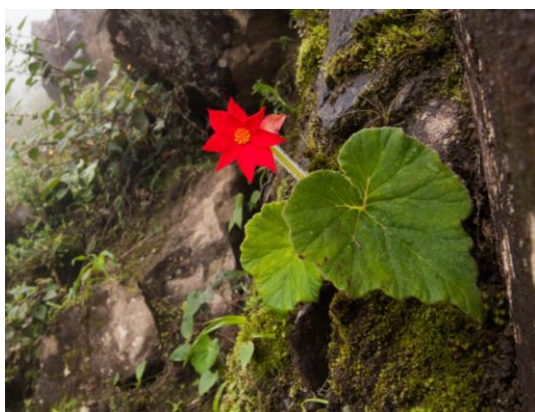# Where the rare plants are: Exploring range size rarity in *Solanum* and *Begonia*

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20th August 2021

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Thesis submitted in partial fulfilment for the MSc in
Biodiversity and Taxonomy of Plants

Abstract

Almost 40% of the world's plant species are restricted in their geographic range size. However, little is known about the mechanisms that shape range sizes, particularly in a tropical context. Because small geographic range size is known to increase extinction risk, there is a need to better understand range size in the face of the ongoing biodiversity and climate crisis. In this study, the patterns of range size rarity within the two megadiverse tropical genera *Solanum* and *Begonia* were explored and the range size-niche breadth hypothesis was tested. The results of this study show that range-restricted *Solanum* and *Begonia* species in Peru inhabit geographically and climatically rare habitats within the Andes. A positive correlation between climatic niche breadth and range size was observed, suggesting that range-restricted species are often climatic specialists. These findings underline the importance of mountainous regions and rare habitats for species with narrow ranges, a pattern observed at the global scale. The results also indicate that range-restricted species might be particularly susceptible to the effects of climate change. With 60% of the range-restricted species having no known populations inside of protected areas, the outcomes of this study underline the importance of additional conservation measures to protect range-restricted species within Peru and globally.

Acknowledgements

First of all, I want to wholeheartedly thank my supervisors Tiina Särkinen, Edeline Gagnon and Peter Moonlight for providing me with advice, ideas, and encouragement whenever I needed it. Our Monday meetings together with Jay Delves, who I also want to thank for the reassurance and support all the way through, gave me a lot of inspiration and the needed enthusiasm to write this thesis.

I also want to thank the whole LATAM-Team for making Tuesdays the highlight of the week and for all the input and ideas that helped me get to this point. This would not have been possible without you.

Thank you also to Antje Ahrends for the advice on statistics. Your Friday courses gave me the courage not to shy away from all the difficult formulas.

At last, I also want to thank everyone from the RBGE-Education Team. With the COVID-19 pandemic persisting, this has been a tough year for everyone, but I have always felt welcome and supported. Thank you for putting in the immense effort to make the course happen despite all the obstacles along the way. You all made me feel like a part of the team.

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Figures & Tables

1. Introduction

1.1. Rarity & extinction risk

The processes that cause rarity in plants are still poorly understood. What is known is that almost 40% of the worlds' plant species are rare (Enquist *et al.*, 2019; Stévart *et al.*, 2019) and that being rare makes species vulnerable to extinction (Harris and Pimm, 2008; Nic Lughadha *et al.*, 2020; Pimm *et al.*, 1995; Pimm and Jenkins, 2010; Staude *et al.*, 2020). Understanding the processes that lead to rarity is an important step to mitigate the risk of future extinctions, particularly in the face of environmental change. The world is facing its sixth mass extinction event with current extinction rates exceeding pre-anthropogenic background rates by 100 to 1000-fold (Humphreys *et al.*, 2019; Pimm *et al.*, 2014) and these rates are likely to increase in the coming years due to accelerating habitat destruction, extinction debt, and climate change (Antonelli *et al.*, 2020; Nic Lughadha *et al.*, 2020). Almost 600 plant species have already gone extinct over the last 270 years since the publication of Linnaeus' revolutionary *Species Plantarum* (Humphreys *et al.* 2019). The prevention of future extinctions is necessary to avert the detrimental impacts of further losses of biodiversity.

1.2. Types of rarity

There are many ways to be rare in nature and being geographically range-restricted is only one of them (Gaston 1994). One of the most comprehensive contributions to our understanding of the multidimensionality of rarity stems from Rabinowitz (1981) who delineated seven categories of rarity based on three distinct parameters: habitat specificity, local abundance, and range size (Table 1) (e.g., Harnik *et al.* 2012; Sætersdal 1994; Yu and Dobson 2000). A more pragmatic definition was formulated by Gaston (1994) who defined rare species as those that have low relative abundances and/or a small geographic range based on the studies scale (e.g., Harcourt 2006; Harcourt *et al.* 2002; Poulsen and Krabbe 1997; Sólymos and Feher 2005).

Table 1. Types of rarity according to Rabinowitz *et al.* (1981), with examples from the two study groups (*Solanum* and *Begonia*) mentioned for each category on the right. The grey row on top represents a widespread species followed by the seven forms of rarity.

Geographic range	Habitat specificity	Local population size	Examples from *Solanum* and *Begonia*
Large	Wide	Large, dominant somewhere	Some tuberous *Begonia* species (*B. octopetala*) many weedy *Solanum* species (e.g., *S. americanum, S. cochabambensis, S. sisymbriifolium, S. interandinum*)
Large	Wide	Small, non-dominant	Many *Solanum* species (montane: e.g., *S. corymbosum, S. caripense; lowland e.g., S. obliquum*)
Large	Narrow	Large, dominant somewhere	Most lowland *Begonias* (e.g., *B. maynensis, B. semiovata, B. albomacualta*) and most lowland *Solanums* (e.g., *S. mite, S. sessile, S. thelopodium, S. anceps, S. nudum*), many montane *Solanum* species (e.g., *S. maturecalvans, S. glutinosum, S. grandidentatum, S. fragile, S. montanum, S. nitidum, S. acaule*)
Large	Narrow	Small, non-dominant	Only a few species in both genera, e.g., *B. aeranthos, S. weddellii* (specialist in loose sand dune habitats ~4000m elevation that occur in small pockets), *S. morellifolium*
Small	Wide	Large, dominant somewhere	Locally abundant in several habitats but geographically rare, very few species globally according to Rabinowitz (1981)
Small	Wide	Small, non-dominant	Constantly sparse and geographically rare, in several habitats, might not exists according to Rabinowitz (1981)
Small	Narrow	Large, dominant somewhere	Most *Begonia* species (e.g., *B. speculum*), some *Solanum* species (e.g., *S. multiinterruptum, S. clivorum*)
Small	Narrow	Small, non-dominant	Some *Solanum* and *Begonia* species (e.g., *S. anomalostemon, B. conoensis*)

The types of rarity have been useful in advancing our knowledge and concept of rarity in nature, but they have been criticised because they are based on arbitrary categories of "small", "large", "wide", and "narrow" (Table 1; Gaston, 1994; Ronnie Drever *et al.*, 2012). Different aspects of rarity should, instead, be measured by continuous variables which better reflects variation observed in nature (Gaston, 1994). By using a categorical definition of rarity, species that fall outside of the defined categories might be disregarded while other species might meet the criteria of several categories. A relative measure of rarity is scale-dependent and runs the risk of disregarding factors that influence species distributions outside of the study area if used at a non-global scale. While these considerations point out certain

limitations to the use of rarity within ecology, studying rarity is still meaningful. A better understanding of the patterns of rarity could have several implications for conservation and macroecology, particularly when studied at a global scale (Enquist *et al.*, 2019).

1.1. Causes of rarity

The underlying mechanisms that cause different types of rarity in plants remain ambiguous. In vertebrates (birds, mammals, and bats), resource breadth (e.g., diet), body size, and ecological specialisation have all been consistently identified as correlates of rarity (Arita *et al.*, 1990; Boyles and Storm, 2007; Cofre *et al.*, 2007; Yu and Dobson, 2000). For example, Yu and Dodson (2000) showed that in their study that included 25% of mammals, mammalian orders with high numbers of large animals (>30 kg) contained higher proportions of species falling into one of the seven forms of rarity (Table 1) than other groups.

The understanding of potential causes of rarity in plants is less clear. Although several traits have been suggested as potential explanations for rarity there is little consistency in the traits examined and comparative studies of closely related species are often lacking (Bevill and Louda 1999). A large-scale comparative study by Murray *et al.* (2002) showed that only 31 out of 94 traits studied so far have been covered by more than one study. Life-history traits such as dispersal mode, growth form, seed size and competitive ability seem to have some influence on species rarity or commonness but their effects are non-directional (Bevill and Louda 1999; Murray *et al.* 2002). Seed production has been found to be the best predictor for plant rarity with a negative response observed in 4 out of 6 studies that were part of the review (Murray *et al.* 2002).

1.2. Rarity in the tropics

Plant rarity has been little studied in areas of high plant diversity, i.e. in the tropics, even though these regions might host disproportionate amounts of rare species (Enquist et al., 2019; Janzen, 1967). Most studies of plant rarity reviewed by Murray *et al.* (2002) come from temperate, arctic, or subtropical regions of the northern hemisphere. It is still a point of contention whether the signal found in these studies also applies to areas of high plant diversity in the tropics, and it can be argued that there is a considerable knowledge gap of plant rarity in megadiverse tropical regions. Secondly, studying plant rarity beyond the heavily industrialised and densely populated areas of Europe and the USA is important to make sure any patterns found are generalisable. Many ecosystems in the northern hemisphere have been heavily affected by human-induced land transformation over the past centuries (Ralska-Jasiewiczowa *et al.* 2003; Vitousek *et al.* 1997). Because of this, patterns of rarity

could be strongly affected by man-made processes in temperate systems where patterns of rarity are a mix of artificial (i.e., man-made) and natural rarity. Habitat transformation has also affected many (if not most) tropical regions but it can be argued that these influences have been less extensive (i.e., less industrialised) in comparison to the northern hemisphere.

In a comparative study of angiosperms, Dominguez-Lozano and Schwartz showed that family size (e.g., species richness per family) is positively correlated with species rarity (Domínguez-Lozano and Schwartz, 2005). Models of global plant rarity patterns add evidence to these hypotheses (Enquist *et al.*, 2019). With more than 20,000 endemic plant species, the tropical Andes in particular show high degrees of natural rarity (Enquist *et al.*, 2019; Lamoreux *et al.*, 2006; Myers *et al.*, 2000). Studies of plant rarity in the Andes are lacking, however, possibly due to the sheer diversity and size of the region and the relatively low collection densities across most of the mountain ranges (Jørgensen *et al.*, 2011).

1.3. Range size as a measure of rarity

Due to the difficulties associated with studying rare plant species, in particular those confined to taxonomically poorly known yet highly diverse areas with low collection densities, range size is often used as a surrogate of plant rarity and threat. Range size is also often used to produce threat assessments for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species because it has been identified as a major predictor of extinction risk across taxonomic groups (Gaston, 1994; Gaston and Fuller, 2009; Harnik *et al.*, 2012; Harris and Pimm, 2008; IUCN, 2021; Leao *et al.*, 2014; Runge *et al.*, 2015).

Our knowledge of global distribution patterns of plants has increased considerably since the earliest biogeographical studies by Wallace and von Humboldt (von Humboldt, 1808; Wallace, 1878), but our understanding of the processes that shape these distributions is lagging behind (Brown *et al.*, 1996; Gaston, 2003; Gregory and Gaston, 2000; Sheth *et al.*, 2020). The slow scientific progress can be traced back to several factors. Firstly, range size is a multidimensional variable that can be explored at various spatial scales (Brown, 1995; Gaston, 2003). At a global scale, a species' geographic range size has long been used to create species distribution maps, but often at a coarse scale (Brummitt *et al.*, 2021; Williams *et al.*, 1994). The lack of detailed global level species distribution maps has prevented fine-scale studies of plant distribution patterns. Meanwhile, most published studies on range sizes in plants are confined to local or regional study areas (Essl *et al.*, 2009; Kelly and Woodward, 1996; Loza *et al.*, 2017; Pilgrim *et al.*, 2004).

Range size can vary tremendously between closely related species with one species exceeding the range size of another by several orders of magnitude (Brown *et al.*, 1996). This has restricted the scope of most detailed early studies of range size to a single widespread species (Brown *et al.*, 1996; Gaston and Fuller, 2009). It is now evident, however, that most of the world's species are geographically rare and that extremely widespread species are somewhat of an exception (Enquist *et al.*, 2019; Gaston, 1996).

1.4. Range size in conservation

The considerable knowledge gap that exists regarding the mechanisms that shape range sizes and rarity has direct consequences for conservation studies and practices. The most comprehensive tool to classify species for conservation prioritisation is the IUCN Red List of threatened species (hereafter as Red List) (IUCN, 2021). In the course of the classification process, species are assigned a specific threat level based on the evaluation of several criteria relating to extinction risk (IUCN, 2019). Geographic range size is one of the main criteria used in the IUCN Red List assessment to categorise extinction risk for plants (IUCN, 2021; Stévart *et al.*, 2019). This approach is particularly common in the tropics because other information is often insufficient or not available (Dauby *et al.*, 2017; Nic Lughadha *et al.*, 2019).

The two most commonly used measurements of range sizes include the Extent of Occurrence (EOO) and Area of Occupancy (AOO), which are both used in the IUCN Red List assessments. EOO is calculated as the minimum area covered by a convex polygon that connects all know occurrences. EOO thereby determines the boundaries of the species' range (Gaston, 1991; IUCN, 2021). AOO complements the EOO by estimating the area within the EOO that is occupied by individuals of the species of interest (Gaston, 1991). Because AOO can be highly correlated with sampling effort in areas with low collection densities, AOO is a less accurate measure of range size in some cases as it underestimates range sizes in areas with low sampling effort (Sheth *et al.*, 2012).

1.5. Niche breadth-range size hypothesis

Several studies propose that range size rarity might be linked to ecological specialisation (reviewed in Slatyer *et al.* 2013). Measuring specialisation is inherently complex, and an abundance of study frameworks exists. One of the ways of measuring specialisation that has become established in studies of rarity is niche breadth, which defines the range of ecological factors (e.g., the degree of specialisation) a given species is able to survive and reproduce under (Colwell and Futuyma, 1971; Hutchinson, 1957). Niche breadth is based around the

concept of the ecological niche which refers to the n-dimensional environmental and biotic space in which a species can persist (Hutchinson, 1957).

The hypothesis that niche breadth might be directly linked to range size was formalised in the niche breadth-range size hypothesis by Brown (1984), which predicts that broader niches to have a positive effect on range sizes mediated by the amount of suitable habitat available to a given species (Sheth and Angert, 2014).

The niche breadth-range size hypothesis has been tested across a number of taxonomic groups, including mammals and other vertebrates, molluscs and crustaceans, insects, and plants. (Briers, 2003; Essl et al., 2009; Gaston and Spicer, 2001; Gregory and Gaston, 2000; Saupe et al., 2015; Sheth and Angert, 2014; Slatyer et al., 2013; Waldock et al., 2020; Walker, 2006; Williams et al., 2006; Yu et al., 2017). Delineating a general trend has been difficult as results largely depend on the study group and the definition of the niches' environmental axis. A review by Slatyer *et al.* (2013) suggests that a general positive correlation between niche breath and range size exists, but most early studies that tested the hypothesis are likely to suffer from distortions by uneven sampling effort. Of the 64 studies reviewed, 45 focused on animals, underlining a general emphasis on vertebrates in niche breadth studies (Slatyer *et al.* 2013).

Most recently, Sheth *et al.* (2014) found evidence for a correlation between climatic niche breadth and range size across 72 North American *Mimulus* species, where species with a larger range tended to have broader environmental niche. A similar relationship was observed across *Rhododendron* species in China by Yu *et al.* (2017). However, it is still a point of contention if these patterns would hold true within tropical regions where species assemblages are often thought to be driven by biotic interactions rather than climatic conditions (Schemske *et al.*, 2009).

Plant studies in tropical regions are particularly underrepresented in the existing literature on niche breadth and geographic rarity and no large scale-comparative study of plant range sizes and niche breadth within the tropics has been published yet. While tropical countries are generally understudied, there is a global bias in conservation studies towards animals (Balding and Williams, 2016). This "plant blindness" highlights the need for studies examining the distribution and processes underlying the patterns underlying rarity in plants within tropical areas.

If ecological specialisation (expressed as niche breadth) and geographic rarity are correlated, geographically rare species could be more vulnerable to environmental changes than previously thought. On one hand, the accelerating rate of habitat loss poses a direct threat to species with restricted range sizes (Nic Lughadha *et al.*, 2020; Pimm *et al.*, 1995; Staude *et al.*, 2020). Under the assumption that these species are specialised to certain environmental conditions changes in these might have an adverse effect on precisely the same species (Breiner *et al.*, 2017; Colles *et al.*, 2009; Enquist *et al.*, 2019). The effects of climate change might be particularly concerning when it comes to plants as their sessile habit could make them particularly vulnerable to the accelerating climatic changes and species distributions are potentially linked to climatic conditions (Enquist *et al.*, 2019; Thuiller *et al.*, 2005). In the worst-case climatic changes could lead to the emergence of a positive feedback loop where the loss of potentially inhabitable habitat prevents species from migrating and evolutionary rescue whereas climate change further reduces the amount of suitable habitat (Colles *et al.*, 2009).

1.6. Aims and objectives

The aim of this project is to explore range size rarity and the relationship between range size and niche breadth using two megadiverse tropical plant genera *Begonia* and *Solanum* as a study group. Specifically, the project is focused on understanding the patterns of range sizes in geographic and climatic space and testing the correlation between range size and climatic niche breadth, with the objective to answer the following questions:

1. **Do range-restricted species form geographic hotspots, i.e., are they geographically clustered?**

   H0: There is no detectable geographical clustering of range-restricted species.

   H1: There is detectable geographic clustering of range-restricted species.

2. **Are there climatic hotspots of range-restricted species?**

   H0: There is no detectable climatic clustering of range-restricted species.

   H1: There is detectable climatic clustering of range-restricted species. We expect a higher proportion of range-restricted species in climatically rare habitats due to lack of available habitat space restricting species' geographic range sizes (Ohlemüller *et al.*, 2008; Sheth and Angert, 2014).

3. **Is geographic range size correlated with climatic niche breadth?**

H0: There is no detectable correlation with geographic range size and climatic niche breadth.

H1: Geographic range size is correlated with climatic niche breadth, where range-restricted species have narrower climatic niches than widespread species (Breiner *et al.*, 2017; Sheth and Angert, 2014; Yu *et al.*, 2017).

In this study the term **range-restricted** is used to describe **geographically rare** species (i.e., species that are rare because of their small range size) (Table 1). **Geographic rarity** is thus hereafter referred to as **range size rarity** to reflect the use of geographic range size as a measure of rarity.

Results from this study will provide insights into the patterns of geographic range size in a tropical context and will help to determine areas for conservation prioritisation in the study region of Peru (see below under Methods section 2.1). If general trends across both study groups (*Solanum* and *Begonia*) are observed results can be applied more generally across tropical countries in setting conservation priorities and establishing protected areas that target range-restricted species. Results will also be used to evaluate the incorporation of niche properties in IUCN threat assessments. The prior expectation is that niche breadth should be used in IUCN threat assessments for plants because of its implications about species' vulnerability to climate change.

2. Methods

2.1. Study region

Peru is among the world's 12 most biodiverse countries, harbouring at least 19,147 plant species, of which 39% are endemic to the country (Ulloa *et al.*, 2017). Peru is environmentally extremely heterogeneous and is characterised by sharp climatic and elevational gradients with examples of all of the world's major biomes found within its borders (Figure 1; Brooks *et al.*, 2002; Josse *et al.*, 2011; Myers *et al.*, 2000). The distribution of climatic conditions is primarily driven by the northern and central Andean mountain chain that spans the entire country from north to south (Young, 2011). This leads to a pronounced east-west gradient in rainfall across Peru (Garreaud, 2009; Josse *et al.*, 2011). The western pacific coastline is dominated by arid conditions of the Sechura desert (Guerrero *et al.*, 2013) while the lowland areas on the eastern side of the country in the Amazon basin are some of the wettest places on the planet dominated by lowland moist rainforest (Young and León, 1999) (Figure 1A-B & G-H). The same east-west gradient applies to the Andean mountains themselves, where the western flanks are generally drier than the eastern flanks (Espinoza *et al.*, 2015). Only small parts of humid mountain cloud forests are found on the western slopes harbouring high amounts of endemic species (Weigend *et al.*, 2005). Montane cloud forests dominate the eastern flanks of the Andes and have long been recognised for the uniqueness of their biodiversity and their high rates of endemism (La Torre-Cuadros *et al.*, 2007) (Figure 1C). Seasonally dry tropical forests are found within the small and fragmented inter-Andean valleys isolated from each other by the high Andean peaks (Kessler *et al.*, 2011; Myers *et al.*, 2000) (Figure 1E). At higher elevations around 4,000m, forests give way to high-elevation grass and shrublands (Josse *et al.*, 2011) (Figure 1D,F).
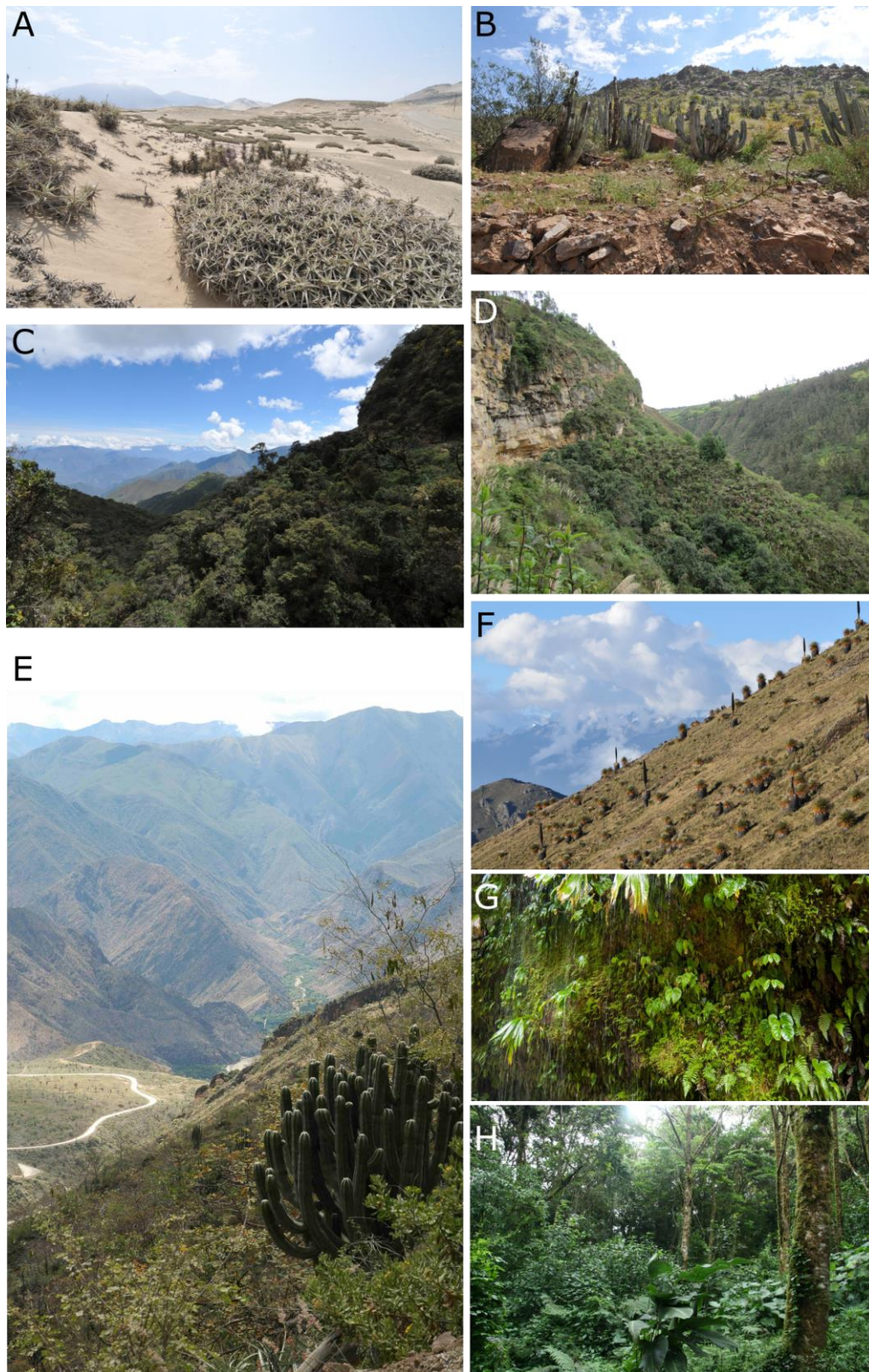
Figure 1. Diversity of biomes across the environmentally heterogeneous study region of Peru. A –Desert along the western coast, B – Coastal desert turning into seasonally dry tropical forest along the western flanks of the Andes, C – Montane cloud forest, D – Scrubland (Matorral), E – Inter-Andean Seasonally dry tropical forest, F – High-elevation grassland (Puna), G & H –Tropical rainforest in the eastern lowlands of Amazon basin. Photos by Peter W. Moonlight, Tiina Särkinen and Zoe Goodwin.

2.2. Study groups

Two megadiverse plant genera *Solanum* (Solanaceae) and *Begonia* (Begoniaceae) were chosen as study groups because (1) both genera are diverse across Peru across different habitats, (2) the taxonomy of both genera is relatively well known, (3) their diversity and distribution within Peru have been recently studied (Särkinen *et al.*, 2015: Moonlight *et al.*, in press.), and (4) there is a taxonomically verified occurrence database available for both genera (Hughes *et al.*, 2015; PBI *Solanum* Project, 2021). These factors make the two genera ideal groups to explore species range sizes across geography and climate space in a tropical highly diverse region. Both genera are amongst the ten most species diverse genera in the world with >1,000 species each (Frodin, 2004). Taxonomic species definitions follow the most recent taxonomic literature available for this region (Moonlight, *in press.*; Särkinen *et al.*, 2015).

Solanum contains 1,234 accepted species and is one of the ten most diverse plant genera in tropical Andes (Echeverría-Londoño *et al.*, 2020; Jørgensen *et al.*, 2011). A total of 276 native species have been recorded for Peru (Särkinen *et al.*, 2015). Within Peru, *Solanum* species occur across all major habitats, with a centre of species diversity in the Andes (Särkinen *et al.*, 2015, 2013). Species ecologies within the genus are incredibly diverse and include dry coastal deserts, seasonally dry tropical forests, humid montane cloud forests, lowland tropical rainforests, as well as high elevation grasslands (Särkinen *et al.*, 2015).

Similar to *Solanum*, *Begonia* is one of the ten most species-rich plant genera globally (Frodin, 2004). The genus has recently surpassed 2,000 accepted species (Hughes *et al.*, 2015). Most of the species diversity of *Begonia* is found within south-east Asia and the Neotropics, with more than 600 species documented in the tropical Americas (Moonlight *et al.*, 2015). In Peru alone, more than 70 species have been collected so far (Moonlight, *in press.*). Ecologically, *Begonia* species cover a broad range of strategies and are found within most habitats present in Peru, ranging from the dry coastal part to the wet tropical forests on the eastern slope of the Andes. Compared to *Solanum*, *Begonia* species often thrive in wetter conditions, found in habitats such as the understories of montane cloud forest (Tebbitt, 2005).

2.3. Occurrence data

Solanum and *Begonia* occurrence data was extracted from the Solanaceae Source database (http://solanaceaesource.org/) and the *Begonia* Resource Centre database (https://padme.rbge.org.uk/Begonia/home), respectively. For both genera, all available global occurrence data of species known to occur in Peru were downloaded. Manual georeferencing

in potentially under-sampled areas was conducted using a combination of Google Earth and Google Maps to trace specimen locations based on the information available on collection labels. When elevation was recorded, the information was used as an additional, independent piece of information. The Path and Line tools were used to measure distances within Google Earth to ensure the accuracy of the added coordinates. Georeferenced specimens were compiled in a list and added to the respective database, increasing the number of georeferenced specimens of the datasets by nearly 200 specimens.

The total raw *Solanum* species occurrence dataset extracted from the Solanaceae Source database encompassed 48,655 specimens, and the raw *Begonia* species occurrence data amounted to 10,734 specimens globally. After removing all potentially inaccurate occurrence data (see Section 2.4) the number of specimens was reduced to 26,199 *Solanum* and 4,615 *Begonia* specimens resulting in a final dataset of 30,586 specimens. This allowed us to investigate the range sizes and distributions of 75 *Begonia* species and 259 *Solanum* species with a total of 334 species analysed in this study. Maps were created using QGIS v3.10.9 to visualise species distributions.
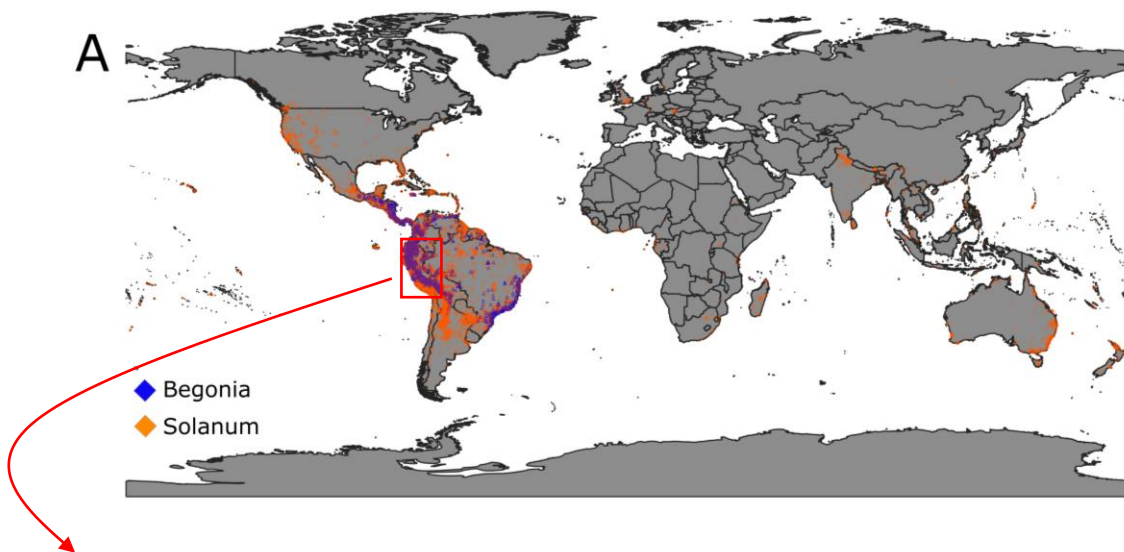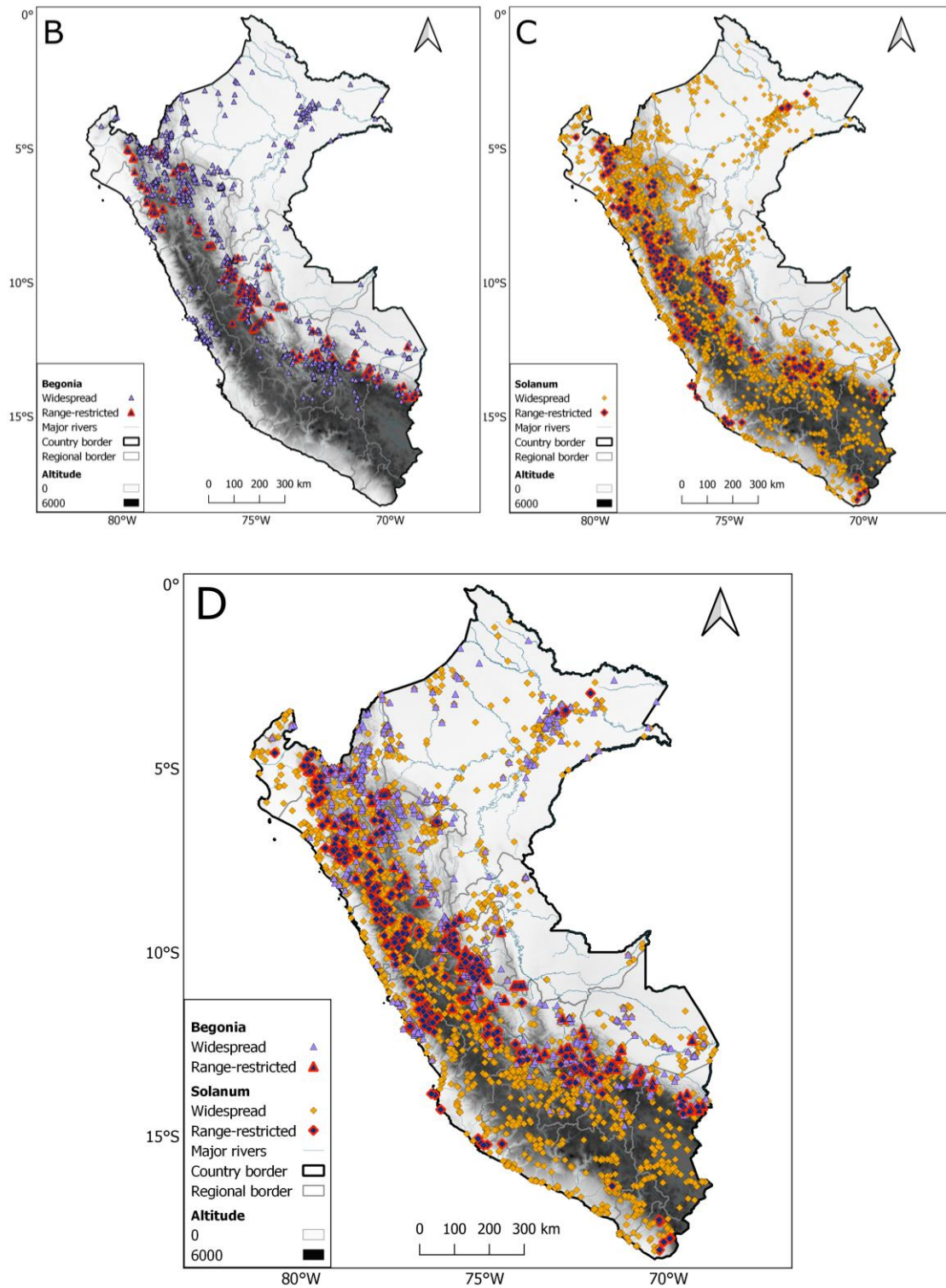
Figure 2. Distribution of the cleaned occurrence data used in the study for the two study groups *Solanum* and *Begonia*. A: Occurrence data at a global scale. B, C, D: Occurrence data within the study area Peru, for *Begonia* (B), *Solanum* (C) and the combined dataset (D) respectively.

2.4. Data cleaning

The occurrence datasets were cleaned thoroughly using several approaches that aimed to (1) remove non-native species and their occurrence records, (2) identify and remove

georeferencing errors, and (3) identify and remove duplicate specimens (Figure 2). Data cleaning and analyses were conducted in R 4.02 (R Core Team, 2013) using a combination of custom-made scripts (Gagnon *et al.*, *unpublished*), and the packages "CoordinateCleaner" (Zizka *et al.*, 2019), "dplyr" (Wickham *et al.*, 2018), "raster" (Hijmans, 2021) and "stringr" (Wickham, 2019). The package "ggplot2" (Hadley, 2016) were used to visualises the results.

			Solanum (48655)	*Begonia* (10735)
Data cleaning	**Non-native species**	Cultivated, naturalised or invasive species	- 13370	- 0
	Georeferencing errors	Occurrences with coordinate conversion errors	- 2	- 0
		Occurrences in the sea	- 125	- 0
		Occurrences without valid coordinates	- 6947	- 2935
		Occurrences in urban areas	- 0	- 22
		Occurrences in the wrong country	- 215	- 11
		Occurrences outside of the altitudinal range	- 1981	- 54
	Duplicates	Herbarium duplicates	- 308	- 3097
		Final data:	**26199**	**4615**

Figure 3. Overview of occurrence data cleaning process that aimed to identify and remove (1) records of non-native species, (2) georeferencing errors, and (3) duplicate specimens. The number of specimens identified and removed at each cleaning step is shown for both study groups and the total number of specimens kept for the analyses is indicated.

Firstly, all non-native species (cultivated, naturalised, or invasive) were removed because the primary focus of this project was to identify patterns within species naturally occurring in Peru. Hence all specimens of introduced, naturalised, and invasive species were removed (Figure 3). The largest amount of data cleaning concerned specimens with erroneous coordinates with six different cleaning steps (Figure 3). First, errors arising from inaccuracies associated with geographic coordinate conversions were detected and the coordinates were adjusted (Figure 3). Secondly, records with coordinates falling outside continental areas were identified using a raster file of climatic variables from the CHELSA repository as a land mask (see Section 2.7). Occurrences identified with this cleaning step were pushed to the closest raster cell with climate data if they were within a 2 km distance of the land mask. All occurrences with a distance of more than >2 km from land were removed (Figure 3). The

third step involved identifying and removing collections without valid coordinates (Figure 3), including specimens with equal longitude and latitude and specimens with zero longitude and latitude (Figure 3). In the fourth step specimens that fell within the borders of urban areas were identified (Figure 3). Many of these specimens were not removed, however, because they coincided with small patches of naturally occurring vegetation elements. For *Begonia fischeri* Schrank*.,* not all ambiguities could be eliminated, and the flagged records were discarded.

The next step involved removing all records falling outside countries indicated on herbarium label data (Figure 3). The results were then compared to the original dataset and occurrences with diverging information were flagged. Lastly, a digital elevation model was used to detect specimens falling outside of the elevation indicated on herbarium label data (Figure 3). Elevation data with a resolution of ~1km was acquired from the topographic database of the Shuttle Radar Topography Mission (SRTM, 2013). Specimens that fell >1,000 m from the elevation specified on the collection label were evaluated and adjusted or discarded depending on the severity of the inaccuracy (Figure 3). Elevation errors <1,000 m was considered acceptable considering the resolution of the elevation model. The final step in the cleaning process was the identification and removal of duplicate specimens i.e., collections with identical collector names and collection numbers (Figure 3).

2.5. Range size

Range size (i.e., geographic range size) was measured at a global scale for all species recorded to occur in Peru using the entirety of the final dataset. Both EOO and AOO were calculated. EOO was calculated using the R package "ConR" (Dauby *et al.*, 2017). A shapefile consisting of global country outlines was utilised to mask areas outside of the terrestrial space reducing the distortion of the EOO of species transcending continental borders.

Because the "ConR" package cannot calculate EOOs for pantropical species that span >180 degrees of longitude (Dauby *et al.*, 2017), the R package "redlistr" (Lee *et al.*, 2019) was used to calculate EOOs for four species (*Solanum americanum* Mill*., S. chrysotrichum* Schltdl*. , S. nitidibaccatum* Bitter *, S. sisymbriifolium* Lam*.*) using the same methodology as described above. EOOs of species with two occurrences or species with occurrences localised along a straight line were calculated as the distance in km between the points multiplied by 0.1 (Dauby *et al.*, 2017). For species with a single occurrence point, AOO values were used

as an approximation of EOO. AOO was determined using the Con R package with a resolution of 4km^2 per grid cell.

Range size was kept as a continuous variable for all analyses and was categorised in order to summarise results following the IUCN Red List criteria version 14 (IUCN, 2019). All species with EOO <20,000 km^2 were considered range-restricted or threatened, following IUCN criterion B1 for Vulnerable species (IUCN, 2019). Following results from previous studies on plants (Sheth *et al.* 2012), the correlation between AOO and sampling effort was tested. The results of a Spearman rank correlation test and a linear model showed that AOOs in *Solanum* and *Begonia* were strongly correlated with sampling effort in the dataset used (R^2: 0.979, ρ: 0.990, Figure 6A-C). AOO was not used for further analyses.

Table 2 Overview of IUCN Criterion B1 following the IUCN Red List criteria version 14 *(IUCN, 2019)*. The near threatened threshold was chosen based on Moat (2007) who extrapolated the value based on the power relationship between the other thresholds *(Moat, 2007)*. Categories in grey (LC-NT) correspond to widespread species in this study. Coloured (VU, EN, CR) categories are classified as range-restricted.

IUCN Category	*EOO (in km^2)*
LC (Least Concern)	> 45,000 km^2
NT (Near Threatened)	< 45,000 km^2
VU (Vulnerable)	< 20,000 km^2
EN (Endangered	< 5,000 km^2
CR (Critically endangered)	< 100 km^2

2.6. Geographic clustering

To study geographic clustering of range-restricted species within Peru, species diversity maps of range-restricted species and proportion of range-restricted species were created at three different spatial scales (10x10 km, 20x20 km, and 50x50 km). The intermediate scale (20x20 km) was identified as the most appropriate scale given the spread and quantity of data. This resolution was used to create further maps of the median EOO of all species, total species richness, and the total number of specimens known per grid cell.

Only occurrence points falling within Peru were used (n = 12,568) to study geographic clustering. Coordinates in these analyses were projected to a Lambert azimuthal equal-area coordinate system centred on Peru in order to minimise the statistical distortions arising from the changes in conversion of longitudinal and latitudinal degrees based on the distance to the equator.

The geographical clustering of range-restricted species was further explored by dividing Peru into four biogeographical regions that reflect major biomes within distinct elevational zones

(Table 3): (1) Coastal lowland ≤500m elevation, (2) West Andes >500m elevation, (3) East Andes >500m, and (4) Amazon lowland ≤500m elevation. A digital elevation model with a resolution of ~ 30m was used to create a raster file with these polygons based on a shapefile of major watersheds across Peru (SERNANP, 2021; SRTM, 2013).

Table 3. Biogeographical division of Peru into four regions that reflect major biomes based on elevational zonation, including dry coastal and moist Amazonian lowland regions, and two higher elevation Andean regions (West and East).

Zone	Definition
Coastal lowland	Areas ≤500m elevation within watersheds flowing into the Pacific
West Andes	Areas >500m elevation flowing into the Pacific
East Andes	Areas >500m elevation flowing into the Atlantic
Amazon lowland	Areas ≤500m elevation flowing into the Atlantic

While the classification of the four regions is based on their geographical attributes, the regional classes have some ecological relevance. Peru's western coastal lowland consists of mostly dry and desert-like environments, whereas the eastern lowlands are dominated by tropical rainforest (Josse *et al.*, 2011; Young, 2011). The Andes were divided into East and West, which are differentiated by different climatic conditions where the West includes pockets of lomas vegetation, dry matorral vegetation, seasonally dry forests, small pockets of Western Andean montane cloud forests, and high elevation puna grasslands. The East includes dry matorral vegetation, small pockets of inter-Andean dry forests, larger stretches of montane cloud forests, high elevation puna grasslands, and pre-montane forests along the Amazonian flanks (Young, 2011) (Figure 1).

In a second step, a raster with a 0.181 arc degrees resolution (~ 20x20 km in Peru) was created and the median EOO of all species found to occur in each cell was calculated. A projection to an equal area grid cell raster was avoided in this case as it would have led to distortions in the altitudinal data and the categorical regional map used to determine the mean altitude and habitat association of each grid cell. This resulted in the creation of a dataset consisting of 1,287 grid cells, containing information about altitude, biogeographic region, and the associated collections. Finally, linear models and Analyses of Variance (ANOVAs)

combined with a Tukey-Kramer post-hoc test were run to examine the relationships between range size, elevation, and biogeographical region using log-transformed data to meet the criteria of parametric statistical analysis. When a log-transformation did not achieve normally distributed residuals, the Spearman rank correlation coefficient (ρ) or Kruskal-Wallis test were calculated.

In a specimen-based approach, the elevation data was used to derive the elevational distribution of the occurrence data by extracting the elevation of the grid cell each occurrence fell in. The extracted values were compared between genera, and between range-restricted and widespread species, and summarised to calculate the elevational distribution and range of each species. Differences between the groups were examined by using standard and permutation t-tests to account for deviations from normal distributions. The R package "GmAMisc" (Alberti, 2021) was used to conduct these analyses. The permutation t-test was chosen as the appropriate non-parametric statistical method due to its robustness to skewed data and differences in group sizes (Moore *et al.*, 2009).

2.7. Climatic clustering

Two analyses were done to test for climatic clustering of range-restricted species within Peru based on (1) grid cells, and (2) specimens. All 19 bioclimatic variables available from the CHELSA repository (https://chelsa-climate.org/) were used at 30 arc-second resolution (~1x1 km in Peru; Table 3; Karger *et al.*, 2017).

Table 4. Overview of the bioclimatic variables utilised for this study. Variables shown in bold were used for both the climatic clustering analysis and niche breadth analyses, and variables not in bold were used climatic clustering analysis only.

Layer name	Corresponding variable
Bio1	**Annual Mean Temperature (℃)**
Bio2	**Mean Diurnal Range (℃)**
Bio3	Isothermality (-)
Bio4	**Temperature Seasonality (℃)**
Bio5	Max Temperature of Warmest Month (℃)
Bio6	Min Temperature of Coldest Month (℃)
Bio7	Temperature Annual Range (℃)
Bio8	Mean Temperature of Wettest Quarter (℃)
Bio9	Mean Temperature of Driest Quarter (℃)
Bio10	Mean Temperature of Warmest Quarter (℃)
Bio11	Mean Temperature of Coldest Quarter (℃)
Bio12	**Annual Precipitation (mm)**
Bio13	Precipitation of Wettest Month **(mm)**
Bio14	Precipitation of Driest Month **(mm)**
Bio15	**Precipitation Seasonality (-)**
Bio16	Precipitation of Wettest Quarter **(mm)**
Bio17	Precipitation of Driest Quarter **(mm)**
Bio18	**Precipitation of Warmest Quarter (mm)**
Bio19	Precipitation of Coldest Quarter **(mm)**

The grid cell-based analyses of climatic clustering of range-restricted species involved identifying grid cells within Peru with observations of range-restricted (n = 245) and widespread species (n = 1,282) within the two datasets. The process followed the approach described in Section 2.6 for the creation of a grid cell raster file. The first dataset included all grid cells with at least one range-restricted species, and the second dataset comprised all grid cells containing at least one widespread species. Climatic conditions for all grid cells were extracted and aggregated to a 20x20 km scale by calculating mean climatic conditions across cells. Differences between the two datasets were tested with a standard t-test as well as a non-parametric permutation-based t-test because both datasets were not normally distributed.

The specimen-based analysis of climatic clustering of range-restricted species was done using a spatially filtered dataset that aimed to reduce the amount of spatial autocorrelation and geographic bias in the occurrence datasets following results from empirical and simulated studies showing that spatial autocorrelation and bias have the potential to considerably distort results in biodiversity studies of remote and poorly known regions (Kramer-Schadt *et al.*, 2013; Moore *et al.*, 2018; Sheth and Angert, 2014). The spatial filtering process included the thinning of species' occurrence points so that only a single record within a 10 km radius was kept for a given species. The radius was deemed appropriate based on the sharp gradient of environmental conditions within the Andes, which also makes it unlikely that species exceeding that range form part of the same population. The spatial filtering process resulted in a dataset consisting of 5,068 specimens within Peru that were used for the analysis. Climatic conditions for all occurrence points within the spatially filtered datasets were extracted from the climatic raster layers. A null model was created based on climatic values extracted for 5,000 randomly selected grid cells from across Peru that represented the climatic space available in Peru, against which the results were compared. The extracted climatic conditions of range-restricted and widespread species were then compared to each other and the background data (i.e., null model) using an ANOVA and a Tukey-Kramer post-hoc test to explore differences between the groups.

2.8. Niche breadth

Climatic niche breadth was calculated for all species native to Peru based on all occurrence data for South America. This meant niche breadth was measured based on all known occurrence points for all species, except for the most widespread species with ranges extending beyond the continent. This was done to accurately represent the climatic conditions each species can survive under for those species that had known distribution beyond Peru.

For widespread species with ranges stretching beyond South America, niche breadth calculations reflect patterns observed on the continent and not those of potentially phylogenetically more distant populations that may have diverged in their niche properties. Spatial filtering of the dataset was applied to reduce the impact of spatial autocorrelation (see Section 2.7.), resulting in a dataset of 13,908 collections.

A set of six not strongly correlated bioclimatic variables were chosen to describe to calculate climatic niche breadth in *Begonia* and *Solanum* based on Principal Component Analysis (PCA) and a Pearson correlation test. The PCA was performed using the R package "factoextra" (Kassambara and Mundt, 2017). Strongly correlated climatic layers were identified (Pearson correlation < 0.8) and the variables with the highest contribution to the two Principal Components (i.e., explanatory power concerning climatic variation with the dataset) were kept (Figure 4). The retained variables included Annual Mean Temperature (Bio1), Mean Diurnal Range (Bio2), Temperature Seasonality (Bio4), Annual Mean Precipitation (Bio12), Precipitation Seasonality (Bio15), and Precipitation of Warmest Quarter (Bio18) (Table 4).
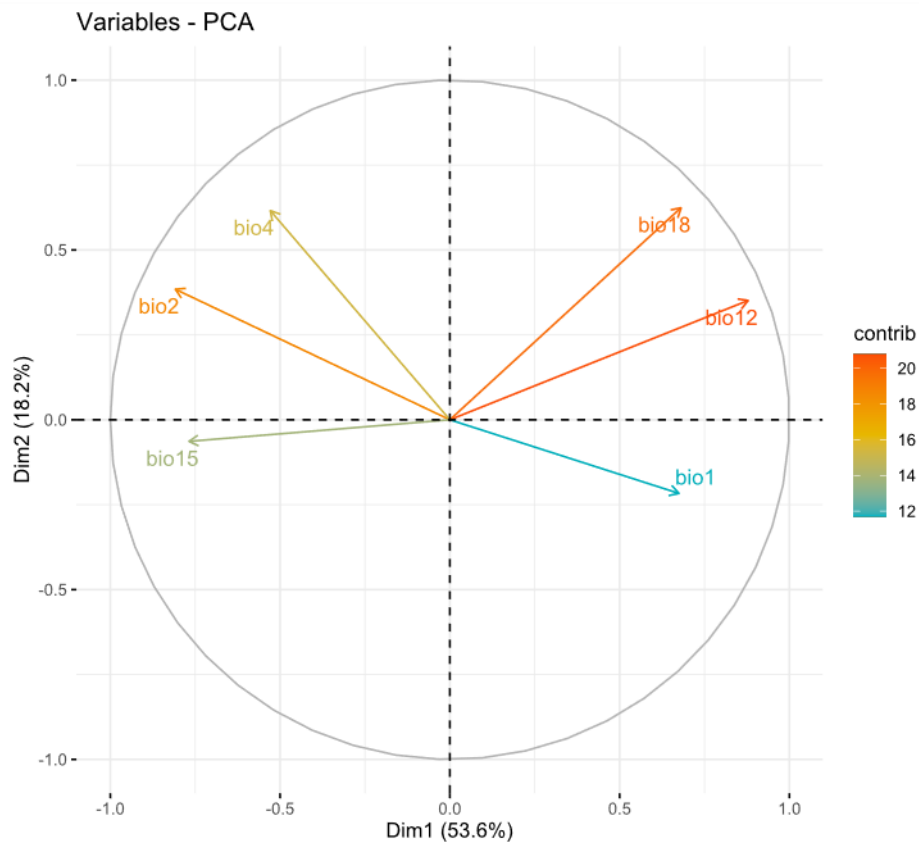
Figure 4. Results of a Principal Component Analysis (PCA) showing the explained variation by the six bioclimatic layers chosen for the analysis of the climatic niche breadth (Table 4. Overview of the bioclimatic variables utilised for this study. Variables shown in bold were used for both the climatic clustering analysis and niche breadth analyses, and variables not in bold were used climatic clustering analysis only.Colour indicates the contribution of each variable to the explanatory power of the first two principal component axes that explained 72% of the variation observed.

Climatic niche breadth was calculated for all species for each individual climatic variable as the difference of the maximum and the minimum value observed, thereby determining the range of values a species was present under. These values were scaled in order to enable comparison between temperature and precipitation variables which operate at different scales, by dividing the observed ranges by the maximum range of the observed values across the entire dataset within a climatic variable. For species with >10 occurrences, a subsampling process was introduced to reduce the impact of climatic outliers. This involved calculating the mean values of 1,000 datasets, containing random occurrences but a stable fraction of the occurrence data available for each species (50%). The process was repeated for each climatic variable with the sum of the individual climatic niches representing the climatic niche breadth of a species. The individual climatic niche breadths were compared by using t-tests to test for significant differences between rare and widespread species. The correlation between climatic niche breadth and range size was examined using a linear model with log-

transformed values to better capture the relation between the two variables and to achieve normality of the residuals.

A null model was designed to compare results to random expectation in order to ensure that the correlation of climatic niche breadth and range size observed within the dataset was higher than just by chance. This was achieved by randomising the climatic distribution of each species 100 times, with a linear model created for each of the 100 randomised datasets, similar to approaches suggest by Sheth *et al.* (2014) and Moore *et al.* (2018). The Coefficient of determination (R^2) of each model was then extracted, and the extracted values were used to determine the 95% confidence interval (CI) of the null model coefficients, with the assumption that an R^2 value outside of the CI represents a result that is significantly different from the variation that can be explained by chance alone. The Spearman rank correlation coefficient was calculated additionally.

3. Results

3.1. Range sizes

Range sizes varied by ten orders of magnitude within the dataset (Figure 5, Table 5), with the maximum range size in *Solanum* surpassing range sizes observed in *Begonia* by one order of magnitude (Figure 5, Table 5). Of the total 334 evaluated species (75 *Begonia* and 259 *Solanum* spp.), 92 (28%) were classified as range-restricted and 242 (72%) as widespread (Table 5). The proportion of range-restricted species was considerably higher in *Begonia* (52%) than in *Solanum* (20%) (Table 5). The specimen numbers underlying these calculations differed between the two genera, where *Solanum* species generally had higher specimen counts than *Begonia* species (Table 5). Overall, 19% of the range-restricted specimens fell into the boundaries of protected areas.
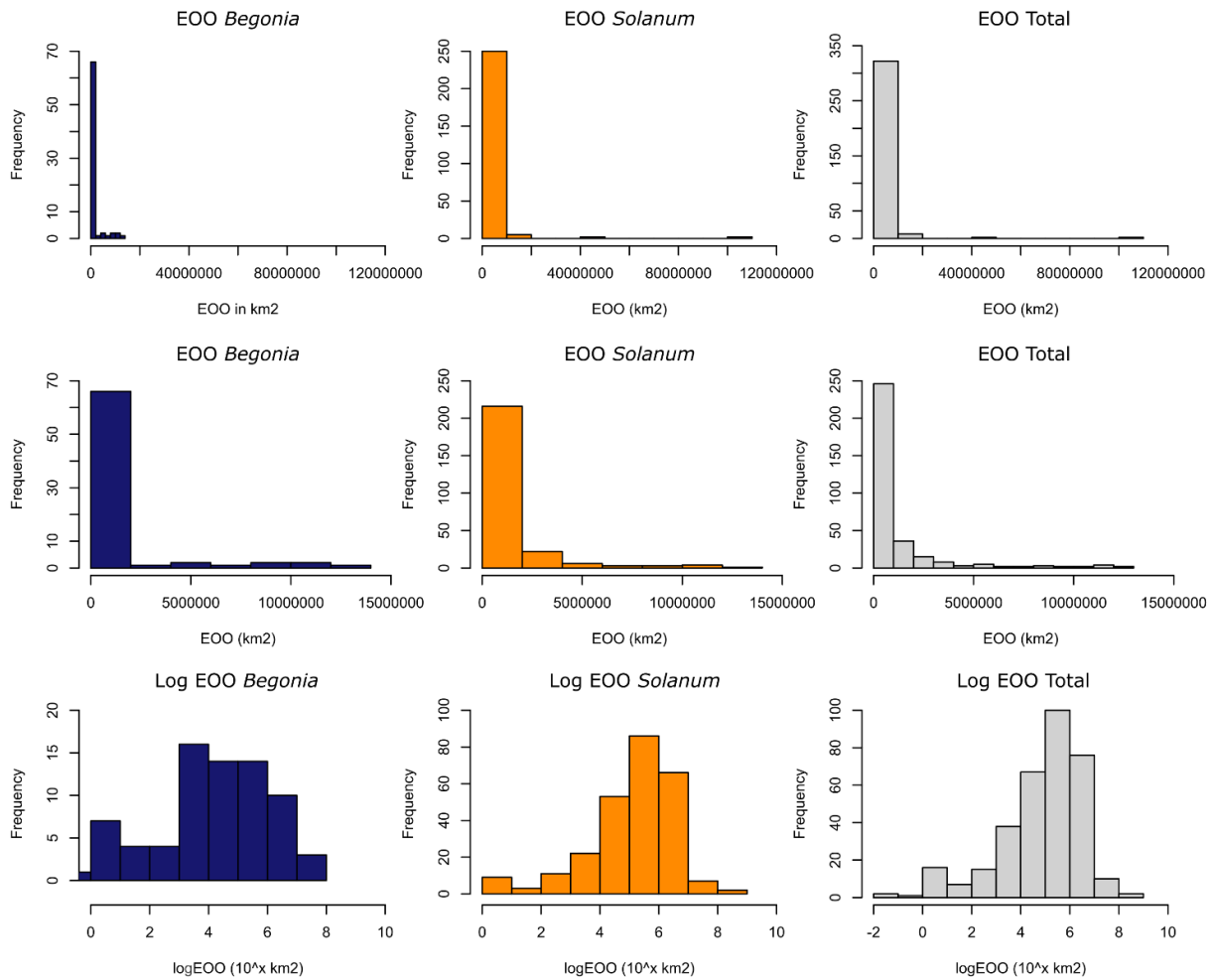
Figure 5. Global range size distributions of *Begonia* (blue) and *Solanum* (orange) species native to Peru as measured by Extent of Occurrence (EOO). In the second row of histograms, outlier species with EOOs spanning more than 180 degrees of longitude ((*Solanum americanum, S. chrysotrichum, S. nitidibaccatum, S. sisymbriifolium*) were removed to better show the frequency distribution of range sizes within the dataset. The third row shows the distrutbion of the log-transformed range sizes.

Table 5. Global range size summary statistics for *Begonia* and *Solanum* species native to Peru as measured by Extent of Occurrence (EOO). Number of specimens used for EOO calculations are shown for both genera, as well as the preliminary IUCN Red List threat assessment categories. All species with EOO <20,000km^2 were considered range-restriced following the threshold for Vulnerable in the IUCN Red List assessment criterion Bi.

	Begonia (n = 75)	*Solanum* (n = 259)	Total (n = 334)
EOO (km2)			
Mean	1,090,239	2,276,622	2,010,219
Median	14,997	285,296	192,639
Q1, Q3	1,185, 258,266	34,188, 1,181,658	13,860, 1,030,202
Min - Max	0.016 – 12,151,657	2 – 108,346,341	0.016 - 108,346,341
Log EOO (10$^{\text{x}}$ km2)			
Mean	4	5	5
Median	4	5	5
Q1, Q3	3, 5	5, 6	4, 6
Min - Max	-2 - 7	0 - 8	-2 - 8
Specimen number			
Mean	61	99	91
Median	16	38	33
Q1, Q3	5, 48	15, 94	12, 87
Min - Max	1 - 737	1 – 2,584	1 – 2,584
Status			
Widespread	36 (48%)	206 (80%)	242 (72%)
Range-restricted	39 (52%)	53 (20%)	92 (28%)
Preliminary IUCN category			
CR	14 (19%)	12 (5%)	26 (8%)
EN	18 (24%)	25 (10%)	43 (13%)
VU	7 (9%)	16 (6%)	23 (7%)
NT	5 (7%)	21 (8%)	26 (8%)
LC	31 (41%)	185 (71%)	216 (65%)
Peruvian specimens in protected area			
Widespread	29%	17%	19%
Range-restricted	24%	17%	19%

A strong correlation between specimen count and AOO was observed across all three datasets tested (*Begonia*, *Solanum*, and the combined dataset; Figure 6). The linear regression explained 98% of the overall variation in AOO in the combined dataset (Figure 6). The strong correlation was also captured by the Spearman rank correlation coefficient (ρ: 0.990, Figure

6). The patterns were less pronounced in the EOO measurements, where only a moderately strong correlation between EOO and specimen count was observed in all three datasets (Figure 6). Specimen count explained 62% of the variation observed in EOO in the overall dataset (Figure 6). The Spearman rank correlation coefficient showed slightly higher values (ρ: 0.812; Figure 6). In all datasets, the correlation between EOO and specimen count was lower than the observed correlation between AOO and specimen count (Figure 6).
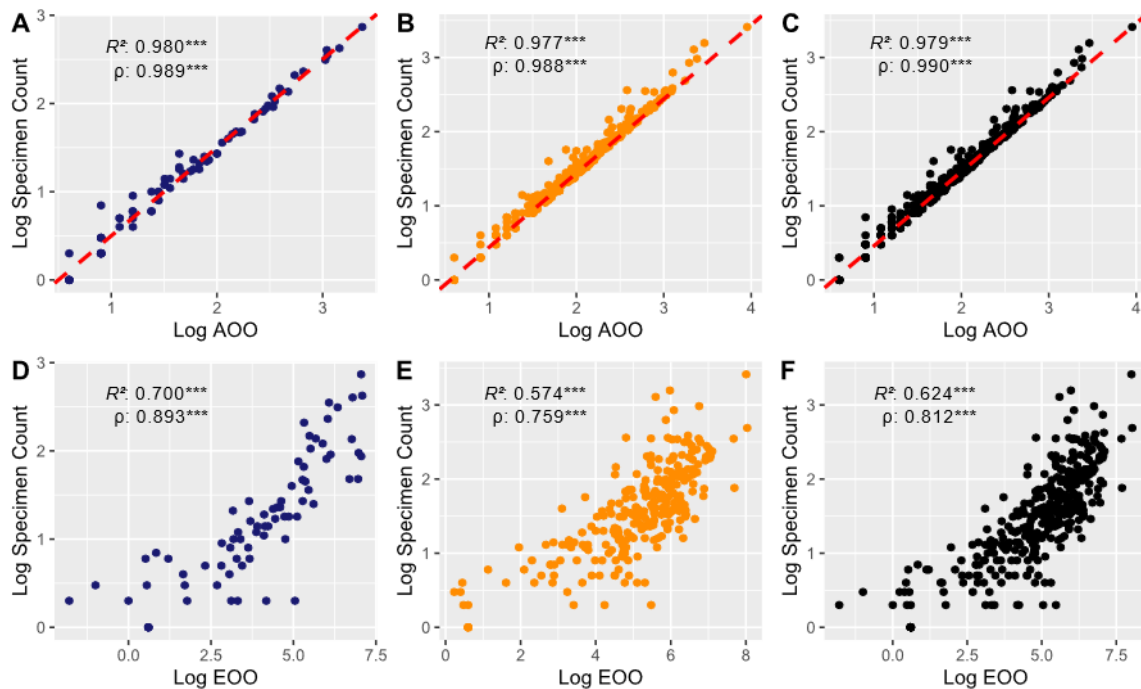
Figure 6. Correlation between range size measurements and collection effort in *Begonia* (blue), *Solanum* (orange), and the combined dataset (black). All variables were log-transformed to better reflect linear relations. A diagonal trendline was added to the three plots at the top to highlight the linearity of the interaction. The Coefficient of determination (R^2) of a linear model and the results of a Spearman rank correlation (ρ) are displayed within each plot.

3.2. Geographic distribution of range-restricted species

Density maps of species distributions at three different spatial scales revealed that in both *Solanum* and *Begonia,* the majority of range-restricted species were situated within the Andes, particularly on the western and eastern slopes of the Andes (Figure 7). In the norther part of Peru, range-restricted *Begonia* species inhabited both sides of the Andes (Figure 7A-C). Towards the south, range-restricted *Begonia* species generally occurred more frequently on the eastern side of the Andes (Figure 7A-C). This trend was consistent across all three scales, with local clusters of cells with higher numbers of range-restricted species found throughout the Andes (Figure 7G-I). The two grid cells with the highest number of range-restricted species both fell into the northern parts of the Andes (Figure 7I). Range-restricted *Solanum* species frequently inhabited the western slopes of the Andes, particularly in the norther part parts of Peru (Figure 7D-F). The inverse was observed in southern Peru, where

clusters of range-restricted *Solanum* species primarily occurred on the western slope of the Andes (Figure 7D-F).
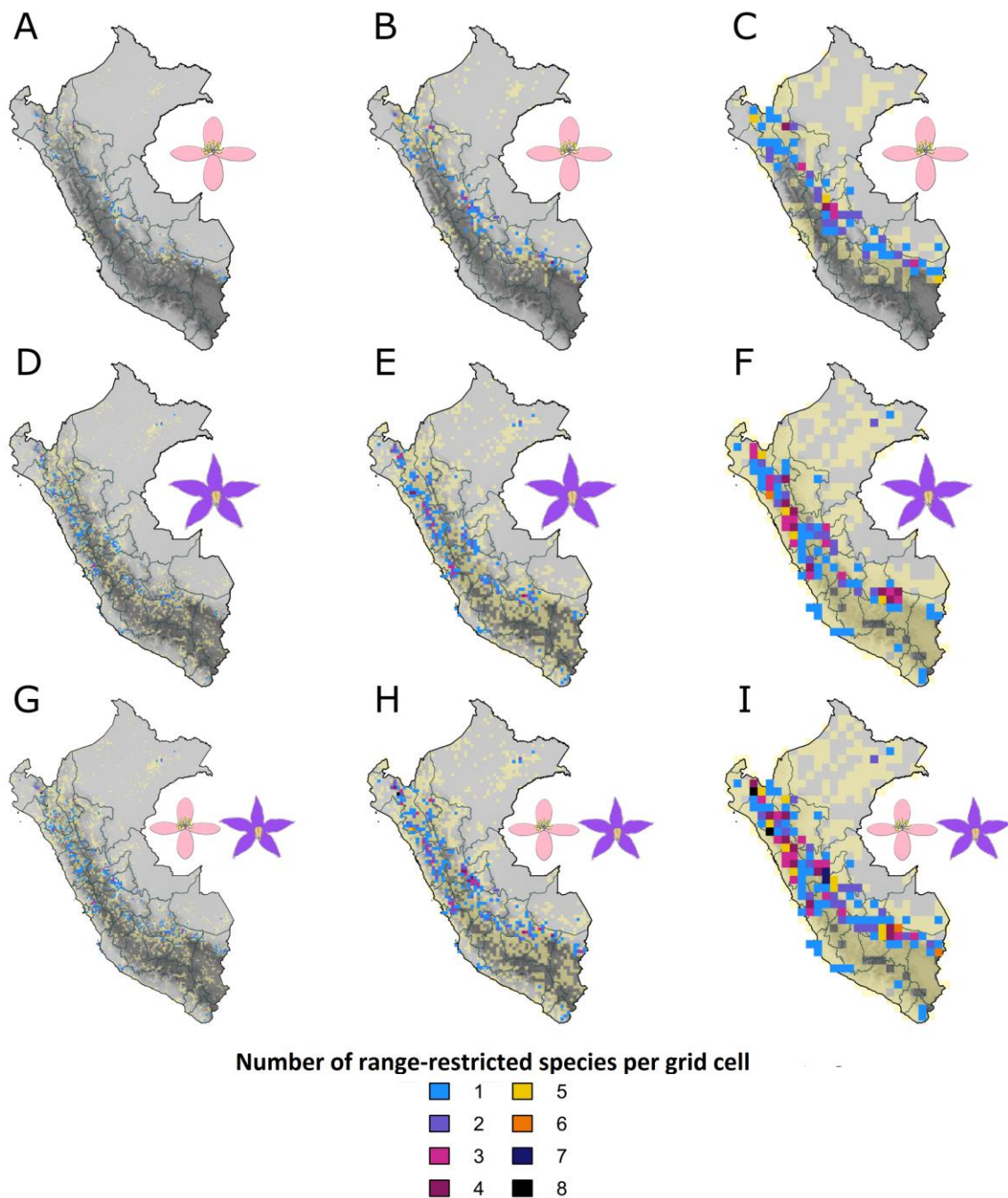
Figure 7. Density maps of the number of range-restricted species within grid cells at a resolution of 10x10km (A-G), 20x20km (B-H), and 50x50km (C-I) in *Begonia* (pink flower)(A-C), *Solanum* (purple flower)(D-F), and the combined dataset (G-I). Flower symbols indicate the dataset used for the calculation. The background shows the elevation patterns of Peru, with darker colours reflecting increasing elevations and in yellow the grid cells with collections of species not classified as rare (with regards to the dataset used). *Begonia* flower illustration was adapted from an illustration of *B. speculum* by Claire Banks and the *Solanum* flower from an illustration of *S. dulcamara* drawn by Bobbi Angell.
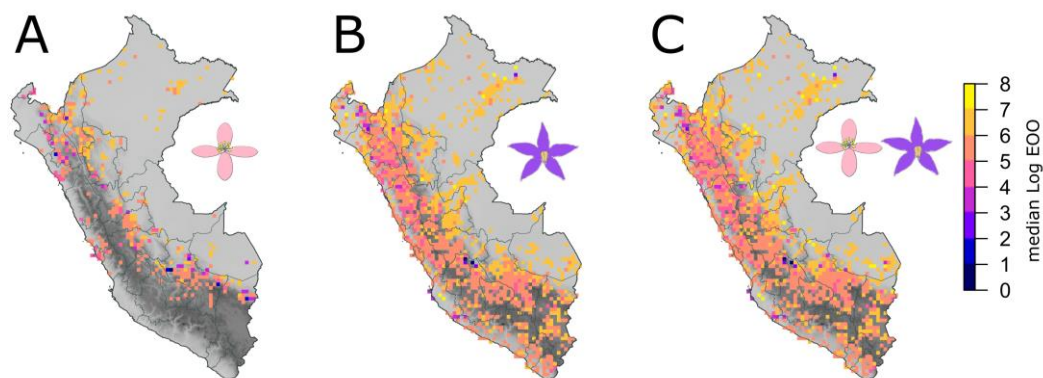
Figure 8. Density maps of the median range size of species within grid cells at a resolution of 20x20km for *Begonia* (pink flower) (A), *Solanum* (purple flower) (B), and the combined dataset (C). Flower symbols indicate the dataset used for the calculation. The data was log-transformed to reduce the impact of outliers. The background shows the elevation patterns of Peru, with darker colours reflecting increasing elevations. *Begonia* flower illustration was adapted from an illustration of *B. speculum* by Claire Banks and the *Solanum* flower from an illustration of *S. dulcamara* drawn by Bobbi Angell.

Median range size per grid cell showed generally higher values in lowland areas outside of the Andes for both *Begonia* and *Solanum* (Figure 8). In both genera, the majority of cells with low median range sizes per grid cell fell within the Andes, with the highest range size rarity values observed in scattered pixels in small pockets across the southern, central, and northern parts of the mountain chains (Figure 8).
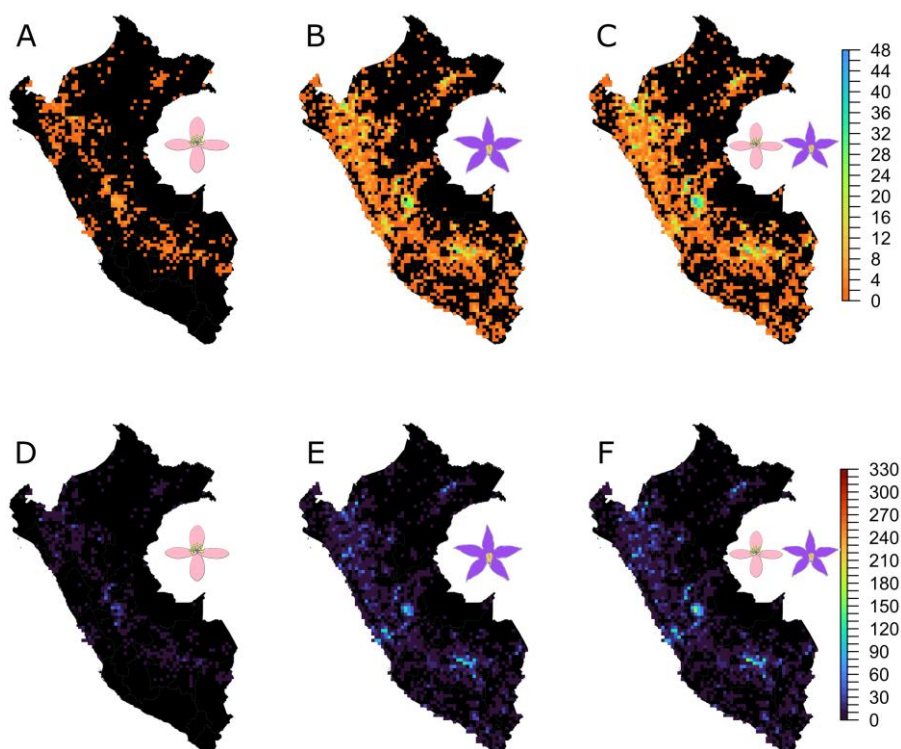
Figure 9. Density maps showing the total species richness (top) and the number of collections (bottom) within grid cells at a resolution of 20x20km for *Begonia* (pink flower) (A, D), *Solanum* (purple flower) (B, E), and the combined dataset (C, F). Flower symbols indicate the dataset used for the calculation. *Begonia* flower illustration was adapted from an illustration of *B. speculum* by Claire Banks and the *Solanum* flower from an illustration of *S. dulcamara* drawn by Bobbi Angell.

Areas of total species richness largely coincided with areas that were extensively collected across both genera and within the combined dataset (Figure 9A-F), reflecting the strong correlation between total species richness and collection effort observed across the study area by both the linear regression and the Spearman rank correlation test (R^2: 0.84, ρ: 0.92, p < 0.001, Figure 10B, D). The relation between range-restricted species richness and collection effort was significant, but the explanatory power of both statistical tests was lower than for total species richness (R^2: 0.19, ρ: 0.40, p < 0.001, Figure 10A, D). When using the same tests to examine the relationship between range-restricted species richness and total species richness, a weak positive correlation was detected by both statistical measurements (R^2: 0.23, ρ: 0.44, p < 0.001, Figure 10C, D).
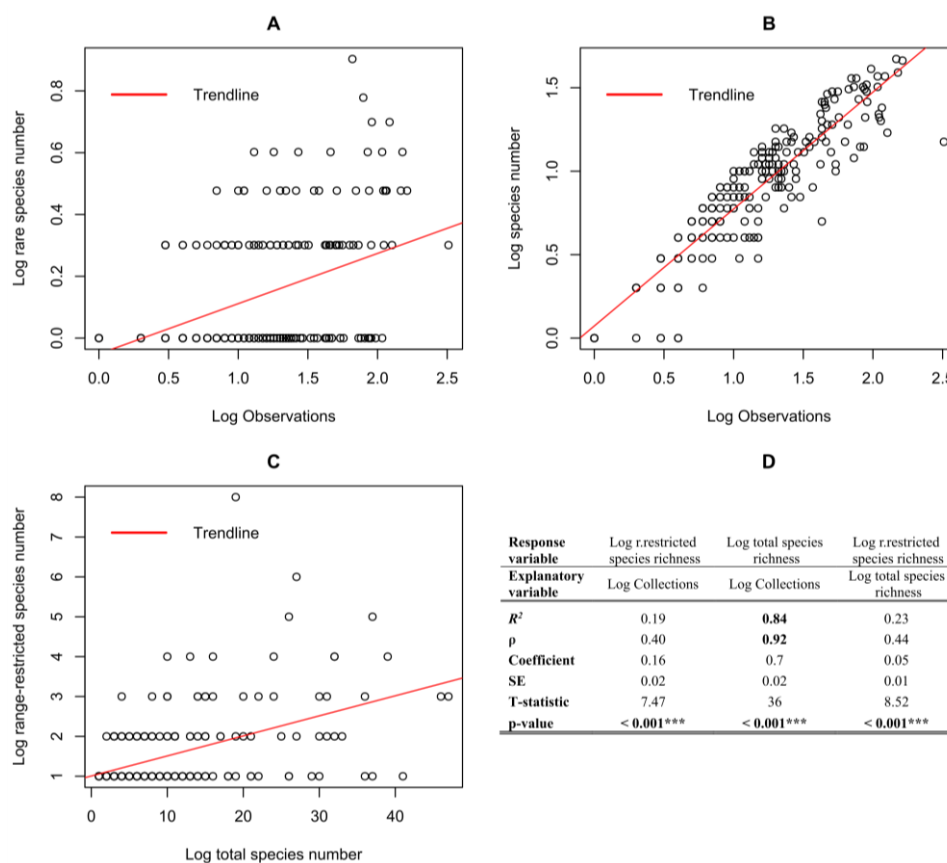
Figure 10. Relation between total species richness, range-restricted species richness and collection effort based on 20x20km raster grid cells of the density maps of the combined dataset of both *Begonia* and *Solanum*. Each dot in the scatterplot represents one raster cell. The trendline resulting from a linear model is shown in red. The table displays the detailed results of the linear model and a Spearman rank correlation test. Bold values indicate the highest variation explained by the statistical methods and significant p-values.

Response variable	Log r.restricted species richness	Log total species richness	Log r.restricted species richness
Explanatory variable	Log Collections	Log Collections	Log total species richness
R^2	0.19	**0.84**	0.23
ρ	0.40	**0.92**	0.44
Coefficient	0.16	0.7	0.05
SE	0.02	0.02	0.01
T-statistic	7.47	36	8.52
p-value	< 0.001***	< 0.001***	< 0.001***

3.3. Geographic clustering

3.3.1. Comparative analysis

Comparison of the distribution of *Begonia* and *Solanum* within the four biogeographic regions of Peru showed that for both genera, the highest number of species was observed in

the Eastern Andes, while the lowest number of range-restricted species was found in the coastal lowlands (Table 6). The coastal lowlands were the geographically smallest and also the least species-rich region, with only 35 species observed in total compared to more than 100 unique species in every other biogeographical unit (Table 5). The proportion of range-restricted species was the highest in the Western Andes (0.18) and the lowest in the Amazonian region (0.09, Table 6). Both Andean regions surpassed the two lowland regions in the number of range-restricted species found per km^2 (Table 6).

Table 6. Species diversity of *Begonia* and *Solanum* across the four biogeographic regions within Peru. For information about the classification process see (Section 3.3, Table 3). The highest values observed in each category are shown in bold.

Category	Coastal lowland	West Andes	East Andes	Amazon lowland
Number of species	35	121	**288**	105
Number of range-restricted Begonia	0	7	**32**	5
Number of range-restricted Solanum	4	22	**39**	9
% range-restricted species	0.11	**0.18**	0.14	0.09
range-restricted species per km2	0.00006	0.00014	**0.00017**	0.00002
Area in km2	72,740	206,647	427,441	**582,532**

3.3.2. Relation of median range size and habitat

Highly significant differences between the median range sizes per 20x20 km grid cell between the four biogeographic regions were detected based on the ANOVA ($p < 0.0001$***, Figure 11). A Tukey-Kramer post-hoc test revealed significant differences between the two Andean regions, with the West Andes exhibiting the lowest median range size values (ANOVA: $p < 0.0001$***, Figure 11). The values observed in the Amazonas region were significantly higher than in all other regions (ANOVA: $p < 0.0001$***, Figure 11). The distribution of the median range size per grid cell of the eastern Andean region closely matched the distribution observed in the coastal lowland and the median range size between the two groups did not differ significantly (ANOVA: $p = 0.878$, Figure 11). A Kruskal-Wallis test showed the same results.

Groups	Difference	Lower CI	Upper CI	p-value
Coastal lowland-Amazonas	-0.74	-0.91	-0.56	< 0.0001***
East Andes-Amazonas	-0.69	-0.80	-0.58	< 0.0001***
West Andes-Amazonas	-0.97	-1.11	-0.84	< 0.0001***
East Andes-Coastal lowland	0.05	-0.12	0.21	0.878
West Andes-Coastal lowland	-0.24	-0.41	-0.06	0.004**
West Andes-East Andes	-0.28	-0.40	-0.17	< 0.0001***
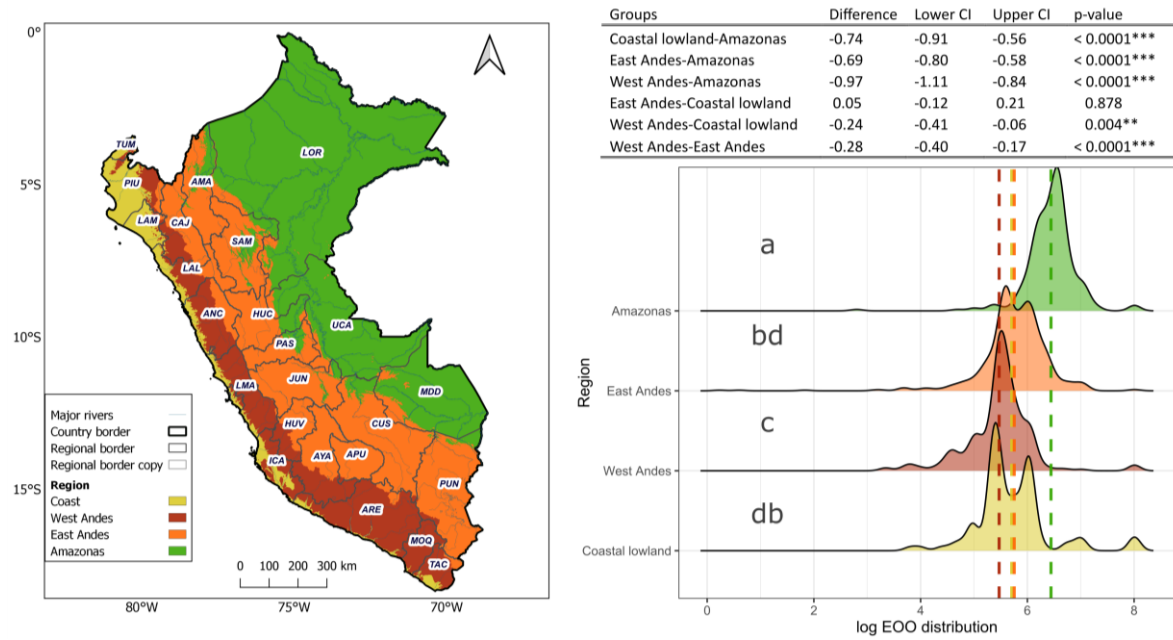
Figure 11. Overview of the range size values observed across the four biogeographic regions of Peru in *Begonia* and *Solanum*. Left: Map of the four biogeographic regions and their distribution within Peru. Top right: Summary table of the results of a Tukey-Kramer post-hoc test, based on an ANOVA, testing the differences between the median range size of 20x20 grid cells per study region. Bottom right: Density distribution of the median range size per grid cells. Dashed lines indicate the mean of each study group. Letters on the left visualise the results of the Tukey-Kramer post-hoc test. The range size measurements were log-transformed for this analysis.

3.3.3. Relation of range size and elevation

Results from the linear model and a non-parametric Spearman rank correlation test suggested a negative correlation between elevation and median range size per grid cell (p-value < 0.001***, Figure 12). The linear model showed a relatively low fit (R^2: 0.14, Figure 12). A stronger correlation between the two variables was observed by the Spearman correlation (ρ: -0.43, Figure 12)
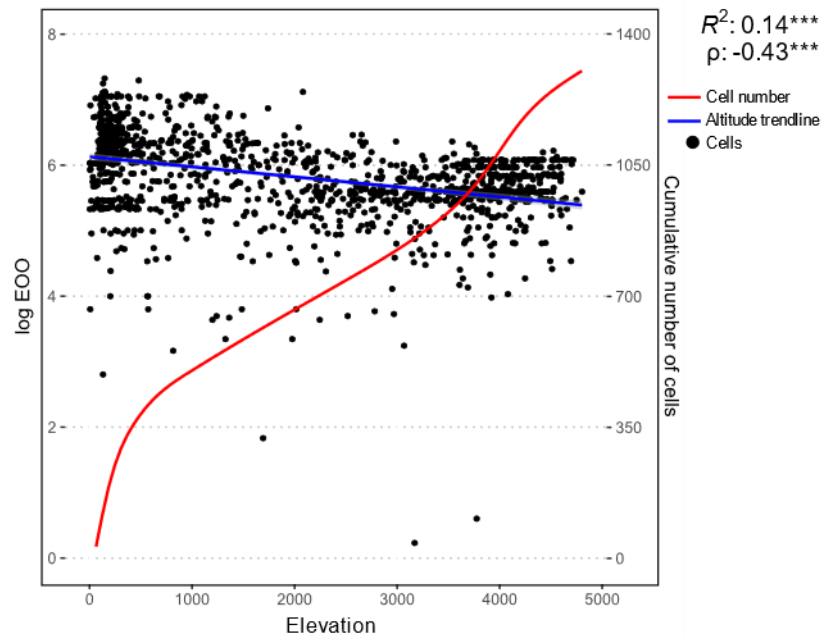
Figure 12. Relation between the median range size per grid cell and elevation shown on the left y-axis. Each dot indicates a grid cell. Trendline of the linear model shown in blue, 95% CI in grey. The right y-axis scales with the number of grid cells per altitude. The cumulative cell number is visualised by the red line.

The specimen-based approach showed significant differences in the elevation distributions of range-restricted and widespread species based on both a t-test and a non-parametric permutation t-test (t-test: p-value <0.001***, perm. t-test: p-value <0.001**, Figure 12C-D, Table 7). The mean difference in mean elevation occupied by range-restricted and widespread species was 271m, while the mean difference in elevational range was 970m (t-test: p-value < 0.001***, perm. t-test: p-value < 0.001**, Table 7).

Range-restricted *Begonia* species were shown to occur at significantly lower elevations than range-restricted *Solanum* species based on parametric and non-parametric tests (t-test: p-value < 0.001***, perm. t-test: p-value < 0.001**, Table 7). Range-restricted species generally grew at higher elevations than widespread species in both genera (Figure 13A-B). The number of unique species was the highest within the elevational band of 1,000 – 2,000m for widespread species. Range-restricted species richness was the highest between 2000-3000m (Figure 13F). The biggest difference in species richness between widespread and range-restricted species was observed in the lowest elevation zone at 0-1000m (Figure 13F).

Table 7. Summary statistics of the results of a t-test and a permutation t-test analysing the elevational distribution of the *Begonia* and *Solanum* species. On the left mean elevation and elevational range are compared between range-restricted and widespread species. On the right, the elevational distribution of the two study genera is compared.

Test	Elevation	Elevational range	Test	Elevation
Mean widespread species	2072.77	2112.60	Mean range-restricted *Begonia*	1754.19
Mean range-restricted species	2343.17	1142.86	Mean range-restricted *Solanum*	2594.29
Mean difference	-271.23	969.74	Mean difference	- 840.01
t-test p-value	< 0.0001***	< 0.0001***	t-test p-value	< 0.0001***
Perm. t-test p-value	< 0.001**	< 0.001**	Perm. t-test p-value	< 0.001**
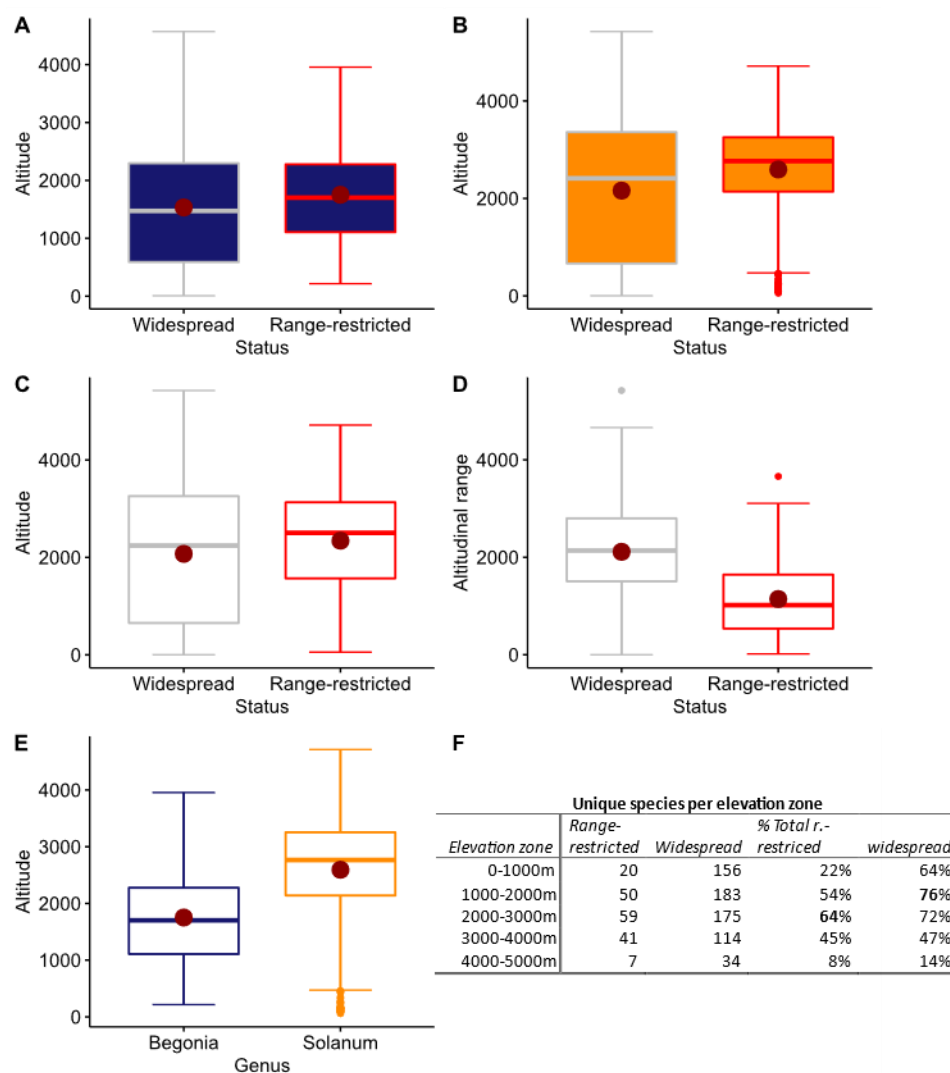
Figure 13. Display of species' mean elevational distributions in *Begonia* (A) and *Solanum* (B), elevational differences between range-restricted and widespread species (C-D), and a comparison between the genera (E). The table in the bottom right corner shows the number of unique species per elevation zone. Bold values show the highest proportions of range-restricted and widespread species respectively.

3.4. Climatic clustering

3.4.1. Habitat scale analysis

Of the 19 bioclimatic variables tested, 12 showed significant differences between range-restricted and widespread species (Figure 14). Of the 12 variables that were significantly different, nine were temperature related, whereas only three of the nine precipitation variables examined showed significant differences between range-restricted and widespread species (Figure 14). Widespread species showed a bimodal distribution in climate space in temperature variables with higher specimen densities in either extreme, while range-restricted species showed the highest densities at intermediate values (Figure 14A, E, F, H, I, J, and K).
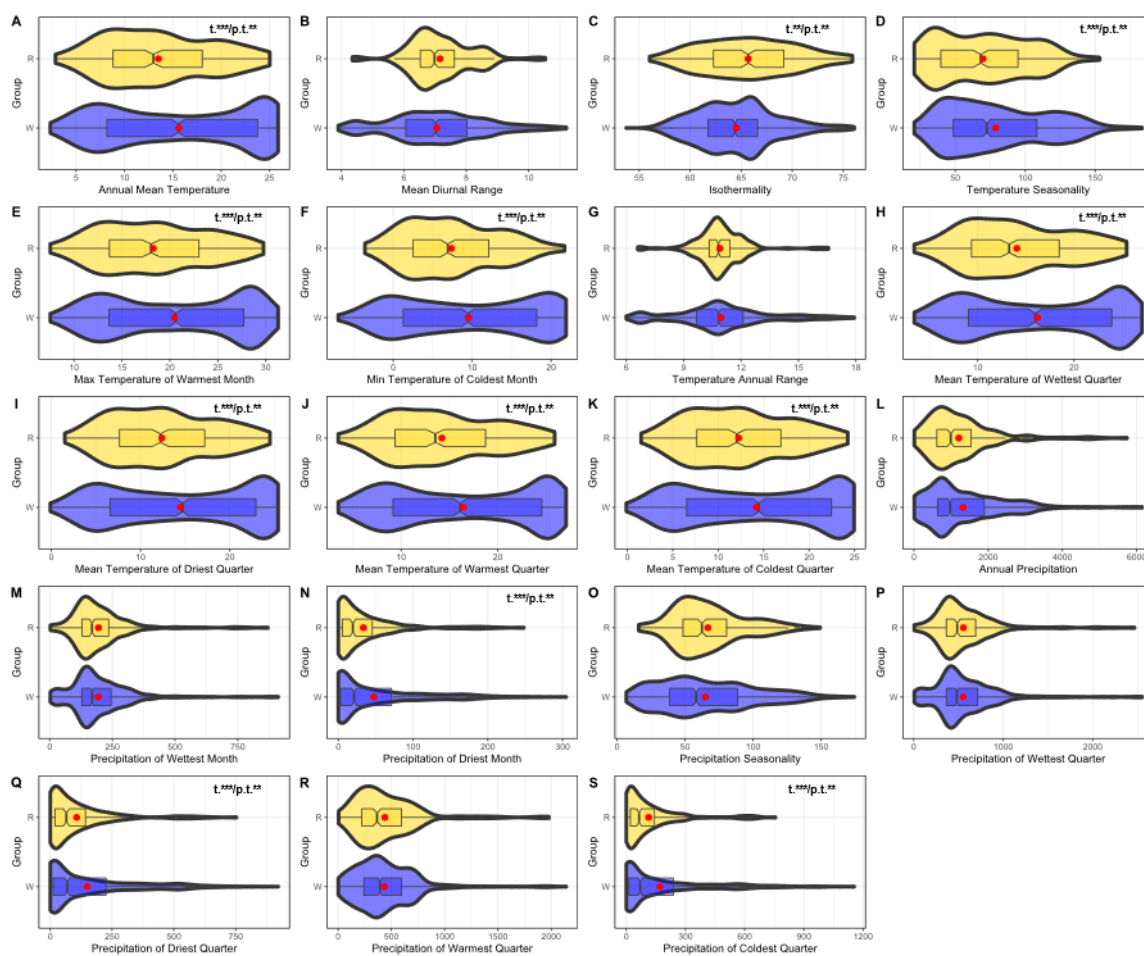
Figure 14. Density distributions of the mean climatic variables of 20x20km grid cells containing at least 1 Range-restricted species (R or gold) or at least 1 widespread species (W or blue). Red dots show the mean of the group. The notches of the boxplots indicate the 95% CI of the median. All temperature variables are measured in °C. Precipitation variables are measured in millimetres of depth. The abbreviations t. and p.t. indicate significant differences between the means of the two groups, based on the results a t-test and a permutation t-test. P-value legend: $p < 0.05*$, $p < 0.01**$, $p < 0.0001***$.

3.4.2. Specimen scale analysis

Significant differences in climate space between range-restricted and widespread species were observed for 16 out of 19 bioclimatic variables when extracting climatic data at a

specimen level based on the results of ANOVAs (Figure 15). The simulated background climatic conditions of Peru significantly differed from the values observed in the dataset containing range-restricted species irrespective of the bioclimatic layer (Figure 15). The values observed in the dataset comprising widespread species differed in 15 out of the 19 climatic variables from the dataset with range-restricted species (Figure 15). No significant difference between the two datasets was observed for Temperature Annual Range (Bio7), Precipitation of Wettest Month (Bio13), Precipitation of Wettest Quarter (Bio16) and Precipitation of Warmest Quarter (Bio18) (Figure 15). The mean difference between the simulated climatic conditions and the climatic conditions observed in the two datasets was always higher in the dataset containing range-restricted species (Table 8).
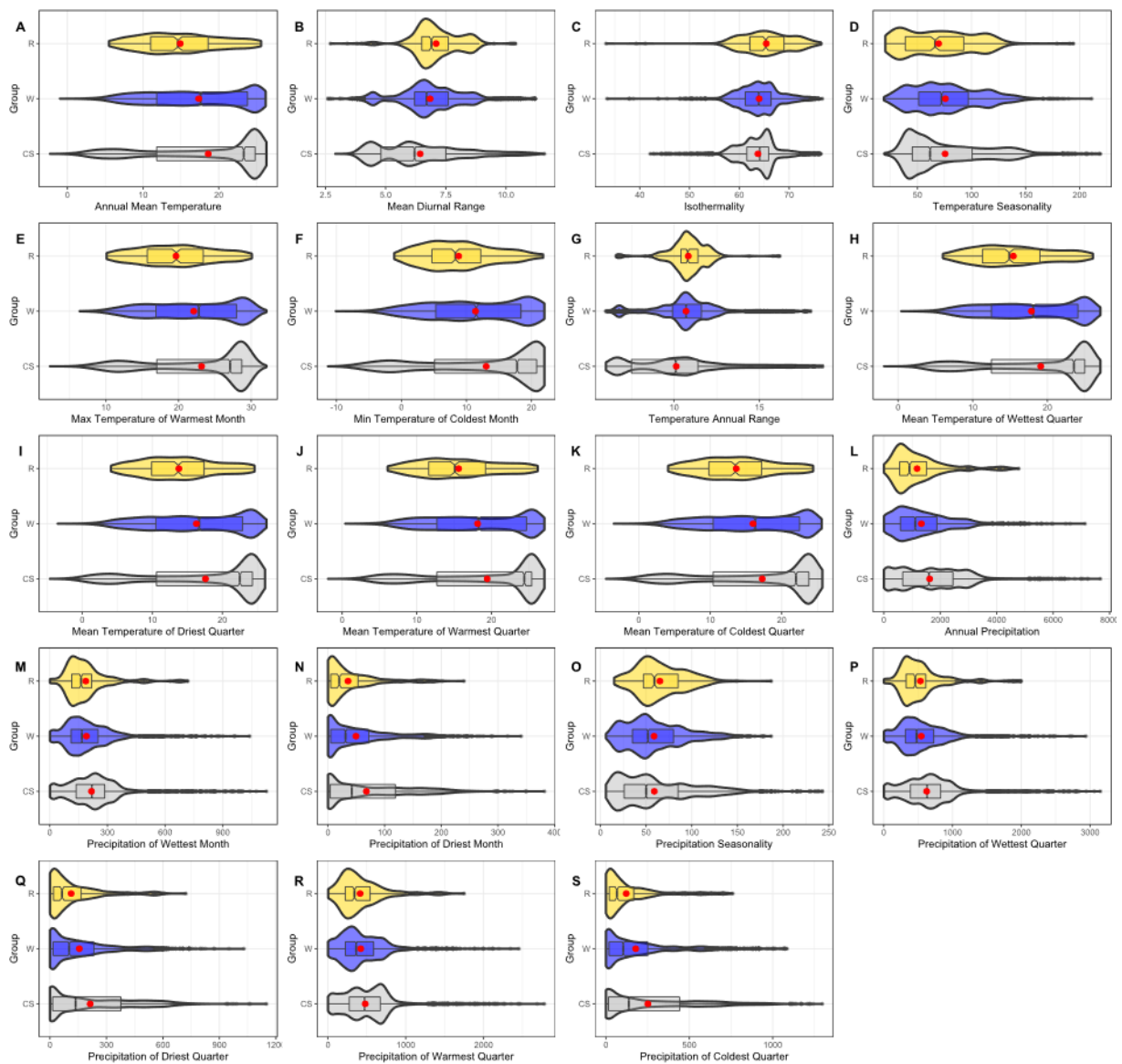
Figure 15. Density distributions of the mean climatic variables of range-restricted species (R or gold), widespread species (C or blue), and the available climatic space in Peru (Background or grey). Red dots show the mean of the group. The notches of the boxplots indicate the 95% CI of the median. All temperature variables are measured in °C. Precipitation variables are measured in millimetres of depth.

Table 8. Results of ANOVAs used to compare the climatic distributions of range-restricted and widespread species, and the available climatic space in Peru, based on 19 climatic variables (See Table 4). Non-significant results are shown in bold red. Lowest mean differences observed in comparison to the available climatic space in Peru have a red background, and highest values in have a green background.

Bioclimatic variable	*Climatic space - Widespread*	*Climatic space – Range-restricted*	*Widespread – Range-restricted*
Bio1	1.26***	3.70***	2.44***
Bio2	-0.41***	-0.66***	-0.25**
Bio3	-0.26**	-1.68***	-1.42***
Bio4	**-0.32**	6.01**	6.33**
Bio5	1.07***	3.52***	2.44***
Bio6	1.65***	4.23***	2.58***
Bio7	-0.57***	-0.71***	**-0.13**
Bio8	1.25***	3.67***	2.42***
Bio9	1.31***	3.80***	2.49***
Bio10	1.29***	3.83***	2.54***
Bio11	1.29***	3.64***	2.35***
Bio12	295.65***	447.74***	152.09*
Bio13	26.57***	29.67***	**3.10**
Bio14	18.36***	32.29***	13.93***
Bio15	**0.30**	-6.09*	-6.39*
Bio16	78.94***	90.93***	**12.00**
Bio17	57.80***	101.16***	43.35***
Bio18	58.52***	66.43***	**7.90**
Bio19	73.14***	129.73***	56.59***

Note: $\qquad$ p < 0.05*, p < 0.01**, p < 0.0001***

3.5. Niche breadth analysis
3.5.1. Individual climate axis

The results of T-tests showed significant differences in the climatic niche breadths of range-restricted and widespread species across all six bioclimatic variables analysed (Figure 16, Table 9). The average climatic niche breadth was smaller in range-restricted species compared to widespread species in all six bioclimatic variables (Figure 16, Table 9).
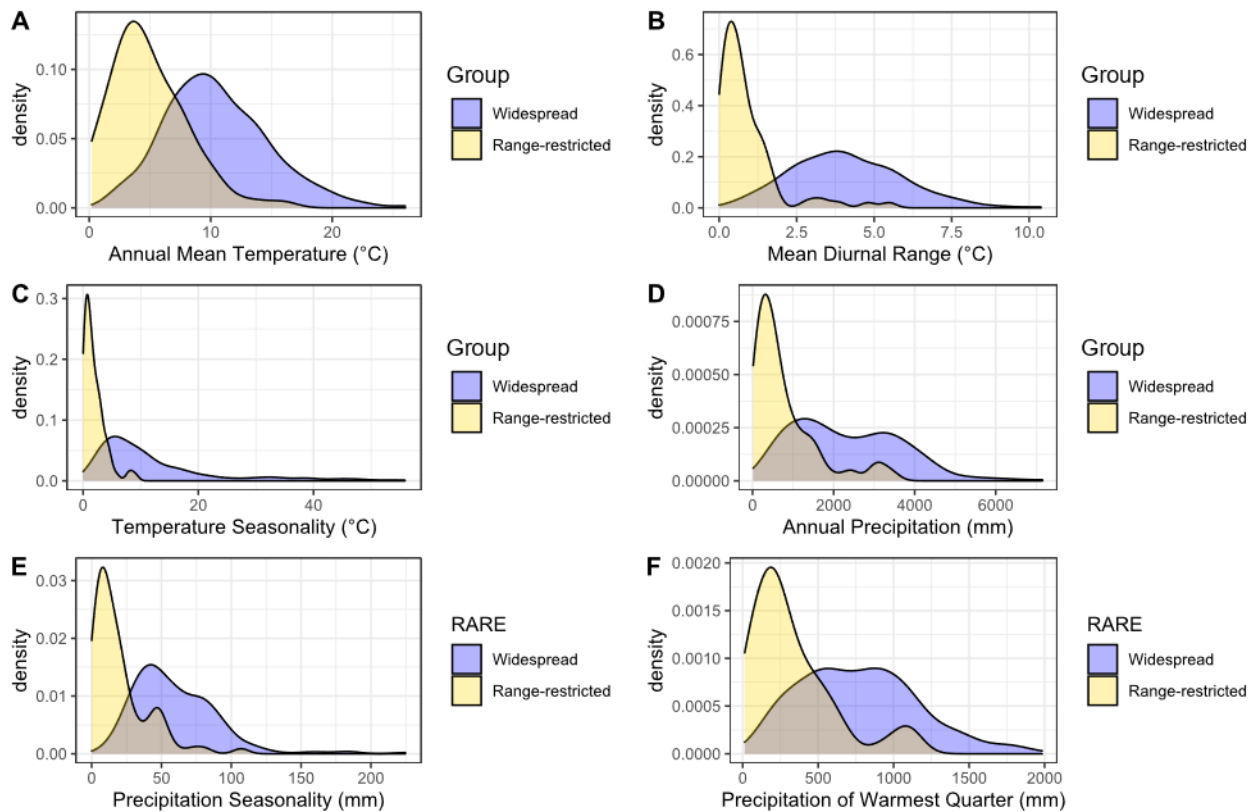
Figure 16. Density distributions of the climatic niche breadths of range-restricted species (yellow) and widespread species (blue) shown for the six climatic layers used for the analysis.

Table 9. Climatic niche breadths of widespread and range-restricted species across six climatic variables examine d(see Figure 16A-F). T. test values reported stem from a t-test and a non-parametric permutation t-test.

Climatic variable	Breadth Widespread	Breadth Range-restricted	Std Error	df	t-test/ p.t-test
Bio1	10.51	4.94	0.44	188.45	***/**
Bio2	4.10	0.88	0.16	248.05	***/**
Bio4	11.92	1.89	0.72	278.28	***/**
Bio12	2321.56	782.56	124.06	230.85	***/**
Bio15	59.66	19.97	2.96	213.84	***/**
Bio18	773.43	328.82	39.99	193.61	***/**
Note:			$p < 0.05^{*}, p < 0.01^{**}, p < 0.0001^{***}$		

3.5.2. Total niche breadth

A significant positive relationship between climatic niche breadth and range size was observed in both genera (Figure 17, Table 10). Overall, the coefficient of determination (R^2) explained 72% of the variation in range size (Table 10). Climatic niche breadth explained more variation in range size in *Begonia* than in *Solanum* (Figure 17, Table 10).
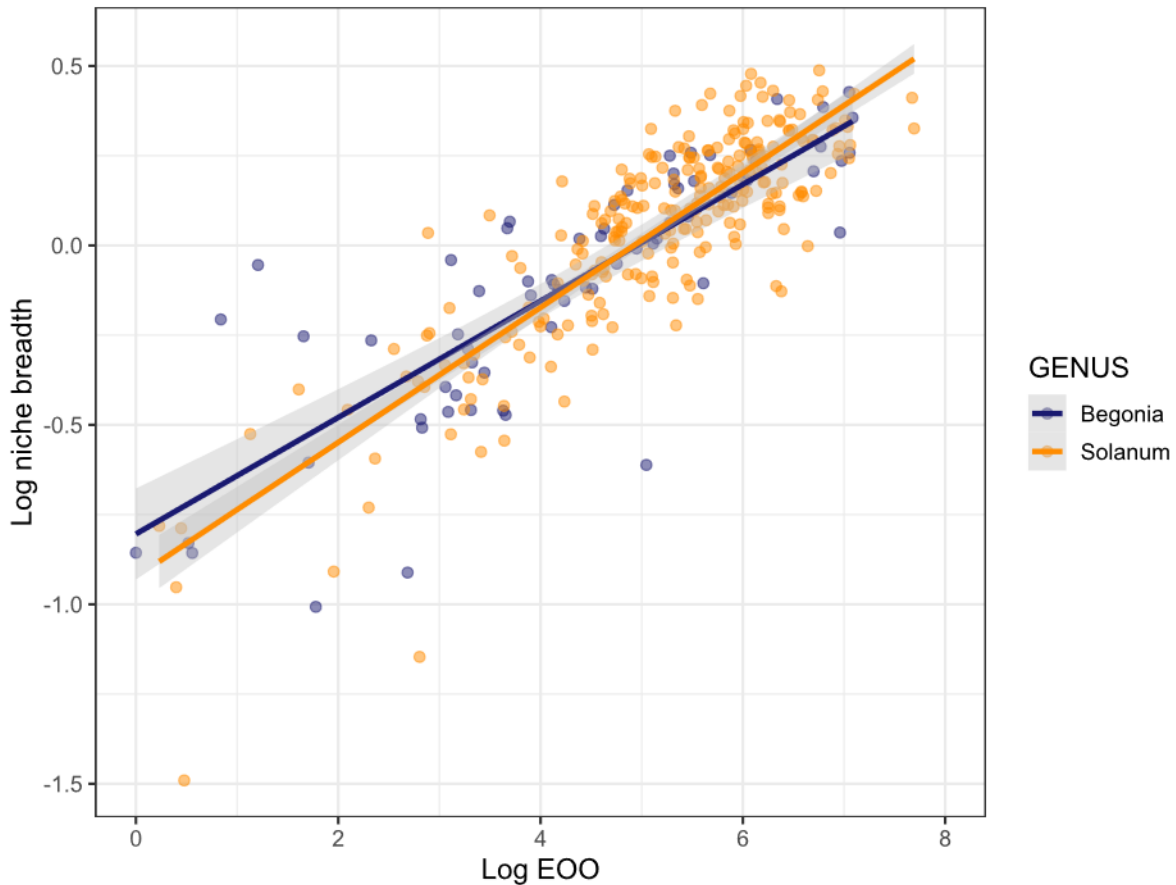
Figure 17. Relation of log-transformed EOO and niche breadth. Blue dots represent *Begonia* species and orange dots represent *Solanum* species. Regression lines resulting from the linear model of log-transformed EOO and niche breadth analyses is shown (see Table 10). Grey shadow represents the 95% CI of the linear model residuals.

Table 10. Summary statistics of the three linear models of log-transformed EOO and niche breadth and a Spearman rank correlation test (Rho (ρ)) of *Begonia*, *Solanum*, and the combined dataset. Significant results are highlighted, see notes at the bottom of the table for more details.

	Dependent variable:		
	Log EOO		
	Begonia	*Solanum*	Combined
	(1)	(2)	(3)
Log niche breadth	4.380[***]	3.898[***]	4.119[***]
	(0.363)	(0.151)	(0.142)
Observations	70	253	323
R^2	0.682	0.727	0.723
Adjusted R^2	0.677	0.726	0.722
Residual Std. Error	1.041 (df = 68)	0.697 (df = 251)	0.793 (df = 321)
F Statistic	145.617[***] (df = 1; 68)	667.783[***] (df = 1; 251)	837.273[***] (df = 1; 321)
Rho (ρ)	0.875[***]	0. 790[***]	0.828[***]
Note:			$p < 0.05^*$, $p < 0.01^{**}$, $p < 0.0001^{***}$

The observed relation between niche breadth and range size was shown to be significantly higher than the values from the null model (95% CI lower boundary = 0.447, 95% CI upper boundary = 0.576), and the R^2 of the observed linear model fell outside of the simulated 95% quantiles of the null models (Figure 18). The average Coefficient of determination of 100 null models was 0.513 (CI: 0.506, 0.520). A null model was designed to test the assumption that the explanatory power of the model was greater than the correlation induced by spatial autocorrelation.
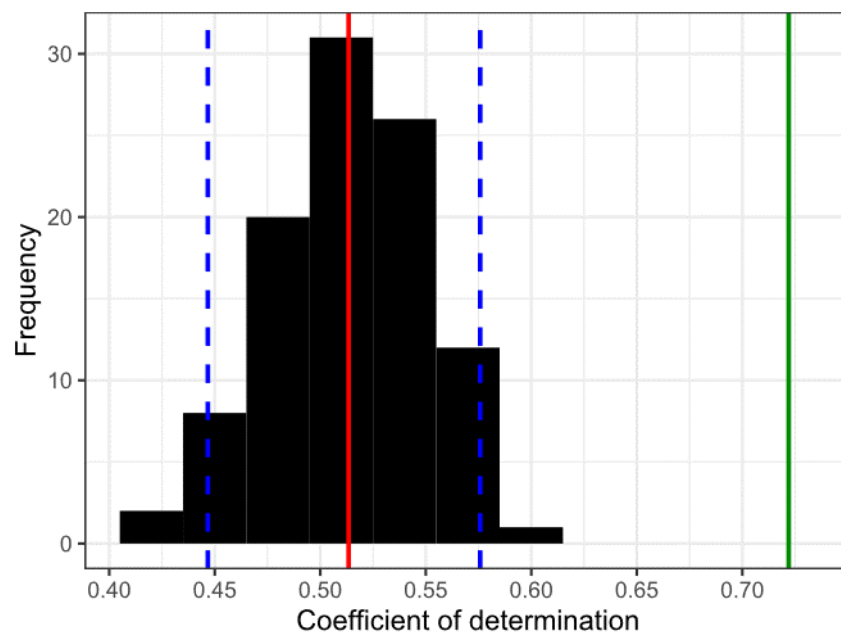
Figure 18. Frequency distribution of the Coefficients of determination (R^2) resulting from 100 linear models examining the correlation between niche breadth and EOO in 100 null models with randomised climatic conditions. The data was log-transformed to better reflect the relation of the two variables. Lines indicate key values, where blue dashed lines refer to the lower and upper boundaries of the 95% quantile, red lines to the mean R^2 determined from the 100 null models, and the green line represents the R^2 value derived from the observed data of spatially filtered *Solanum* and *Begonia* data.

4. Discussion

A high proportion of tropical species have small ranges and could be particularly threatened by environmental change (Colles *et al.*, 2009; Enquist *et al.*, 2019). Studies that examine range size in plants especially in the tropics context remain rare, despite the fact that tropical regions accommodate most of the world's biodiversity (Myers *et al.*, 2000). Although range size is one of the main axes of rarity (Table 1; (Rabinowitz, 1981) and a major predictor of extinction risk across taxonomic groups, other factors such as ecological specialisation and niche breadth may play an equally if not more important role in determining threat in plants.

In this large-scale comparative study, the patterns of geographic and climatic clustering of range size in the two megadiverse genera *Begonia* and *Solanum* and the relationship between range size and climatic niche breadth were examined in a neotropical context. The results presented here have several implications for the conservation of range-restricted species and raise further questions regarding the study of range size within a tropical context.

4.1. Range-restricted species occur in rare climates

The study results demonstrate that the majority of range-restricted species of Peruvian *Begonia* and *Solanum* are found in climatically and geographically rare habitats and highlight the importance of climatically and geographically rare montane habitats for range-restricted species globally. Range-restricted species primarily occurred in marginal (i.e., rare) climates and were found to inhabit climatically different habitats compared to widespread species in Peru. The habitats where range-restricted species were found to show higher densities were generally rarer when compared to the climatic space available in the study region (Figure 14, Figure 15). This is underlined by the fact that mean differences between range-restricted species and the available climatic space in Peru were higher than the differences observed for widespread species. This pattern was consistent across all 19 bioclimatic variables examined (Table 8). The differentiation is particularly strong when it comes to temperature variables, where the overall trends of range-restricted and widespread species show an almost inverse pattern (Figure 14, Figure 15). The finding that range-restricted species occur in marginal environments is in accordance with the niche position hypothesis as observed by Gregory and Gaston (2000) in British birds. The hypothesis assumes species with small ranges often have a marginal position relative to the central tendencies of the environment. If range-restricted species are dependent on stable climates because of their marginal position within the climatic space, range-restricted species might be particularly vulnerable to climatic changes.

A study of range size dynamics of range-restricted species within a tropic-paleoclimatic context would be an interesting approach to validate the relation between climatic stability and rarity to range size in future studies.

These findings also support the climatic-rarity hypothesis established by Ohlemüller *et al.* (2008), who found a correlation between climatically rare habitats and areas of range-restricted species richness across several different taxonomic groups, including Western-Hemisphere bird species, and European plants and butterflies.

The authors also hypothesised that range-restricted species might occur in cooler habitats, in what they referred to as the "climatic relict hypothesis" (Ohlemüller *et al.*, 2008). Cooler habitats have been widespread during glacial periods within the Northern Hemisphere, meaning that persistent cool areas could act as refugia for cold-adapted species during warming periods (Willis and Whittaker, 2000). The contraction of these areas could lead to a correlation of cool habitats and species with small range sizes (Ohlemüller *et al.*, 2008). This assumption was only partly supported by the patterns observed in European plant species in their study, but in general range-restricted species occurred in drier and cooler areas than range-restricted species (Ohlemüller *et al.*, 2008). A similar pattern was observed in range-restricted species of *Solanum* and *Begonia,* which were also found to occur in cooler and drier habitats in comparison to more widespread species in this study. This effect was observed at both the habitat and the specimen scale (see Appendix, Figure 14, Figure 15), indicating that such a pattern might be generalizable in montane habitats.

To what extent such refugia existed in the Neotropics is debatable, as many species likely have been persistent over glacial periods (Willis and Whittaker, 2000). However, a large-scale study examining range size patterns in plants of the Americas has shown that small range sizes are associated with stable climates, suggesting that the stability of climatic conditions might be of importance for the persistence of range-restricted species within a tropical context as well (Morueta-Holme *et al.*, 2013).

4.2. Range-restricted species differ from widespread species in their elevational preferences

The habitats in which range-restricted species generally occur are not only rare from a climatic perspective but also from a geographic point of view. These findings show that range-restricted species occur at higher elevations on average than more widespread species in both *Solanum* and *Begonia*. Only 22% of the range-restricted species inhabit elevations

under 1,000m, compared to 64% of widespread species (Figure 13). Range-restricted species also show narrower elevational ranges, with widespread species surpassing the mean elevational range of range-restricted species by roughly 84% on average (Figure 12, Table 7). Similar patterns have been observed in other studies of endemics and range-restricted species. In a study of Austrian alpine endemic plant species, Essl *et al.* (2009) showed that endemic species had considerably smaller elevational ranges than more widespread species and differed in their elevational distribution.

4.3. Niche breadth is correlated with range size

The results of this study indicate that there is a significant positive relationship between range size and climatic niche breadth across *Solanum* and *Begonia*, even when accounting for spatial autocorrelation and uneven collection densities (Figure 17, Figure 18, Table 10). This suggests that range-restricted species are generally climatic specialists and is in accordance with the findings of Sheth *et al.* (2014). In their study of niche breadth of North American *Mimulus* species, species distribution models were used to create a binary map of habitat suitability. The results of the analysis showed that climatic niche breadth explained most of the variation in range size observed in their study (Sheth and Angert, 2014). A similar pattern was observed by Yu *et al.* (2017) in their study of 80 *Rhododendron* species endemic to China.

Contrastingly, a study of the climatic and biotic niche of *Fagus* species native to the Northern Hemisphere, Cai *et al.* (2021) found no correlation between species' realized climatic niche and range size. This shows that the generality of the pattern is still a point of contention. One possible explanation could be that there is not yet a standardized method to estimate the climatic niche. This makes comparisons between studies difficult, as studies use differing ways to calculate niche breadth. For example, Sheth et al 2014 calculated the climatic niche breadth based on the climatic variances derived from Species Distribution Models (SDMs), while other authors use a multivariate analysis that measures niche breadth and position based on the distance to the mean habitat conditions (i.e., the Outlying Mean Index (OMI); Dolédec *et al.*, 2000).

This dilemma could be solved by implementing a niche-based measurement within the IUCN Red List, thereby standardizing the process as seen with the EOO for range size. As shown by Breiner et al (2017) niche properties could act as a complementary measure to range size within the framework of the IUCN Red List. Particularly a climate-based measurement could be beneficial, as it could enable the quantification of species vulnerability to climate change.

This information could be used to foresee migration patterns of plants, which will be important for the establishment of protected areas in the future. While this approach might not be appropriate for organisms that do not respond directly to climatic changes, the inclusion of climatic niche measurements in Red List assessments of plants should be evaluated (Breiner *et al.*, 2017; Enquist *et al.*, 2019; Morueta-Holme *et al.*, 2013).

4.4. The tropical Andes as a rarity hotspot

The results of this study highlight the importance of the tropical Andes for neotropical biodiversity and the conservation of range-restricted species. A staggering 94% of the range-restricted specimens examined in this study are found at elevations above 500m within the Andes, with the vast majority of range-restricted *Begonia* and *Solanum* species occurring in the East and West Andes. Only 15% of the tropical Andes are currently protected on a global scale (Hoffmann et al., 2011). Within Peru, the number is even lower, with only 11% were protected at a national level in 2011 (Hoffmann *et al.*, 2011). A study of deforestation patterns within Peru revealed that there is a mismatch between the forests most likely to experience deforestation and the placement of protected areas (Bax and Francesconi, 2018). Based on a random forest model that classified deforestation likelihood in reference to environmental conditions the authors showed that more than 80% of the forests vulnerable to future deforestation were situated outside of protected areas in Peru (Bax and Francesconi, 2018).

Mountains house a disproportionate amount of the world's biodiversity (Myers *et al.*, 2000; Rahbek *et al.*, 2019). Particularly in tropical regions the pattern is striking. In an earlier hypothesis Janzen assumed that the higher environmental divergence between lowland and mountain tops in the tropics might act as physiological barriers for tropical species, leading to the smaller geographic range sizes and higher species richness seen in the tropics (Janzen, 1967). This led to Janzen famously stating that "mountain passes are higher in the tropics" (Janzen, 1967). While several of the studies statements have been called into question in a recent review (Ghalambor *et al.*, 2006), the fact that mountainous regions are centres of range size rarity still stands based on these findings and is also supported by several earlier studies at a global or regional scale (Morueta-Holme *et al.*, 2013; Ohlemüller *et al.* 2008; Essl *et al.* 2009; Enquist *et al.* 2019; Rahbek *et al.* 2019).

4.5. Can the results of this study be generalised?

The results show highly similar patterns of rarity in terms of geographic and climatic preferences of range-restricted species in both of the study genera *Begonia* and *Solanum*, two

megadiverse genera that occur throughout all major habitats and biogeographic regions of the study region Peru, although both genera can be argued to have Andean-centred distributions. The majority of range-restricted species in both of the genera were found in climatically and geographically rare habitats in the Andes.

While the two genera are similar in having large numbers of species and an Andean-centred distribution, the similarity of rarity patterns in the two genera are somewhat striking considering that *Begonia* and *Solanum* differ in many important aspects of their reproductive biology (breeding system, pollination biology) and ecological preference (moist microhabitats in *Begonia* versus drier and more disturbed habitats in *Solanum*) (Anderson and Symon, 1988; Echeverría-Londoño et al., 2020; Tebbitt, 2005). In fact, most field biologists would identify these two genera as the two extremes, where *Begonia* is known for its extremely narrow range-sized species that are ecologically highly specialised to occupy moist microclimates (Tebbitt, 2005). *Solanum*, in contrast, is known for many weedy species with no clear ecological specialisation and much wider range sizes (Echeverría-Londoño et al., 2020).

This raises the question whether the results presented here can be generalised to other plant groups and/or geographic areas? The pattern recovered here in two Andean-centered suggests that similar patterns could be applied to other Andean-centred or mountain-centred genera, independent of their pollination biology and/or breeding system. This is because the breadth of the climatic conditions and the diverging ecological properties of the two genera studied here make it particularly remarkable that range-restricted species across both genera occur in similar, rare climates and have narrow niches, highlighting the strength of the pattern observed here.

The fact, however, that two genera follow a typical Andean-centered distribution described by Gentry (1982), with high numbers of species occurring in the Andes and decreasing diversity towards the Amazon lowlands (Gentry, 1982; Moonlight *et al.*, 2015), calls into question whether patterns discovered here would be general across all plant groups. The expectation would be that pattern for Amazon-centered genera would differ from those discovered here and would reveal important aspects of niche specialisation within lowland moist tropical forest habitats that dominate large areas of South America.

Choosing study groups in studies such as presented here is challenging, because it requires a combination of taxonomic and distribution data which do not exist for many species-rich

plant groups. Similarly, it is difficult to find plant genera that span large elevational and environmental gradients. Only a few plant genera in South America expand across the entire elevational and environmental gradient from the Amazon to the peaks of the Andes. The two study groups used here (*Begonia* and *Solanum*) are some of the largest and most environmentally broad genera currently known.

4.6. Hotspots of rarity within the Andes

The two richest hotspots of range-restricted species were located in the transitional zone between the Northern and Central Andes (Figure 7). The two Andean subdivisions are separated by the Porculla Pass in the Huancabamba Depression that spans northern Peru and southern Ecuador (Josse *et al.*, 2011) (Figure 19). Hotspots of range-restricted species in this area occur in both *Solanum* and *Begonia* (Figure 7). The mountain pass is the lowest point in the tropical Andes where the mountain tops lower to 2,145m elevation and acts as a topographical barrier for many high elevation plant and animal species, impeding migration from the Northern to the Central Andes (Josse *et al.*, 2011; Weigend, 2002). It has been suggested that this has led to the two zones largely diverging in their species composition (Josse *et al.*, 2011). The area of the Huancabamba Depression, also termed "Amotape-Huancabamba Zone", is considered as a transitional zone between the two phytogeographic regions, hosting species from both the Northern and the Central Andes with overlapping distributions (Josse *et al.*, 2011; Weigend, 2004, 2002; Weigend *et al.*, 2005). At the same time, earlier studies also have documented high amounts of endemism in the region, such as the biodiversity of the Marañón valley (e.g. Särkinen *et al.*, 2011; Koch, 2014). With clusters of range-restricted species found in the same area, the results of this study, thus, add further support to the assumption that the Amotape-Huancabamba Zone might be a particularly important biodiversity and rarity hotspot (Herzog and Kattan, 2011; Särkinen *et al.*, 2011; Weigend *et al.*, 2005). As of now, no large-scale protected areas exist in the region and based on the results shown here the implementation of conservation measures in the Amotape-Huancabamba Zone should be a priority for the conservation of biodiversity in Peru.
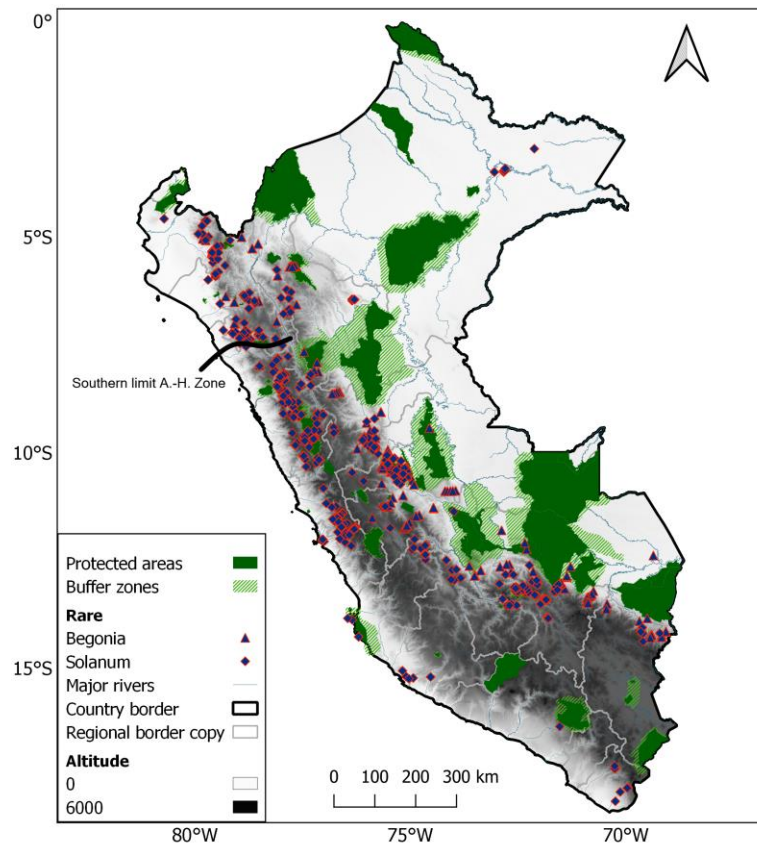
Figure 19. Distribution of range-restricted species and protected areas within Peru. The black stripe shows the southern limit of the Amotape-Huancabamba Zone according to Weigend (2002).

The threat of land-use change and habitat loss is a major concern for range-restricted species. Less than 20% of the range-restricted specimens examined in this study fell within the boundaries of protected areas or their buffer zones (Table 5). 60% of the range-restricted species had no collections from within the boundaries of a protected area (see Appendix). To determine priority areas for the conservation of range-restricted species it is important to understand factors that influence their distributions.

4.7. Range-restricted species are highly vulnerability to climatic changes

Together with the marginal climatic distribution of range-restricted species highlighted by the climatic clustering and the evidence that range-restricted species have narrow climatic niches, the results of this study show that range-restricted tropical plant species are highly vulnerable to climatic changes. The patterns of climatic and elevational clustering of range-restricted species recovered followed the general ecological preferences observed for each genus, with *Solanum* generally occurring in drier, colder habitats at higher elevations than *Begonia* (see Appendix and Figure 13). As species from almost all major *Solanum* clades and for two of the four major *Begonia* clades were included in this study this implies that the species might

be constrained in their evolutionary potential and have a limited adaptive capacity (Moonlight, *in press*.; Särkinen *et al.*, 2015).

While the threat of climatic changes to range-restricted species has been highlighted for the species of the Northern Hemisphere in previous studies (e.g., Essl *et al.*, 2009; Ohlemüller *et al.*, 2008), the results of this study suggest that range-restricted plants in the Neotropics are equally threatened. This is supported by global studies and cross-continental studies (Enquist *et al.*, 2019; Morueta-Holme *et al.*, 2013). Some future climate scenarios project the tropical Andes to undergo major transformations, with cloud forests and the Andean páramos particularly threatened by the climatic changes (Young *et al.*, 2011).

Studies of tropical systems often emphasise the importance of biotic interactions in tropical regions (Schemske *et al.*, 2009). A high proportion of species that depend on mutualistic biotic interactions are range-restricted, just by the nature of these relationships. As seen by the global bleaching of coral reefs, major changes in climate can cause the patterns of biotic interactions such as symbiosis and mutualism to change drastically (Hughes *et al.*, 2017). The results of this study show macroclimatic conditions might play an important role when it comes to the distribution of range-restricted species. While models of future climates are full of uncertainties and some projections show less detrimental scenarios for the Andes (e.g., Tovar *et al.*, 2013) the results of this study underline the need to include climatic changes in conservation planning. Protecting areas that might as refugia for species with narrow climatic niches will be key to maintain ecosystem functions and preserve biodiversity in the future.

4.8. Caveats and further work

4.8.1. EOO as a measure of range size

As part of the study, range size measurements were evaluated for their correlation to collection effort. A strong relationship between AOO and collection effort was observed, with the AOO increasing almost linearly with the number of collections (Figure 6). A weaker, but still significant, correlation was observed for EOO (Figure 6). This result is in line with earlier observations that show that the AOO should be used with caution when it comes to evaluating range sizes and conservation statuses within areas with uneven collections depths. While using the EOO alone as a range size measurement is more robust to these biases, there are also disadvantages to such an approach, particularly in heterogeneous regions such as the tropical Andes.

The problem with EOO is best exemplified by *Solanum trachycarpum* Bitter.*,* a trailing subshrub from the Basarthrum Clade of *Solanum* (Anderson, 1975). The species occurs in dry forests and dry montane scrublands between (700-)1,000-2,600(3,000) m elevation. These habitats only occur in small pockets in Ecuador and northern and Central Peru (Banda *et al.*, 2016). The species is currently only known from four unique populations, which leads to an AOO of 12km^2 yet the EOO for the species is much larger (59,276km^2) due to the fragmented nature of the known populations that follow the distribution of suitable habitat along the Andes. The large EOO results in the species being considered as Least Concern, despite the low number of known populations that would merit a threatened status within the IUCN threat categorisation (IUCN, 2019).

Another very similar example is *Begonia conoensis* Moonlight. This species grows on isolated hills close to the borders of Peru and Brazil (Cerro el Cono) and in montane forests in southern Colombia (Moonlight *et al.*, in press.). *Begonia conoensis* is currently only known from two collections. Similar to *S. trachycarpum,* the AOO is only 8km^2, while the EOO (111,193km^2) is heavily affected by the large distance between the two isolated populations.

As shown by Table 1, there are examples *Solanum* and *Begonia* for almost all of the seven categories of rarity. This suggests that using geographic range size alone as a measure of rarity might lead to underestimations of rarity, which could limit this study. However, while the estimation of rarity used here is purely based on range size, the results suggest that range size alone as used here is accurately estimating the number of rare and threatened species in *Begonia.* This is based on the fact that this study classified 52% of Peruvian *Begonia* species as threatened categories compared to a strikingly similar 51% based on provisional IUCN Red List assessments by Moonlight *et al.* (*in prep*.).

Species distribution models (SDMs) could be a way to further minimise the outlined problems of AOO and EOO as range size measurements. By modelling the amount of suitable habitat, SDMs would allow range size measurements to be restricted to suitable habitats instead of potentially including habitat that is not suitable for a given species because of its environmental properties. This could increase the accuracy of the range size estimates.

A similar approach has been suggested by Brooks *et al.* (2019), who proposed the inclusion of the Area of Habitat (AOH) as an additional measure of range size within the IUCN Red List. In their article, the AOH is defined as the area within a species range that is available to

the species as habitat. The available habitat is thereby inferred from the species elevational distribution and land cover maps (Brooks *et al.*, 2019). Combined with SDMs, this approach could allow for more accurate predictions of species' geographic range sizes.

If SDMs were to be used for estimated range sizes, it is important to consider that the quality of SDMs depends largely on the quality of the data that is used to train these models. Thus, accounting for and minimising uncertainties intrinsic to the data-based predictions of SDMs is necessary to make appropriate conclusions about the spatial distribution of species (Beale and Lennon, 2012). Measures can range from data cleaning measures, such as the removal of inaccurate data records to more sophisticated controls such as improved model evaluation and selection (Araújo and Guisan, 2006).

Still, when employed within the right framework, SDMs can be a powerful tool in the exploration of range sizes of range-restricted species. Particularly in under collected, SDMs could improve our understanding of the distribution of range-restricted species and can even lead to the discovery of new species (Särkinen *et al.*, 2013). A re-evaluation of the IUCN Red List criteria for range size would, thus, be an important step towards increasing the accuracy of extinction risk estimates in poorly collected regions, such as the Andes.

4.8.2. Niche evaluation and fundamental versus realized niche

A significant positive relationship between range size and climatic niche breadth was observed in our study, even when spatial autocorrelation and uneven sampling depths were accounted for. The generality of this pattern is still a point of contention, and it is important to acknowledge that outliers that were not captured by the linear model used, were also observed in this study. For example, *Solanum yanamonense* S.Knapp. *,* and *S. mariae* Särkinen & S.Knapp. both had considerably narrower niches than expected by the linear model. Contrastingly, *B. speculum* Moonlight & Tebbitt. had a broader niche than its range size would suggest. To better capture these outliers a Generalized linear mixed model (GLMM) could be used in the future to account for random effects and interactions within the data (Bolker *et al.*, 2009).

One explanation for these deviations could be the method that was used for range size measurements in this study (see Section above for detailed discussion). The EOO tends to overestimate the realised range size of species, as unsuitable habitat is included within the calculation. This could distort the relation of range size and niche-breadth and would explain some of the variation observed here. The assumption is supported by the results of the

measurements of the aforementioned *B. conoensis*. As discussed in Section 4.8.1, the method used for the calculation of the range size of *B. conoensis* overestimated the species realised range. We can observe this effect within the niche breadth study, as the observed values (0.24) for *B. conoensis* are significantly lower than we would expect based on the observed correlation of niche breadth and range size.

Based on the overestimation of the climatic niche of *B. conoensis*, a similar trend should be visible for *S. trachycarpum*. With a niche breadth of 1.18, *S. trachycarpum* fails to show the same pattern. A possible explanation for the absence of such a trend could be that the species occupies specific micro-climatic niches that fall below the resolution of the climatic data used in this study (30 arc-seconds, i.e. ~ 1km^2). While the potentially highly specific climatic conditions in the small dry forest pockets that *S. trachycarpum* typically inhabits, could still be similar, the aggregated climatic conditions within 1km^2 might exhibit higher fluctuations.

It is important to highlight that the relationship observed here is the correlation between range size and the realised climatic niche of a species i.e., the climatic space the species occupies in the presence of biotic interaction. It would be important to evaluate if the correlation also exists at the level of the fundamental climatic niche i.e., the climatic space a species could potentially occupy due to its intrinsic capabilities.

Similar to the suggested improvements to range size measurements, SDMs could be a possibility to evaluate the properties of the fundamental climatic niche, as shown by Sheth *et al.* (2014). It is still a point of contention, however, to what extent SDMs can predict the niche of organisms, particularly in highly dynamic tropical regions where occurrence data is limited (Araújo and Guisan, 2006).

As suggested by Sheth *et al.* (2020) examinations of the niche breadth-range size hypothesis are most robust when observed in an experimental setting. An experimental approach would also allow for observations at a finer scale, thereby enabling the quantification of microclimatic factors such as the importance of microhabitats, which might play a particularly important role in *Begonia* species that often occur in the understories of rain forest canopies (Tebbitt, 2005). Unfortunately, experiments are difficult to establish in a tropical setting, due to the remoteness and costs associated with such a project. With the general lack of funding for plant studies, an implementation seems unlikely at the moment. Still, an experimental approach to measure climatic niche breadth in a tropical setting would be necessary for a better understanding of its influence on geographic range size.

The climatic niche is only one of many approaches to examine the niche-breadth-range size hypothesis. Other traits, such as species intrinsic attributes (e.g., dispersal ability and seed production), biotic interactions (e.g., pollination and herbivory), but also environmental factors like soil properties and geographical barriers, might constrict a species range size, independent of its climatic niche breadth, as reviewed by Murray *et al.* (2002) and Sheth *et al.* (2020). Particularly in the mountainous regions, such as the Andes, geographical barriers might influence species range sizes (Morawetz and Raedig, 2007; Rahbek *et al.*, 2019). As documented by studies of inter-Andean dry forests, species are often only found within a few isolated valleys (Linares-Palomino *et al.*, 2011; Särkinen *et al.*, 2011). Range size in this study is also examined statically and the dynamics of range size expansions and contractions are disregarded due to their complexity and the lack of data. In a next step, it would be important to further explore why these species are constricted to their habitats by investigating the interaction and dynamics between the different mechanisms that constrict range size, as in Sheth et al (2014).

4.8.3. Low collection densities across biodiverse areas in the tropics

Large biodiversity databases, such as GBIF (Global Biodiversity Information Facility), are often criticised for their potential spatial biases (Beck *et al.*, 2014). Especially in a tropical context these biases often confine large-scale studies of range size rarity, as collection densities vary considerably. Additionally, most of the more recently collected occurrence data of local herbaria is not readily available online, as resources for the digitalisation process are often lacking. In this study, both databases are curated by taxonomic experts of the respective study groups and the enhancement of occurrence data of range-restricted species in Peru has been a particular focus over the last years. This highlights the importance of curated species occurrence databases and is what allows this study to accurately quantify range size rarity.

Almost all ecological methods depend on sampling effort and the outcome of analyses can only be as robust as the data that it is built on. Even though the effects of uneven sampling were accounted for, their influence is still visible in this study. Total species richness was highly correlated to collection effort, best visualised by the density maps shown in (Figure 9). The patterns observed are almost identical, indicating two hotspots of collection density and species richness – one near Cusco and one near Oxapampa. Both areas have are known for their association with botanical institutes and collections such as the Jardin Botanico de Missouri in Oxapampa, with the "Herbario Selva Central Oxapampa" (HOXA) and the

herbarium of the "Universidad Nacional de San Antonio Abad del Cusco" (CUZ). Additionally, the proximity of Cusco to heavily visited sites such as Machu Picchu might explain the high number of collections in this region of Peru.

While spatial filtering can reduce the effects of uneven sampling depths, this approach is difficult for range-restricted species. Due to the nature of range-restricted species, generally, fewer collections are available (often below 10), making further thinning often not feasible with regards to appropriate sample sizes. The tropical Andes alone accommodate more than 20,000 endemic plant species and are among the richest hotspot of biodiversity worldwide (Jørgensen *et al.*, 2011; Myers *et al.*, 2000). At the same time, the tropical Andes are one of the most under-explored regions, with Peru and Ecuador projected to accommodate 29% of the undescribed plant species (Joppa *et al.*, 2011; Jørgensen *et al.*, 2011). This highlights the need for further fieldwork, to gain a holistic picture of the species richness present in the "hyperspot" of diversity that is the tropical Andes.

4.8.4. Adding phylogenetic perspective

Further research to explore the patterns that cause range size rarity is needed. Species distribution modelling was already highlighted as one possible direction for future range size and niche studies at a large scale. At the same time, it is important to look at the processes that shape these patterns at a finer level. In this study, phylogenetic relationships among the *Solanum* and *Begonia* species were not considered. Future studies should remove or control for phylogenetic relatedness between study species because these patterns could provide further insights into the mechanisms behind range size rarity. Little is known about these patterns in tropical plants, but the few studies conducted suggest that there could be a phylogenetic signal in relation to range size rarity.

In their study of range size rarity in woody tropical plants, Loza *et al.* (2016) found that closely related species had similar properties along all three axes of rarity, geographic range, habitat breadth and abundance. There is also evidence that species richness is negatively correlated with geographic range size (Dexter and Chave, 2016; Leao *et al.*, 2014; Leão *et al.*, 2020). In Brazilian Atlantic forests lineages with high recent diversification rates in particular show high amounts of range-restricted species (Leão *et al.*, 2020). A similar trend in Andean-centred genera would add evidence to a more general pattern across tropical floras. If there are common traits that make some clades particularly susceptible to extinction the results

could have important implications for conservation prioritisation (Leao *et al.*, 2014; Leão *et al.*, 2020).

4.9. Conclusion

The focus on temperate species in range size studies has led to a considerable asymmetry in ecological research with most ecological theories developed based on the study of widespread species as these were perceived as disproportionally important (Kunin and Gaston, 1993). Almost half of the world's plant species are rare and thus particularly threatened by environmental change (Enquist *et al.*, 2019). More recent studies suggest that rare species play an important role in ecosystem functioning highlighting the need for a better understanding of rarity (Lyons *et al.*, 2005; Mouillot *et al.*, 2013).

The aim of this study was to explore the patterns of range size and the species in a neotropical context to start to close this knowledge gap. In a large-scale study, the geographic and climatic clustering of range-restricted *Begonia* and *Solanum* species native to Peru was explored and the relation of climatic niche breadth and range size was tested. The results demonstrate that range-restricted species are climatic specialists in mountainous habitats that might be restricted by the amount of suitable habitat available. This could make them highly vulnerable to climate change and habitat loss, as their specialist nature might not give them room for adaption (Colles *et al.*, 2009). Additionally, the vast majority of the collections of range-restricted species examined for this study fall outside of protected areas (Figure 19, Table 5). Particularly the area around the Huancabamba Depression is still largely unprotected but shows hotspots of range-restricted species. This highlights the need for scientifically guided conservation measures to ensure that the resources available to safeguard biodiversity are used in the most efficient way possible. This goal can only be achieved by further exploring the diversity of biodiversity hotspots, such as the tropical Andes, to achieve a better understanding of the patterns that lead to range size rarity and, thus, an increased susceptibility to extinction.

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6. Appendix
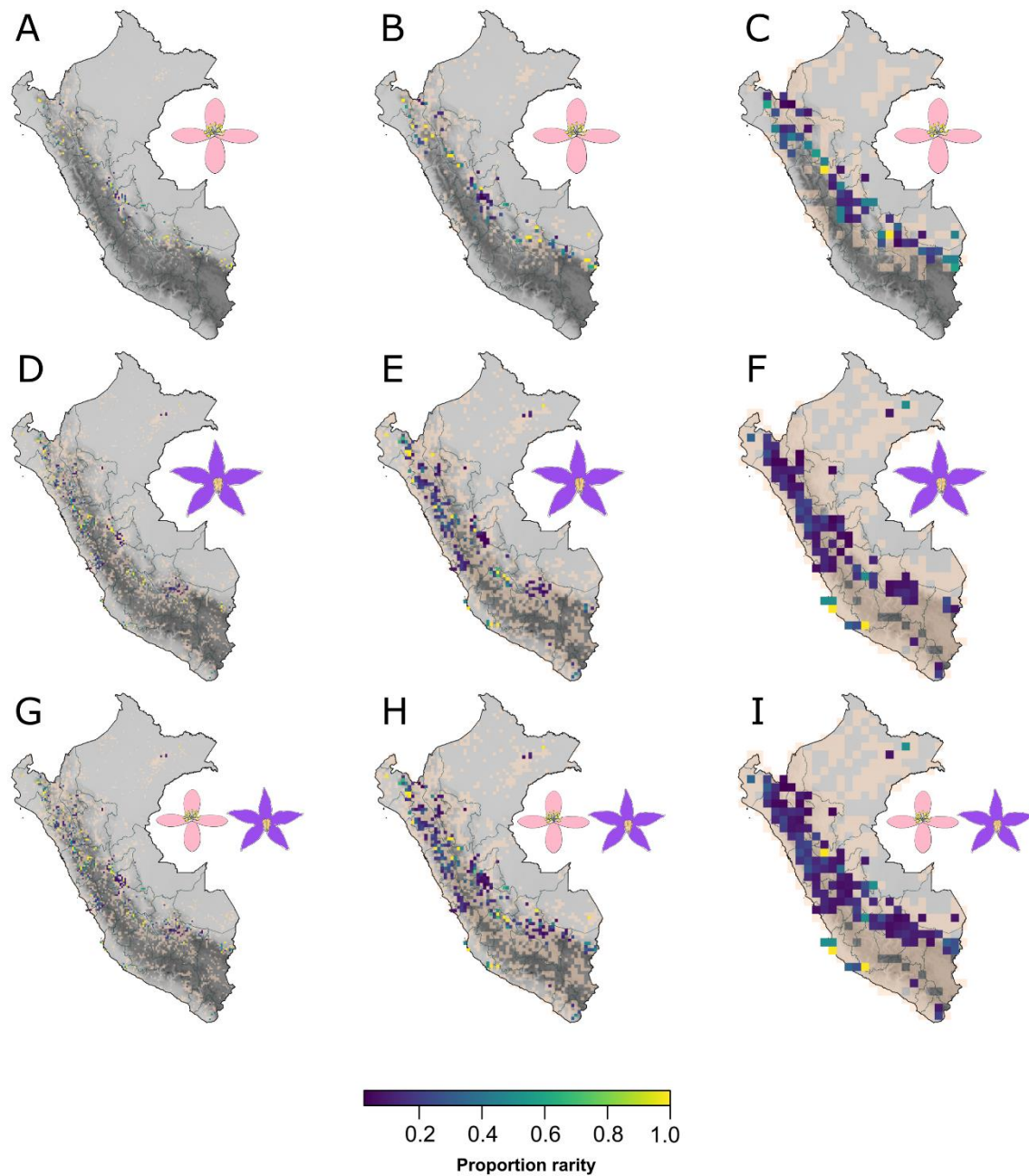
Figure 1 AP. Density maps of the proportion of range-restricted species within grid cells at a resolution of 10x10km (A-G), 20x20km (B-H), and 50x50km (C-I) for *Begonia* (A-C), *Solanum* (D-F), and the combined dataset (G-I). Flower symbols indicate the dataset used for the calculation. The background shows the elevation patterns of Peru, with darker colours reflecting increasing elevations and in yellow the grid cells with collections of species not classified as range-restricted (with regards to the dataset used). The illustration of a *Begonia* flower was adapted from an illustration of *B. speculum* by Claire Banks and the template for the *Solanum* flower stems from an illustration of *S. dulcamara* drawn by Bobbi Angell.

Table 1 AP. Overview of specimen data for Peru used in this study with summary statistics.

	Begonia (N=1,888)	*Solanum* (N=10,680)	Total (N=12,568)
EOO			
Mean	2549126	3288129	3,177,114
Median	329287	393276	393276
Q1,Q3	206683, 2181878	214447, 1495660	210208, 1495660
Min - Max	0.016 - 12151657	2 - 108346341	0.016 - 108346341
AOO			
Mean	681	846	821
Median	408	392	408
Q1,Q3	224, 1060	196, 852	196, 1020
Min - Max	4 - 2368	4 - 9008	4 - 9008
Altitude			
Mean	1524	2054	1982
Median	1542	2300	2179
Q1,Q3	640, 2250	500, 3300	500, 3200
Min - Max	80 - 4073	0 - 4600	0 - 4600
Status (Widespread, Range-restricted)			
Common	1644 (87%)	10101 (95%)	11745 (93%)
Rare	244 (13%)	579 (5%)	823 (7%)
Preelimnary IUCN category			
CR	42 (2%)	39 (0%)	81 (1%)
EN	129 (7%)	255 (2%)	384 (3%)
LC	1615 (86%)	9501 (89%)	11116 (88%)
NT	29 (2%)	600 (6%)	629 (5%)
VU	73 (4%)	285 (3%)	358 (3%)
Range-restricted species in protected area			
inside	59 (24%)	96 (17%)	155 (19%) (representing 40% species)
outside	185 (76%)	483 (83%)	668 (81%) (representing 60% species)
Protected area total			
inside	543 (29%)	1832 (17%)	2375 (19%)
outside	1345 (71%)	8848 (83%)	10193 (81%)

Table 2AP. Overview of specimen data for range-restrcited species in Peru with summary statistics.

	Begonia (N=39)	*Solanum* (N=53)	Total (N=92)
EOO (km2)			
Mean	3220	4149	3755
Median	1221	1743	1300
Q1,Q3	12, 4395	200, 6145	50, 5016
Min - Max	0 - 17186	2 - 18652	0 - 18652
logEOO (km2)			
Mean	2	3	3
Median	3	3	3
Q1,Q3	1, 4	2, 4	2, 4
Min - Max	-2 - 4	0 - 4	-2 - 4
AOO			
Mean	20	30	26
Median	16	24	20
Q1,Q3	8, 30	12, 40	8, 36
Min - Max	4 - 68	4 - 104	4 - 104
Specimen number			
Mean	7	11	10
Median	6	8	7
Q1,Q3	2, 10	4, 13	3, 13
Min - Max	1 - 27	1 - 57	1 - 57
Preelimnary IUCN category			
CR	14 (36%)	12 (23%)	26 (28%)
EN	18 (46%)	25 (47%)	43 (47%)
VU	7 (18%)	16 (30%)	23 (25%)
NT	0 (0%)	0 (0%)	0 (0%)
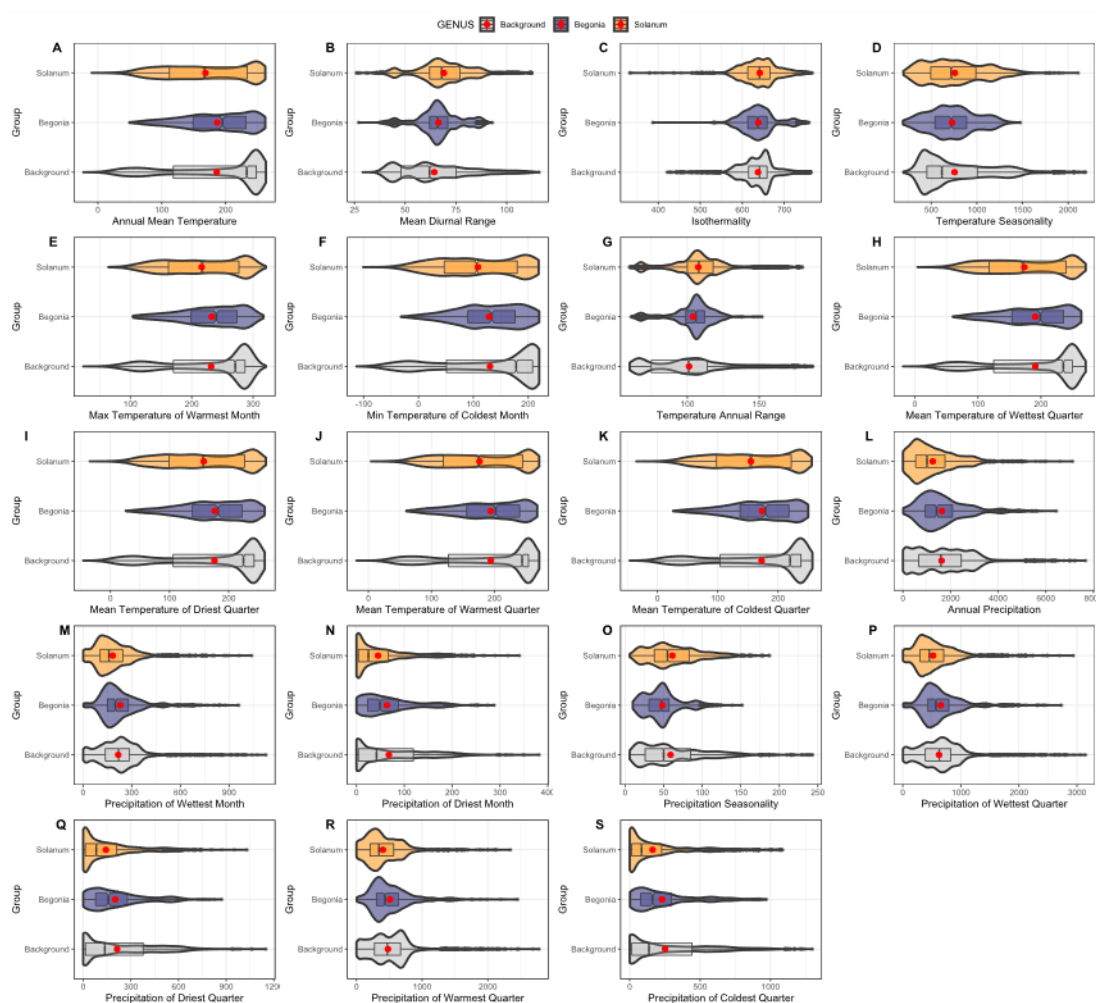
Figure 2 AP. Density distributions of the mean climatic variables of *Solanum* species (orange) and *Begonia* species (dark blue) and the available climatic space in Peru (Background or grey). Red dots show the mean of the group. The notches of the boxplots indicate the 95% CI of the median. All temperature variables are measured in 10x°C. Precipitation variables are measured in millimeters of depth.

Table 3 AP. Expanded statistics of Table 6 regarding the distribution of species and specimens in the four biogeographic regions created for this study.

Category	Coastal lowland	West Andes	East Andes	Amazonas
Species	35	121	**288**	105
Range-restricted *Begonia*	0	7	**32**	5
Range-restricted *Solanum*	4	22	**39**	9
Proportion of r.-restricted species	0.11	**0.18**	0.14	0.09
Range-restricted specimens per km2	0.00006	0.00014	**0.00017**	0.00002
Total species per km2	0.00054	0.00073	**0.00084**	0.0002
Specimens per km2	0.01048	0.01283	**0.01693**	0.00324
Area in km2	72724	206647	427441	**582532**

Table 4AP. Summary statistics of the results of t-tests to test for differences between the climatic position of *Begonia* and *Solanum*. The higher mean is marked by a bold font.

CHELSA variables	p.value	Mean *Begonia*	Mean *Solanum*	stderr
bio1	3E-18	**18.67**	16.85	0.21
bio2	6.36E-10	6.64	**6.91**	0.04
bio3	0.025502	63.82	**64.17**	0.16
bio4	0.00418	72.82	**75.80**	1.04
bio5	5.38E-16	**23.25**	21.62	0.20
bio6	1.31E-17	**12.86**	10.85	0.23
bio7	2.96E-10	10.39	**10.77**	0.06
bio8	5.54E-17	**19.09**	17.38	0.20
bio9	3.5E-17	**17.64**	15.79	0.22
bio10	4.33E-17	**19.40**	17.64	0.21
bio11	7.86E-18	**17.33**	15.49	0.21
bio12	2.42E-22	**1640.34**	1253.81	38.89
bio13	2.51E-20	**229.27**	182.58	4.95
bio14	2.34E-18	**63.79**	45.22	2.09
bio15	1.71E-39	48.21	61.28	0.96
bio16	2.81E-20	**656.35**	522.78	14.19
bio17	6.38E-19	**201.35**	142.78	6.47
bio18	6.82E-19	**510.41**	402.83	11.89
bio19	2.11E-16	**229.65**	162.69	8.02

Table 5AP. Summary statistics of the results of t-tests to test for differences between the climatic position of range-restricted *Begonia* and *Solanum* species. The higher mean is marked by a bold font. Non-significant fonts in bold red

Climatic variable	p.value	Mean range-restricted *Begonia*	Mean range-restricted *Solanum*	stderr
bio1	8.96585E-15	**17.16**	13.42	0.46
bio2	**0.303973963**	7.04	**7.13**	0.09
bio3	0.004333037	64.56	**65.98**	0.49
bio4	0.042787224	**73.33**	67.04	3.10
bio5	5.86289E-15	**21.88**	18.17	0.46
bio6	4.89512E-13	**11.00**	7.36	0.49
bio7	**0.55715473**	**10.87**	10.81	0.10
bio8	3.33726E-14	**17.65**	13.98	0.47
bio9	9.24066E-14	**15.99**	12.36	0.47
bio10	2.09238E-14	**17.85**	14.11	0.47
bio11	7.68906E-14	**15.78**	12.22	0.46
bio12	1.50326E-09	**1510.80**	955.27	89.03
bio13	1.69495E-09	**230.89**	158.29	11.63
bio14	1.14886E-08	**50.61**	25.42	4.30
bio15	7.0054E-13	54.73	71.86	2.31
bio16	2.00289E-09	**657.25**	450.99	33.22
bio17	8.91235E-09	**160.22**	80.92	13.42
bio18	1.52857E-06	**498.21**	356.23	28.94
bio19	2.32183E-08	**174.76**	86.51	15.38

Table 6AP. Results from 100 randomised climatic null models testing the relationship between range size and climatic niche breadth. R-squared and p-value are the results from a linear model. Rho (ρ) is the correlation coefficient resulting from an additional Spearman rank correlation test.

Model index	Rsquared	p-value	Rho (ρ)	Model index	Rsquared	p-value	Rho (ρ)
1	0.560	4.18E-56	0.749	51	0.530	4.31E-52	0.729
2	0.495	9.85E-46	0.705	52	0.568	5.63E-57	0.754
3	0.449	2.76E-41	0.671	53	0.528	7.49E-52	0.728
4	0.490	1.09E-46	0.701	54	0.501	9.86E-48	0.709
5	0.457	2.54E-42	0.678	55	0.571	1.23E-57	0.756
6	0.522	2.07E-51	0.724	56	0.500	9.16E-48	0.708
7	0.507	2.23E-49	0.713	57	0.485	6.73E-46	0.697
8	0.485	1.11E-45	0.698	58	0.543	3.83E-53	0.738
9	0.567	2.31E-57	0.754	59	0.524	6.68E-50	0.725
10	0.526	2.16E-52	0.726	60	0.545	6.26E-54	0.739
11	0.532	7.95E-52	0.731	61	0.506	1.05E-48	0.713
12	0.517	4.05E-50	0.720	62	0.489	2.59E-46	0.701
13	0.488	1.29E-45	0.700	63	0.487	3.45E-46	0.699
14	0.421	1.32E-38	0.650	64	0.614	6.71E-66	0.785
15	0.510	6.70E-49	0.715	65	0.544	1.44E-54	0.739
16	0.516	3.11E-50	0.720	66	0.540	1.59E-53	0.736
17	0.481	1.06E-45	0.695	67	0.507	2.16E-48	0.713
18	0.476	1.33E-44	0.691	68	0.526	4.07E-52	0.726
19	0.515	1.25E-49	0.719	69	0.480	2.23E-45	0.694
20	0.524	8.51E-52	0.725	70	0.535	3.74E-52	0.732
21	0.516	2.01E-49	0.720	71	0.486	7.43E-46	0.698
22	0.538	3.92E-53	0.735	72	0.507	1.73E-48	0.713
23	0.513	7.98E-49	0.717	73	0.517	5.12E-50	0.720
24	0.550	1.45E-54	0.743	74	0.499	2.18E-48	0.708
25	0.486	1.23E-45	0.698	75	0.530	1.65E-51	0.729
26	0.531	2.27E-51	0.730	76	0.528	6.81E-50	0.728
27	0.422	2.28E-37	0.651	77	0.558	9.68E-55	0.748
28	0.480	1.50E-45	0.694	78	0.530	1.36E-51	0.729
29	0.478	8.28E-45	0.693	79	0.516	5.51E-50	0.719
30	0.532	2.52E-51	0.731	80	0.524	7.63E-51	0.725
31	0.539	3.69E-53	0.735	81	0.457	8.27E-42	0.678
32	0.499	9.92E-48	0.707	82	0.456	4.02E-41	0.677
33	0.521	1.94E-50	0.723	83	0.479	3.15E-45	0.694
34	0.512	4.14E-50	0.717	84	0.455	6.28E-42	0.676
35	0.542	2.13E-52	0.738	85	0.571	4.44E-58	0.757
36	0.560	1.72E-56	0.749	86	0.533	3.98E-52	0.731
37	0.573	3.23E-59	0.758	87	0.547	5.53E-55	0.741
38	0.535	2.39E-53	0.732	88	0.497	9.10E-48	0.706
39	0.480	9.59E-46	0.694	89	0.554	1.07E-55	0.746
40	0.517	1.29E-48	0.720	90	0.577	4.58E-58	0.761
41	0.491	5.92E-47	0.702	91	0.457	2.09E-42	0.677
42	0.495	5.00E-47	0.704	92	0.556	2.78E-55	0.747
43	0.529	1.58E-51	0.728	93	0.501	4.42E-47	0.709
44	0.490	6.86E-47	0.701	94	0.538	1.39E-52	0.734
45	0.507	2.66E-48	0.713	95	0.505	6.09E-48	0.712
46	0.496	7.51E-47	0.705	96	0.504	1.48E-48	0.711
47	0.525	5.28E-51	0.726	97	0.574	1.05E-58	0.759
48	0.445	1.83E-40	0.668	98	0.585	1.93E-59	0.766
49	0.498	7.96E-47	0.707	99	0.479	6.24E-45	0.694
50	0.512	5.90E-48	0.717	100	0.453	1.48E-41	0.674

Table 7 AP. Correlation table of the 19 bioclimatic variable tested in this study. Fields in orange show Pearson corrleations above 0.8, fields in blue show Pearson correlations below -0.8.

	bio1	bio2	bio3	bio4	bio5	bio6	bio7	bio8	bio9	bio10	bio11	bio12	bio13	bio14	bio15	bio16	bio17	bio18	bio19
bio1	1.00	0.60	-0.03	-0.20	0.96	0.96	0.42	0.98	0.97	0.98	0.97	0.49	0.42	0.44	0.43	-0.43	0.44	0.21	0.46
bio2	-0.60	1.00	0.26	0.55	-0.38	0.75	0.86	0.52	0.67	-0.50	0.69	0.54	0.47	0.47	0.51	-0.48	0.47	0.34	-0.48
bio3	-0.03	0.26	1.00	-0.86	0.22	0.19	0.67	0.17	0.14	0.21	0.18	0.19	0.14	0.21	0.18	0.14	0.22	0.07	0.24
bio4	-0.20	0.55	-0.86	1.00	0.04	-0.44	0.89	-0.04	-0.37	0.01	0.42	0.31	0.27	0.28	0.31	0.27	0.28	0.12	0.30
bio5	0.96	0.38	0.22	0.04	1.00	0.85	0.16	0.97	0.89	0.99	0.88	0.40	0.34	0.36	0.35	0.35	0.36	-0.13	0.39
bio6	0.96	0.75	0.19	-0.44	0.85	1.00	-0.66	0.89	0.99	0.89	0.99	0.55	0.47	0.49	0.50	0.48	0.50	-0.24	0.53
bio7	0.42	0.86	0.67	0.89	0.16	0.66	1.00	0.29	0.57	-0.25	-0.61	-0.46	-0.40	-0.41	-0.44	-0.41	-0.42	-0.26	-0.44
bio8	0.98	0.52	0.17	-0.04	0.97	0.89	0.29	1.00	0.91	0.99	0.91	0.43	0.38	0.38	0.35	0.38	0.38	0.21	0.38
bio9	0.97	0.67	0.14	-0.37	0.89	0.99	0.57	0.91	1.00	0.91	0.99	0.53	0.45	0.48	0.47	0.46	0.49	0.20	0.52
bio10	0.98	0.50	0.21	0.01	0.99	0.89	0.25	0.99	0.91	1.00	0.90	0.43	0.37	0.38	-0.37	0.38	0.39	0.18	0.40
bio11	0.97	0.69	0.18	0.42	0.88	0.99	0.61	0.91	0.99	0.90	1.00	0.53	0.45	0.47	0.47	0.46	0.47	0.22	0.50
bio12	0.49	0.54	0.19	0.31	0.40	0.55	0.46	0.43	0.53	0.43	0.53	1.00	0.94	0.88	0.62	0.94	0.89	0.79	0.83
bio13	0.42	0.47	0.14	0.27	0.34	0.47	0.40	0.38	0.45	0.37	0.45	0.94	1.00	0.70	0.43	1.00	0.70	0.78	0.73
bio14	0.44	0.47	0.21	0.28	0.36	0.49	0.41	0.38	0.48	0.38	0.47	0.88	0.70	1.00	0.70	0.70	1.00	0.68	0.81
bio15	0.43	0.51	0.18	0.31	0.35	0.50	0.44	0.35	0.47	-0.37	0.47	0.62	0.43	0.70	1.00	0.44	0.71	0.43	0.54
bio16	0.43	0.48	0.14	0.27	0.35	0.58	0.41	0.38	0.46	0.38	0.46	0.94	1.00	0.70	0.44	1.00	0.71	0.78	0.74
bio17	0.44	0.47	0.22	0.28	0.36	0.50	0.42	0.38	0.49	0.39	0.47	0.89	0.70	1.00	0.71	0.71	1.00	0.68	0.82
bio18	0.21	0.34	0.07	0.12	0.13	0.24	0.26	0.21	0.20	0.18	0.22	0.79	0.78	0.68	0.43	0.78	0.68	1.00	0.46
bio19	0.46	0.48	0.24	0.30	0.39	0.53	0.44	0.38	0.52	0.40	0.50	0.83	0.73	0.81	0.54	0.74	0.82	0.46	1.00

Table 8 AP. Table of species used in this study, indicating total number of collections, collections in Peru, and the preliminary threat status based on the IUCN Red List assessment.

Index	Species name	Collections total	Collections Peru only	Threat status
1	Begonia acerifolia Kunth	27	2	NT
2	Begonia aeranthos L.B.Sm. & B.G.Schub.	10	8	LC
3	Begonia albomaculata C.DC.	36	32	LC
4	Begonia altoperuviana A.DC.	18	5	LC
5	Begonia amoeboides Moonlight	12	12	VU
6	Begonia andina Rusby	4	1	EN
7	Begonia anemoniflora Irmsch.	10	10	EN
8	Begonia arrogans Irmsch.	11	11	VU
9	Begonia bifurcata L.B.Sm. & B.G.Schub.	14	11	VU
10	Begonia bracteosa A.DC.	209	207	LC
11	Begonia brevicordata L.B.Sm. & B.G.Schub.	3	3	EN
12	Begonia buddleiifolia A.DC.	91	15	LC
13	Begonia chemillenensis Moonlight	21	21	EN
14	Begonia condorensis Jara & Moonlight	5	4	EN
15	Begonia conoensis Moonlight	2	1	LC
16	Begonia cyathophora Poepp. & Endl.	4	4	CR

17	Begonia deltoides Moonlight	6	5	EN
18	Begonia elachista Moonlight & Tebbitt	2	2	CR
19	Begonia erythrothrix Tebbitt & Moonlight	2	2	CR
20	Begonia fischeri Schrank	423	57	LC
21	Begonia foliosa Kunth	81	11	LC
22	Begonia geraniifolia Hook.	40	40	LC
23	Begonia glabra Aubl.	737	211	LC
24	Begonia glauca (Klotzsch ex Klotzsch) A.DC.	19	19	VU
25	Begonia granpajatensis Moonlight	1	1	CR
26	Begonia guaduensis Kunth	136	11	LC
27	Begonia harlingii L.B.Sm. & Wassh.	18	1	LC
28	Begonia heliantha Tebbitt	2	2	CR
29	Begonia herrerae L.B.Sm. & B.G.Schub.	2	1	VU
30	Begonia hirta (Klotzsch ex Klotzsch) L.B.Sm. & B.G.Schub.	14	14	VU
31	Begonia hirtella Link	87	8	LC
32	Begonia hitchcockii Irmsch.	66	22	LC
33	Begonia humilis Dryand.	95	40	LC
34	Begonia imbrexiformis Moonlight	1	1	CR
35	Begonia joshii Moonlight	5	5	EN
36	Begonia lamolina Moonlight	6	6	CR
37	Begonia longitepala Moonlight	3	3	CR
38	Begonia lophoptera Rolfe	47	46	LC
39	Begonia lucifuga Irmsch.	5	5	EN
40	Begonia ludwigii Irmsch.	17	5	NT
41	Begonia maynensis A.DC.	121	71	LC
42	Begonia monadelpha (Ruiz ex Klotzsch) A.DC.	76	76	LC
43	Begonia neoharlingii L.B.Sm. & Wassh.	18	16	LC
44	Begonia nunezii Moonlight	2	2	EN
45	Begonia obtecticaulis Irmsch.	6	6	EN
46	Begonia occultata Moonlight & J.P.Allen	1	1	CR
47	Begonia octopetala L'HŽr.	138	119	LC
48	Begonia parcifolia C.DC.	22	9	NT
49	Begonia parviflora Poepp. & Endl.	312	148	LC
50	Begonia pastoensis A.DC.	25	3	LC
51	Begonia peruviana A.DC.	148	144	LC
52	Begonia piedmontana Moonlight	27	1	LC
53	Begonia piurensis L.B.Sm. & B.G.Schub.	14	5	VU
54	Begonia pleiopetala A.DC.	45	26	LC
55	Begonia polypetala A.DC.	9	9	EN
56	Begonia pseudopleiopetala Tebbitt	10	10	EN
57	Begonia rodriguezii Moonlight	3	3	CR
58	Begonia rossmanniae A.DC.	231	97	LC
59	Begonia scorpiocaulis Moonlight & Tebbitt	1	1	CR
60	Begonia semiovata Liebm.	403	63	LC
61	Begonia serotina A.DC.	23	1	NT
62	Begonia speculum Moonlight & Tebbitt	3	3	CR
63	Begonia stenotepala L.B.Sm. & B.G.Schub.	16	16	EN
64	Begonia subspinulosa Irmsch.	6	6	CR
65	Begonia thyrsoidea Irmsch.	2	2	EN
66	Begonia tumbezensis Irmsch.	23	12	NT
67	Begonia ulmifolia Willd.	48	1	LC
68	Begonia unilateralis Rusby	27	2	EN
69	Begonia urticae L.f.	352	60	LC
70	Begonia urubambensis Tebbitt	8	8	EN
71	Begonia veitchii Hook.f.	106	73	LC
72	Begonia velata L.B.Sm. & B.G.Schub.	8	8	EN
73	Begonia weberbaueri Irmsch.	12	12	EN
74	Begonia wollnyi Herzog	48	2	LC
75	Begonia yuracyacuensis Moonlight	7	7	CR
76	Solanum abitaguense S.Knapp	60	23	LC
77	Solanum acanthodes Hook.f.	86	58	LC
78	Solanum acaule Bitter	849	335	LC
79	Solanum acerifolium Dunal	206	15	LC
80	Solanum achorum S.Stern	19	15	LC
81	Solanum acroglossum Juz.	8	8	EN
82	Solanum acroscopicum Ochoa	24	24	LC
83	Solanum actaeibotrys Rusby	27	11	LC
84	Solanum acuminatum Ruiz & Pav.	69	50	LC
85	Solanum adenobasis M.Nee & Farruggia	23	9	LC
86	Solanum albicans (Ochoa) Ochoa	57	54	LC
87	Solanum albidum Dunal	211	92	LC
88	Solanum aligerum Schltdl.	386	25	LC
89	Solanum altissimum Benítez	95	30	LC
90	Solanum amayanum Ochoa	4	4	EN
91	Solanum amblophyllum Hook.	37	37	VU
92	Solanum americanum Mill.	2584	192	LC
93	Solanum amnicola S.Knapp	17	16	LC

94	Solanum amotapense Svenson	33	28	LC
95	Solanum anamatophilum Ochoa	13	13	EN
96	Solanum anceps Ruiz & Pav.	351	181	LC
97	Solanum ancophilum (Correll) Ochoa	14	14	EN
98	Solanum angustialatum Bitter	6	6	CR
99	Solanum anisophyllum Van Heurck & Müll.Arg.	99	29	LC
100	Solanum anomalostemon S.Knapp & M.Nee	8	8	EN
101	Solanum antisuyo Särkinen & S.Knapp	103	46	LC
102	Solanum apaporanum R.E.Schult.	16	3	LC
103	Solanum aphyodendron S.Knapp	250	48	LC
104	Solanum appressum K.E.Roe	74	55	LC
105	Solanum arcanum Peralta	72	72	LC
106	Solanum arenicola Särkinen & P.Gonzáles	41	7	LC
107	Solanum arequipense Bitter	66	66	LC
108	Solanum asperolanatum Ruiz & Pav.	314	92	LC
109	Solanum augustii Ochoa	7	7	EN
110	Solanum aureum Dunal	72	3	LC
111	Solanum ayacuchense Ochoa	5	5	EN
112	Solanum barbeyanum Huber	152	70	LC
113	Solanum barbulatum Zahlbr.	129	54	LC
114	Solanum baretiae Tepe	22	19	NT
115	Solanum basendopogon Bitter	40	39	LC
116	Solanum bellum S.Knapp	25	5	LC
117	Solanum boliviense Dunal	627	41	LC
118	Solanum brevicaule Bitter	1569	126	LC
119	Solanum brevifolium Dunal	54	5	LC
120	Solanum buesii Vargas	14	14	EN
121	Solanum burkartii Ochoa	13	13	EN
122	Solanum cacosmum Bohs	21	17	LC
123	Solanum cajamarquense Ochoa	13	13	EN
124	Solanum cajanumense Kunth	9	3	LC
125	Solanum calidum Bohs	38	8	LC
126	Solanum callianthum C.V.Morton	37	15	LC
127	Solanum campechiense L.	31	3	LC
128	Solanum candidum Lindl.	36	9	LC
129	Solanum candolleanum Berthault	1283	1277	LC
130	Solanum cantense Ochoa	34	34	NT
131	Solanum caricaefolium Rusby	65	45	LC
132	Solanum caripense Dunal	104	36	LC
133	Solanum catilliflorum G.J.Anderson, Martine, Prohens & Nuez	10	10	LC
134	Solanum chachapoyasense Bitter	2	2	VU
135	Solanum chacoense Bitter	963	8	LC
136	Solanum chamaepolybotryon Bitter	11	11	NT
137	Solanum chilense (Dunal) Reiche	186	46	LC
138	Solanum chimborazense Bitter & Sodiro	4	3	LC
139	Solanum chiquidenum Ochoa	115	115	NT
140	Solanum chmielewskii (C.M.Rick, Kesicki, Fobes & M.Holle) D.M.Spooner, G.J.Anderson & R.K.Jansen	13	11	LC
141	Solanum chomatophilum Bitter	353	340	LC
142	Solanum chrysotrichum Schltdl.	76	12	LC
143	Solanum clandestinum Bohs	35	20	LC
144	Solanum clathratum Sendtn.	25	19	LC
145	Solanum clivorum S.Knapp	21	21	NT
146	Solanum cochabambense Bitter	345	146	LC
147	Solanum cochoae G.J.Anderson & Bernardello	8	8	VU
148	Solanum colombianum Dunal	361	3	LC
149	Solanum confertiseriatum Bitter	31	2	LC
150	Solanum confine Dunal	42	38	LC
151	Solanum conglobatum Dunal	22	8	LC
152	Solanum conicum Ruiz & Pav.	41	40	LC
153	Solanum contumazaense Ochoa	12	12	CR
154	Solanum corneliomulleri J.F.Macbr.	154	154	LC
155	Solanum corymbosum Jacq.	90	68	LC
156	Solanum cruciferum Bitter	5	3	VU
157	Solanum cucullatum S.Knapp	25	10	LC
158	Solanum curtilobum Juz. & Bukasov	5	2	LC
159	Solanum cutervanum Zahlbr.	50	39	LC
160	Solanum cyathophorum M.Nee & Farruggia	52	2	LC
161	Solanum daphnophyllum Bitter	9	1	LC
162	Solanum dianthum Rusby	68	2	LC
163	Solanum dillonii S.Knapp	33	31	LC
164	Solanum dolichocremastrum Bitter	31	31	VU
165	Solanum dolichorhachis Bitter	4	2	EN
166	Solanum edmondstonii Hook.f.	11	11	VU
167	Solanum endopogon (Bitter) Bohs	68	36	LC
168	Solanum evolvulifolium Greenm.	82	1	LC
169	Solanum fiebrigii Bitter	89	3	LC

170	Solanum filiforme Ruiz & Pav.	10	10	LC
171	Solanum fragile Wedd.	45	33	LC
172	Solanum glutinosum Dunal	92	89	LC
173	Solanum goniocaulon S.Knapp	25	17	LC
174	Solanum gonocladum Dunal	101	9	LC
175	Solanum goodspeedii K.E.Roe	73	27	LC
176	Solanum gracilifrons Bitter	3	3	CR
177	Solanum grandidentatum Phil.	80	54	LC
178	Solanum grandiflorum Ruiz & Pav.	109	44	LC
179	Solanum habrocaulon S.Knapp	6	1	NT
180	Solanum habrochaites S.Knapp & D.M.Spooner	208	174	LC
181	Solanum hastiforme Correll	13	13	VU
182	Solanum hazenii Britton	284	2	LC
183	Solanum heleonastes S.Knapp	26	2	LC
184	Solanum hispidum Pers.	1	1	CR
185	Solanum huancabambense Ochoa	19	19	EN
186	Solanum huaylasense Peralta	23	23	VU
187	Solanum humectophilum Ochoa	14	14	EN
188	Solanum hutchisonii (J.F.Macbr.) Bohs	16	15	NT
189	Solanum hypacrarthrum Bitter	47	47	NT
190	Solanum iltisii K.E.Roe	42	36	LC
191	Solanum immite Dunal	31	31	NT
192	Solanum incarceratum Ruiz & Pav.	59	13	LC
193	Solanum incasicum Ochoa	1	1	CR
194	Solanum incurvum Ruiz & Pav.	39	38	LC
195	Solanum inelegans Rusby	19	5	NT
196	Solanum interandinum Bitter	314	99	LC
197	Solanum jamaicense Mill.	259	23	LC
198	Solanum juglandifolium Dunal	132	4	LC
199	Solanum junctum S.Stern & M.Nee	16	16	LC
200	Solanum juninense Bitter	37	36	LC
201	Solanum kioniotrichum Bitter ex J.F.Macbr.	23	21	LC
202	Solanum kulliwaita S.Knapp	5	2	NT
203	Solanum laxissimum Bitter	35	35	LC
204	Solanum leiophyllum Benth.	15	4	NT
205	Solanum lepidotum Dunal	137	35	LC
206	Solanum leptocaulon Van Heurck & Müll.Arg.	38	1	LC
207	Solanum leptopodum Van Heurck & Müll.Arg.	60	32	LC
208	Solanum leucocarpon Dunal	281	21	LC
209	Solanum leucopogon Huber	123	61	LC
210	Solanum lignicaule Vargas	40	40	EN
211	Solanum limbaniense Ochoa	6	6	EN
212	Solanum lindenii Rusby	48	36	LC
213	Solanum longifilamentum Särkinen & P.Gonzáles	125	68	LC
214	Solanum luteoalbum Pers.	34	32	LC
215	Solanum lycopersicoides Dunal	20	10	VU
216	Solanum macbridei Hunz. & Lallana	15	10	LC
217	Solanum malletii S.Knapp	45	35	LC
218	Solanum mariae Särkinen & S.Knapp	2	2	CR
219	Solanum maturecalvans Bitter	185	143	LC
220	Solanum medians Bitter	204	199	LC
221	Solanum megaspermum Agra	11	11	LC
222	Solanum mite Ruiz & Pav.	197	139	LC
223	Solanum mochiquense Ochoa	55	55	LC
224	Solanum monadelphum Van Heurck & Müll.Arg.	52	49	LC
225	Solanum monarchostemon S.Knapp	28	21	LC
226	Solanum montanum L.	203	198	LC
227	Solanum morellifolium Bohs	47	35	LC
228	Solanum multifidum Lam.	97	95	LC
229	Solanum multiinterruptum Bitter	145	145	NT
230	Solanum naucinum S.Knapp	3	3	EN
231	Solanum nemorense Dunal	127	100	LC
232	Solanum neorickii D.M.Spooner, G.J.Anderson & R.K.Jansen	30	27	LC
233	Solanum nitidibaccatum Bitter	489	3	LC
234	Solanum nitidum Ruiz & Pav.	177	137	LC
235	Solanum nubicola Ochoa	2	1	CR
236	Solanum nudum Dunal	312	60	LC
237	Solanum nutans Ruiz & Pav.	108	69	LC
238	Solanum obliquum Ruiz & Pav.	46	43	LC
239	Solanum oblongifolium Dunal	90	12	LC
240	Solanum oblongum Ruiz & Pav.	32	32	VU
241	Solanum occultum Bohs	58	28	LC
242	Solanum ochranthum Dunal	86	41	LC
243	Solanum ochrophyllum Van Heurck & Müll.Arg.	27	11	LC
244	Solanum olmosense Ochoa	4	3	EN
245	Solanum oppositifolium Ruiz & Pav.	183	111	LC
246	Solanum ovalifolium Dunal	111	27	LC

247	Solanum oxapampense S.Knapp	13	13	EN
248	Solanum oxycoccoides Bitter	16	16	NT
249	Solanum oxyphyllum C.V.Morton	33	26	LC
250	Solanum pachyandrum Bitter	8	7	NT
251	Solanum pallidum Rusby	117	49	LC
252	Solanum paposanum Phil.	51	36	LC
253	Solanum paucissectum Ochoa	2	2	EN
254	Solanum pectinatum Dunal	45	3	LC
255	Solanum pedemontanum M.Nee	84	26	LC
256	Solanum pendulum Ruiz & Pav.	39	32	LC
257	Solanum pennellii Correll	58	57	LC
258	Solanum pentlandii Dunal	71	51	LC
259	Solanum perlongistylum G.J.Anderson, Martine, Prohens & Nuez	4	3	LC
260	Solanum peruvianum L.	182	158	LC
261	Solanum phaseoloides Pol.	15	1	LC
262	Solanum physalifolium Rusby	36	6	LC
263	Solanum pillahuatense Vargas	7	7	EN
264	Solanum pimpinellifolium L.	342	163	LC
265	Solanum piurae Bitter	12	12	EN
266	Solanum placitum C.V.Morton	28	7	LC
267	Solanum plowmanii S.Knapp	39	37	NT
268	Solanum poinsettiifolium Rusby	38	21	LC
269	Solanum polytrichostylum Bitter	64	39	LC
270	Solanum proteanthum Bohs	29	14	LC
271	Solanum pseudoamericanum Särkinen, P.Gonzáles & S.Knapp	41	40	LC
272	Solanum pseudosycophanta Farruggia	20	18	NT
273	Solanum quaesitum C.V.Morton	33	7	LC
274	Solanum quitoense Lam.	35	10	LC
275	Solanum radicans L.f.	124	80	LC
276	Solanum raphanifolium Cárdenas & Hawkes	362	362	LC
277	Solanum raquialatum Ochoa	15	15	EN
278	Solanum rhomboideilanceolatum Ochoa	1	1	CR
279	Solanum rhytidoandrum Sendtn.	158	3	LC
280	Solanum riparium Pers.	112	68	LC
281	Solanum robustifrons Bitter	110	95	LC
282	Solanum roseum Bohs	16	10	LC
283	Solanum rubicaule S.Stern	21	16	LC
284	Solanum rugosum Dunal	227	11	LC
285	Solanum ruizii S.Knapp	8	8	VU
286	Solanum salasianum Ochoa	4	4	CR
287	Solanum sanchez-vegae S.Knapp	33	32	LC
288	Solanum saponaceum Dunal	81	80	LC
289	Solanum savanillense Bitter	8	3	LC
290	Solanum scabrifolium Ochoa	5	5	EN
291	Solanum schlechtendalianum Walp.	191	37	LC
292	Solanum selachophyllum Bitter	39	36	LC
293	Solanum sericeum Ruiz & Pav.	3	3	CR
294	Solanum sessile Ruiz & Pav.	233	181	LC
295	Solanum simplicissimum Ochoa	8	8	EN
296	Solanum sinuatiexcisum Bitter	41	5	LC
297	Solanum sisymbriifolium Lam.	350	35	LC
298	Solanum smithii S.Knapp	17	11	LC
299	Solanum sogarandinum Ochoa	47	47	NT
300	Solanum solum J.F.Macbr.	2	1	LC
301	Solanum splendens (Dunal) Bohs	178	11	LC
302	Solanum stenophyllum Dunal	63	4	LC
303	Solanum stramoniifolium Jacq.	201	28	LC
304	Solanum suaveolens Kunth & C.D.Bouché	41	30	LC
305	Solanum subtusviolaceum Bitter	32	15	LC
306	Solanum sumacaspi S.Knapp	13	13	VU
307	Solanum superbum S.Knapp	10	9	NT
308	Solanum sycophanta Dunal	59	13	LC
309	Solanum tabanoense Correll	16	1	LC
310	Solanum talarense Svenson	20	20	VU
311	Solanum tenuisetosum (Bitter) Bohs	38	28	LC
312	Solanum tenuispinum Rusby	21	7	LC
313	Solanum tergosericeum Ochoa	1	1	CR
314	Solanum ternatum Ruiz & Pav.	136	116	LC
315	Solanum thelopodium Sendtn.	114	65	LC
316	Solanum tovarii S.Knapp	5	5	VU
317	Solanum trachycarpum Bitter & Sodiro	4	43	LC
318	Solanum trinitense Ochoa	59	4	LC
319	Solanum uleanum Bitter	4	25	CR
320	Solanum uncinellum Lindl.	33	56	LC
321	Solanum unilobum (Rusby) Bohs	237	1	LC
322	Solanum ursinum Rusby	12	2	LC
323	Solanum urubambaense Agra	5	12	NT

324	Solanum velardei Ochoa	12	1	VU
325	Solanum velutinum Dunal	74	33	LC
326	Solanum velutissimum Rusby	9	4	LC
327	Solanum verecundum M.Nee	24	15	LC
328	Solanum violaceimarmoratum Bitter	68	34	LC
329	Solanum weddellii Phil.	62	7	LC
330	Solanum wittmackii Bitter	57	57	VU
331	Solanum xanthophaeum Bitter	26	24	LC
332	Solanum yanamonense S.Knapp	7	7	EN
333	Solanum youngii S.Knapp	18	14	NT
334	Solanum zumbense Bohs	12	11	LC