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Tree genetic resources at risk in South America: A spatial threat assessment to prioritize populations for conservation

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Abstract

Background: Humans threat the populations of tree species by overexploitation, deforestation, land use change, and climate change. We present a novel threat assessment at intraspecific level to support the conservation of genetic resources of 80 socioeconomically viable tree species in South America. In this assessment, we evaluate the threat status of Ecogeographic Range Segments (ERSs). ERSs are groups of populations of a specific species in a certain ecological zone of a particular grid cell of a species' geographic occupancy.

Methods: We used species location records to determine the species distributions and species-specific ERSs. We distinguished eight threat situations to assess the risk of extirpation of the ERSs of all 80 species. These threat situations were determined by *large* or *little* tree cover, *low* or *high* human pressure, and *low* or *high* climate change impact. Available layers of tree cover and threats were used to determine the levels of fragmentation and direct human pressure. Maxent niche modelling with two Global Circulation Models helped determining climate change impact by the 2050s.

Results: When all 80 species are considered, in total, 59% of the ERSs are threatened by *little* tree cover or *high* human pressure. When climate change is also considered, then 71-73% of the ERSs are threatened. When an increased risk of extirpation of populations outside protected areas is considered, then 84–86% of the ERSs are threatened. Seven species warrant special attention because all their ERSs are threatened across their whole distribution in South America: *Balfourondendron riedelianum*, *Cariniana legalis*, *Dalbergia nigra*, *Handroanthus pulcherrimus*, *Pachira quintana*, *Prosopis flexuosa*, and *Prosopis pallida*.

Conclusions: Our results confirm the urgency to set up a regional action plan for the conservation of tree genetic resources in South America. With this threat assessment, we aim to support governments and organizations who are taking up this task.

KEYWORDS

climate change, ecogeography, evolutionary significant units, intraspecific diversity, reserve selection, risk assessment, Latin America, circa situm conservation, in situ conservation

1 | INTRODUCTION

Humans use more than 8,000 tree species worldwide for timber, food, fibre, medicine, and cultural activities (FAO, 2014). As much as humans need and value tree species, we threaten their populations by overexploitation, deforestation, land use change, and climate change. The genetic variation maintained in these populations is the source for adaptation to environmental changes and enables species and populations to evolve over time (Graudal et al., 2014; Ottewell, Bickerton, Byrne, & Lowe, 2015). This genetic variation is also a source for seed material and breeding efforts (Graudal et al., 2014). Aichi Target 13 of the Convention of Biological Diversity (CBD) states that by 2020 strategies need to be established to conserve the genetic resources of socioeconomically valuable species (CBD, 2010). This includes tree species of value to humans. The conservation of the genetic resources of these tree species requires coordinated actions between different organizations and countries as demonstrated by the European network of dynamic gene conservation units (Koskela et al., 2013). South America harbours much more tree genetic resources than Europe. But in contrast to Europe no clear conservation strategies are in place to safeguard tree genetic resources in South America, except perhaps for a few tree species, which are listed at the Convention on International Trade in Endangered Species (CITES).

Most tree genetic resources are exclusively maintained in situ in their natural habitat in or outside protected areas, or circa situm in home gardens, orchards, livestock, or agroforestry systems (Dawson et al., 2013). Ex situ conservation is an alternative and complementary approach to rescue genetic material of highly threatened populations. Ex situ conservation of tree species is done mostly in live collections, in botanical gardens, or in provenance trials. To a lower degree genetic material is conserved in vitro, cryopreserved, or maintained in seed collections. Ex situ is only an option for a limited number of prioritized species and populations because of the costs related to maintaining live collections due to the longevity of tree species and the often recalcitrant nature of their seeds. In situ and circa situm conservation remain the recommended conservation options.

We present a spatial approach to assess the threats of fragmentation, direct human pressure, and climate change to the genetic resources of 80 socioeconomically valuable tree species in South America. With this study, we aim to support the development of a regional action plan to safeguard tree genetic resources in South America.

In our approach, we assess threats at intraspecific level, for groups of conspecific populations, which are genetically similar. As far as we know, this is the first systematic threat assessment of plant species at intraspecific level. Our approach complements spatial threat assessments at species and ecosystem level (Jarvis, Touval, Schmitz, Sotomayor, & Hyman, 2010; Ramirez-Villegas, Jarvis, & Touval, 2012; Underwood, Viers, Klausmeyer, Cox, & Shaw, 2009).

The concept of Evolutionary Significant Units has been proposed for intraspecific assessments. Evolutionary Significant Units are defined as "groups of conspecific populations that have substantial reproductive isolation, which has led to adaptive differences so that the populations represent a significant evolutionary component of the species" (Palsbøll, Bérubé, & Allendorf, 2007). For most tropical tree species, however, it is currently not possible to define Evolutionary Significant Units across their distribution because limited or no genetic data exist about their adaptive variation and reproductive isolation between populations (Dawson et al., 2017). As an alternative to Evolutionary Significant Units, Eco-Geographic Units have been proposed to prioritize *range segments of species* for conservation (Zhivotovsky et al., 2015).

Here, we rename *Eco-Geographic Units* to Ecogeographic Range Segments (ERSs), to avoid confusion in spatial assessments with *Geographic Units* of measurements such as countries or grid cells. We define an Ecogeographic Range Segment (ERS) as a group of populations of a specific species in a certain ecological zone of a particular grid cell of a species' geographic occupancy. These criteria are in line with recommendations to prioritize areas for conservation of genetic resources on the basis of ecological zones (Graudal et al., 2014; Phillips, Asdal, Magos Brehm, Rasmussen, & Maxted, 2016; Taylor et al., 2017), and to use geographic distance as a measure of reproductive isolation (Rivers, Bachman, Meagher, Lughadha, & Brummitt, 2010; Rivers, Brummitt, Nic Lughadha, & Meagher, 2014).

2 | METHODS

2.1 | Species prioritization

A total of 80 woody perennials were analysed in our study, including one bamboo species and eight palm species (Appendix S1). These species were selected based on their socioeconomic value for industrial wood; fuel wood, posts, poles; non-timber products; and/or edible fruits according to FAO (2001) and the New World Fruit Database (Appendix S2—links data sources). The species were selected by FAO's forest genetic resources panels in 2001 and 2003 (Baskaran et al., 2003; FAO, 2001) and by experts of the Latin American Forest Genetic Resources Network (LAFORGEN) during meetings carried out in 2006, 2008 and 2010.

For this regional exercise, only species native to at least two countries in South America (or at least two states in the case of Brazil) were considered following Zeven and de Wet (1987) and the database of the USDA Germplasm Resources Information Network (Appendix S2—links data sources). Furthermore, to ensure the representativeness of tree species from all South American countries, species were selected in such a way that there were at least five native species per South American country. Lastly, only species with at least 30 unique georeferenced species location records were included, to allow spatial analyses to be conducted with a minimum level of reliability (Wisz et al., 2008). All species names were adjusted according to The Plant List (Appendix S2—links data sources).

2.2 | Species distribution

We obtained georeferenced species location records from data made available by herbaria, field studies, and genebanks through the Global Biodiversity Information Facility (Appendix S2—links data sources), the Information System for Biological Collections in Brazil (Appendix

S2—links data sources) and participants of the Latin America Forest Genetic Resources Network (LAFORGEN). Even though some species location records may belong to botanical gardens and tree plantations, most species location records in our database come from natural populations or from managed trees in farming systems, which may hold unique genetic diversity not found any more in natural systems (Boshier, Gordon, & Barrance, 2004; Miller & Schaal, 2005). We assume that collecting species location records from these different settings together ensures to capture all genetic resources within the native distribution ranges of these 80 tree species. In addition, we assume that each species location record stands for a number of individuals of the same species at the indicated location, which form together a population.

Data were curated by removing species location records with inconsistencies between countries reported in the passport data of the species location records and corresponding administrative units resulting from map projection (Hijmans, Schreuder, De La Cruz, & Guarino, 1999). To accommodate for imprecisions for otherwise accurate spatial coordinates, we maintained species location records in a border buffer zone of 10 arc minutes (~18 km at the equator) near administrative boundaries. Coordinates of species location records located in coastal waters within a 10 arc minutes buffer to the coastline were modified to the nearest point in the coastline, which is a common precision issue in biological data georeferencing (Record, Charney, Zakaria, & Ellison, 2013). Species location records located further in the sea were removed.

Species location records with extreme climate values beyond species niche margins were removed from our dataset because these are likely errors in coordinates or taxonomy. Species location records were removed when the values of 5 or more of 19 bioclimatic variables as defined by Hijmans, Cameron, Parra, Jones, and Jarvis (2005) were outside 2.5 times the interquartile range below the first quartile or above the third quartile. Our thresholds are 40% more conservative compared to recommended ones from literature (Chapman, 2005; Hijmans, Guarino, & Bussink, 2004). In this way, we aimed to avoid the removal of species location records from marginal populations with valuable genetic resources in our analysis. Our final dataset consisted of 15,601 species location records from South America.

2.3 | Ecogeographic range segments

For each of the 80 species, species-specific ecogeographic range segments (ERSs) were defined in an attempt to capture for each species all its genetic variation across its distribution in South America. To define ERSs for each species, we overlaid FAO ecological zones with the grid cells of species' geographic occupancy (Figure 1a,b; FAO, 2012). Per species, we then allocated the species location records among its ERSs (Figure 1c,d). In this way, each ERS is a group of species location records of species *x* in ecological zone *y* of grid cell *z* of a species' geographic occupancy.

We used the map of FAO ecological zones because it harmonizes several existing ecological zoning maps (FAO, 2012). The grid cells of species' geographic occupancy represent the spatial structure in genetic variation and reproductive isolation between populations. For each species, the size of the grid cells of species' geographic occupancy can vary given the species range and was calculated as the 10% maximum inter-point distance as this ratio is species-specific and not sensitive to collection density (Rivers et al., 2010).

2.4 | Tree cover

We distinguished between species location records in areas with *large* tree cover (30% or more) and species location records in areas with

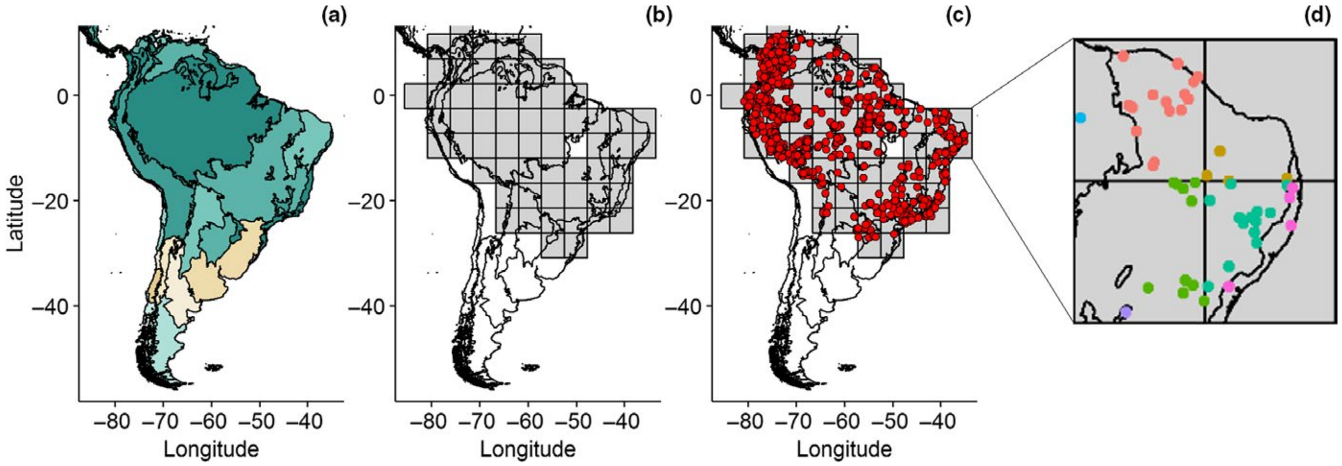

FIGURE 1 Development of species-specific Ecogeographic Range Segments (ERSs) and the assignment of species location records to these ERSs. To illustrate the development of ERSs, *Cedrela odorata* is used here as an example. (a) Ecological zones in South America according to FAO (2012). (b) Grid cells of the geographic occupancy of *Cedrela odorata* are overlaid with the ecological zones to define ERSs across the species distribution of *Cedrela odorata*. The size of grid cells of the species' geographic occupancy is calculated as the 10% maximum inter-point distance between species location records of *Cedrela odorata*. (c) Species location records of *Cedrela odorata* are allocated across the defined ERSs. (d) Each ERS is species-specific and consists of a group of species location records of a specific species of a certain ecological zone of a particular grid cell of a species' geographic occupancy [Colour figure can be viewed at wileyonlinelibrary.com]

little tree cover (less than 30%). We extracted for each species location record the percentage tree cover per aggregated grid cell of arc 5 minutes resolution from the 30 m resolution 2010 Global Tree Canopy Cover database (Hansen et al., 2013). We used 30% tree cover as a threshold because this is a tipping point between ecosystem states of *large* and *little* tree cover (Hirota, Holmgren, Van Nes, & Scheffer, 2011). The tree cover in the locations of our species location records followed a bimodal distribution with most species records either located in areas with more than 80% tree cover or less than 20% tree cover (Appendix S3). We consider species location records in areas with *large* tree cover as exempted from fragmentation, whereas species records located in areas with *little* tree cover are vulnerable to fragmentation.

2.5 | Direct human pressure

We combined six maps showing different types of threats associated with human pressure on ecosystems, developed by Jarvis et al. (2010), into one map of direct human pressure, which reflects the maximum value among the six threats in each pixel. The six depicted threats are due to (1) human accessibility; (2) conversion to agriculture; (3) fires; (4) grazing pressure; (5) infrastructure; and (6) land clearance because of oil and gas. The threat maps have a 2.5 arc minutes resolution and indicate a threat magnitude from 0 (no threat) to 3 (maximum threat), which is determined by the threat exposure on the basis of freely available datasets and threat sensitivity at ecosystem level according to experts (Jarvis et al., 2010).

In the combined map of direct human pressure, *low* threat areas were distinguished from areas with *high* threats. We chose 1.2 as the threshold value, which is 2/5 of the maximum value of 3, distinguishing *low* threat values from *medium* and *high* threat values (>2/5 of the maximum value). For choosing this threshold, we followed a 5-point threat scale after IUCN-CMP (2007) and modified by Gaisberger et al. (2017).

2.6 | Indirect human pressure: climate change

To assess climate change impacts, we applied ecological niche modelling with Maxent, a widely used modelling algorithm (Elith et al., 2011). We modelled the distribution of each species under historic climate conditions (1960–1990) and the projected future climate during the period between 2040 and 2069 (2050s). The 19 bioclimatic variables available from the WORLDCLIM 1.4 database, with a downscaled resolution of 2.5 arc minutes, were used as environmental variables in the modelling (Appendix S2—Links data sources). This set of variables returned good quality distribution maps according to species experts who were asked for 5 of the 80 species (van Zonneveld, Castañeda, Scheldeman, van Etten, & Van Damme, 2014). Even though our analysis focused on South America, modelling was done with a total of 27,283 species location records from whole Latin America and the Caribbean to capture the whole realized niche of the 80 species in their native distribution. Future climate modelling was done separately with two climate models: MRI-CGCM3 (MG) (Yukimoto et al., 2012) and HadGEM2-CC (HG) (Collins et al., 2011) under two Representative Concentration Pathways (RCPs) 4.5 and 8.5. These models and scenarios have been used in the Fifth Assessment Report by the Intergovernmental Panel on Climate Change (IPCC) (Flato et al., 2013). We used the threshold value of maximum specificity + sensitivity to distinguish suitable from not-suitable areas (Liu, White, & Newell, 2013). On the basis of these thresholds, we distinguished for each species: (1) areas with *low* climate change impact where habitat conditions are expected to remain suitable, and thus populations of tree species are likely to persist under global climate change; and (2) areas with *high* climate change impact where the climate eventually becomes unsuitable for existing populations of tree species.

To reduce the possible effect of sampling bias on modelling results, we averaged for each species the Maxent results from three runs, each time using 80% of randomly resampled species location records. These species locations records were resampled from grid cells with a size corresponding to 10% of the longest inter-point distance after Fourcade, Engler, Rödder, and Secondi (2014). Second, to allow Maxent to discriminate areas with species location records from the areas with no data, we randomly extracted five times more background points from the area enclosed by the species' convex hull. This convex hull was extended with a buffer corresponding to 10% of the longest inter-point distance. Third, to reduce the risk of including modelled areas where the species does not occur in reality, we limited the modelled distribution range by the area enclosed by the extended convex hull polygon. Finally, we restricted the modelled distributions to land cover types where we assumed populations to occur, namely, in natural vegetation and mixed agricultural systems as classified by the Global Land Cover 2000 Project (Fritz et al., 2003). For the mangrove species *Rhizophora mangle*, we limited the modelled distribution of this species to a distance of 10 arc minutes land-inwards from the coastal line.

2.7 | Threat assessment

We assessed the risk of extirpation for each individual species location record in each ERS, considering eight threat situations that consisted of areas with *large* or *little* tree cover, with *low* or *high* human pressure, and with *low* or *high* climate change impact. As a result, we were able to determine for all ERSs of all 80 species in which of the eight threat situations their species location records are located (Figure 2). In addition, as a fourth level of extirpation risk, we determined for each record whether it was located in or outside a protected area according to the 2010 WDPA database (UNEP-WCMC, 2010).

The eight threat situations:

Little tree cover

1. *High* direct human pressure and *high* climate change impact: *high* threat areas where populations of tree species are increasingly at risk to extirpate under the combined threat of fragmentation because of *little* tree cover, climate change and direct human pressure.
2. *High* direct human pressure and *low* climate change impact;
3. *Low* direct human pressure and *high* climate change impact: *low* threat areas in fragmented landscapes with *little* tree cover where populations are predicted to become progressively vulnerable to climate change;

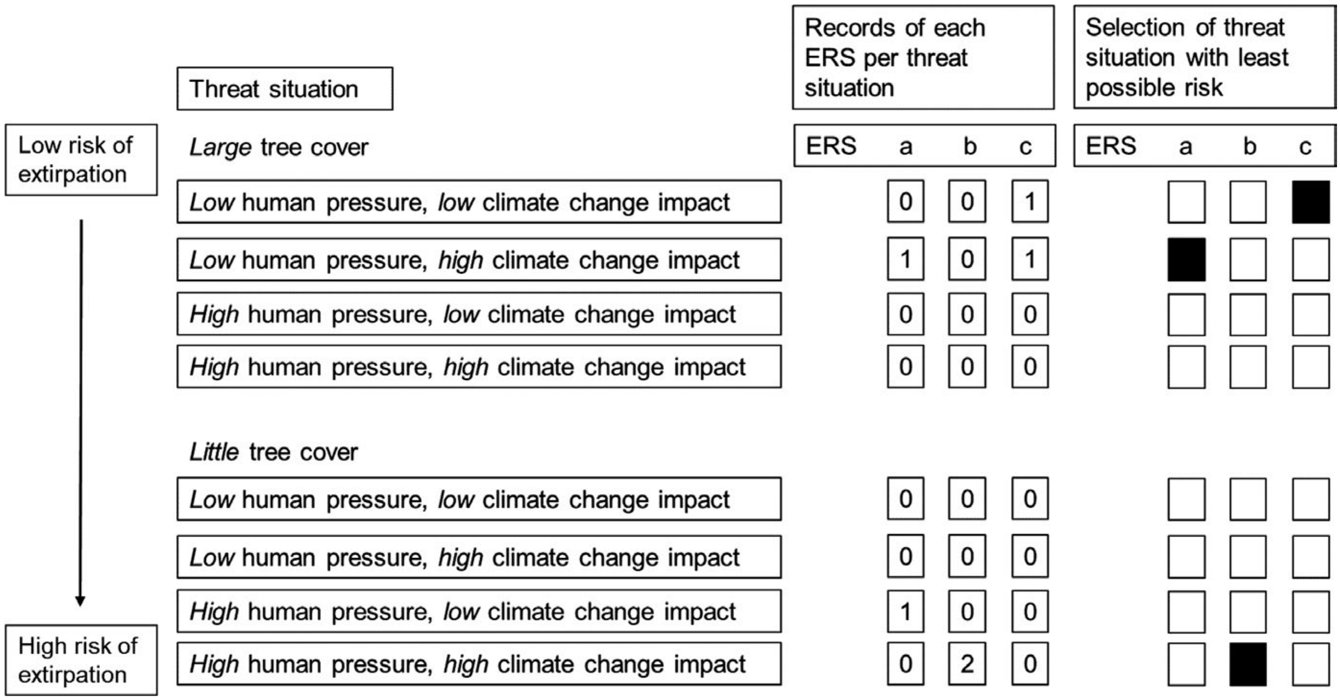

FIGURE 2 Schematic representation of the selection of the threat situations with least possible extirpation risk for each Ecogeographic Range Segment (ERS) to target conservation actions. For ERS “a”, “b”, and “c”, the number of species location records for every one of the eight threat situations is determined. Species location records in the threat situation with the lowest risk of extirpation are selected to target conservation actions. The risk of extirpation is determined on the basis of three hierarchic levels of threats: level 1: *large* or *little* tree cover; level 2: *low* or *high* direct Human Pressure (HP); level 3: *low* or *high* climate change impact. Some ERSs such as ERS “b” can only be conserved in the least-preferred threat situation of *little* TC, *high* HP, and *high* climate change impact

4. *Low* direct human pressure and *low* climate change impact: *low* threat areas in fragmented landscapes with *little* tree cover.

Large tree cover

1. *High* direct human pressure and *high* climate change impact; *high* threat areas where *large* tree cover could help mitigate the negative effects of climate change and direct human pressure to maintain species′ populations;
2. *High* direct human pressure and *low* climate change impact;
3. *Low* direct human pressure and *high* climate change impact; *low* threat areas where *large* tree cover could create a suitable habitat for species populations to adapt to climate change;
4. *Low* direct human pressure and *low* climate change impact; *low* threat areas with *large* tree cover are the most desirable areas for in situ and circa situm conservation of genetic resources of tree species.

2.8 | Complementary reserve selection

We followed the complementary reserve selection algorithm of Rebelo and Siegfried (1992) to prioritize areas for conservation in two steps: (1) prioritize for each ERS the threat situation with least possible risk to extirpate; and (2) prioritize per threat situation, the areas with highest number of ERSs to target conservation actions (Figure 2).

Step (1) Prioritize for each ERS the threat situation with least possible risk to extirpate. In a first iteration, we started with identifying all ERSs with at least one record in the preferred situation for conservation: areas with *large* tree cover, *low* direct human pressure, and *low* climate change impact. In a second iteration, ERSs in areas of the second-most preferred situation were identified: areas with *large* tree cover, *low* direct human pressure, and *high* climate change impact. Records from the ERSs, which were identified in the previous iteration, were excluded from this and further subsequent analysis. This procedure was repeated until the eighth threat situation with highest extirpation risk in areas with *little* tree cover, *high* direct human pressure, and *high* climate change impact. In this final iteration, we identified the remaining ERSs, which exclusively occur in this least-preferred threat situation.

Step (2) Prioritize per threat situation, the areas with highest number of ERSs. Per threat situation, we determined the minimum number of grid cells required to conserve all ERSs, which were allocated to that specific threat situation in step 1. Grid cells with a resolution of 2 arc degrees were used as the geographic unit for reserve selection at continental scale. Per threat situation, we ran the reserve selection algorithm 25 times and selected the run with the least number of grid cells required to capture all the ERSs in that specific situation. Per threat situation, the grid cell with the highest number of different ERSs was determined as the first priority area for conservation. Second priority was given to the grid cell, which covers the highest number of species location records from additional ERSs, which did not occur in the grid cell of first priority. This iteration continues until species location records from all ERSs are covered by grid cells.

2.9 | Software

All analyses were performed in R version 2.15.1 with the packages ‘raster’ (Hijmans, van Etten, & Cheng, 2015), ‘dismo’ (Hijmans, Phillips, Leathwick, & Elith, 2016), ‘sp’ (Pebesma, Bivand, & Rowlingson, 2013) and ‘maptools’ (Bivand & Lewin-Koh, 2013). Graphs and maps were created in R with the use of ‘ggplot’ (Wickham, 2009). Maps were developed with the geographical latitude/longitude projection and WGS84 datum. The R code is available on request.

3 | RESULTS

We identified a total of 2,631 ERSs summed up across all 80 species. The number of ERSs per species varies between 8 ERSs for *Cariniana legalis* to 101 ERSs for *Cedrela odorata* and *Hymenaea courbaril* respectively (Appendix S1).

A total of 705 ERSs (27% of all ERSs) only occur in areas with *little* tree cover (Table 1). When direct human pressure in areas with *large* tree cover is added, then 1,561 ERSs (59% of all ERSs) are threatened. When climate change is also considered, then all species location records in 1,857–1,930 ERSs (71-73% of all ERSs) are threatened. When the increased extirpation risk of populations outside protected areas is added, then all species location records in 2,223–2,252 ERSs (84–86% of all ERSs) are threatened.

TABLE 1 Number of ERSs per threat situation considering all 80 species: (1) in areas with *large* or *little* tree cover; (2) in areas with *low* or *high* direct human pressure; (3) in areas with *low* or *high* climate change impact; and (4) in and outside protected areas

	***Large* Tree Cover**								***Little* Tree Cover**							
Nr per group	1,926								1,396							
Complementary[a]	1,926								705							
	***Low* HP**				***High* HP**				***Low* HP**				***High* HP**			
Nr per group	1,070				1,359				249				1,278			
Complementary	1,070				856				117				588			
	***Low* CC**		***High* CC**		***Low* CC**		***High* CC**		***Low* CC**		***High* CC**		***Low* CC**		***High* CC**	
Nr per group																
RCP 4.5 MG[b]	774		457		995		550		172		85		860		663	
RCP 4.5 HG	710		530		935		626		159		101		796		734	
RCP 8.5 MG	744		485		957		592		161		95		802		714	
RCP 8.5 HG	701		519		914		644		154		105		781		736	
Complementary																
RCP 4.5 MG	774		296		594		262		78		39		323		265	
RCP 4.5 HG	710		360		552		304		69		48		281		307	
RCP 8.5 MG	744		326		567		289		71		46		288		300	
RCP 8.5 HG	701		369		551		305		70		47		276		312	
	***Low* HP**				***High* HP**				***Low* HP**				***High* HP**			
	***Low* CC**		***High* CC**		***Low* CC**		***High* CC**		***Low* CC**		***High* CC**		***Low* CC**		***High* CC**	
Protected areas	**In**	**Out**	**In**	**Out**	**In**	**Out**	**In**	**Out**	**In**	**Out**	**In**	**Out**	**In**	**Out**	**In**	**Out**
Nr per group																
RCP 4.5 MG	408	559	215	328	295	876	107	491	34	145	14	71	149	820	57	635
RCP 4.5 HG	379	502	245	390	276	826	127	558	35	131	12	89	140	753	64	703
RCP 8.5 MG	397	538	232	346	285	846	121	530	31	137	16	80	135	767	67	683
RCP 8.5 HG	382	494	244	393	273	807	133	572	34	127	15	91	140	741	63	707
Complementary																
RCP 4.5 MG	408	366	128	168	171	423	41	221	16	62	3	36	44	279	13	252
RCP 4.5 HG	379	331	159	201	160	392	52	252	17	52	2	46	40	241	15	292
RCP 8.5 MG	397	347	150	176	165	402	52	237	14	57	5	41	39	249	16	284
RCP 8.5 HG	382	319	165	204	159	392	55	250	16	54	3	44	41	235	15	297

HP, direct Human Pressure; CC, climate change impact.

[a] Complementarity: ERSs are assigned to situations with the lowest risk of extirpation using the complementary reserve selection algorithm.

[b] RCP 4.5 MG, RCP 4.5 HG, RCP 8.5 MG, RCP 8.5 HG: future climate models.

A total of 1,057 of ERSs (40%) just had one species location record. Forty-three species have on average less than one species location record per ERS in areas with *large* tree cover and *low* direct human pressure (Figure 3). Three species are severely threatened because they have zero species location records in areas with *large* tree cover and *low* direct human pressure: *Cariniana legalis*, *Prosopis flexuosa*, and *Prosopis pallida* (Figure 3).

All ERSs of 5 of the 80 species (*Balfourondendron riedelianum*, *Cariniana legalis*, *Dalbergia nigra*, *Handroanthus pulcherrimus*, and *Pachira quintana*) are threatened to extirpate in South America when climate change is considered (Figure 4). *Cariniana legalis* and *Dalbergia nigra* are most vulnerable to extirpate because more than 50% of their ERSs only occur in areas with *little* tree cover.

Of the seven threatened species identified above, *Prosopis pallida* is not covered by any protected area (Appendix S1). *Cariniana legalis*, *Handroanthus pulcherrimus*, *Pachira quintana*, and *Prosopis flexuosa* are poorly covered by protected areas with, respectively, 1 of its 8 ERSs, 1 of its 11 ERSs, 2 of its 18 ERSs, and 1 of its 16 ERSs covered by protected areas. *Balfourondendron riedelianum* and *Dalbergia nigra* are somewhat better covered by protected areas with 6 of its 27 ERSs and 5 of its 26 ERSs respectively.

3.1 | Complementary reserve selection

Priority areas for the conservation of populations in ERSs in the least-preferred threat situation, in areas with *little* tree cover, *high* direct human pressure and *high* climate change impact, include southern Brazil (Paraná, São Paulo) and eastern Bolivia (Santa Cruz) (Figure 5a). Priority areas with *little* tree cover, *high* direct human pressure, but *low* climate change impact include the Atlantic forests in Brazil (Minas Gerais, São Paulo, Rio de Janeiro, Goiás) (Figure 5b). Priority areas with *little* tree cover, *low* direct human pressure, but *high* climate change impact include northern Bolivia (Beni) (Figure 5c). Priority areas with *little* tree cover, *low* direct human pressure, and *low* climate change impact include the Atlantic forests in northern Brazil (Rio Grande do Norte, Paraiba) (Figure 5d).

Priority areas with *large* tree cover, *high* direct human pressure, and *high* climate change impact include the northern Andes in Ecuador and central-western Colombia (Antioquia, Chocó, central coffee zone), the border zones of Paraguay with Brazil and Argentina, and the border zone between Bolivia and Brazil (Figure 5e). Priority areas with *large* tree cover, *high* direct human pressure and *low* climate change impact include the northern Andes in Ecuador and central-western Colombia (Antioquia, Chocó, central coffee zone), the Atlantic forests

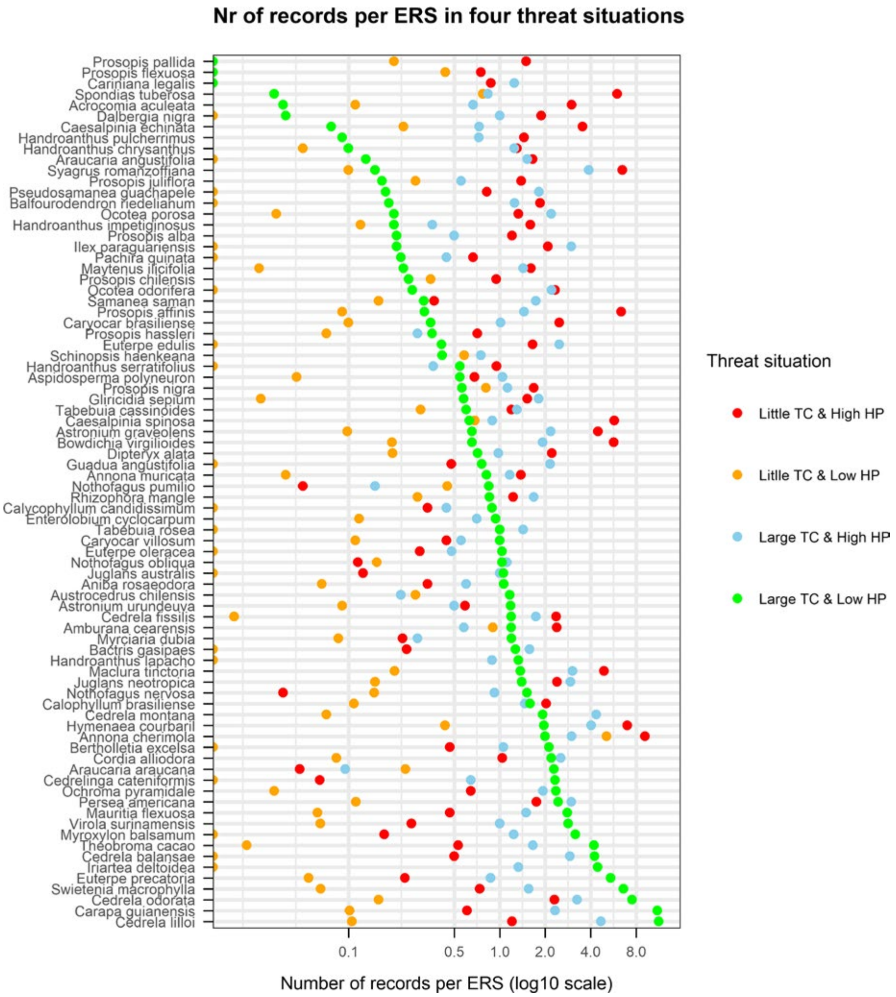

FIGURE 3 Mean number of species location records per Ecogeographic Range Segment (ERS) in four threat situations for each of the 80 species considering *large* or *little* Tree Cover (TC) and *low* or *high* Human Pressure (HP). Species are ordered in order of their threat status from top to bottom. *Prosopis flexuosa*, *Prosopis pallida*, and *Cariniana legalis* are listed on top with zero species location records per ERS in areas with *large* TC and *low* HP. All the ERSs of these three species are threatened to extirpate [Colour figure can be viewed at wileyonlinelibrary.com]

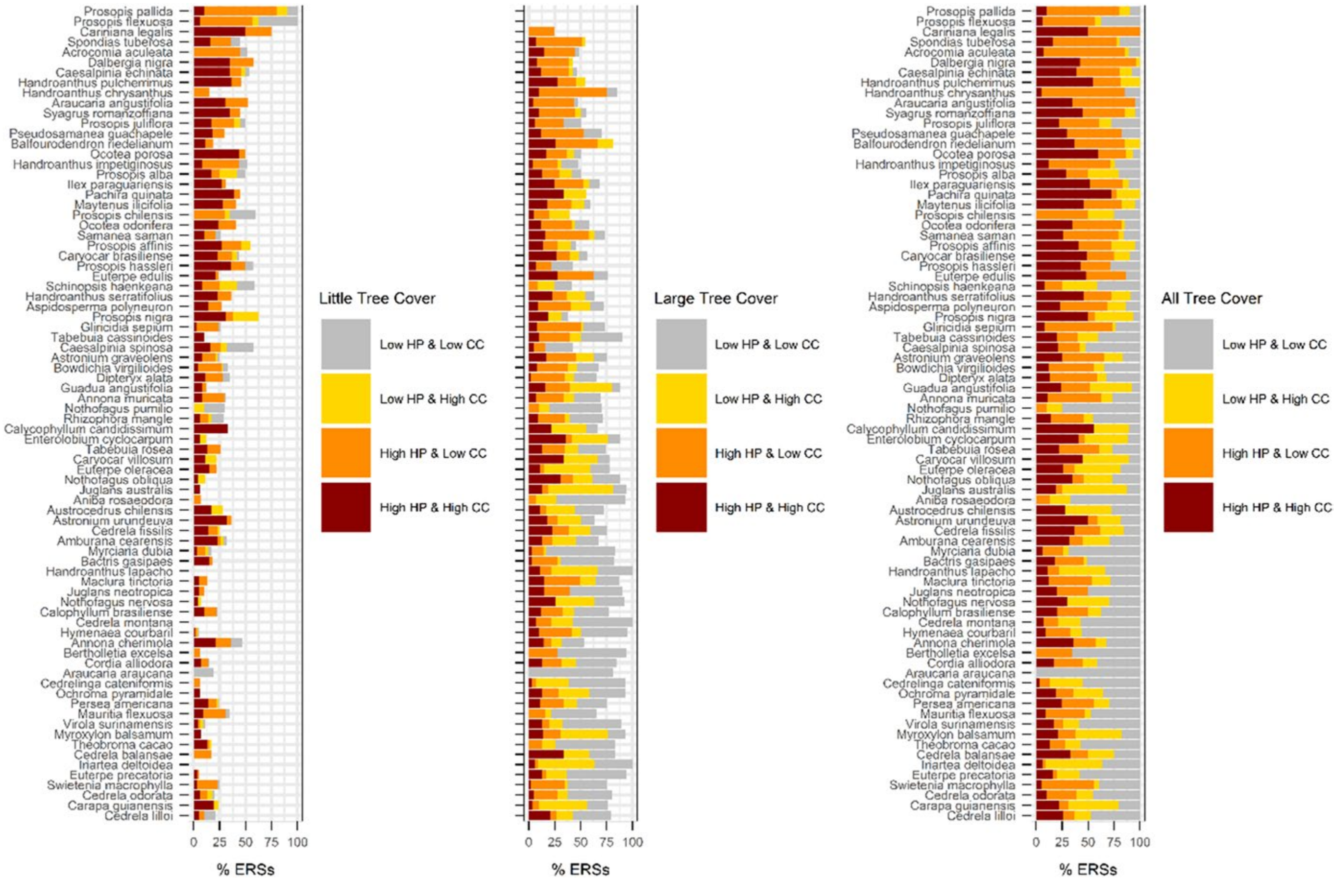

FIGURE 4 Threat assessment of the Ecogeographic Range Segments (ERSs) for each of the 80 species under *little* Tree Cover (TC), *large* TC, and all TC. For each ERS, the threat situation with the lowest possible risk of extirpation was determined considering Human Pressure (HP) and Climate Change (CC) impact by the 2050s under climate model HG and RCP 8.5. The species are sorted by their threat status from *high* to *low* after Figure 3 [Colour figure can be viewed at wileyonlinelibrary.com]

in Brazil (São Paulo, Paraná, Rio de Janeiro, Bahia), and central Bolivia (Figure 5f). Priority areas with *large* tree cover, *low* direct human pressure, and *high* climate change impact include the Amazonian regions of Ecuador and Peru, north-western Bolivia (Madidi park), western Colombia (Antioquia, Chocó), the border zone between Peru and Ecuador (Cajamarca, Amazonas and Zamorano), eastern Bolivia (Beni), southern Bolivia (Tarija), and Surinam (Figure 5g).

The border zone between Peru and Ecuador is the highest priority area to conserve and manage populations from ERSs in the preferred threat situation for conservation with *large* tree cover, *low* direct human pressure, and *low* climate change impact. Other priority areas in this preferred threat situation include western Colombia (Antioquia, Chocó), Peruvian Amazon (Madre de Dios), and southern Chile (Araucanía, Los Lagos) (Figure 5h).

4 | DISCUSSION

Our results suggest that more than 59% of the Ecogeographic Range Segments (ERSs) of the prioritized 80 tree species are threatened by extirpation in South America. Seven species warrant special attention because they are highly threatened across their whole distribution in South America: *Balfourondendron riedelianum*, *Cariniana legalis*, *Dalbergia nigra*, *Handroanthus pulcherrimus*, *Pachira quintana*, *Prosopis flexuosa*, and *Prosopis pallida*. Many other tree species also require targeted conservation because a high number of their ERSs is at risk to extirpate. Ideally, at least two populations per ERS need to be targeted for conservation to have a duplicate. For 40% of the ERSs, however, it is not clear if this will be possible because we only found one species location record of them. This makes these ERSs extra vulnerable to extirpate.

ERSs in areas with *little* tree cover, *high* direct human pressure, and *high* climate change impact are mostly, but not exclusively, located in the Atlantic forests of Brazil and eastern Bolivia. Populations in these ERSs require urgent conservation actions to safeguard their genetic resources. The combination of current fragmentation, continuous human pressure, and climate stress will reduce substantially the safe operating space of tree species populations in this *high* threat situation (Scheffer et al., 2015). We expect that populations exposed to these threat conditions will be affected by a reduction in the number of reproductive trees and reduction in regeneration success. Without conservation actions to create a safe operating space for populations under these threat conditions, it is likely that these populations will extirpate.

Conservation actions in South America should take into account interests of local communities to be just and effective (Southgate &

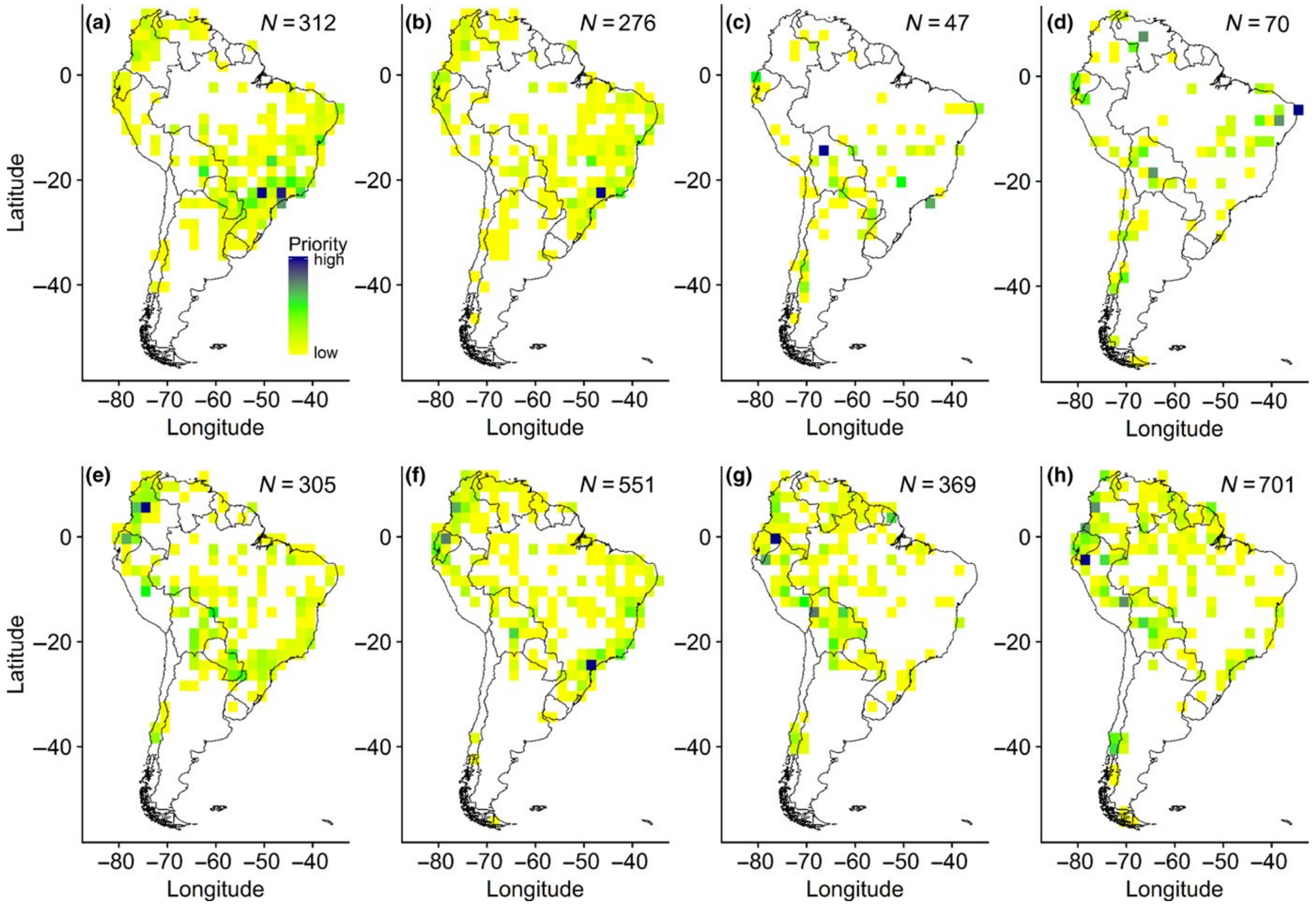

FIGURE 5 Priority setting to safeguard as many Ecogeographic Range Segments (ERSs) with the lowest possible risk of extirpation using the complementary reserve selection method and considering climate model HG and RCP 8.5 to assess climate change impact by the 2050s. A grid cell size of 2 arc degrees was used as the geographic unit of reserve selection at continental scale. Panel a: reserve selection of ERSs exclusively occurring in areas with *little* Tree Cover (TC), *high* Human Pressure (HP), and *high* climate change impact. Panel b: reserve selection of ERSs in areas with *little* TC, *high* HP, and *low* climate change impact. Panel c: reserve selection of ERSs in areas with *little* TC, *low* HP, and *high* climate change impact. Panel d: reserve selection of ERSs in areas with *little* TC, *low* HP, and *low* climate change impact. Panel e: reserve selection of ERSs exclusively occurring in areas with *large* TC, *high* HP, and *high* climate change impact. Panel f: reserve selection of ERSs in areas with *large* TC, *high* HP, and *low* climate change impact. Panel g: reserve selection of ERSs in areas with *large* TC, *low* HP, and *high* climate change impact. Panel h: reserve selection of ERSs in areas with *large* TC, *low* HP, and *low* climate change impact [Colour figure can be viewed at wileyonlinelibrary.com]

Clark, 1993). Second, these actions should explore complementarities between socioeconomic development and conservation. Third, these actions need to anticipate potential conflicts with mining and livestock and other economic interests in frontier areas to ensure conservation success and to consider the safety for persons who are involved in the conservation of tree genetic resources. For in situ and circa situm conservation of ERSs, it is therefore recommended to interact with the several stakeholders who use the land in these areas for their livelihoods and economic activities. We propose *MATE*, four steps to implement conservation actions to safeguard tree genetic resources:

1. *Motivate*: Connect in situ and circa situm conservation of tree genetic resources to social, economic, ecological, and cultural values of community members, producers, concerned urban citizens, local and regional policy makers, conservationists, among other actors (Wallace, 2012; van Zonneveld, Loo, Maselli, Madrid, & Echeverria, 2018). These values could be related to forest products, cultural heritage, ecosystem services, certification schemes, nutrition, among others.
2. *Articulate*: Explain to these persons in plain but precise language why genetic resources matter for species conservation and how the conservation of genetic resources relate to social, economic, ecological, and cultural values (van Zonneveld et al., 2018).
3. *Technical solutions*: Estimate the minimum number of reproductive trees required to maintain genetic resources, and the minimum distance between them (Boshier et al., 2004; Graudal et al., 2014). When needed, technical solutions should be developed to facilitate regeneration and seed dispersal of wild growing tree populations (Boshier et al., 2004), or to distribute diverse seed material for planting and restoration (Thomas et al., 2014).

4. *Evaluate*: Measure indicators of gene flow, progeny vigour, and regeneration success over time to monitor implementation and effectiveness of conservation actions (Graudal et al., 2014).

In some cases, the four points of *MATE* may not be sufficiently effective for in situ and circa situm conservation actions in *high* threat situations. In those cases, ex situ conservation approaches could serve as an alternative to safeguard genetic material.

Restoration and rehabilitation activities could be a good option in areas with *little* tree cover because these actions combine conservation with the provision of ecosystem services, which can be connected to human values such as water provision and soil retention. Most ERSs in areas with *little* tree cover, however, are also threatened by *high* human pressure, *high* climate change impact, or both, which makes it a challenge to carry out conservation and restoration actions in these areas. Only some ERSs are present in areas with *little* tree cover but *low* threats, such as in northern Brazil and northern Bolivia.

In multi-functional landscapes with *large* tree cover but *high* human pressure, in situ and circa situm conservation of tree genetic resources requires collaboration with local and regional policy makers, farmer organizations, among other actors. Areas with this threat situation include the northern Andes in Ecuador and central-western Colombia, the Atlantic forests in Brazil, and Central Bolivia.

Populations in ERSs with *low* direct human pressure and *high* climate change impacts are located in the Amazonian regions of Ecuador and Peru, in north-western Bolivia (Madidi park), the border zone between Peru and Ecuador, eastern Bolivia, southern Bolivia, and Surinam. These populations do not require urgent conservation actions but climate change is likely to affect them progressively. These populations can be useful to study the response of the 80 tree species to climate change.

Our reserve selection analysis indicates that areas with *large* tree cover, *low* direct human pressure, and *low* climate change impact in the border zone between Peru and Ecuador should be prioritized for in situ and circa situm conservation followed by central-western Colombia, Amazonian Peru, and southern Chile. This *low* threat situation allows to keep a safe operating space for populations of tree species, and is therefore the desirable threat situation for in situ and circa situm conservation.

5 | LIMITATIONS AND FUTURE RESEARCH

Our study is limited to 80 tree species and to South America, but similar analyses can be carried out for other tree species and for other continents. The threat maps used in this study were made with freely available data. It is straightforward to develop your own threat maps with this freely available data (Gaisberger et al., 2017; Samuel, Drucker, Andersen, Simianer, & Zonneveld, 2013). We used historical species location records, freely available through online portals such as the Global Biodiversity Information Facility (GBIF), which facilitates repeatability of spatial threat assessments for other species. Highly threatened populations at these recorded locations, however, could have been extirpated after they have been reported. This increases the urgency to monitor and conserve these populations.

The maps of direct human pressure, which were used in our analysis, indicate sensitivity to threat exposure at ecosystem level but not at species level (Jarvis et al., 2010). Although these maps can be used for continental threat assessments, the threat values should be interpreted carefully for specific species. For example, some species tolerate threats such as grazing pressure and fire better than others because of specific traits. We recommend further research to understand which traits can be linked to species-specific threat sensitivity. This would complete our current threat assessment. Expert feedback is an alternative approach to indicate species-specific threat sensitivity, and social science methods can be used to formalize the feedback from experts (Gaisberger et al., 2017; Metcalf & Wallace, 2013).

6 | CONCLUSIONS

This threat assessment at intraspecific level can help managers of governmental and conservation organizations in South America to reach Aichi Target 13 to conserve the genetic resources of socioeconomically important species from this region by 2020. Our findings confirm the urgency to set up a regional action plan to conserve the genetic resources of the 80 prioritized tree species and other useful tree species in South America.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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