by habitat loss due to agricultural intensification, the impact of invasive species, deforestation, overgrazing and overexploitation (Maxted et al., 2008; VMABCC-BIOVERSITY, 2009). In addition to these direct threats, global climate change is expected to become a long-term threat to CWRs (Jarvis et al., 2008). The Convention on Biological Diversity (CBD, 2010), the Status of Plant Genetic Resources for Food and Agriculture (FAO, 2010) and the Global Network for *In Situ* Conservation of Crop Wild Relatives (Maxted and Kell, 2009), all highlight that active *in situ* (in wild populations and on farm) and *ex situ* conservation of CWRs is essential for future crop improvement. Several global initiatives are currently being implemented to improve both *in situ* (VMABCC-BIOVERSITY, 2009) and *ex situ* conservation (GCDT, 2010) of CWRs.

Bolivia is located in one of the main centres of origin of domesticated plants in the world (Vavilov, 1951), and its high diversity of climatic conditions, soils and habitats combined with the high cultural wealth of indigenous peoples played a key role in the process of domestication (Ibisch and Mérida, 2003). Bolivia is an important centre of diversity of several globally important staple crops such as potatoes (*Solanum tuberosum* L.), peanuts (*Arachis hypogaea* L.) and chili peppers (*Capsicum* spp.), but also crops of local importance such as the Andean grains, quinoa (*Chenopodium quinoa* Willd.) and amaranth (*Amaranthus* spp.), and Andean roots and tubers. Bolivia is also an important secondary centre of diversity of several other species such as maize (*Zea mays* L.), cassava (*Manihot esculenta* Crantz) and pineapple (*Ananas comosus* [L.] Merr.), and home to many wild relatives of all these crops.

Potato is production-wise the fourth most important crop in the world, after rice, wheat and maize. The crop (and its wild relatives) is therefore included in Annex I of the International Treaty on Plant Genetic Resources for Food and Agriculture, which facilitates the access to these genetic resources (http://www.planttreaty.org/texts_en.htm). In Bolivia, potato is the most important food crop for the local population with over 1000 native potato cultivars being cultivated by over 200,000 families (Zeballos et al., 2009; Cadima and Gandarillas, 2009).

Despite the previously mentioned potential for breeding programmes, CWRs are still underutilized in the development of new cultivars, albeit new technologies are available to better target their use (i.e. molecular maps, QTL analysis) (Hajjar and Hodgkin, 2007). In the case of wild potato relatives, several endemic Bolivian species have been studied, revealing traits important for future potato breeding (see Table 1). Ten species were found to show resistance against late blight (*Phytophthora infestans*), the main disease affecting potato production in Bolivia and elsewhere, while twelve species are resistant to nematodes (*Globodera* spp.). Seven species show tolerance to abiotic stress, such as high temperature, drought or frost (Hawkes and Hjerting, 1989; Ochoa, 1990; Coleman, 2008).

<< Table 1>>

Wild potato relatives occur in the Americas from south-western United States to central Argentina and Chile. Some species, such as *Solanum acaule*, have a wide distribution range but most of them are confined to limited areas and ecological zones (Hijmans et al., 2002; Spooner and Salas, 2006; Hawkes, 1990). Overall distribution of all wild potato species is wider than that of the native cultivated potatoes which are confined mainly to the South American Andes. The highest number of wild potato (*Solanum* spp.) relatives is also found in the Andes area from north-central Peru to central Bolivia.

In Bolivia, 35 wild species have been recorded following the classification of Spooner and Salas (2006), of which 21 species are endemic to the country. Wild potato species grow at altitudes between 700 to 4500 m (Ochoa, 1990) and occupy many different ecological niches in mesothermic and inter-Andean valleys, and in the subtropical Andean rainforest (Yungas). They are only absent from the Bolivian tropical lowland forests (Spooner et al., 1994).

Potato species can be reproduced both sexually through insect-mediated pollination and asexually by means of stolons (e.g. runners) and tubers (Camadro et al., 2012). The role of these two reproduction strategies and relative importance of either one of them under different environmental conditions still needs to be determined for wild potato species (Camadro et al., 2012). Most potato species are allogamous (Salas et al., 2008; Camadro, 2011). However, polyploidy species may have higher rates of autogamy (Camadro, 2011). The latter species also tend to occur in more extreme climates (Hijmans et al., 2007). For example, the broadly distributed species *S. acaule* occurs at high altitudes in cold, harsh environments (Camadro, 2011). This habitat lacks sufficient pollinators and the species reproduction thus relies mostly on self-fertilization and asexual propagation (Camadro, 2011).

In principle, potato species are annual. Yet tubers of wild potato plants can persist for more than a year and resprout under favourable environmental conditions (pers. obs. X. Cadima). Moreover, natural hybridization between sympatric species can occur. From a breeding perspective, there has been a lot of interest in crossings between wild and cultivated species (Table 1; Camadro, 2011). The probability of a successful cross between two species depends on their ploidy level and Endosperm Balance Number (EBN) (Hijmans et al., 2002). EBNs are putative genetic factors that influence species crossing potential (Hijmans et al. 2002). Incompatibility of species with similar ploidy level is thus explained by differences in EBN (Hijmans et al., 2002). Almost all wild potato species endemic to Bolivia are diploids except for *S. xsucrense*, *S. ugentii*, *S. hoopesii* and *S. bombicynum* (Appendix A). These species are tetraploid (four sets of chromosomes, 4x) (Appendix A).

There have been several efforts to collect germplasm of wild potato species in Bolivia. Nevertheless a significant amount of the diversity remains unrepresented in collections (Hijmans et al., 2000). For several species, only a few observation records exist and they are not conserved *ex situ*. At the same time, there is a limited knowledge about the *in situ* conservation status of these potato relatives (VMABCC-BIOVERSITY, 2009). Geographic information systems (GIS) are an effective tool that can contribute to generate new knowledge on the conservation status of plant species (Brummitt et al., 2008). GIS is widely applied in different areas of environmental sciences and biodiversity, and has become an important tool in the development of strategies for the conservation and use of plant genetic resources (Jarvis et al., 2003). GIS is increasingly used to evaluate the geographic distribution and *in situ* conservation status of plant species, including CWRs (Scheldeman et al., 2007; Penn et al., 2009; Hauptvogel et al., 2010; González-Orozco et al., 2012) as well as to guide targeted germplasm collection (Jarvis et al., 2005; Scheldeman et al., 2007). Since species with a narrow distribution range are more prone to become extinct (Baillie et al., 2004; Işik, 2011), spatial analysis has been widely used to assess species conservation status by identifying the extent of species distribution range (Willis et al., 2003). Spatial layers that contain information about human intervention (e.g. roads, agricultural conversion) can be overlaid with GIS over maps of species distribution and provide further information about the threats and conservation status of cultivated plant species and their relatives (Willemen et al., 2007; Maxted et al., 2008) or ecosystems (Jarvis et al., 2010).

Recent collection missions by the Fundación para la Promoción e Investigación de Productos Andinos (PROINPA) have increased the number of accessions for *ex situ* conservation (Patiño et al., 2008; Patiño and Cadima, 2009). This new wild potato occurrence data combined with existing information about wild potato relatives' distribution and with new spatial information about threats allows a comprehensive survey of the conservation status of endemic potato wild relatives in Bolivia. In this study, we will (1) evaluate the *in situ* and *ex situ* conservation status of wild potato relatives based on spatial analysis; and (2) identify hotspots of endemic wild potato diversity, including areas that are threatened by human activities that cause disturbance to the habitat of the wild potato. The newly obtained results will all add to improve the conservation status efforts of several species and contribute to assure a future base for potato breeding.

Methods

Data sources

Georeferenced passport data from existing genebank databases (Centre for Genetic Resources of The Netherlands, United States Potato Genebank, Institute of Plant Genetics and Crop Plant Research of Germany, Intergenebank Potato Database and International Potato Center of Peru) were used to map the geographic coverage of the 21 Bolivian endemic, wild potato species. Herbarium records on wild potato species developed by Hawkes and Hjerting (1989), Ochoa (1990) and Hijmans and Spooner (2001) were used to verify and improve the species´ distribution data. Duplicates were removed after merging the different data sets, where after 331 georeferenced observation points remained. One hundred and one new presence points, obtained through PROINPA's germplasm collecting missions during 2006 to 2010 were added to this dataset. Additionally, 52 georeferenced herbarium and genebank records (presence points) were obtained from existing bibliography, herbaria and genebank databases (through the Global Biodiversity Information Facility [GBIF]). Twelve records from GBIF without coordinates were georeferenced based on locality descriptions with the use of Google Earth® and www.geonames.org, and were added to the analysis. Presence point datasets were checked for inconsistencies between coordinates and department information in the passport data after Scheldeman and van Zonneveld (2010) and removed accordingly.

Species identification followed the taxonomy of Spooner and Salas (2006) which is commonly used in global databases and also in the Bolivian germplasm bank. We are aware that the results made in this study could eventually change if we take into account the last taxonomic treatment of wild potatoes reported in 2011 in the Solanaceae source website (http://www.solanaceaesource.org) that questions the delimitation between various species of the "brevicaule complex" as defined by van den Berg et al. (1998) (See Appendix B).

Species richness

A layer of the observed species richness based on presence points was created in DIVA-GIS using a five-minute resolution grid and applying a circular neighbourhood of 30-minute diameter (about 50 km around the equator) (see Scheldeman and van Zonneveld, 2010). To estimate complete natural distribution ranges, we used a species distribution modelling approach. This technique defines the ecological niche, based on different environmental layers at the sites of the records, and identifies areas with similar environmental conditions as zones where the species could potentially occur and discriminates it from areas with an environment outside the ecological niche. Maxent is a distribution modelling tool (Phillips et al., 2006; Elith et al., 2011) for which the applied algorithm has been evaluated as performing very well, in comparison to other similar modelling software (Elith et al., 2006; Hernandez et al., 2006; Aguirre-Gutiérrez et al., 2013). Therefore, Maxent was selected to model the potential natural distribution of species. Nineteen bioclimatic variables representing different interannual bioclimatic conditions important for a plant's natural establishment and survival (Busby, 1991), were used as environmental layers, derived from the Worldclim dataset and downscaled to a resolution of 30 seconds (~1 km) (Hijmans et al., 2005). Distribution modelling with Maxent and these climate variables were used successfully to predict the occurrence of a wild potato species in Bolivia that was thought to only occur in Mexico and Central America (Simon et al., 2011). We expect that this variable set will also return also good quality modelling outcomes for the wild potato species in our study.

To train the model for each species, we used background points within a 50 km radius around the presence points. Model outcomes were generated with logit probability values. All other Maxent settings were kept default. As a threshold probability value to distinguish potential areas of occurrence from areas where a species would be absent, we chose the probability value where the value of sensitivity (true positive rate) plus specificity (true negative rate) is maximum. This is a recommended threshold value in distribution modelling (Liu et al. 2005).

Then, to develop a potential richness map that is comparable to the observed richness map, we aggregated for each species its presence-absence map to the same resolution as the observed richness map, i.e. five minutes. The aggregated cells received a value for species presence (grid cell value = 1) when species presence was modelled in one or more of its composing cells. Our final potential richness map consisted of the sum of all aggregated presence-absence maps.

Species with only few occurrence data may be sensitive to over-prediction in Maxent, although Maxent may even produce useful models with only 5-10 observations if these species have a rare and narrow distribution (Hernandez et al., 2006). This is likely true for several of our potato species that have a narrow distribution restricted to Bolivia: five of the 21 species had less than 10 unique locations (Table 2). Therefore, we restricted the generated potential distribution layers with a buffer zone around the Extent of Occurrence (EOO) to avoid overestimation of the modelled distribution ranges. A circular radius of 50 km was chosen for this buffer zone after the potato distribution maps developed by Hijmans and Spooner (2001). By restricting the model outcomes with the buffer zones, our predictions of modelled species richness remain relatively conservative.

<<*Table 2*>>

Ecogeographic analysis

We identified for each endemic wild potato species, the different climatic zones in its distribution range according to the Köppen climate classification (see Kottek et al., 2006). This allows us to identify for each species putative ecotypes adapted to different environmental conditions, including rare and unusual ones. Such an analysis helps to determine potentially interesting germplasm for potato breeding that would use adaptive traits to unusual and interesting environmental conditions.

Köppen´s system was the first quantitative global climate classification and is still very widely used (Kottek et al., 2006). This classification has also an ecological plant meaning; because of differences in plant physiology, vegetation groups can be distinguished by climate zones (Kottek et al., 2006).

We used 30 s resolution monthly precipitation and mean temperature layers from the Worldclim dataset (www.worldclim.org) to define the different climate zones according to the criteria provided by Kottek et al. (2006). We calculated these zones using the R statistical environment (R Development Core Team 2010; for the final map please refer to Appendix C). In addition, we provided for each endemic wild potato species the altitudinal range in which it is occurring. Elevation data was derived from the 30 s resolution elevation data from the Worldclim dataset.

In situ *conservation status*

As an indicator of *in situ* conservation status and on the basis of the presence points, we calculated for each species the Extent of Occurrence (EOO), the Area of Occupancy (AOO) (in km^2) and corresponding preliminary IUCN red list category based on these outcomes. Species' EOO and AOO were calculated on the basis of observed species distribution in ArcView 3.2

with the CATS tool (Willis et al., 2003). The CATS tool calculates the areas using the Equal Area Cylindrical Projection.

EOO is defined as the area within the shortest boundary that encompasses all occurrence sites. In our study, we use the convex hull that encompasses all points. It is a measure of the distribution range in which a taxon occurs (IUCN 2010). Taxa with a higher EOO have a broader distribution range and are therefore less vulnerable to extinction compared to narrowly distributed taxa. AOO is a parameter that represents the area of the most suitable habitat for a species´ occurrence within its EOO (IUCN 2010). AOO is calculated as the area of all grid cells in which one or more species records are located (IUCN 2010). Following Willis et al. (2003), we chose for each species the 10% of the maximum geographic distance between two collection sites to define the size of AOO grid cells. The more suitable habitat a taxon has within its EOO, the less likelihood of extinction in the short term.

The taxon must then meet at least two of three other options listed for criterion B to qualify for the vulnerable or worse conservation status (IUCN 2010). These options are 1) the species´ occurrence is severely fragmented or known to exist in not more than a certain amount of locations; 2) species´ occurrence is in continuous decline; or extreme fluctuations in populations (IUCN 2010). However, this information requires intensive monetary monitoring of specific populations, which requires a substantial investment of funding. As a first indication for the number of locations where the species occurs, we counted for each species the number of unique locations on the basis of our georeferenced species database. We calculated in ArcGIS10 (ESRI, Redlands, California, USA), the number and percentages of records per species within protected areas. The protected area layer was derived from the World Database on Protected Areas (WDPA) (UNEP-WCMC, 2010). All classes of protected areas were considered, i.e. national, international and private protected areas in different UICN categories.

As an estimation of potential population decline, we used threat maps for natural ecosystems developed by Jarvis et al. (2010) to understand the major factors affecting endemic wild potato species and how these threats affect species distributions and richness. The layers consisted of six threats expected to occur over the 2012 and 2015 period, i.e. accessibility to humans, conversion to agriculture, fires, livestock pressure, infrastructure, and oil and gas.

Jarvis et al. (2010) calculated the threats´ levels for specific locations by 1) mapping the geographic distributions of recorded human disturbances related to these threats; 2) developing threat-specific decay functions after expert consultation. These were used to calculate the relation between threat exposure and geographic distance; 3) the magnitudes of the threats´ impacts on 608 ecosystems according to experts; and 4) the response of these ecosystems to specific threats according to experts. These specialists indicated whether the threats´ impacts to specific ecosystems were linear, exponential (low levels of threat would have a minimal impact), logarithmic (any level of threat has large impacts), or polynomial (low impact in mid-threat levels). Final threat values for locations were between 0 (low) and 3 (high). For further details please refer to Jarvis et al. (2010).

The ecosystem map followed the Nature Serve classification that was developed by Josse et al. (2003) The following datasets are described by Jarvis et al. (2010) to determine the geographic distribution of each threat in South America:

- Accessibility to humans: road, river and rail access per capita using data from the Digital Chart of the World (DCW), Vector Map (VMAP), and the Center for International Earth Science Information Network (CIESIN) (1:250,000 to 1:1,000,000 scale);
- Conversion to agriculture: number of major crops per 10 km resolution grids as indicated by distribution maps for the 22 principal crops developed by You and Wood (2006);
- Fire: 250 m resolution MODIS satellite-based fire occurrence;
- Livestock pressure: 8 km resolution maps of cattle, goat and sheep density from FAO´s Livestock Atlas of the World (FAO 2004);
- Infrastructure: airport or dam presence according to DCW and King's College London database of dams (1:1,000,000 scale);
- Oil and gas: recorded oil and gas drill sites according to the World Petroleum Assessment 2000 Digital Data Series (DDS) 60 (1:5,000,000 scale).

The spatial resolution of these maps was defined to 30 seconds (~1km) considering the accuracy of the various data sources and ease of applicability for practitioners in the field (Jarvis et al., 2010).

Because the sensitivity was determined on ecosystem level, the threat values should be interpreted with caution at species level because some taxa may be more sensitive to a specific threat than others. However, in our threat analysis, we assume that all wild potato species that occur in a specific ecosystem have a similar level of sensitivity to the different threats.

For each species, we determined threat values as identified at the locations where they were recorded when they were overlaid with the threat maps in DIVA-GIS. Based on this information, we calculated for all species the mean overall threat value among the collection sites (the average of all threat values per species) and accordingly, we identified the major threats for each species.

Prioritization of areas for in situ *conservation*

We carried out a complementary analysis (Rebelo and Siegfried, 1992) in DIVA-GIS (www.diva-gis.org), using a 30 minutes-resolution grid (~50 km^2) to prioritize areas for species *in situ* conservation. This analysis identifies the minimum number of grid cells required to conserve all species of interest. Different approaches to define priority conservation areas were tested. The grid cell with the highest number of species records is determined as the first priority area for *in situ* conservation. Second priority is given to the grid cell that covers the highest number of additional species that did not occur in the first priority cell. This prioritization exercise goes on until all species are covered in one or more cells.

We considered 30 minutes (~50 km^2) an appropriate scale to detect spatial patterns at country level. It is also a representative size for a protected area. The median size of the protected areas that are listed for Bolivia in the WDPA database is 36 km^2. The mean size of these registered conservation areas is 61 km^2. In a first analysis, a complementary analysis was carried out without taking into account whether the locations of presence points are threatened or not. Secondly, only presence points at locations below the 75% percentile of average threat value were included in protected area selection. The areas that are most susceptible to threats like human accessibility, livestock pressure and agricultural production can be very costly to conserve compared to more isolated and less-threatened areas (Carwardine et al. 2008). Limited budgets for conservation planning can thus be used more efficient in these isolated and less-threatened areas.

The reserve selection exercise was then repeated with only occurrence sites from protected areas. We carried out this analysis to evaluate how well the current protected area network in Bolivia conserves endemic potato wild relatives. Protected areas are the principal system for *in situ* conservation at national level. The representativeness of wild potato species in these conservation areas is thus an indicator for the conservation status of wild potato species. Finally, we carried out the reserve selection considering different putative ecotypes within each species that occur in the different climatic zones.

Ex situ *conservation status*

To identify *ex situ* conservation status of endemic wild potato relatives of Bolivia, we consulted the Global Strategy for the *Ex Situ* Conservation of Potato (van Soest, 2006) which provides an overview of collected, and conserved, material in genebanks from Bolivia. We identified species not yet conserved in any genebank or with only a few accessions (less than five) conserved *ex situ*. We identified the areas where most of these species occur (gap analysis) on the basis of their occurrence sites, targeting future collection needs to improve the Bolivian wild potato species *ex situ* conservation status.

Results

Species richness

Wild potato relatives can be found from the northern high Andean part of Bolivia across the Andean-Amazon transition zone towards dry subtropical south-central Bolivia (Figure 1). Observed species richness is highest in south-central Bolivia (Figure 2), in Santa Cruz (mesothermal valleys of Florida and Vallegrande provinces), and in Chuquisaca (Provinces Zudañez, Azurduy Tomina and Oropeza). According to the potential species richness map, most species are expected to occur in northern Chuquisaca and, to a lower degree, in Cochabamba (Figure 3). This area is situated more towards the centre of Bolivia than towards the mesothermal valleys of Santa Cruz where currently most species are known to occur. The areas of observed high diversity are outside protected areas. A high number of species is predicted to occur in the protected area 'El Palmar', but currently no wild potato species have been collected nor recorded from that area (Figures 2 and 3). To a lower degree, the national park 'Carrasco' harbours several endemic wild potato species (Figure 2 and 3).

<< Figure 1>>

<< Figure 2>>

<< Figure 3>>

Ecogeographic analysis

Almost all species (20) were observed in warm temperature climates with dry winters and warm summers according to our Köppen climate map (Table 3). In this climate zone, half of all observations was registered. In general, these areas correspond to inter-Andean valleys and mid-elevation subtropical forests. The second most diverse climate zone is the cold arid steppe climate (Table 3). This area corresponds to highland grass vegetation. With respect to breeding for adaptive traits for climate change adaptation such as for drought and heat tolerance and/or water use efficiency, materials from the hot arid steppe climate are interesting. This is the third-most rich and abundant zone in endemic wild potato species (Table 3). All species occur above 1,200 m.a.s.l. (Table 3; Figure 4). It is common to find species above 3,000 m.a.s.l. (Table 3; Figure 4). Some species occur even up to elevations above 4000 m.a.s.l. Almost all species occurred in two or more climate zones.

<< Table 3>>

<<Figure 4>>

In situ *conservation status and threat assessment*

Following the preliminary IUCN red listing according to AOO (Area of Occupancy) and EOO (Extent of Occurrence), 24 % (five of the 21 species) of the endemic wild potato relatives is critically endangered (CR), which is due to their restricted observed distribution areas (Table 2). Another 19% (four of the 21 species) is endangered (EN) according to these parameters, whereas 28 % (six of the 21 species) has a vulnerable status (VU). The remaining six species are not threatened (NT) or of low concern (LC) based on the herbarium and genebank records.

To get a comprehensive picture of the species' conservation status following Red listing criterion B (IUCN 2010), we combined the AOO/EEO analysis with the threat assessment to identify which potato species require a IUCN conservation status of vulnerable or worse.

According to our threat maps, the areas with highest average threat levels can be found in the western part of Cochabamba, and to a lower degree in northern Chuquisaca and western Santa Cruz where currently the highest numbers of species are observed (Figure 5). The most significant threats for all species considered in this study are accessibility to humans, fire and, to a lower degree, livestock pressure (Table 2). A substantial part of the protected area 'Tunari' where potentially several potato species occur is also being threatened as well by these pressures (Figure 5). The seven most-threatened species are *S. achacachense* (EN), *S. arnezii* (VU), *S. brevicaule* (LC), *S. flavoviridens* (CR), *S. hoopesii* (EN), *S. ugentii* (EN) and *S.* ×*sucrense* (NT).

Of these seven species, five have a vulnerable conservation status or worse according to the EOO/AOO analysis. Whether these five species, four have only been observed in a low number of locations. *S. achacachense* has been observed in less than 10 locations and *S. flavoviridens*, *S. hoopesii* and *S. ugentii* in less than 15 locations (Table 2).

<<Figure 5>>

Prioritization for in situ *conservation*

All 21 species can be conserved *in situ* in eight areas of ~50 km^2 when 25% of the most threatened collection sites are not taken in account (Table 4). This is only one more area of ~50 km^2 than when all collection sites are considered in the prioritization of conservation areas, including those most-threatened.

<< Table 4>>

By excluding 25% of the most-threatened collection sites, the areas of highest species richness, i.e. northern Chuquisaca and western Santa Cruz, were less taken in account in the reserve selection because large parts of natural vegetation in those areas are threatened due to accessibility by human, fires and livestock pressure (Figure 6). Instead, the area of highest priority is in south-eastern Cochabamba, where six species can be conserved *in situ* in an area of 50 km^2. The second priority is the northern highlands in western La Paz where three additional species can be conserved in an area of 50 km^2, which moreover is within a protected area (Area Natural de Manejo Integrado de Apolobamba [Figure 6]). The third priority area for conservation is western Santa Cruz were two additional species could be conserved. The fourth priority area is located in La Paz too. The latter prioritized area also comprises the only observed locations of the endangered species *S. achacachense* (Figure 6, Appendix D). The endangered and highly threatened species *S. hoopesii* and *S. ugentii* are both located in Chuquisaca (Figure 6, Appendix E). When we restrict the reserve selection to only the protected areas, only seven (33 %) of the 21 species could be conserved. Of the four most endangered species only *S. flavoviridens* was included.

<< *Figure 6*>>

Ex situ *conservation*

According to data reported in the Global Strategy for the *Ex Situ* Conservation of Potato (van Soest, 2006) updated with data from PROINPA, there are 10 genebanks in the world holding 1062 accessions of 21 endemic wild potato species from Bolivia (Appendix E). The *ex situ* collection in Bolivia maintained in the National Genebank of Andean tubers and roots is the result of repatriated materials from the Centre of Genetic Resources the Netherlands (CGN) and new collection trips in recent years. This national collection has currently 235 accessions of the 21 endemic species (the total potato wild collection has 618 accessions, including other non-endemic species occurring in Bolivia), 65 of these are new materials collected over the 2006 to 2010 period.

Some species are well-represented in the genebank collections, such as *S. berthaultii* which has the largest number of accessions (228), followed by *S. ×sucrense* (195) and then *S. boliviense* (141). On the other hand, no germplasm of *S. bombycinum* and *S. ×litusinum* is conserved in any *ex situ* collection. Other species poorly conserved are *S. neovavilovii* (two accessions), *S. soestii* (two) and *S. flavoviridens* (four), and exist only in the Bolivian collection. The small number of samples for these species in genebanks also coincides with a restricted distribution in the field and limited accessibility to reach the natural habitats of occurrence of these species. Prioritized areas for collection trips are La Paz (Provinces Tamayo and Saavedra) where populations of *S. flavoviridens, S. neovavilovii* and *S. bombycinum* have been observed (Figure 7). *Solanum soestii* could be explored in La Paz (Province Inquisivi) and Cochabamba (Province Ayopaya). *Solanum ×litusinum* is most likely to occur in the Cochabamba-Santa Cruz border area and at the frontier between Potosi and Chuquisaca (Figure 7).

<<Figure 7>>

Comparison of conservation priorities of species and putative ecotype diversity

In addition to a reserve selection exercise at species level, we also carried out a prioritization of areas for conservation considering genecological zones separately. Recorded species´ plant individuals from different climate zones possibly represent distinct ecotypes within wild potato species that can be useful in breeding programs for different adaptive traits. In total, we identified 56 putative ecotypes. Only 49 of these potential ecotypes can be conserved when we exclude 25% of the most threatened collection sites (Table 4). These are scattered across the wild potato distribution range in Bolivia and can be conserved in 19 grid cells.

When we exclude 25% of the most-threatened collection sites, the area with most ecotype diversity coincides with the one that has highest observed species diversity (Figure 8). Other areas of unique putative ecotype diversity coincide with areas of high species diversity such as the northern highlands in western La Paz. In addition to the previously defined areas for species *in situ* conservation, a new prioritized area of unique high putative ecotype diversity is located in eastern Potosí.

<< Figure 8>>

Seven of the 56 putative ecotypes occur exclusively in the most-threatened collection sites. These are *S. circaeifolium*, *S. gandarillasii* and *S. neocardenasii* populations in cold arid steppe climate; *S. virgultorum* and *S. xsucrense* populations in hot arid steppe climate; *S. neovavilovii* population in tundra climate; and *S. violaceimarmoratum* in equatorial savannah environments with dry summers. These seven putative ecotypes were represented by only one occurrence site and are therefore likely to be species populations in extreme environments with potentially interesting traits. In addition to the prioritized species for targeted germplasm collection, these putative ecotypes should be targeted for germplasm collection as they are susceptible to *in situ* extinction (Figure 9).

<<Figure 9>>

Discussion

Some 70 % (15 species) of the endemic wild potato relatives that we studied has a preliminary vulnerable or worse status according to IUCN´s criterion B category AOO (Area of Occupancy) and EOO (Extent of Occurrence). Of these, five species are of particular concern for protection because they are facing significant threats, particularly by fire (*S. achacachense, S. arnezii, S. flavoviridens, S. hoopesii* and *S. ugentii*) (Table 2). *S. achacachense, S. flavoviridens, S. hoopesii* and *S. ugentii* were only been observed in a restricted number of locations (<15). These four species qualify most for a conservation status of vulnerable or worse according to criterion B of the IUCN red listing assessment and should therefore be prioritized for conservation.

Among these species, *S. flavoviridens* is underrepresented in genebanks. Of the other species, fortunately a considerable number of accessions is conserved *ex situ*. Collection sites of two species that have a broader distribution than the five species mentioned above, i.e. *S. brevicaule* and *S. ×sucrense*, are also highly threatened. Although these threats may have a substantial impact on the genetic diversity of the populations of these species, new collection sites in less-threatened parts of their distribution range may be identified for their *in situ* conservation. Species distribution modelling will help in identifying those areas.

In addition to *S. flavoviridens*, four other species should be prioritized for targeted collection because they are either not yet conserved in any genebank (*S. bombycinum S. ×litusinum*) or are underrepresented (*S. neovavilovii, S. soestii*) (Appendix E). The department of highest priority for collection is La Paz (Provinces F. Tamayo and B. Saavedra) within the protected area “Area Natural de Manejo Integrado de Apolobamba” where three of the five species have been documented to occur. The areas in the northwest of La Paz are locations of difficult access which would explain the few samples collected in these areas.

We preferred the scenario in which we excluded 25% of the most threatened collection sites to prioritize areas for *in situ* conservation. The reduced cost of *in situ* conservation in less-threatened areas may outweigh the cost of implementing conservation measures in an additional area. However, all priority areas identified for conservation are areas where farming is important, except one that lies within a protected area in northern La Paz (Apolobamba). In the case of Santa Cruz, livestock is also important. These areas are not related to any system of conservation or protection, so even while we excluded 25% of the most-threatened occurrence sites, the other locations may still be vulnerable to threats as a result of human activities. For example, although *S. virgultorum* collection sites do not have particular high threat values, known populations of these species reported in the past (Ochoa, 1990) were not found in recent field visits (between 2006 and 2010), Similar indications of decline may even be more pronounced in populations of species that are highly threatened according to our analysis.

Studies on the effectiveness of conservation efforts of vertebrates to reduce their threat level demonstrate a significant contribution of protected areas (Hoffmann et al., 2010). This could be similarly true for higher plants and more specifically for CWRs. In Bolivia there are 22 protected areas established to protect wild populations of flora and fauna, but none consider explicitly CWRs in their inventories (SERNAP, 2011). According to our study, only one third of the wild potato species endemic to Bolivia (seven species) have been observed to occur within the protected areas. This clearly demonstrates the poor coverage of the actual protected area network in Bolivia in protecting wild potato relatives' populations. The remaining species occur in natural vegetation habitats, sometimes even as weeds in agricultural fields or on the edges of roads, dispersed by human activities. As a consequence, an inventory should be made in protected areas that we modelled to have high species richness but have not yet been visited for collection, particularly "El Palmar" at the border of Chuquisaca and Cochabamba (Figure 3), to get a full understanding as to what extent the existing protected area network in Bolivia can contribute to *in situ* conservation of endemic wild potato diversity. Assisted migration to less-threatened areas, e.g. to existing close-by protected areas, may be an option. We are not aware of examples of such measures, but this option may be worthwhile to explore with the national government body responsible for the protected areas.

We also observed in a few protected high threat levels (Figure 5). So even within these conservation areas, species may be threatened by human disturbance. On the other hand, national networks of protected areas are the principal measure for *in situ* conservation of biodiversity. But even protected areas can become susceptible to human pressure. This is of great conservation concern. According to our analysis, several parts of protected area 'Tunari', for example, are severely being threatened. This protected area is close by some urban populations with people exploiting the natural resources in this area (Valenzuela and Padilla Suáre, 2002).

On-farm conservation may be an alternative way to conserve these species, especially those that grow in disturbed areas. Recently, the UNEP/GEF-supported project "*In situ* conservation of wild crop relatives through enhanced information management and field application" (VMABCC-BIOVERSITY, 2009) worked on raising awareness of indigenous communities and farmers on the importance of building a participatory conservation strategy for CWRs. Guidelines or protocols help raise consciousness and guide farmers in the conservation of CWRs (Dulloo et al., 2010). However, there is an on going discussion about the feasibility to protect CWRs on farm, especially how farmers will benefit from this when these wild relatives may not have direct use (e.g. only in breeding programs), or even may have negative effects on the productivity of their crops through cross-pollination.

Threat assessment is an important step in setting conservation priorities. In this study, we did that based on threat maps developed by (Jarvis et al., 2010). These maps are made on a continental scale and may lose their precision at a local scale. Therefore, these threat analyses are exploratory and where relevant, such as in the area of highest threat levels, a locally more-detailed threat analysis should be carried out. In addition to the observed immediate threats, i.e. accessibility and fire, field observations denote livestock pressure as an important threat. This threat has been identified in our analysis as a third immediate threat after accessibility and fire.

Since fire seems to be the most important threat for half of the endemic wild potato species, it would be interesting to investigate how tolerant these species are to fire events. Many plant species have adapted to such conditions (Pekin et al., 2009; Ansley et al., 2010; Segarra-Moragues and Ojeda, 2010), and for them fire may not be a threat and even favour colonization and regeneration. Hijmans et al. (2002) state that wild potatoes are fire-tolerant. Yet no further details are provided. It could be that these species can survive fire events underground due to their tubers and resprout in more favourable environmental conditions. On the other hand, human-induced fire events can become so frequent and intense that even ecosystems adapted to natural fire events become degraded and thus also the species that inhabit these ecosystems. Ecological research is required to understand the impact of fire on natural wild potato species.

Most collection sites are located in areas of natural vegetation. A possible reason could be that these species don't thrive well in areas disturbed by agriculture. However, Hijmans et al. (2002) state that wild potatoes can grow well in disturbed areas even though they do not explain this in further detail. Another possibility is that there has been a sampling bias towards collecting wild potato species in natural vegetation. It is therefore worthwhile to monitor or set up experiments to determine how well these species may survive in disturbed habitats following conversion to agriculture, which would be relevant for on farm conservation.

This study has identified eight areas where the 21 species could be conserved *in situ*, although this analysis does not take in account the conservation of genetic diversity within species. Endemic species, such as the wild potato species in our study, in general have low levels of genetic diversity within the species, whereas relatively high levels of genetic differentiation between their populations can be observed (Hamrick and Godt, 1996). Populations of these species are therefore susceptible to inbreeding effects. Consequently, the viability of endemic and narrowly distributed species populations may be more sensitive to fragmentation and habitat reduction compared to more widespread species. We therefore recommend that population genetic studies be carried out on these wild potato species.

On the other hand, species with a larger distribution area may consist of several ecotypes that are adapted to different environmental conditions across the species distribution range. In that case, different ecotypes should be conserved to capture as much of the genetic diversity within the species as possible. In our study we found that most wild endemic potato species occur in different climate zones. We anticipate that these species´ populations have developed different adaptive traits to be able to survive in these environments.

In general, the areas with high putative ecotype diversity coincided with the eight prioritized areas for species conservation. An additional area with high putative ecotype richness was identified in Potosí. To maximize the conservation of wild potato genetic resources, the latter area may be relevant to consider in an *in situ* conservation strategy.

Related studies of other wild potato species have shown clear genetic distinctiveness and wide variations in pest and disease resistance between accessions collected in different localities

(Ronning et al., 2000; Del Rio et al., 2001). Because it is not possible to preserve large areas for *in situ* conservation to keep all the genetic diversity, one must consider complementary conservation strategies such as genebanks. We identified seven putative ecotypes that are most threatened. For these materials, we recommend *ex situ* conservation. Moreover, genebanks can facilitate the use of these species in genetic improvement programs. On the other hand, the management of *ex situ* collections also has a cost and addition of new accessions implies extra costs in storage, regeneration, etc. *Ex situ* conservation is also a static form of conservation while under *in situ* conditions plant populations can evolve in interaction with their environment. *In situ* conservation is therefore preferred for long-term conservation of wild species.

We followed the classification of Spooner and Salas (2006), which is widely accepted and used in genebanks. Yet new taxonomic studies suggest that several accepted species are synonyms to other already existing species (http://www.solanaceaesource.org). The results of our study would differ substantially if this new taxonomy was followed. Fewer areas would be required to conserve all species and several of the prioritized species would be a synonym to a species with a good conservation status. As long as this taxonomic classification is not clarified, we follow the accepted wild potato taxonomy of Spooner and Salas (2006). Molecular characterization studies can help to delineate species and estimate their phylogenetic relationships (González-Orozco et al. 2012). This information provides additional information about genetic distinctiveness to prioritize species for conservation (Weitzman 1998).

Final remarks

Considering the wide distribution of wild potato species in Bolivia and the often limited resources for germplasm conservation, this study provides guidelines to direct *in situ* conservation efforts to priority areas where there is a higher concentration of species and which have a relatively low level of threat. We prioritized eight areas of about 50 km^2 for *in situ* conservation, but only one is situated in a protected area, i.e. Area Natural de Manejo Integrado de Apolobamba, where three species are known to occur. A high number of wild potato species is predicted to occur in the protected area "El Palmar" in north Chuquisaca (Figure 3). A field inventory should be carried out in that area to assess how many wild potato species it contains.

Ex situ conservation of Bolivian wild potato species is widely-represented in 10 genebanks in different countries. Of the 21 endemic species, three are poorly represented in these genebanks, whereas there are no living specimens of two additional species. The protected area "Area Natural de Manejo Integrado de Apolobamba" has highest priority for additional collection because three of these five species occur in this park. Other areas for targeting collection include La Paz (Province Inquisivi), Cochabamba (Province Ayopaya), the Cochabamba-Santa Cruz and Potosi-Chuquisaca border areas (Figure 7).

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Figure legends

Figure 1. Distribution of the 21 endemic wild potato relatives on the basis of herbarium and genebank records.

Figure 2. Observed wild potato species richness with a five-minute resolution grid-cell and 30-minute circular neighbourhood based the herbarium and genebank records of the 21 endemic wild potato relatives.

Figure 3. Potential wild potato species richness with a five-minute resolution grid-cell of the 21 endemic wild potato relatives using species distribution modelling in Maxent

Figure 4. Distribution of endemic wild potato species across altitude ranges.

Figure 5. Mean threat values (average of human accessibility, conversion to agriculture, fires, livestock pressure, infrastructure, and oil and gas) in a thirty-second resolution map across the modelled distribution range of endemic wild potato species in Bolivia.

Figure 6. Prioritized areas to conserve *in situ* 21 endemic wild potato species with the use of the complementary reserve selection and excluding 25 % of the most threatened locations where the species have been collected or recorded.

Figure 7. Map with prioritized cells to target germplasm collections of the five potato wild relatives for which no or less than five accessions are currently conserved (*S. bombycinum, S.* ×*litusinum S. neovavilovii*, *S. soestii* and *S. flavoviridens*).

Figure 8. Prioritized areas to conserve *in situ* the 56 putative ecotype of the 21 endemic wild potato species with the use of the complementary reserve selection and excluding 25 % of the most threatened locations where the species have been collected or recorded.

Figure 9. Map with prioritized cells to target germplasm collecting trips of the seven putative ecotypes that occur exclusively in the 25 % most threatened collection sites.

Table 1. Documented properties of endemic wild potato relatives of Bolivia.

Species	Uses (Resistances)*	References
S. achacachense	Cyst nematode (*Globodera pallida*)	Hawkes y Hjerting, (1989) Ochoa, (1990) Centre for Genetic Resources (CGN), Netherlands Intergenebank Potato Database (USDA) International Potato Center (CIP), Peru Institute of Plant Genetic Resources and Crop Plant Research (IPK), Germany.
S. alandiae	Wart (*Synchytrium endobioticum*) Blackkeg (*Erwinia carotovora*) Cyst nematode (*Globodera pallida*) Flea beetle (*Epitrix cucumeris*), Potato aphid (*Macrosiphum euphorbiae*) Heat tolerance	
S. arnezii	Late blight (*Phytophthora infestans*) Blackkeg (*Erwinia carotovora*) Root-knot nematode (*Meloidogyne* spp.) Cyst nematode (*Globodera pallida*)	
S. avilesii	Late blight (*Phytophthora infestans*), Wart (*Synchytrium endobioticum*) Blackkeg (*Erwinia carotovora*) Root-knot nematode (*Meloidogyne* spp.), Cyst nematode (*Globodera pallida*) Flea beetle (*Epitrix cucumeris*), Potato aphid (*Macrosiphum euphorbiae*).	
S. berthaultii	Late blight (*Phytophthora infestans*), Wart (*Synchytrium endobioticum*), Black scurf (*Rhizoctonia solani*), Verticillium wilt (*Verticillium* spp.) Blackkeg (*Erwinia carotovora*), Common scab (*Streptomyces scabies*), Bacterial wilt (*Ralstonia solanacearum*) Root-knot nematode (*Meloidogyne* spp.), Cyst nematode (*Globodera spp*.) Virus resistance PVX, PVY, PSTV Colorado beetle (*Leptinotarsa* spp.), Peach-potato aphid (*Myzus persicae*), Leaf hopper (*Empoasca fabae*), Flea beetle (*Epitrix* sp.), Leaf miner (*Liriomyza* spp.), Chinche (*Lygus* sp.), Spider mite (*Tetranychus* spp.)	
S. circaeifolium	Late blight (*Phytophthora infestans*). Blackkeg (*Erwinia carotovora*) Cyst nematode (*Globodera pallida*). Heat and Drought tolerance	
S. ×doddsii	Wart (*Synchytrium endobioticum*).	
S. flavoviridens	Peach-potato aphid (*Myzus persicae*), Colorado beetle (*Leptinotarsa* sp.), Spider mite (Tetranichus spp.), Leaf hopper (*Empoasca* sp.), Leaf miner (*Lyriomiza* spp.)	
S. ×litusinum	Late blight (*Phytophthora infestans*), Wart (*Synchytrium endobioticum*), Black scurf (*Rhizoctonia solani*) Cyst nematode (*Globodera* spp.) Colorado beetle (*Leptinotarsa* spp.), Chinche (*Lygus lineolaris*)	
S. neocardenasii	Peach-potato aphid (*Myzus persicae*, *Macrosiphum euphorbiae*), Leaf hopper (*Empoasca fabae*), Flea beetle (*Epitrix cucumeris*), Spider mite (*Tetranichus urticae*).	

	Drought tolerance	
S. soestii	Late blight (*Phytophthora infestans*) Blackkeg (*Erwinia carotovora*) Cyst nematode (*Globodera* spp.) Heat tolerance.	
S. ugentii	Late blight (*Phytophthora infestans*) Cyst nematode (*Globodera* spp.)	
S. virgultorum	Late blight (*Phytophthora infestans*), Wart (*Synchytrium endobioticum*) Blackkeg (*Erwinia carotora*) Cyst nematode (*Globodera* spp.)	
S. gandarillasii	Drought tolerance Cyst nematode (*Globodera* spp.)	Same references plus Coleman (2008)
S. ×sucrense	*Verticillium* resistance Late blight (*Phytophthora infestans*), Wart (*Synchytrium endobioticum*). Cyst nematode (*Globodera* spp.) Blackkeg (*Erwinia carotovora*) Virus resistance PVX, PVA Potato tuber moth (*Phthorimaea operculella*) Frost resistance	Same references plus Spooner and Bamberg (1994)
S. violaceimarmoratum	Colorado beetle (*Leptinotarsa* spp.) White mold (some) Late blight (*Phytophthora infestans*) Frost resistance	Same references plus Jansky *et al.*, (2008)

*Uses found (only) for 16 Bolivian wild potato species.

Table 2. Total number of presence points of each endemic wild potatoes species in Bolivia, number of points in protected areas, preliminary IUCN conservation status, average threat value and identification of most important threats per species.

Species	Nr. of locations	Nr. of locations in protected areas	AOO (km^2)	EOO (km^2)	Tentative AOO/EEO Red listing status*	Mean threat value	Largest threat **	Second largest threat**
S. achacachense	10	0	29	129	EN	0.35	fires (0.86)	access (0.75)
S. alandiae	34	0	6874	20586	NT	0.30	access (0.60)	fires (0.53)
S. arnezii	23	0	5124	5488	VU	0.36	access (0.78)	livestock (0.71)
S. avilesii	19	0	38	59	CR	0.30	access (0.74)	Convers (0.61)
S. berthaultii	71	0	25085	36307	NT	0.30	access (0.84)	livestock (0.61)
S. boliviense	33	0	5205	10076	VU	0.29	access (0.95)	livestock (0.45)
S. bombycinum	3	3	5	0.3	CR	0.16	fires (0.39)	access (0.37)
S. brevicaule	47	13	111659	105673	LC	0.36	fires (1.05)	access (0.70)
S. circaeifolium	42	4	42095	46386	NT	0.27	fires (0.68)	access (0.56)
S. flavoviridens	7	4	39	67	CR	0.34	fires (0.95)	convers (0.46)
S. gandarillasii	21	0	2913	12308	VU	0.27	access (0.68)	livestock (0.49)
S. hoopesii	11	0	264	430	EN	0.34	fires (1.00)	livestock (0.57)
S. neocardenasii	14	0	37	507	CR	0.28	access (0.75)	fires (0.56)
S. neovavilovii	17	17	61	180	EN	0.17	fires (0.52)	access (0.35)
S. soestii	6	0	1	3	CR	0.16	access (0.57)	livestock (0.29)
S. ugentii	12	0	324	401.4	EN	0.42	fires (1.28)	livestock (0.60)
S. violaceimar Moratum	22	9	8830	13703	VU	0.28	fires (0.73)	access (0.65)
S. virgultorum	9	2	18792	25035	NT	0.18	access (0.63)	livestock (0.22)
S. ×doddsii	18	0	3268	11985	VU	0.20	access (0.65)	livestock (0.55)
S. ×litusinum	9	0	1663	10161	VU	0.29	access (0.80)	livestock (0.58)
S. ×sucrense	66	0	25436	48284	NT	0.37	fires (0.99)	access (0.86)

*CR: Critically Endangered; EN: Endangered; VU: Vulnerable; LC: Lower Concern; NT: Not threatened.
** access: accessibility to humans; livestock: livestock activities pressure; convers: conversion to agriculture.

Table 3. Distribution of species occurrence sites across Köppen climate zones and the altitude range in which they occur.

Species	As[1]	ET[2]	BWk[3]	BSh[4]	BSk[5]	Cfb[6]	Cwb[7]	Cwc[8]	min. alt. (masl)	max. alt. (masl)
S. achacachense		9					1		3,745	4,165
S. alandiae				9	3	1	21		1,633	3,377
S. arnezii				5	6		12	23	1,738	2,771
S. avilesii							19	19	2,145	2,841
S. berthaultii				16	20		35		1,692	3,219
S. boliviense					16		17		2,869	3,732
S. bombycinum		2					1		2,610	4,643
S. brevicaule		11		1	13		18	4	2,152	4,315
S. circaeifolium		3			2		36	1	1,933	4,753
S. flavoviridens	2						5	7	1,336	2,850
S. gandarillasii				19	1		1		1,411	2,740
S. hoopesii							11		2,360	3,950
S. neocardenasii				13	1				1,392	1,867
S. neovavilovii		1					16		2,444	4,155
S. soestii							6	6	2,862	3,595
S. ugentii							12	12	2,700	3,950
S. violaceimarmoratum	1					2	18	22	1,226	4,002
S. virgultorum		2		1			6		1,441	4,714
S. xdoddsii				5	8		5		1,977	2,762
S. xlitusinum				2	5		2		1,925	3,090
S. xsucrense		2	3	1	47		13		2,117	4,550
Total species richness	2	7	1	10	11	2	20	3		
Total observations	3	30	3	72	122	3	255	6		

[1]As = equatorial savannah with dry summer; [2]ET = tundra climate; [3]BWk = cold desert climate; [4]BSh = hot steppe climate; [5]BSk = cold steppe climate; [6]Cfb = warm temperature climate, fully humid and with warm summer; [7]Cwb = warm temperature climate with dry winter and warm summer; [8]Cwc = warm temperature with dry summer and cool summer.

Table 4. Results of reserve selection analysis to prioritize areas for *in situ* conservation.

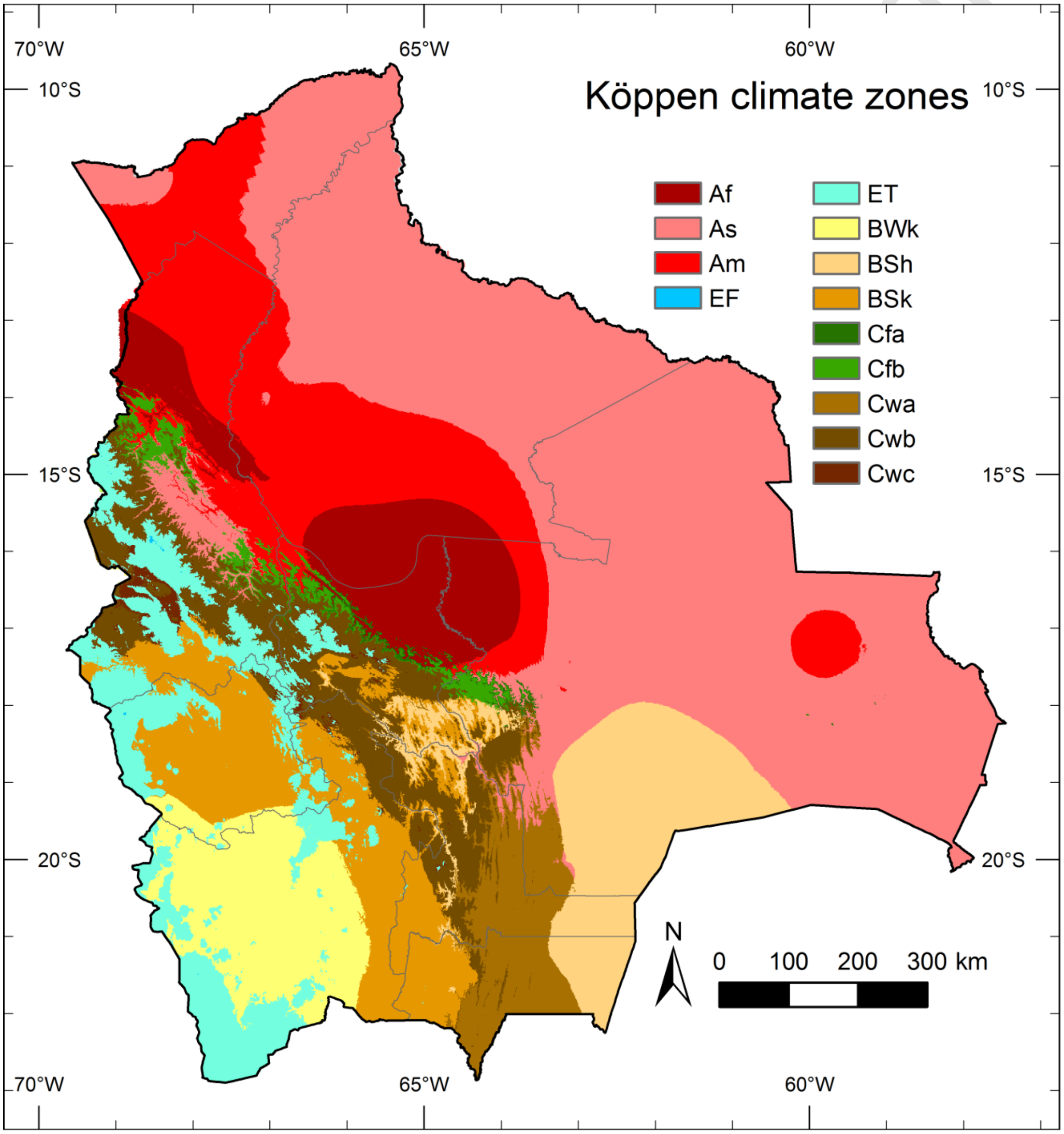
Methodology	Nr. of cells Included	Nr. of putative ecotypes included
All occurrence sites are included in the reserve selection (threats not taken into account)	20	56
25 % of the occurrence sites with the highest average overall threat not included in the reserve selection	19	49
Only occurrence sites protected areas are included in the reserve selection	7	12

Appendix A Ploidy level and endosperm balance numbers (EBN) of the Bolivian endemic wild potato species.

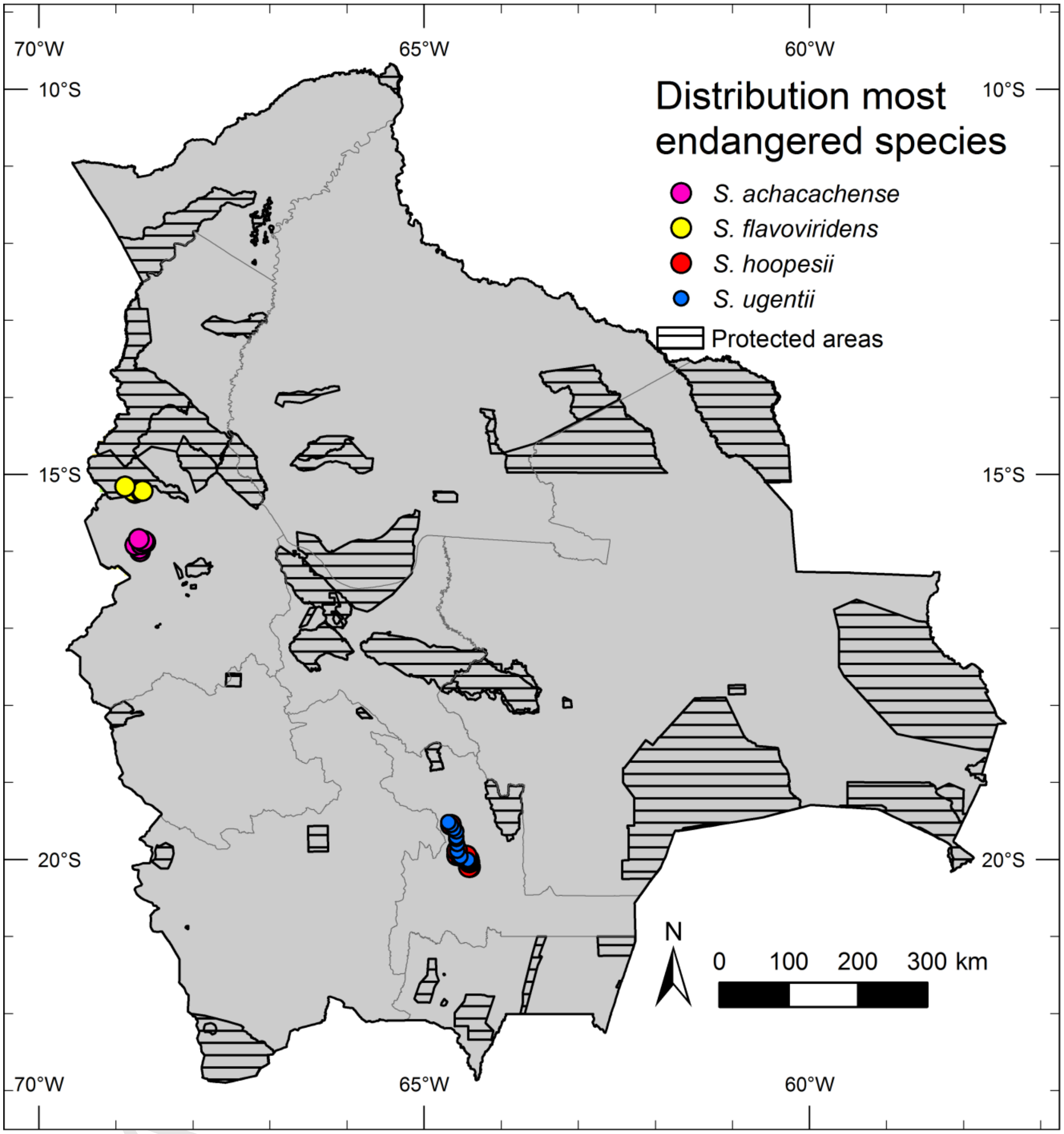
Species	Ploidy and (EBN)*
S. achacachense Cárdenas	2x
S. alandiae Cárdenas	2x
S. arnezii Cárdenas	
S. avilesii Hawkes and Hjrt.	2x
S. berthaultii Hawkes	2x (2EBN)
S. boliviense Dunal	2x (2EBN)
S. bombicynum Ochoa	4x
S. brevicaule Bitter	2x (2EBN)
S. circaeifolium Bitter	2x (1EBN)
S. x doddsii Correl (aln x chc)	2x (2EBN)
S. flavoviridens Ochoa	
S. gandarillasii Cárdenas	2x (2EBN)
S. hoopesii Hawkes and K.A. Okada	4x
S. x litusinum Ochoa (ber x tar)	2x (2EBN)
S. neocardenasii Hawkes and Hjert.	2x
S. neovavilovii Ochoa	2x (2EBN)
S. soestii Hawkes and Hjert.	2x
S. x sucrense Hawkes (adg x opl)	4x (4EBN)
S. ugentii Hawkes and K.A. Okada	4x
S. violaceimarmoratum Bitter	2x (2EBN)
S. vilgultorum (Bitter) Cárdenas and Hawkes	2x

*Ploidy and EBN determinations follow Spooner and Hijmans 2001. EBN refers to a genetic isolating mechanism that allows crosses between species with the same EBN and prevents crosses between different EBN groups (Hawkes 1990).

Appendix C Köppen climate classification on the basis of the criteria provided by Kottek et al. (2006) and calculated with 30-seconds resolution monthly precipitation and mean temperature data from Worldclim. Af = equatorial rainforest, fully humid; As = equatorial savannah with dry summer; Am = equatorial monsoon; EF = tundra climate; ET = frost climate; BWk = cold desert climate; BSh = hot steppe climate; BSk = cold steppe climate; Cfa = warm temperature climate, fully humid and hot summers; Cfb = warm temperature climate, fully humid and warm summer; Cwa = warm temperature climate, dry winter and hot summer; Cwb = warm temperature climate, dry winter and hot summer; Cwc = warm temperature climate, dry winter and cool summer.



Appendix D Distribution of most endangered wild potato species.



Appendix E Number of accessions per endemic wild species conserved *ex situ* in genebanks according to the potato germplasm conservation strategy (van Soest, 2006) and updated with new accessions collected by PROINPA.

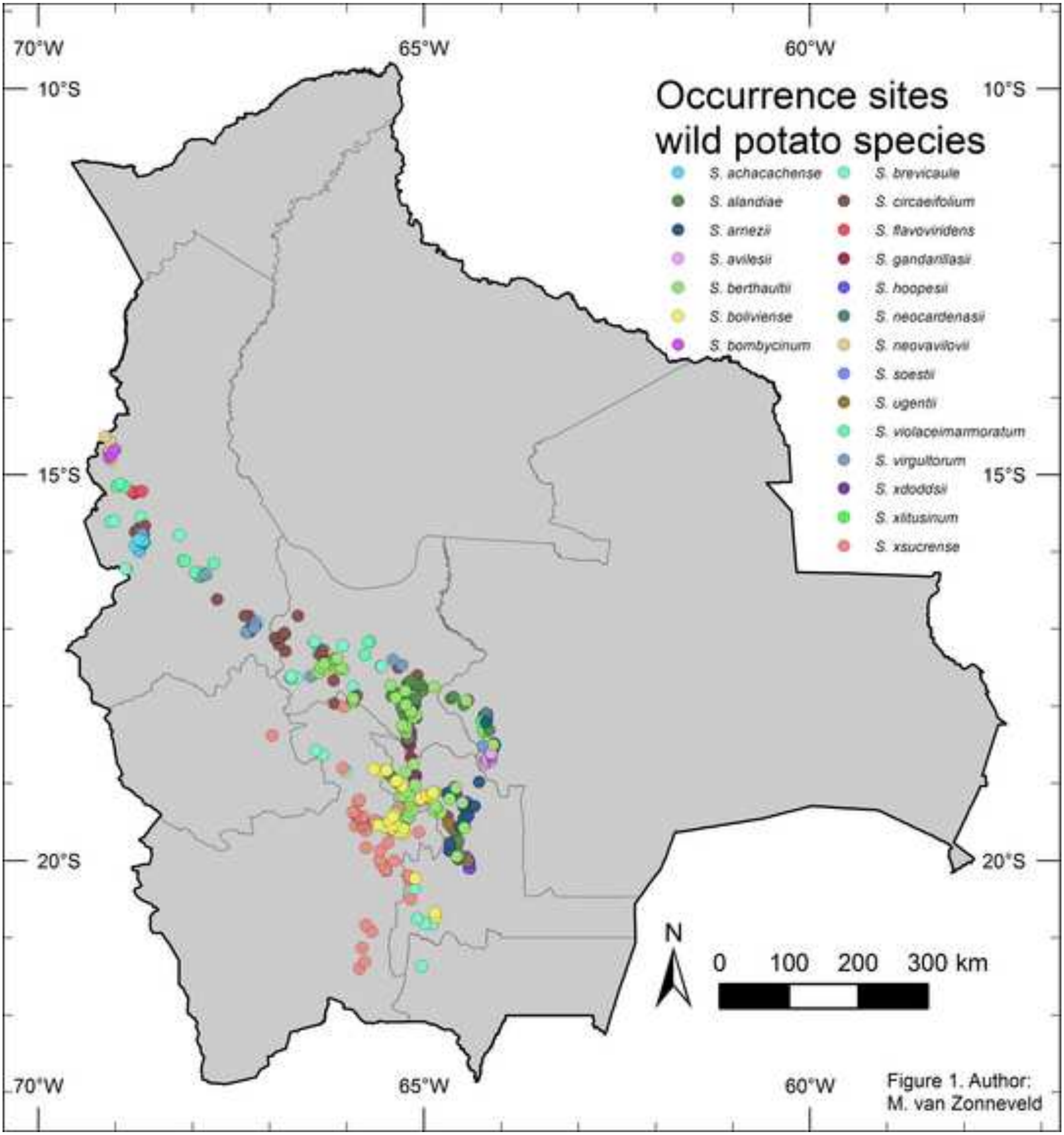
Species	INTA	BOL	CIP	PI	CGN	CPC	IPK	VIR	POL	CZE	Sum
S. achacachense		4		1	4		1				10
S. alandiae		20	15	17	13	2	8	6			81
S. arnezii		7		6	2		4				19
S. avilesii		17	3	3	3		3	5			34
S. berthaultii	1	31	33	62	34	12	12	41	1	1	228
S. boliviense	13	23	10	25	25	6	14	25			141
S. bombycinum		0									0
S. brevicaule	1	15	9	27	14	2	5	15			88
S. circaeifolium		20	9	15	16	3	11	7			81
S. flavoviridens		4									4
S. gandarillasii		11	1	7	3	3	5	6			36
S. hoopesii		9	2	8	4		2				25
S. neocardenasii		4	1	2	1	1	2	2			13
S. neovavilovii		2									2
S. soestii		1					1				2
S. ugentii		3	2	5	3		2				15
S. violaceimarmoratum		8	8	8	5	1	4	7			41
S. virgultorum		6	1		7	1	2	1			18
S. ×doddsii		2	2	13	3	2	4	5			31
S. ×litusinum		0									0
S. ×sucrense		48	20	40	52	10	8	15			193
Total:	15	235	116	239	189	43	88	135	1	1	1062

Where INTA= Estación Experimental Balcarce -Instituto Nacional de Tecnología Agropecuaria, Argentina; BOL=Bolivian potato collection; CIP=International Potato Center, Peru; PI= Potato Introduction Project, USA; CGN=Centre for Genetic Resources, Netherlands; CPC=Common Wealth Potato Collection, UK; IPK=Institute of Plant Genetic Resources and Crop Plant Research, Germany; VIR= Vavilov Research Institute of Plant Industry, Russia; POL=Plant Breeding and Acclimatization Institute, Poland; CZE=Potato Research Institute, Czech Republic.

Reference: van Soest, L.J.M., 2006. Global strategy for the ex situ conservation of potato. Global Crop Diversity Trust. http://www.croptrust.org/documents/web/Potato-Strategy-FINAL-30Jan07.pdf.

Appendix B Differences between two taxonomies for Bolivian wild potato species

No.	**Wild potato taxa accepted for Bolivia by Spooner and Salas (2006)**	Endemic	No.	**Wild potato taxa suggested in the Solanaceae source website** (http://www.solanaceaesource.org)	Endemic
1	*Solanum acaule* Bitter		1	*Solanum acaule* Bitter	
2	*S. achacachense* Cárdenas	*		Synonym of *S. candolleanum* Berthault	
3	*S. alandiae* Cárdenas	*		Synonym of *S. brevicaule* Bitter	
4	*S. arnezii* Cárdenas	*		Synonym of *S. chacoense* Bitter	
5	*S. avilesii* Hawkes and Hjrt.	*		Synonym of *S. brevicaule* Bitter	
6	*S. berthaultii* Hawkes	*	2	*S. berthaultii* Hawkes	*
7 8	*S. boliviense* Dunal subsp. *astleyi* (Hawkes and Hjert.) D.M. Spooner, M. Ugarte, and P.M. Skoch*	*	3	*S. boliviense* Dunal	*
9	*S. bombicynum* Ochoa	*	4	*S. bombicynum* Ochoa	*
10	*S. brevicaule* Bitter	*	5	*S. brevicaule* Bitter	*
11	*S. candolleanum* Berthault		6	*S. candolleanum* Berthault	
12	*S. chacoense* Bitter		7	*S. chacoense* Bitter	
13 14	*S. circaeifolium* Bitter var. *capsicibaccatum* (Cárdenas) Ochoa*	*	8	*S. circaeifolium* Bitter	*
15	*S.* ×*doddsii* Correl (aln x chc)	*	9	*S. doddsii* Correl	*
16	*S. flavoviridens* Ochoa	*		Awaiting *Solanum* status designation	(*)
17	*S. gandarillasii* Cárdenas	*		Awaiting *Solanum* status designation	(*)
18	*S. hoopesii* Hawkes and K.A. Okada	*		Synonym of *S. brevicaule* Bitter	
19	*S. infundibuliforme* Phil.		10	*S. infundibuliforme* Phil	
20	*S. leptophyes* Bitter			Synonym of *S. brevicaule* Bitter	
21	*S.* ×*litusinum* Ochoa (ber x tar)	*		Synonym of *S. berthaultii* Hawkes	
22 23	*S. megistacrolobum* Bitter subsp. *toralapanum* (Cárdenas and Hawkes) R.B. Giannattasio and D.M. Spooner			Synonym of *S. boliviense* Dunal	
24 25	*S. microdontum* Bitter var. *montepuncoense* Ochoa (mcd x vio) *		11	*S. microdontum* Bitter	
26	*S. neocardenasii* Hawkes and Hjert.	*	12	*S. neocardenasii* Hawkes and Hjert.	*
27	*S. neovavilovii* Ochoa	*	13	*S. neovavilovii* Ochoa	*
28	*S. okadae* Hawkes and Hjert.		14	*S. okadae* Hawkes and Hjert.	
29	*S. oplocense* Hawkes			Synonym of *S. brevicaule* Bitter	
30	*S. puchupuchense* Ochoa			Synonym of *S. candolleanum* Berthault	
31	*S. soestii* Hawkes and Hjert.	*		Synonym of *S. circaeifolium* Bitter	
32	*S. sparsipilum* (Bitter) Juz. and Bukasov			Synonym of *S. brevicaule* Bitter	
33	*S.* ×*sucrense* Hawkes (adg x opl)	*		Synonym of *S. brevicaule* Bitter	
34	*S. tarijense* Hawkes			Synonym of *S. berthaultii* Hawkes	
35	*S. ugentii* Hawkes and K.A. Okada	*		Synonym of *S. brevicaule* Bitter	
36	*S. vidaurrei* Cárdenas			Synonym of *S. brevicaule* Bitter	
37	*S. violaceimarmoratum* Bitter	*	15	*S. violaceimarmoratum* Bitter	*
38	*S. virgultorum* (Bitter) Cárdenas and Hawkes	*		Synonym of *S. brevicaule* Bitter	
39	*S. yungasense* Hawkes			Synonym of *S. chacoense* Bitter	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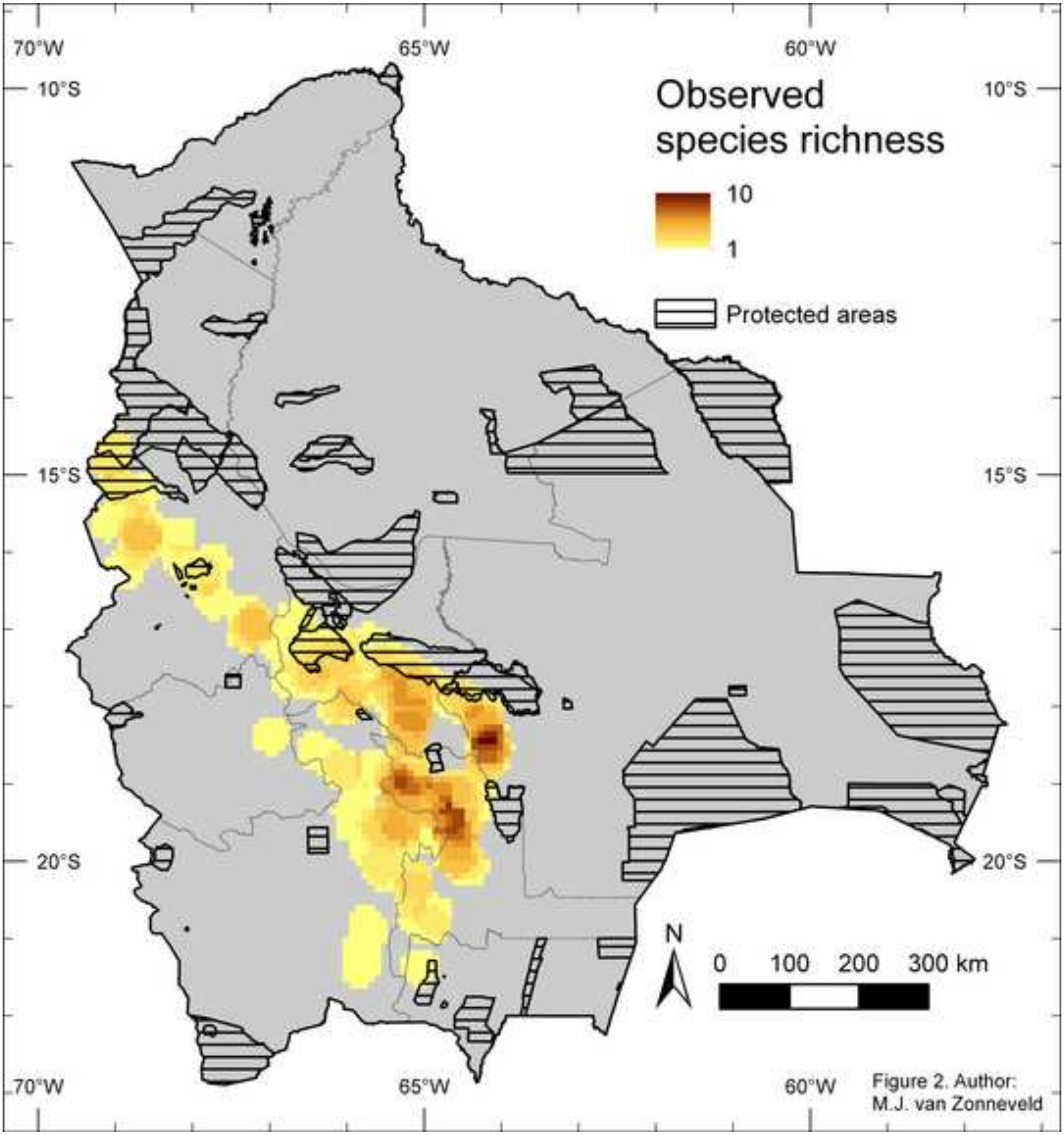
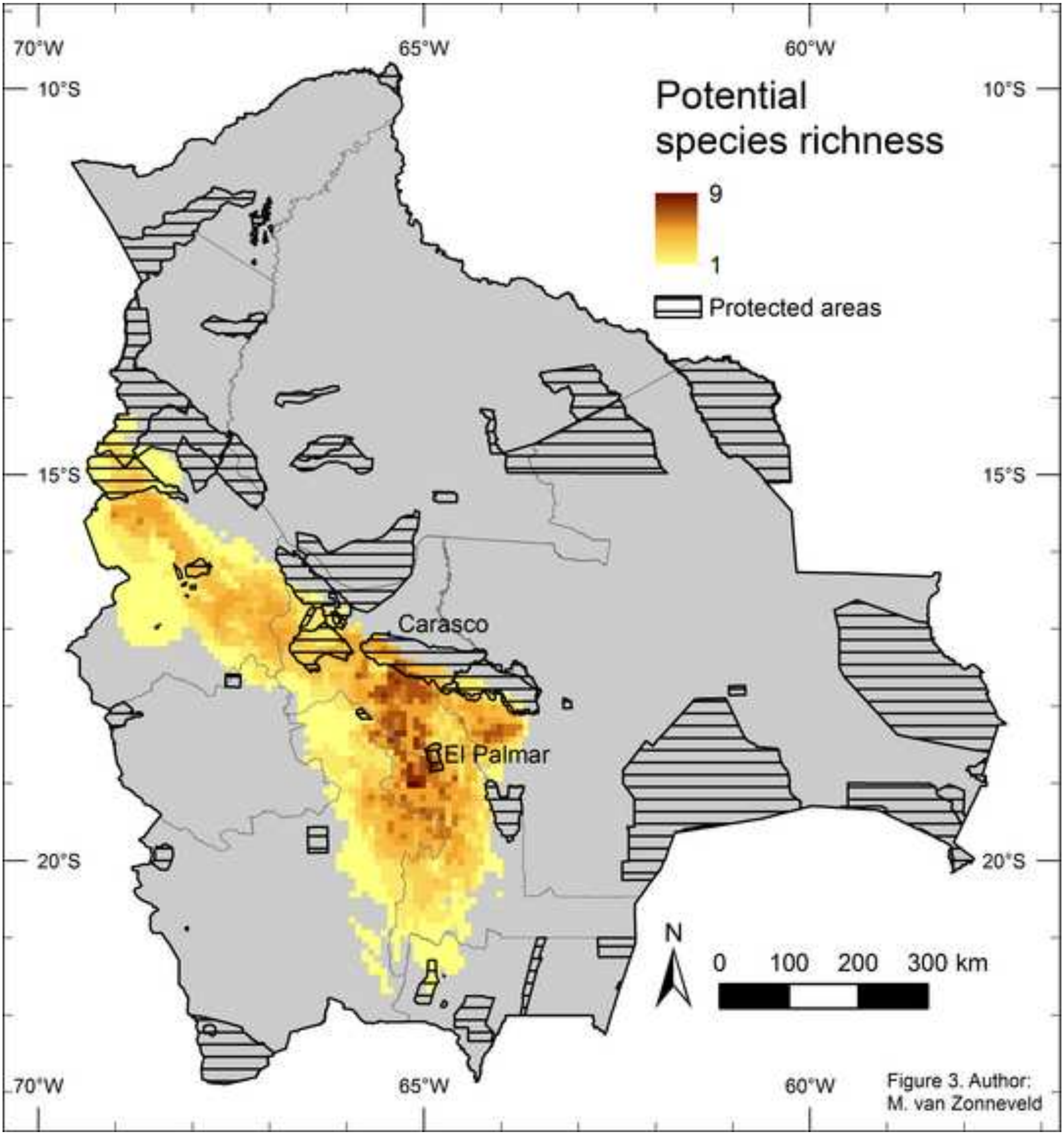
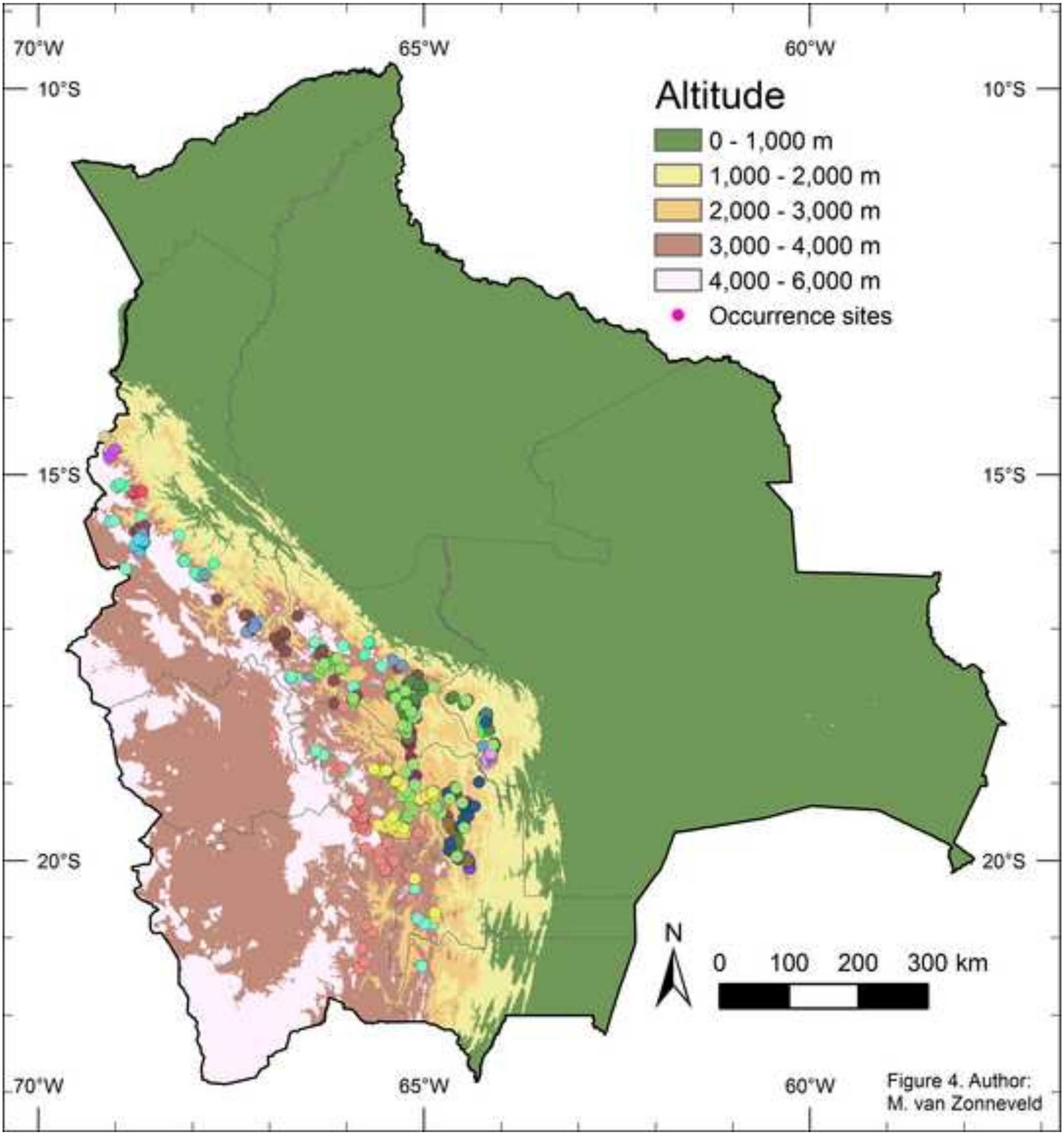
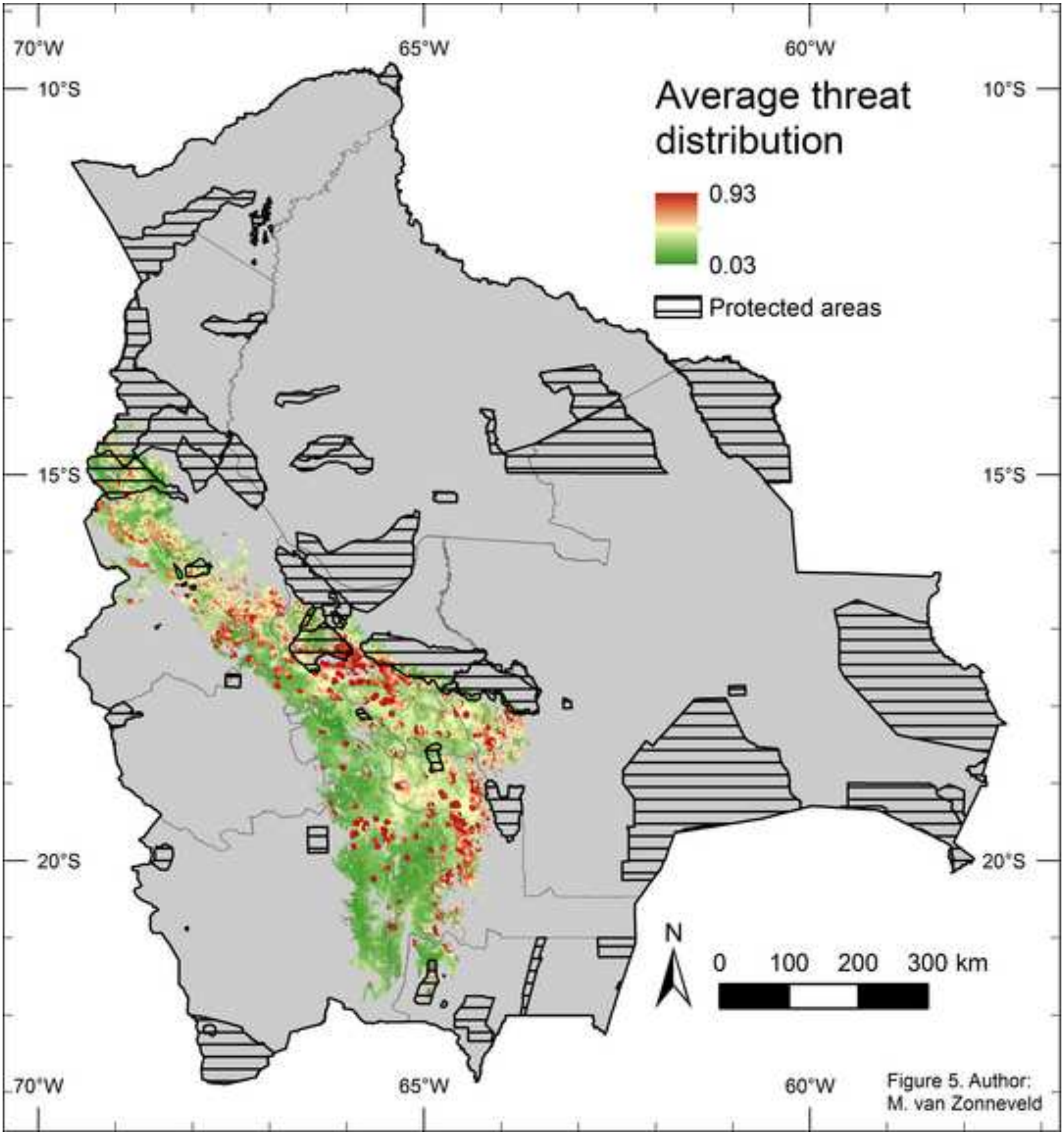
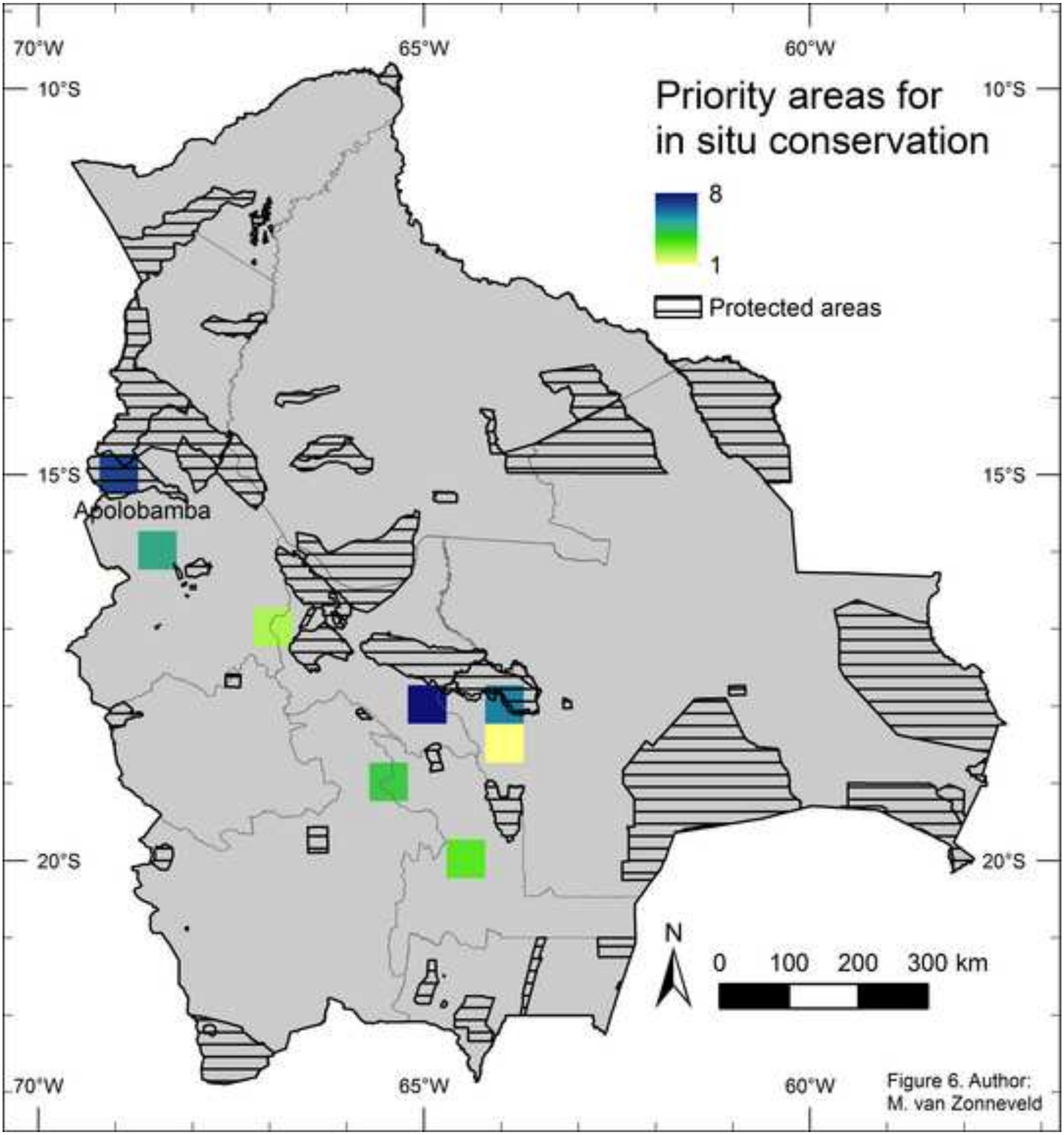
65°W
60°W
10°S
15°S
20°S
Occurrence sites
wild potato species
S. achacachense
S. alandiae
S. arnezii
S. avilesii
S. berthaultii
S. boliviense
S. bombycinum
S. brevicaule
S. circaeifolium
S. flavoviridens
S. gandarillasii
S. hoopesii
S. neocardenasii
S. neovavilovii
S. soestii
S. ugentii
S. violaceimarmoratum
S. virgultorum
S. xdoddsii
S. xitusinum
S. xsucrense
N
0 100 200 300 km
Figure 1. Author:
M. van Zonneveld

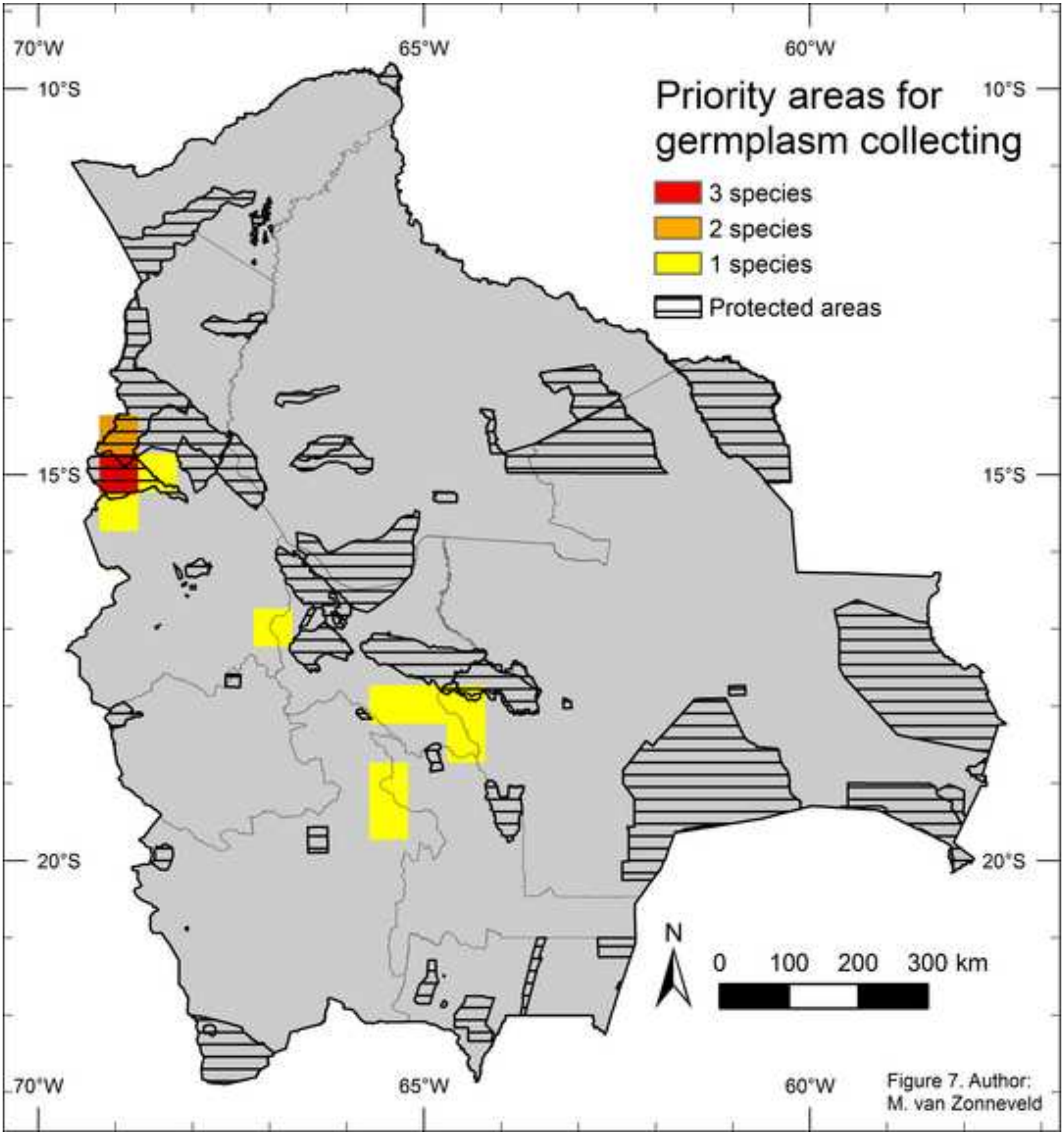

70°W
65°W
60°W
10°S
15°S
20°S
Observed species richness
10
1
Protected areas
N
0 100 200 300 km
Figure 2. Author:
M.J. van Zonneveld

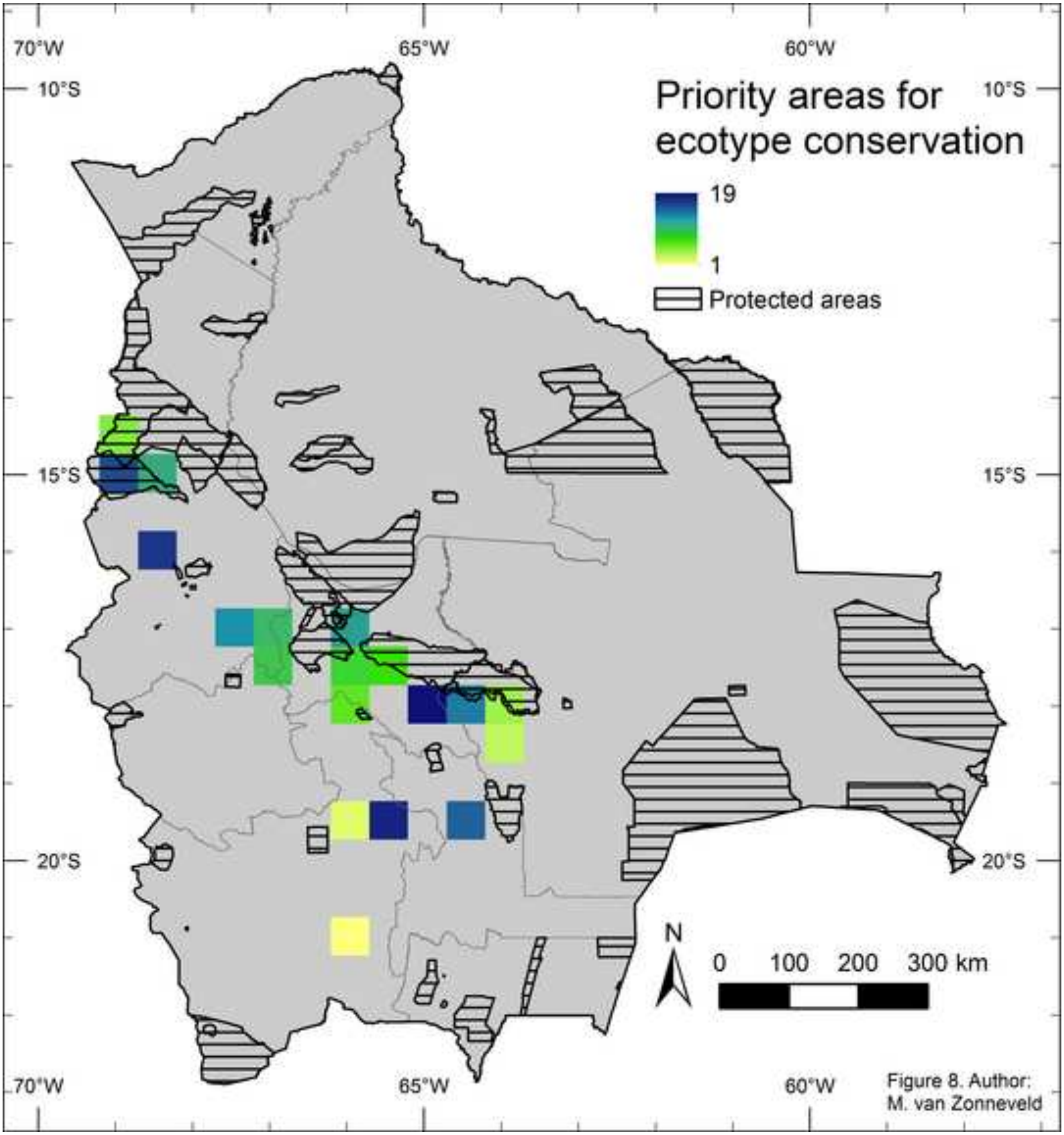

70°W
65°W
60°W
10°S
15°S
20°S
Potential species richness
9
1
Protected areas
Carasco
El Palmar
N
0 100 200 300 km
Figure 3. Author:
M. van Zonneveld

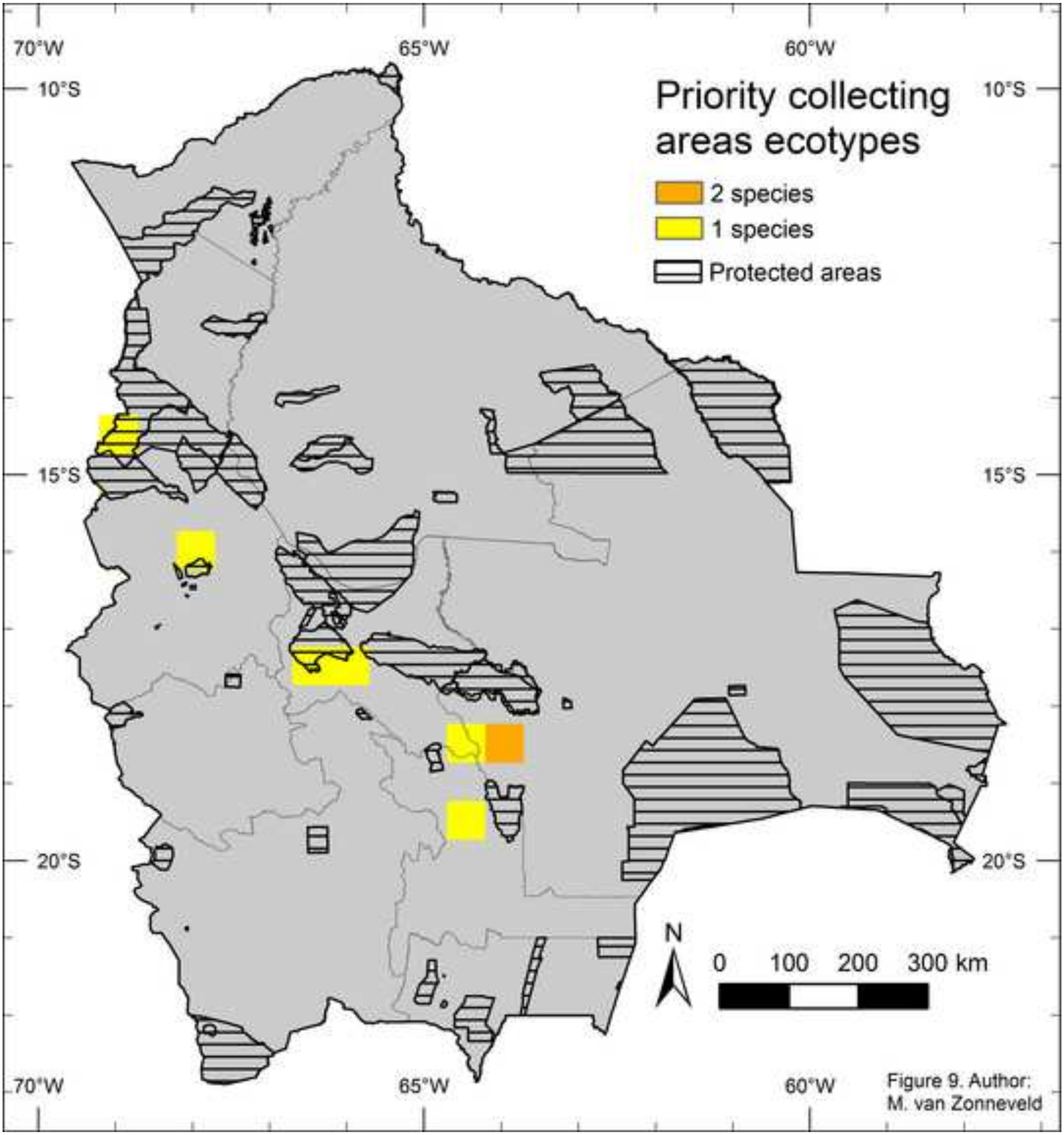

70°W
65°W
60°W
10°S
15°S
20°S
Altitude
0 - 1,000 m
1,000 - 2,000 m
2,000 - 3,000 m
3,000 - 4,000 m
4,000 - 6,000 m
Occurrence sites
N
0 100 200 300 km
Figure 4. Author:
M. van Zonneveld


70°W
65°W
60°W
10°S
15°S
20°S
Average threat distribution
0.93
0.03
Protected areas
N
0 100 200 300 km
Figure 5. Author: M. van Zonneveld


Priority areas for in situ conservation
8
1
Protected areas
70°W
65°W
60°W
10°S
15°S
20°S
Apolobamba
N
0 100 200 300 km
Figure 6. Author: M. van Zonneveld


70°W
65°W
60°W
10°S
15°S
20°S
Priority areas for germplasm collecting
3 species
2 species
1 species
Protected areas
N
0 100 200 300 km
Figure 7. Author:
M. van Zonneveld


70°W
65°W
60°W
10°S
15°S
20°S
Priority areas for ecotype conservation
19
1
Protected areas
N
0 100 200 300 km
Figure 8. Author: M. van Zonneveld


70°W
65°W
60°W
10°S
15°S
20°S
Priority collecting areas ecotypes
2 species
1 species
Protected areas
N
0 100 200 300 km
Figure 9. Author: M. van Zonneveld