*Conservation Biology*

# Effects of trade and poaching pressure on extinction risk for cacti in the Atacama Desert

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**Article impact statement**: *Copiapoa* cacti face an alarming risk of extinction from legal and illegal trade and other drivers.

## Abstract

In this era of a global biodiversity crisis, vascular plants are facing unprecedented extinction rates. We conducted an assessment of the extinction risk of 32 species and 7 subspecies of *Copiapoa*, a genus endemic to Chile's fog-dependent coastal Atacama Desert. We applied the International Union for Conservation of Nature Red List Categories and Criteria enhanced by expert insights and knowledge. Our primary aim was to analyze the impact of trade and poaching on their extinction risk. We employed machine learning models, including multinomial logistic regression (MLR), decision tree (DT), and random forest (RF), to analyze the relationships between conservation status and various factors. These factors encompassed trade and poaching activities, landscape condition, human footprint, monthly cloud frequency, and biological traits such as evolutionary distinctiveness and maximum diameter. Seven taxa had an area of occupancy (AOO) of <10 km$^2$, 10 additional taxa had an AOO of <20 km$^2$, and 16 taxa had an AOO of ≤100 km$^2$. This reassessment exposed a critical level of extinction risk for the genus; 92% of the taxa were classified as threatened, 41% as critically endangered, 41% as endangered, and 10% as vulnerable. MLR, DT, and RF exhibited accuracies of 0.784, 0.730, and 0.598, respectively, and identified trade and poaching pressure and landscape condition as the primary drivers of extinction risk. Our assessment of *Copiapoa* showed trade, poaching, habitat degradation, and their synergic impacts as the main drivers of the genus' extinction risk. Our results highlight the urgent need for nations to develop and enforce strategies to monitor and control trade and poaching pressure because these factors are crucial for the long-term persistence of desert plants.

**KEYWORDS**
Cactaceae, CITES, extinction risk, IUCN red list, poaching

## INTRODUCTION

Global biodiversity is currently experiencing an unprecedented extinction rate, driven primarily by anthropogenic factors, such as land-use change, direct exploitation of organisms, climate change, pollution, and the introduction of non-native species (de Vos et al., 2015; IPBES, 2019; Maxwell et al., 2016). Vascular plants, in particular, face extinction rates exceeding historical trends (Haddaway & Leclère, 2020; Le Roux et al., 2019; Nic Lughadha et al., 2020). Despite recognizing the alarming rate of extinction and the limited evaluation of only around 16% of all described flowering plant species based on International Union for Conservation of Nature (IUCN) Red List Categories and Criteria (IUCN, 2023), resources allocated to global plant species assessment and conservation remain scarce (Margulies et al., 2019; Stuart et al., 2010). Furthermore, detecting shifts in extinction risk trends necessitates periodic species reassessments, posing an additional challenge. To develop accurate predictions and effective conservation strategies, a comprehensive examination of anthropogenic drivers and their interactions with environmental and biological factors is critical.

Extinction risk has a nonrandom pattern among lineages, indicating that shared biological traits among closely related species influence their vulnerability to human impacts (Davies et al., 2008; Russell et al., 1998). Anthropogenic threats, including habitat loss, overexploitation, and invasive species, have significant spatial variation and vary across lineages (Pollock et al., 2020). Accurately predicting extinction risk requires an integrated understanding of area-specific threats, species traits, and phylogenetic relationships in the studied group. Particularly vulnerable are the world's arid and hyperarid deserts (Martínez-Valderrama et al., 2020), including certain regions in the Atacama Desert characterized by remarkable levels of endemism, especially among cacti (Amaral et al., 2022; Duarte et al., 2014; Guerrero et al., 2011, 2013). The biodiversity unique to these coastal arid zones is increasingly imperiled by expanding industrial activities, such as mining (Stotz et al., 2021), that threaten the very fabric of the ecosystems that harbor the highest concentrations of endemism.

Although global studies might overlook regional variations in threats and species traits, taxonomically focused analyses offer more precise insights into extinction risk inferences and the factors inducing these risks (Fisher & Owens, 2004; Purvis, 2008). The underrepresentation of certain biological groups and ecosystems in conservation efforts underscores the urgency to prioritize conservation research, particularly in sensitive and poorly studied ecosystems (Wilson et al., 2016). Such ecosystems may be subject to unique threats that are often missed in conventional conservation evaluations. Notably, the threat posed by illegal plant trafficking is often overlooked, yet it poses a significant risk to species sought after by collectors (Margulies et al., 2019). This includes highly endangered species of cacti and other succulents from arid ecosystems, such as those found in the fog oasis of Chile's coastal Atacama Desert (Gonzales et al., 2023; Moat et al., 2021).

The fog oases in the coastal Atacama Desert are renowned for their rich and endemic diversity of organisms, including the cactus genus *Copiapoa* (Charles, 1998). Chile stands out as a remarkable location, home to over 140 species of endemic cacti that are predominantly concentrated in the northern and central regions (Guerrero et al., 2011). Unfortunately, extensive land-use changes have resulted in habitat loss and fragmentation, imposing significant threats to these species (Larridon et al., 2014). Extirpations of *Copiapoa solaris* and cacti from other genera have been documented and attributed to the intensification of aridity (Larridon et al., 2014; Macaya-Berti & Bustamante-Monroy, 2009; Pinto & Kirberg, 2005). Among the diverse cacti genera in Chile, *Copiapoa* is particularly significant. Thirty-two endemic species and 7 infraspecific taxa are confined to a relatively small and narrow area from 22° S to 31° S in the Chilean Winter Rainfall–Valdivian Forests hotspot (Larridon et al., 2015). Their restricted distribution and specialized fog-dependent niche make them highly vulnerable to direct exploitation by seed and adult plant extractions (Figure 1), development, and environmental changes (Joppa et al., 2011).

The taxonomy of *Copiapoa*, like other Chilean cactus genera, has a lengthy history of taxonomic changes and uncertainty (Duarte et al., 2014). Nevertheless, recent DNA-based phylogenetic analyses (Larridon et al., 2015, 2018) have shed light on the evolutionary relationships within the genus, leading to a more stable classification (Walter & Guerrero, 2022). Recent taxonomic revisions (Korotkova et al., 2021; Larridon et al., 2015, 2018; Walter & Guerrero, 2022), coupled with persistent environmental threats, necessitate the reassessment of the conservation categories of *Copiapoa* taxa. New classifications have led to a redefinition of previously singular species into a more complex array of distinct species or subspecies. Accurate and up-to-date taxonomic classification is essential to effectively assess the extinction risk of these taxa and accurately evaluate the contribution of environmental and biological factors in determining their current extinction risk.

Species endemic to the Atacama Desert face threats from industrial activities, such as mining and energy production and transmission, that destroy critical habitats (Urbina et al., 2021). Metal mining and related infrastructure can threaten *Copiapoa* by significantly affecting habitat quality and directly affecting individual plants (Duran et al., 2013; Sträter et al., 2010; Urbina et al., 2021). Additionally, their dependence on specific climatic conditions (Schulz, 2006; Schulz et al., 2012), including oceanic fog and irregular rainfall patterns in the Coastal Atacama Desert, makes them highly vulnerable to climate dynamics (Hultine et al., 2023; Larridon et al., 2014; Pillet et al., 2022; Schulz et al., 2012).

These conservation challenges are exacerbated by a significant rise in illegal collection, often facilitated by social media networks, which has led to increased poaching of succulent plants (Lavorgna, 2014; Lavorgna et al., 2020; Margulies et al., 2019). Recent seizures of thousands of specimens highlight that the genus *Copiapoa* has become a target for plant traffickers (Lavorgna et al., 2020; Nuwer, 2021). Even legal wildlife trade can be linked to poaching (Mozer & Prost, 2023); there is evidence of a positive correlation between legal imports and seizures. This phenomenon suggests that legal trade can sometimes be used to cover up or facilitate illegal activities. However,
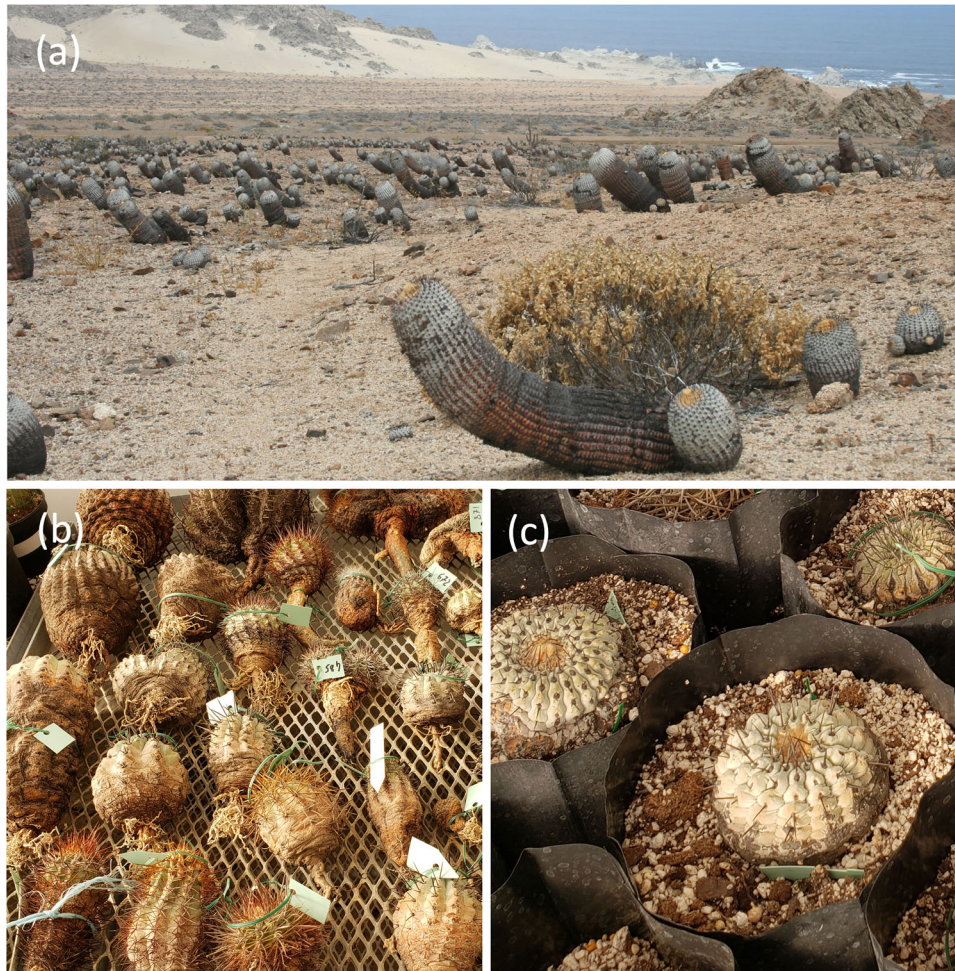
**FIGURE 1** (a) *Copiapoa cinerea* subsp. *columna-alba* in its habitat, (b) seizure of several *Copiapoa* taxa in Operation Atacama in 2021, and (c) seized plants replanted after being repatriated to Chile.

the occurrence and magnitude of this phenomenon necessitate further investigation. Legal trade in plants, often linked to the availability of germplasm for plant cultivation, may present a hidden but substantial risk due to frequent massive seed extractions from natural habitats (Goettsch et al., 2015; Novoa et al., 2017). Although legally permissible, this practice is largely unregulated and has led to excessive seed extraction, which exacerbates the pressure on natural populations (Lavorgna et al., 2020; Novoa et al., 2017). The combined effects of habitat degradation and species exploitation may have created a critical situation for the *Copiapoa* genus. This situation suggests a thorough reassessment of *Copiapoa* extinction risk is needed urgently. Moreover, there is a pressing need to delve deeper into the specific factors contributing to its potential extinction risk so that conservation strategies are both effective and responsive to the evolving challenges faced by these species.

We aimed to update the extinction risk assessment for the 37 recognized taxa of the *Copiapoa* genus. The last Global Cactus Assessment (Goettsch et al., 2015) showed that within the *Copiapoa* genus, 10% of species were categorized as critically endangered, 18% as endangered, 3% as vulnerable, 8% as near threatened, and 18% as least concern. However, 44% of the taxa, following the updated taxonomic classification, remained categorized as not evaluated. To address this gap and evaluate all taxa of *Copiapoa*, we used an automated approach to assign preliminary IUCN Red List categories. The results from the preliminary assessment were reviewed and improved by cactus and biodiversity experts, including professionals from the Chilean Ministry of the Environment and the IUCN. We then used our assessment results to evaluate the role of trade and poaching pressures relative to other threats. Our central hypothesis posits that the current extinction risk of *Copiapoa* taxa is significantly shaped by trade and poaching pressures. We expected the machine learning models to reveal a strong relationship between trade and poaching activities and extinction risk. With this work, we sought to offer crucial guidance for targeted conservation efforts and more effective strategies to mitigate the identified threats.

## METHODS

### Extinction risk reassessment

The reevaluation process for the taxa of the genus *Copiapoa* was conducted in sequential stages by us as members of the IUCN Species Survival Commission Cactus and Succulent Plants Specialist Group (https://iucn-cssg.org). To ensure the taxonomic stability of the reassessment, we aligned our reevaluation with the latest DNA-based studies and updated taxonomic classification. Data from the IUCN Species Information Service (SIS), IUCN's central database, were compiled and combined with updated georeferenced population occurrence data to calculate essential spatial metrics. This extensive data set included details on species distributions, population trends, habitat preferences, ecology, conservation actions, use, and trade following Goettsch et al. (2015) and Guidelines for Using the IUCN Red List Categories and Criteria 15.1.

In adherence to IUCN standard procedures, our assessments were comprehensive and underwent rigorous review during workshops, which included participation from Chilean government experts, researchers, and IUCN facilitators. We meticulously reviewed data on each species. The species evaluations were conducted in accordance with the IUCN Red List Categories and Criteria 3.1 under the guidance of trained and highly experienced IUCN facilitators. This approach ensured that the methodology was applied correctly and consistently, thereby enhancing the reliability and validity of our extension risk assessments.

Our reassessment process began with reviewing and updating the taxonomy of *Copiapoa* according to the most recent taxonomic sources (Korotkova et al., 2021; Larridon et al., 2015, 2018; Walter & Guerrero, 2022). We then compiled georeferenced occurrence point data for all 32 species and 7 subspecies of the *Copiapoa* genus from Chilean (Universidad de Concepción [CONC], Universidad de La Serena [ULS], Museo Nacional de Historia Natural [SGO]) and international herbaria with online public access digital repositories (New York Botanical Garden [NY], United States; Utrecht Herbarium [U], Netherlands). An updated version of our previously published taxonomic and georeferenced data set was also included (Duarte et al., 2014; Larridon et al., 2015). Subsequently, the georeferenced data set was curated, and the nomenclature was standardized. Imprecise and redundant data were removed, and errors were resolved (e.g., misclassification of taxa, occurrence data outside species range). This assessment was done using specialized literature (Charles, 1998; Kattermann, 2018, 2019; Ritter, 1980; Schulz, 2006; Schulz & Kapitany, 1996) and our personal field observations.

Using criterion B of the IUCN Red List Categories and Criteria 3.1 (IUCN, 2022), we conducted preliminary assessments by analyzing species' known distribution ranges. We used the R package ConR 1.2.2 (Dauby et al., 2017), an automated tool, and the georeferenced occurrences previously processed to calculate the extent of occurrence (EOO), area of occupancy (AOO), and number of locations for each taxon (Table 1). The EOO is defined as the area contained within the shortest continuous imaginary boundary or convex polygon that can be drawn to encompass all known, inferred, or projected occurrence points of a species (IUCN, 2022). This polygon often includes areas where the species is not present, and it is not meant to depict the actual area inhabited by the species. This measure is usually used to calculate the extent of area a threat needs to spread to affect all populations in the species' known distribution range. The AOO is defined as the area in its EOO occupied by a species, excluding cases of vagrancy (IUCN, 2022). For the AOO calculations, ConR follows the IUCN Red List methodology in which a 2 × 2-km grid is used to generate minimum convex polygons to calculate the species' EOO (IUCN, 2022).

The assessments were updated using IUCN's SIS database. The species distribution range and AOO and EOO values were updated, as were the population trend, use, trade, habitat, ecology, and threats. A qualitative evaluation of the magnitude and extent of threats observed in the field was conducted as part of the reassessment. Based on this information, extinction risk categories were assigned to all species and subspecies of *Copiapoa*. These preliminary evaluations underwent further validation by national and international experts who participated in the Integrated Conservation Plan for the Genus *Copiapoa* workshop. This review enabled us to conduct a thorough, up-to-date, and accurate reassessment of the *Copiapoa* genus.

### Extinction risk drivers

We carefully selected extinction risk drivers so as to consider both extrinsic and intrinsic factors crucial for *Copiapoa* species' survival. Our analyses encompassed key anthropogenic drivers, including trade and poaching, human footprint, and landscape condition. We considered traits such as maximum stem diameter, evolutionary distinctiveness, and phylogenetic clustering.

We included trade and poaching pressure by building a composite variable from *Copiapoa* trade data available from CITES (2023). The decision to combine legal trade and poaching variables in our analyses was made to capture the overarching impact these factors have on wild populations. The CITES database predominantly reports legal trade involving the sale of cultivated plants. Nonetheless, this does not preclude the possibility that some plants could have been initially extracted from their natural habitats and later laundered or grown from seeds harvested in the wild. The information on poaching, derived from seizure records, likely represents only a small fraction of the total illegal trade, thus not fully capturing its magnitude.

By integrating both forms of trade in a single variable, we aimed to offer a more comprehensive measure that more accurately reflects the overall impact of the plant trade on the extinction risk of *Copiapoa* species. This methodology marks the first attempt in Chile to explore the collective impact of legal and illegal trade on cacti. We used the most recent version (2023.1 available at https://trade.cites.org) of the CITES Trade Database, which offers comprehensive insights into global wildlife trade and serves several key objectives. Its purposes

**TABLE 1** Summary of relative variable importance in multinomial logistic regression (MLR), random forest (RF), and decision tree (DT) machine learning models for assessing the relationship between extinction risk and the drivers trade and poaching pressure, landscape condition, maximum diameter, midrange latitude, evolutionary distinctiveness, human footprint, monthly cloud frequency, and phylogenetic clustering of *Copiapoa* species.

| Driver | MLR (endangered) | MLR (least concern) | MLR (vulnerable) | DT | RF |
|---|---|---|---|---|---|
| Trade and poaching pressure | 0.701 | −1.517 | 0.483 | 5.319 | 100.000 |
| Landscape condition | 18.447 | −102.811 | −69.063 | 5.066 | 98.280 |
| Maximum diameter | 0.055 | 4.287 | 0.145 | 1.900 | 67.380 |
| Midrange latitude | Not used | Not used | Not used | 4.415 | 76.77 |
| Evolutionary distinctiveness | −0.661 | −1.764 | 7.336 | 2.587 | 81.671 |
| Human footprint | 0.001 | 3.197 | −0.350 | 3.619 | 82.12 |
| Cloud frequency | 0.0002 | 0.019 | 0.001 | 1.520 | 59.630 |
| Phylogenetic clustering II | −2.935 | −18.089 | −29.321 | Not used | 0.000 |
| Phylogenetic clustering III | −16.624 | 46.022 | 73.212 | Not used | 18.150 |
| Phylogenetic clustering IV | −1.713 | −57.184 | 33.754 | Not used | 1.781 |
| Phylogenetic clustering V | 0.651 | −4.406 | 33.314 | Not used | 10.841 |

*Note*: In MLR, the coefficients represent the relative contribution of each variable with their positive or negative direction. The RF model uses overall importance to indicate the average importance of variables for model accuracy. The relative variable importance in DT is measured through information gain. Missing values indicate variables that were not used in the optimized models. Assigned statuses of endangered, vulnerable, and least concern follow criterion B of the International Union for Conservation of Nature Red List Categories and Criteria 3.1. The critically endangered category does not have coefficients in the MLR model output because it was used as the baseline category.

include enabling the monitoring of trade levels, trends, and potential impacts on wildlife populations at various scales. Additionally, it facilitates the identification of the most extensive trade, emerging trends, and changes in specimen sources over time (CITES Secretariat & UNEP-WCMC, 2022). We complemented the data set with poaching data from Operation Atacama (Nuwer, 2021) and other seizure data that were made available by the CITES Chilean Scientific Authority for plants, Instituto Forestal. To assess the impact of trade and poaching, we constructed a variable that is the sum of the total number of specimens traded and poached per species from 1997 to 2023. To provide a proportional distribution of commercially traded or poached specimens by species, we calculated the percentage of each *Copiapoa* taxa relative to the total number of specimens. This approach, wherein the total number of *Copiapoa* specimens was used, allowed us to determine the relative frequency of each species in trade or involved in poaching activities.

We employed raster data sets representing the annual dynamics of the global human footprint from 2000 to 2018. These data sets encompass 8 variables that reflect human pressure, including urbanization, population density, night lighting, agriculture, grasslands, roads, railways, and navigable waterways (di Marco et al., 2018). The human footprint values (from 0, minimal impact, to 100, maximum impact) indicate the degree of human influence on land cover (Sanderson et al., 2002) and are available at a spatial resolution of 1 km². Additionally, we integrated the landscape condition index, which amalgamates data related to transport, urban and industrial development, and altered land cover, presented in a raster at 30-m resolution (Hak & Comer, 2017). This index (from 0, complete human-induced transformation, to 1, unaffected by human activity) gauges the ecological condition of a site. Employing principles of landscape ecology and mapped data, landscape condition assessments offered a spatially explicit analysis of an area's eco-

logical state that benefited from increasingly available mapping resources for human land-use and land-cover changes.

We incorporated monthly cloud frequencies as a significant factor because of their direct connection to advection fog formation in the coastal Atacama Desert (del Río et al., 2021; Moat et al., 2021). Cloud cover is crucial in explaining the environmental conditions where *Copiapoa* populations occur along Chile's northern coast (Malik et al., 2015; Schulz et al., 2011). The Humboldt Current, transporting cold water from sub-Antarctic latitudes, creates a substantial temperature difference between the ocean and the atmosphere. This discrepancy leads to extensive stratocumulus cloud formation, which prevails for much of the year along the coast, extending from northern Peru to central Chile (del Río et al., 2021). These cloud conditions have a significant impact on the coastal ecosystems, introducing humidity as a dense fog band into hyper-arid zones and thereby increasing moisture availability for plants (Gonzales et al., 2023). Specifically, we included cloud frequencies based on 1-km² monthly cloud frequencies from 15 years of twice-daily Moderate Resolution Imaging Spectroradiometer (Wilson & Jetz, 2016). Satellite images revealed spatiotemporal cloud cover dynamics. To characterize the values of cloud frequency, human footprint, and landscape condition for each taxon, we obtained these values from raster files by extracting the data at each occurrence point and then averaged them by species.

We included biological traits of *Copiapoa* that are crucial for their survival: evolutionary distinctiveness, maximum diameter of plant branches, midrange latitude, and phylogenetic clustering. Diameter of plant branches is closely linked to cactus' water storage capacity, a key adaptation for arid conditions (Geller & Nobel, 1987; Guerrero et al., 2019; Mauseth, 2006). Midrange latitude, obtained from compiled and filtered occurrences, was used to account for the species' geographic position, acknowledging the latitudinal arid gradient in the habitat. This gradient

ranges from hyperarid conditions in the north to less intense aridity in the south and thus imposes distinct environmental filters and affects species survival differently based on location. These data were extracted from Ritter (1980), Schulz and Kapitany (1996), Charles (1998), Hoffmann and Walter (2004), and Schulz (2006). Evolutionary distinctiveness measures the extent of unique evolutionary history represented by each species. This analysis calculated the frequency distributions of the equal-splits scores (Redding & Mooers, 2006) and was conducted using the picante package in R (Daru et al., 2020). Branch length information was incorporated in the calculation of evolutionary distinctiveness in 2 ways: equal splits (Redding & Mooers, 2006) and fair proportions (Isaac et al., 2007). The variable phylogenetic cluster, which describes distinct infrageneric sections formed by the species, was also used (Larridon et al., 2015, 2018).

We rebuilt a molecular phylogenetic tree for *Copiapoa* mainly based on the study by Larridon et al. (2015) to obtain evolutionary distinctiveness and phylogenetic clustering. Additional taxa and markers were incorporated to conduct an updated and more comprehensive analysis, which produced a concatenated matrix for 2 plastid DNA loci, one noncoding intron (rpl32-trnL) and one gene (ycf1). The extraction and amplification protocols followed the methods of Larridon et al. (2015). *Blossfeldia liliputana*, *Calymmanthium substerile*, and *Eriosyce aurata* were the outgroups. New and published accession codes are in Appendix S1. Partitioned analyses were conducted using Bayesian inference in the program MrBayes 3.2.3 (Ronquist et al., 2012). The GTRGAMMA model of sequence evolution was the best-fitting model for each nucleotide partition. This is the first study to include all members of *Copiapoa* (32 species and 7 subspecies) in phylogenetic inferences. The summary of DNA sequence data for the *Copiapoa* genus and outgroups, the phylogenetic tree, and the phylogenetic distance is in Appendices S2, S3, and S4, respectively.

## Evaluation of drivers as predictors of extinction risk

To assess the impact of various factors on the conservation status of species, we used the following machine learning models: multinomial logistic regression (MLR) (Venables & Ripley, 2003), decision tree (DT) (Therneau et al., 2022), and random forest (RF) (Breiman, 2001). These models provide a variety of predictive capabilities for data analysis. All the data used in the model analyses are in Appendix S5. MLR calculates log odds for each category of a multiclass target variable and selects the class with the highest probability. DT models generate branching solutions to minimize data impurity measures, resulting in a single category for a target variable. The RF model, an ensemble method, leverages bootstrap samples and random feature selection to decrease prediction error variance and enhance accuracy. It combines multiple DTs built on different samples and decides on a category of a target variable through majority voting on outcomes of individual trees. These analyses were implemented in R (R core Team, 2023) and libraries such as

nnet, which uses the multinom function for MLR modeling (William, 2023), rpart for DT model fitting (Therneau et al., 2022), and randomForest for RF modeling (Wiener, 2022). The response variable was the extinction risk status according to our reassessment of *Copiapoa*, and the predictors were phylogenetic cluster, evolutionary distinctiveness, trade and poaching pressure, human footprint, monthly cloud frequency, landscape condition, maximum diameter, and midrange latitude.

The performance of each model was evaluated using 10-fold cross-validation. The train function from the caret package was used for cross-validation in the case of RF modeling (Kuhn, 2008). The accuracy of the model predictions was calculated by predicting extinction risk category on the same training data set and comparing results with the actual extinction risk category using a confusion matrix.

Each model adopts a different approach for assessing variable importance. MLR assigns higher importance with larger absolute coefficients and smaller *p* values. The DT model computes importance based on the reduction in the Gini index (Therneau et al., 2022), whereas the RF model does this through the mean decrease in accuracy when a variable is excluded. This diverse approach to variable importance assessment and performance evaluation resulted in a comprehensive data analysis.

## RESULTS

### Extinction risk reassessment

We compiled 1242 occurrence data points for the 37 *Copiapoa* taxa. After data curation, 892 unique occurrence point data remained, 75 of which corresponded to existing records in herbaria (20, CONC; 14, SGO; 4, VEG; 30, GENT) and botanical gardens (6, ANT; 1, DES), 295 were from the literature, including papers and books, and 501 were occurrence data from our fieldwork. Of the 37 taxa evaluated, 29 had sufficient locations (minimum 3) to generate a minimum convex polygon.

Seven taxa (*Copiapoa aphanes*, *Copiapoa australis*, *Copiapoa decorticans*, *Copiapoa humilis* subsp. *tenuissima*, *Copiapoa leonensis*, *Copiapoa longispina*, and *Copiapoa mollicula*) had an AOO of <10 km$^2$. Ten other taxa (*Copiapoa angustiflora*, *Copiapoa cinerea* subsp. *krainziana*, *Copiapoa conglomerata*, *Copiapoa desertorum*, *Copiapoa esmeraldana*, *Copiapoa hypogaea*, *Copiapoa humilis* subsp. *tocopillana*, *Copiapoa humilis* subsp. *variispinata*, *Copiapoa laui*, and *Copiapoa taltalensis*) had an AOO of <20 km$^2$. Sixteen taxa (*Copiapoa armata*, *Copiapoa atacamensis*, *Copiapoa calderana*, *Copiapoa cinerascens*, *C. cinerea* subsp. *cinerea*, *Copiapoa dealbata*, *Copiapoa fiedleriana*, *Copiapoa grandiflora*, *C. humilis* subsp. *humilis*, *Copiapoa longistaminea*, *Copiapoa marginata*, *Copiapoa megarhiza*, *Copiapoa montana*, *Copiapoa rupestris*, *Copiapoa serpentisulcata*, and *C. solaris*) had an AOO of ≤100 km$^2$. The remaining 4 taxa had an AOO of >100 km$^2$. *Copiapoa gigantea* had the highest AOO value (208 km$^2$).

The distribution of evaluated species across threat categories, according to the IUCN Red List extinction risk classification, was as follows: 14 taxa, including *C. angustiflora* and *C. australis*,
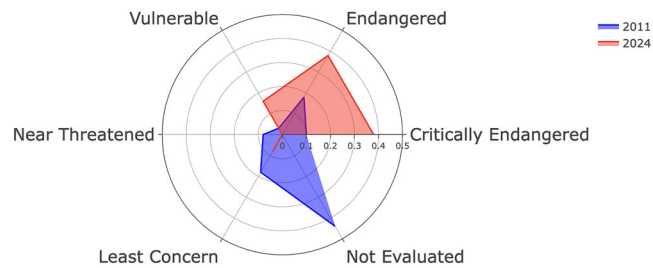
**FIGURE 2** Proportion of *Copiapoa* species and subspecies classified by conservation status categories (endangered, vulnerable, and critically endangered) in 2011 and in 2024 (the reassessment).

critically endangered (CR); 14 taxa, such as *C. atacamensis* and *C. cinerascens*, endangered (EN); 6 taxa, including *C. armata* and *C. calderana*, classified as vulnerable (VU); and 3 taxa, including *Copiapoa coquimbana* and *C. dealbata*, least concern (LC). These results reflect a significant change compared with the previous assessment conducted in 2011; there was a notable increase in extinction risk between assessments (Figure 2).

## Extinction drivers

The combined data set of *ycf1* and *rpl32-trnL* showed 323 variable characters across 2366 base pairs (Appendix S2). Coverage for ingroup taxa was complete, and outgroup taxa were well represented at 88%. Phylogenetic clades for sections *Echinopoa*, *Mammilopoa*, *Cinerei*, and *Copiapoa* were placed as expected (Appendix S3).

Traits varied notably among species (Figure 3). Evolutionary distinctiveness values ranged from 0.001 in *C. mollicula* to 0.015 in *C. australis*. *Copiapoa solaris* and *C. laui*, the closest relatives of *C. australis*, exhibited high evolutionary distinctiveness values (Figure 3; Appendices S3 & S5), consistent with their significant phylogenetic distance from the rest of the genus (Appendices S4 & S5).

Trade and poaching pressure varied considerably among species. *Copiapoa montana* had the highest level at 29.2%, followed by *C. cinerea* subsp. *cinerea* (20.3%) and *C. humilis* subsp. *humilis* (11.1%). *Copiapoa hypogaea*, *C. coquimbana*, and *Copiapoa echinoides* also exhibited notable trade pressure: 8.2%, 7.8%, and 7.3%, respectively. In contrast, *C. cinerascens* (5.5%), *C. calderana* (2.9%), *C. cinerea* subsp. *krainziana* (2.2%), *C. marginata* (1.6%), *C. cinerea* subsp. *columna-alba* (0.9%), *C. dealbata* (0.9%), *C. fiedleriana* (0.4%), *C. serpentisulcata* (0.3%), and *C. esmeraldana* (0.2%) showed relatively low trade and poaching pressure. All *C. cinerea* infraspecific taxa were included in the highest levels of this ranking.

Our data showed other differences in potential extinction drivers among *Copiapoa* (Figure 3). Human footprint scores varied notably from a high of 26 for *C. humilis* subsp. *tocopillana* to a low of 0 for *Copiapoa cinerea* subsp. *cinerea*. The landscape condition was best for *C. esmeraldana*, 0.91 (meaning low levels of habitat conversion), and worst for *C. coquimbana*, 0.43. Cloud frequency varied from 4650 for *C. serpentisulcata* to 647 for *C.*

*megarhiza* and 653 for *C. longispina*. Branch diameters spanned from a modest 1.0 cm for *C. laui* to a substantial 34 cm for *C. cinerea* subsp. *columna-alba*. Midrange latitudes indicated species-specific ranges, underscoring the diverse habitats occupied by these species.

The MLR model converged after 100 iterations, with a final negative log-likelihood value of 15.970. The in-sample accuracy of this model was 0.784. The DT model resulted in an in-sample accuracy of 0.730, and the RF model yielded an accuracy of 0.598.

Trade and poaching pressure consistently showed high variable importance across all models (Table 1). In the MLR model, trade and poaching pressure exhibited variable importance. Coefficients were 0.701 for EN, −1.517 for LC, and 0.483 for VU. Landscape condition showed the highest importance, particularly with a coefficient of −102.811 in the LC category and −69.063 in the VU category.

In the DT model, trade and poaching pressure displayed the highest importance (5.319), followed by landscape condition (5.066) and midrange latitude (4.415). The RF model revealed trade and poaching pressure as the most significant variable, with an importance score of 100. Other variables, such as landscape condition (98.280), evolutionary distinctiveness (81.671), and maximum diameter (67.380), also exhibited substantial importance. Cloudiness frequency was notable with an importance score of 59.630. Phylogenetic cluster III had an importance score of 18.150. Phylogenetic cluster II had no significant importance in this model.

## DISCUSSION

Our findings showed an alarming increase in extinction risk compared with previous assessments; most taxa (76 %) were categorized as CR or EN. This shift in conservation status underscores the exacerbating threats to the biodiversity of the coastal Atacama Desert (Duarte et al., 2014; Gatica-Castro et al., 2015). Our models showed trade and poaching pressure as consistent predictors of extinction risk, underlining their detrimental role in species persistence.

Our results showed that 17 taxa are microendemics, 7 of which had an AOO of <10 km², and 10 others had an AOO of <20 km² (Appendix S5). Furthermore, 16 species exhibited an AOO of ≤100 km² (Appendix S5). The prevalent microendemism in the cactus family significantly contributes to its vulnerability and the observed escalation in extinction risks (Duarte et al., 2019; Goettsch et al., 2015; Hernández & Bárcenas, 1996; Hultine et al., 2023). This pattern of localized distribution heightens the susceptibility of cactus species to a range of threats, including stochastic environmental events and direct anthropogenic pressures (Duarte et al., 2019; Yesuf et al., 2021). The specific and often isolated habitats of these species make them particularly sensitive to environmental changes and plants or seed harvesting, underscoring the need for targeted conservation strategies that address both natural and human-induced challenges. Indeed, we found a considerable increase in extinction risk compared with the previous extinction risk
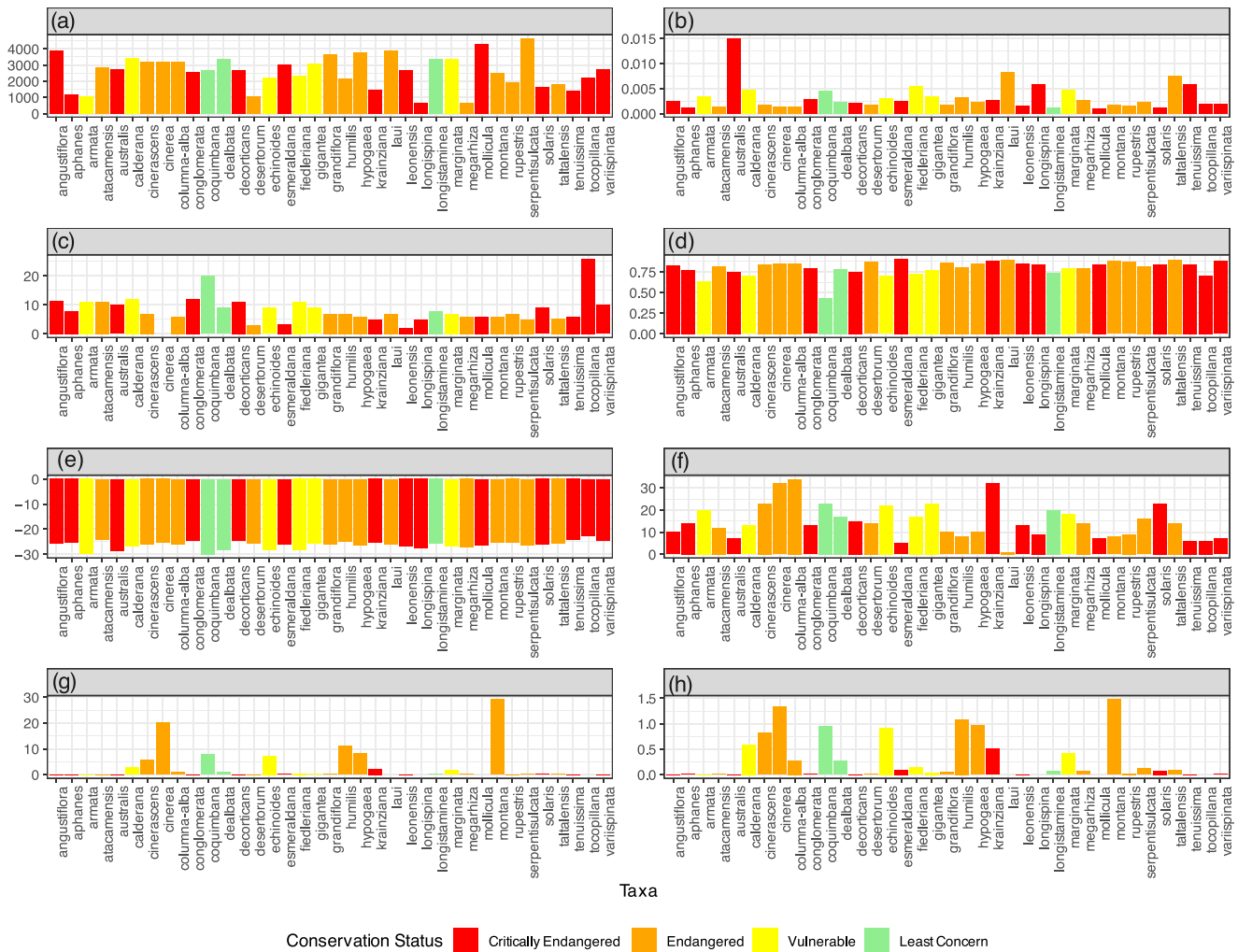
**FIGURE 3** *Copiapoa* species and subspecies extinction drivers used in machine learning models (multinomial logistic regression, random forest, and decision tree): (a) monthly cloud frequencies, (b) evolutionary distinctiveness (frequency distributions of the equal-splits scores), (c) human footprint index (0–100), (d) landscape condition model (0–1), (e) midrange latitude (degrees), (f) maximum branch diameter (cm), (g) trade and poaching pressure (%), and (h) trade and poaching pressure after log transformation ($\log_{10} + 1$).

assessment; 77% of taxa were classified as CR or EN based on IUCN Red List guidelines.

Our results highlight the vulnerability of the biodiversity found in fog oases in the coastal Atacama Desert (Moat et al., 2021), emphasizing its fragility and the high risk of species extinction in this system. High levels of threat or habitat degradation are often overlooked in arid and desert biomes (Martínez-Valderrama et al., 2020). Our study brings attention to the conservation value of arid biomes, which have significant knowledge gaps concerning the impacts of human activities on species richness (Murphy & Romanuk, 2016). Arid regions face significant anthropogenic pressures, notably from mining activities that transform and degrade habitats and pose threats to species and protected areas (Durán et al., 2013; Gajardo & Redón, 2019; Urbina et al., 2021). Specifically, several *Copiapoa* species, such as *C. armata*, *C. cinerea*, *C. desertorum*, *C. megarhiza*, and *C. taltalensis*, are threatened by metal mining operations. The risks are not limited to the mineral extraction processes but

extend to the accompanying industrial infrastructure, including energy transmission lines, mine tailings disposal areas, the construction of new industrial roads, and pollution. These operations jeopardize not only *Copiapoa*, but also other cacti and endemic angiosperm species in the region (Faundez et al., 2013, 2017; Lavandero et al., 2021). Furthermore, the vulnerability of a significant number of *Copiapoa* species echoes the broader biodiversity crisis in Latin America (Ramos, 1988; Raven et al., 2020).

Among our models, trade and poaching pressure emerged as a significant threat. A recent seizure, known as Operation Atacama, uncovered over a thousand Chilean cacti being smuggled illegally, and the genus *Copiapoa* was the most represented among them (Nuwer, 2021). This problem is not exclusive to the Atacama Desert and reflects a broader global trend, as observed in other species of succulents, orchids, cycads, and timber species of economic importance (Hinsley et al., 2017; Kleinschmit et al., 2016; Margulies, 2020; Williamson et al., 2016).

The extraction of plants with small ranges or low abundances from their natural habitats, even at low levels, can have severe impacts on their demography. Among these sensitive species, cacti exhibit a high vulnerability to adult removal (Esparza-Olguín et al., 2002; Jiménez-Sierra et al., 2007; Rae & Ebert, 2002). Despite the severity of this issue, it is often overlooked (Margulies et al., 2019). Furthermore, global trends indicate a concerning rise in the extraction of wild plants, illegal trade, and unscrupulous collection (Harfoot et al., 2018; Lavorgna et al., 2020).

Our results highlight that trade and poaching pressure are linked to the critically threatened status of *Copiapoa* taxa; nearly 90% are affected by either legal or illegal trade. The observed relationship between trade and poaching pressure and extinction risk in *Copiapoa* species may be caused primarily by 2 interacting factors: direct impact of severe human exploitation on the species' survival and consumer preference for rare and endangered species over more common species (Hinsley et al., 2015; Lavorgna et al., 2020). The CITES database provides insights into the legal market by documenting transactions involving legally traded specimens, which, for *Copiapoa*, predominantly consist of artificially cultivated plants. Although it is likely that many of these plants are grown from seeds obtained from artificially propagated specimens, the current data did not allow us to rule out the possibility that some plants may have been extracted from their natural habitats and subsequently laundered or grown from seeds collected in the wild. Deciphering these activities from the CITES database is challenging and necessitates additional efforts to scrutinize the origins of traded plants more closely. Moreover, data on poaching likely represent only a fraction of all illegally traded plants because these activities occur in the black market for which there are no formal records and because our data were derived primarily from seizures by authorities. Integrating legal and illegal forms of trade into a single variable offers a more robust measure that better reflects the overall impact of plant trade on the extinction risk of *Copiapoa* species. This approach constitutes the first effort in Chile to decipher the combined impact of legal and illegal trade on cacti, setting an important precedent for future research and serving as a cautionary signal to stakeholders to delve deeper into these dynamics.

Trade and poaching pressure is particularly acute for *C. cinerea*, *C. humilis*, and *C. montana*, which cumulatively represented over 60% of the species subjected to trade and poaching. The disproportionate exploitation of these species highlights a significant threat. However, even *Copiapoa* species with lower exploitation levels face risks due to their restricted distribution ranges and populations (Larridon et al., 2014). Addressing this crisis involves developing sustainable trade practices and improved compliance with CITES regulations, especially in online markets (Margulies, 2020; Phelps et al., 2016; Thomas-Walters et al., 2021). Not all collectors are compliant with regard to CITES rules, highlighting the need for improved awareness and clarity regarding trade regulations, particularly in online commerce and social media platforms (Lavorgna, 2014; Margulies et al., 2023). Newly discovered populations or species, such as *C. angustiflora*, are particularly vulnerable to the ongoing

threat posed by the demand for wild cacti specimens (Novoa et al., 2017). Trade in cacti has experienced significant growth in the past decade; it encompasses approximately 75% of the world's cactus species traded since 1976 (Lavorgna et al., 2020). Overcollection of wild plants and seeds is recognized as the most significant driver of extinction for 47% of threatened cactus species on the IUCN Red List (Goettsch et al., 2015). The market for wild cacti remains robust, as evidenced by a substantial 64% increase in domestic US trade between 2012 and 2017, generating a multimillion-dollar industry (Lavorgna et al., 2020). Addressing the pressures of trade and poaching on cacti and other plant species requires a comprehensive strategy. This strategy must not only raise public awareness but also strengthen monitoring and international legal measures; thus, a united effort across various sectors and countries is needed. Moreover, to reduce the impact on species harvested from the wild, implementing and enforcing strict protocols for sustainable seed harvesting that aim to lessen the long-term effects on natural populations are crucial. Although generally not recommended, seed harvesting of *Copiapoa* species may be allowed under strict guidelines for species that are less threatened, facilitating the establishment of good practices, certification, and regulation of artificial cultivation. Such initiatives should be coordinated and endorsed by governmental regulatory bodies, which can drive a network of CITES-certified greenhouses that can supply artificially grown plants for markets. This approach helps mitigate the risk of extinction associated with the ornamental use of these species.

Our assessment of habitat quality degradation revealed that *C. coquimbana* and *C. humilis* subsp. *tocopillana* inhabit regions with the most pronounced human influence levels. Key factors contributing to habitat degradation include industrial activities and unregulated residential development along coastal areas. These factors are commonly recognized as drivers of biodiversity loss because they are a direct measure of habitat anthropization (Cantera et al., 2022). Specifically, habitat quality degradation caused by land- and sea-use change is the dominant direct driver of biodiversity loss worldwide (Jaureguiberry et al., 2022). We conducted a thorough analysis of the current extinction risks to the *Copiapoa* genus, primarily due to direct anthropogenic impacts. However, climate change may be a potentially significant threat to these species. The decision to exclude climate-change-related variables from our model was driven by the difficulties in accurately forecasting future climate and fog dynamics in the coastal Atacama region. This challenge is particularly pronounced due to the high spatial resolution needed to account for microendemic species.

Certain fog oases that contain multiple *Copiapoa* species hold significant value due to their evolutionary information, as evidenced by the incorporation of evolutionary distinctiveness metric. The presence of unique genetic characteristics in these species may play a crucial role in their adaptability to environmental changes, especially in hyper-arid conditions. An analysis conducted at the family level reveals that the Atacama Desert exhibits a high degree of endemism (Amaral et al., 2022) and moderate phylogenetic diversity. This pattern is shared by *Copiapoa*, along with other cactus genera, such as *Eriosyce* (Guerrero

et al., 2019) and *Eulychnia* (Merklinger et al., 2021). Legally protected areas in Chile play a vital role in preserving the evolutionary heritage (Scherson et al., 2017). However, the limited number and extent of these areas still leave several species without adequate protection (Duarte et al., 2014; Durán et al., 2013; Goettsch et al., 2019).

We delivered a pivotal reassessment of the extinction risk for the *Copiapoa* genus, highlighting the effects of compounded threats of legal and illegal trade and habitat degradation on their current extinction risk levels. Integrating diverse methodologies, our results significantly advance the understanding of extinction drivers and their interplay with biological traits. The strength of our study lies in the innovative use of advanced statistical methods, offering deep insights crucial for *Copiapoa* conservation. Nonetheless, the reliance on available data could underrepresent the full extent of illegal activities, and their impact may be even more harmful. We emphasize the urgent necessity for robust conservation strategies in the Atacama Desert and advocate for species monitoring, promotion of legal trade alongside effective poaching control, proactive habitat protection, and the use of predictive modeling in conservation planning. This comprehensive strategy could serve as a model for other regions facing similar conservation challenges, demonstrating the effectiveness of thorough analyses in driving effective conservation measures on a global scale.

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**How to cite this article:** Villalobo-Lopez, A., Peña, C. M., Varas-Myrik, A., Pillet, M., Jahnsen, P., Pliscoff, P., Goettsch, B., & Guerrero, P. C. (2024). Effects of trade and poaching pressure on extinction risk for cacti in the Atacama Desert. *Conservation Biology*, *38*, e14353. https://doi.org/10.1111/cobi.14353