

RESEARCH ARTICLE

Extinction risk of Mesoamerican crop wild relatives

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Societal Impact Statement

Crop wild relatives (CWR) are plant taxa closely related to crops and are a source of high genetic diversity that can help adapt crops to the impacts of global change, particularly to meet increasing consumer demand in the face of the climate crisis. CWR provide vital ecosystem services and are increasingly important for food and nutrition security and sustainable and resilient agriculture. They therefore are of major biological, social, cultural and economic importance. Assessing the extinction risk of CWR is essential to prioritise in situ and ex situ conservation strategies in Mesoamerica to guarantee the long-term survival and availability of these resources for present and future generations worldwide.

Summary

- Ensuring food security is one of the world's most critical issues as agricultural systems are already being impacted by global change. Crop wild relatives (CWR)—wild plants related to crops—possess genetic variability that can help adapt agriculture to a changing environment and sustainably increase crop yields to meet the food security challenge.
- Here we report the results of an extinction risk assessment of 224 wild relatives of some of the world's most important crops (i.e. chilli pepper, maize, common bean, avocado, cotton, potato, squash, vanilla and husk tomato) in Mesoamerica—an area of global significance as a centre of crop origin, domestication and of high CWR diversity.
- We show that 35% of the selected CWR taxa are threatened with extinction according to The International Union for Conservation of Nature (IUCN) Red List demonstrates that these valuable genetic resources are under high anthropogenic

threat. The dominant threat processes are land use change for agriculture and farming, invasive and other problematic species (e.g. pests, genetically modified organisms) and use of biological resources, including overcollection and logging. The most significant drivers of extinction relate to smallholder agriculture—given its high incidence and ongoing shifts from traditional agriculture to modern practices (e.g. use of herbicides)—smallholder ranching and housing and urban development and introduced genetic material.

- There is an urgent need to increase knowledge and research around different aspects of CWR. Policies that support in situ and ex situ conservation of CWR and promote sustainable agriculture are pivotal to secure these resources for the benefit of current and future generations.

KEYWORDS

agrobiodiversity, conservation, crop wild relatives, extinction risk, food security, IUCN Red List, threat drivers, threatened species

1 | INTRODUCTION

Reducing the environmental impact of agriculture and simultaneously feeding an exponentially growing human population in the face of climate change (Godfray et al., 2010; Vermeulen et al., 2012) is one of the world's most pressing challenges. The effects of climate change on agriculture are already observed (Banerjee et al., 2018; Brás et al., 2021; Gourdj et al., 2015; Huq et al., 2015; Jaramillo et al., 2011; Läderach et al., 2017) and are expected to worsen without mitigation and adaptation actions (Barros & Field, 2014; Campbell et al., 2016; Dawson et al., 2016; Lobell et al., 2011; Porter et al., 2014) with overall global crop yield declines between 3% and 10% predicted with each degree of warming (Challinor et al., 2014). Changes to crops and varietal production resulting from climate change or through synergistic effects with other drivers caused by land use change (e.g. soil degradation or loss of pollination services) include reduced genetic diversity, variable crop yields and increased vulnerability to emerging pathogens and pests (FAO, 2010; Foley et al., 2005; Groenen, 2018; Keneni et al., 2012; Ricketts et al., 2008; Scheffers et al., 2016). The adaptation of crops to environmental stresses such as drought, soil salinity and flooding, as well as to consequent changes in the prevalence of pests and diseases, while ensuring high nutritional value and yields, will be key in responding to food demand (Campbell et al., 2016; FAO, 2008, 2010, 2011; Ford-Lloyd et al., 2011; Guarino & Lobell, 2011; Maxted et al., 2012; Maxted et al., 2014; Nabhan et al., 2020; Ortiz, 2015; Zamir, 2001). For example, the Mexican wild potato *Solanum demissum* has been used extensively in breeding programs against late blight (Ross, 1986). Likewise, *S. pinnatisectum* and *S. cardiophyllum* show resistance to the Colorado potato beetle (Chen et al., 2004). Thus, a rich source of genetic variability to help adapt crops to changing environmental conditions can be found in crop wild relatives (CWR)—wild plant species related to crops—including their ancestors, which persist in a wide variety of habitats and under heterogeneous environmental

conditions, and have not passed through the domestication genetic bottleneck (Maxted et al., 1997; Tanksley & McCouch, 1997). Therefore, it is so far recognised that they have undergone evolutionary processes without human intervention and sustain a breadth of genetic diversity not found in crops (FAO, 2008; Flores-Hernández et al., 2018; Hawkes et al., 2000; Mariac et al., 2006; Maxted & Kell, 2009; van de Wouw et al., 2001; Vaughan, 1994). However, there is ethnobotanical evidence that suggests that some artificial selection could have been exerted on CWR. Recent studies indicate a range of human management practices of wild resources, including Mesoamerican CWR, which probably were sustained over long periods of time (Casas et al., 2016; de Luna-Ruiz et al., 2018; Levis et al., 2018).

The importance of CWR in achieving food security has long been recognised (Ford-Lloyd et al., 2011; Harlan, 1976; Hoyt, 1988; Maxted et al., 1997; McCouch et al., 2013; Prescott-Allen & Prescott-Allen, 1990). Food security has become an integral element of both the agricultural and environmental sectors as is reflected in international policy frameworks, including the United Nations Sustainable Development Goals (SDG). Aichi Biodiversity Target 13 of the Convention on Biological Diversity (CBD) Strategic Plan for Biodiversity 2011–2020 called for the maintenance and safeguarding of the genetic diversity of CWR (CBD, 2010), which is also highlighted in the Post 2020 Biodiversity Framework (e.g. Target 8 and Target 9; CBD, 2019). Target 2.5 of SDG 2 (Zero Hunger) calls to maintain the genetic diversity of seeds, cultivated plants and farmed and domesticated animals and their related wild species (United Nations, 2015).

Mesoamerica is a centre of origin, diversity and domestication of crops and of important CWR diversity (Maxted & Vincent, 2021; Vavilov, 1935; Vincent et al., 2019). An estimated 8% of the world's most important crops (Vavilov, 1935), including maize, squash, chilli pepper, bean, avocado, vanilla and cotton, were domesticated in the region around 10,000 to 5000 years ago (Clement et al., 2021;

Hummer & Hancock, 2015; Piperno & Smith, 2012). The evolutionary process that results from human manipulation of plant genotypes to satisfy human requirements is still part of the domestication process in the region (Hajjar & Hodgkin, 2007). Further, agriculture is a production process in which both cultivation and domestication of plants were involved (Casas & Caballero, 1995; Perry & Flannery, 2007). Accordingly, and because many of these crops are considered of global importance due to their food, nutritional, economic and other values (CONABIO et al., 2019a, 2019b; Shiferaw et al., 2011; Wei et al., 2012), Mesoamerica has been identified as a global conservation priority centre in which to conduct in situ and ex situ conservation of CWR (Castañeda-Álvarez et al., 2016; Vincent et al., 2019).

There are good reasons to believe that a high proportion of CWR occurring in Mesoamerica are threatened with extinction. Mesoamerica harbours an estimated 3000 endemic flowering plant species yet had lost more than 80% of its original native vegetation cover by the beginning of the 21st century (Mittermeier et al., 2011). The annual deforestation was calculated in 395,000 ha between 2005 and 2010 (Elizondo et al., 2015), making it one of the world's 36 biodiversity hotspots (Rodríguez Olivet & Asquith, 2004). Mesoamerica will suffer severe impacts from climate change (BID and CEPAL, 2010; Thomas et al., 2016), yet its biodiversity holds key adaptive solutions that should be conserved (e.g. genetic diversity and functional genomics; Mastretta-Yanes et al., 2018). Although national (e.g. SEMARNAT-2010-NOM-059; DOF, 2010) and international extinction risk assessments have been completed for some plant groups in the region (Goettsch et al., 2015; IUCN, 2020; Rivers, 2017), CWR have not been targeted.

We present here the first assessment of extinction risk of wild relatives of some of the world's most important crops that occur within Mesoamerica. We focus on the nature of the threats affecting them and discuss actions and policies that can be implemented to strengthen their conservation. We included CWR of six Mesoamerican staple foods of which maize, common bean, chilli pepper, husk tomato and squash are typically part of the ancestral multicrop milpa system. The milpa remains the main means of production and subsistence by direct consumption and trade of surplus for smallholder farmers in the region (Bellon et al., 2018; Lopez-Ridaura et al., 2021; Zizumbo-Villarreal & Colunga-GarcíaMarín, 2010).

2 | MATERIALS AND METHODS

2.1 | Study area

The study focused mainly on the Mesoamerican region (Figure 1a; Kirchoff, 1960), which includes central and southern Mexico, Guatemala, El Salvador and Honduras. In some instances, areas outside Mesoamerica that are part of the Aridamerica region (Nabhan et al., 2020) such as northern Mexico were considered in the analyses to evaluate complete genera in which some taxa were not strictly distributed within Mesoamerica, thus accounting for the full extent of the geographic range of a taxon (Figure 1b,c).

2.2 | Taxa selection criteria

A list of approximately 3000 CWR taxa (i.e. species, subspecies, varieties and subpopulations; Dataset S1) belonging to the same genus of a crop cultivated or domesticated in Mesoamerica was compiled from different sources (e.g. Acevedo Gasman et al., 2009; Azurdia et al., 2011; Bellon et al., 2009; Perales & Aguirre, 2008). The list included 310 high priority CWR for Mexico (Contreras-Toledo et al., 2018), 105 taxa in Guatemala (Azurdia et al., 2011), 50 taxa in El Salvador (Chízar-Fernández et al., 2009; Echeverría et al., 2008) and around 54 taxa in Honduras (Núñez & Alvarado, 1995). A subset of genera and their taxa (with the exception of *Tripsacum*, a tertiary gene pool relative of *Zea mays*) was selected for the present study following a set of criteria considered most relevant for the social, economic and biological characteristics of the region, identified during a stakeholder workshop (Methods S1).

2.3 | Extinction risk assessment

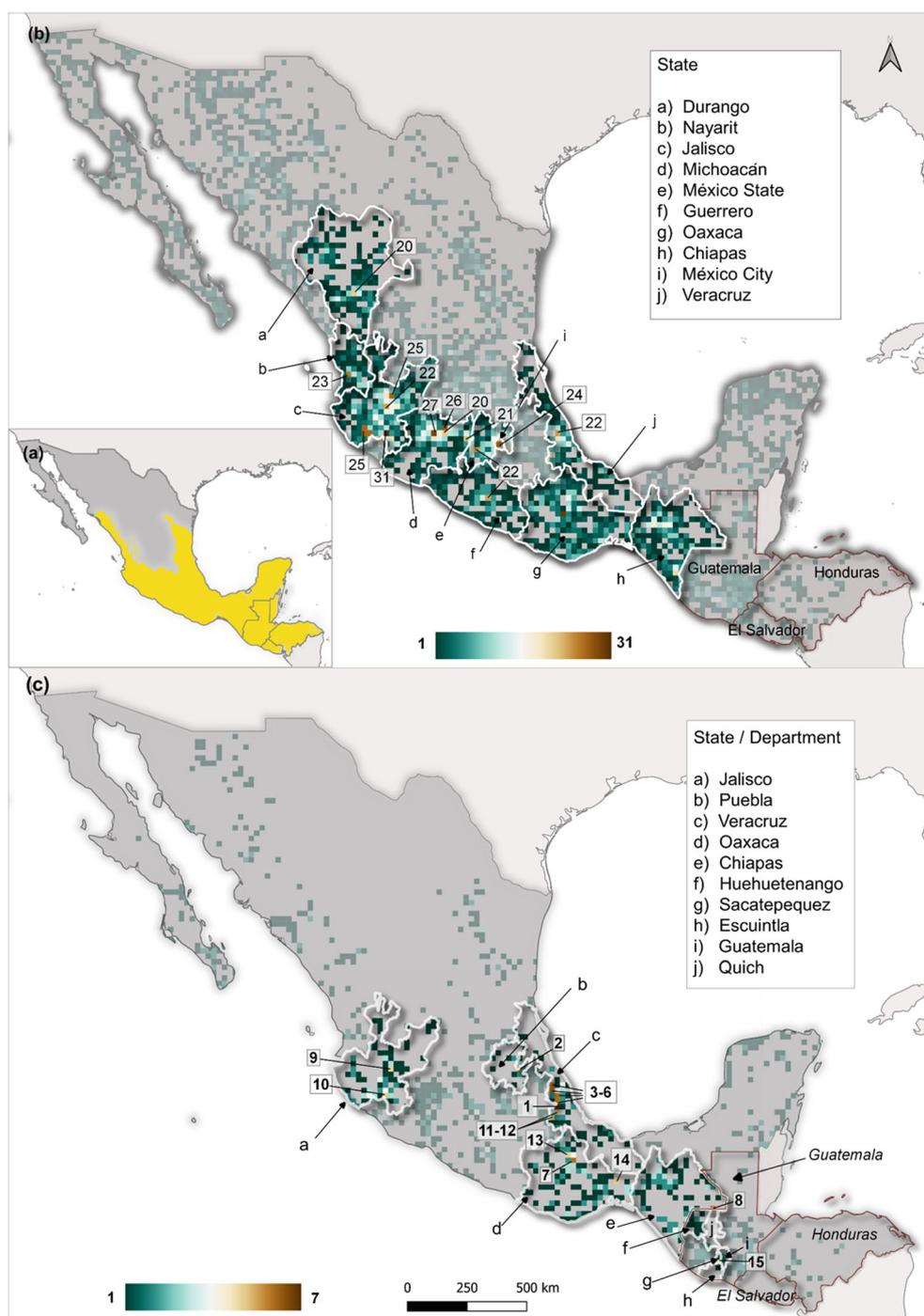
We evaluated extinction risk for the selected taxa of Mesoamerican CWR according to the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria (IUCN, 2012) during an expert workshop (Methods S2). Information on the distribution, population trends, ecology, conservation actions, use and trade was reviewed for each taxon. As part of this process, range maps were generated using over 28,000 reviewed occurrence data points from different sources (e.g. CONABIO, 2016; Crop Trust, 2016; GBIF, 2016; and personal databases; Dataset S2). Data are also available on the IUCN Red List website (IUCN, 2020). These data were used to show the spatial distribution of CWR as well as to generate richness maps (Methods S3) showing areas of high CWR diversity and areas with high diversity of threatened taxa (Methods S4). Detailed data on the threats affecting taxa were also collated from the literature and from direct observations of the experts participating in the assessment process and were coded following the IUCN Threats Classification Scheme (based on Salafsky et al., 2008; version 3.2 available from <https://www.iucnredlist.org/resources/threat-classification-scheme>). Because the assessments for the IUCN Red List of Threatened Species are global, we assessed the extinction risk of taxa throughout their entire range.

3 | RESULTS

3.1 | Selected taxa and their extinction risk

A total of 224 taxa of wild relatives of the following crops were selected: chilli pepper (*Capsicum* spp.), squash (*Cucurbita* spp.), cotton (*Gossypium* spp.), avocado (*Persea* spp.), bean (*Phaseolus* spp.), husk tomato (*Physalis* spp.), potato (*Solanum* sect. *Petota*), maize (*Zea* spp. and *Tripsacum* spp.) and vanilla (*Vanilla* spp.) (Table S1). For each of the taxonomic groups, all taxa occurring within the four countries were included. In the case of *Solanum* and *Vanilla*, they represent less than 10% of the total number of known taxa globally, while all known *Zea* taxa are included (Table S2).

FIGURE 1 (a) Mesoamerican region highlighted in yellow according to Kirchhnoff (1960). (b) Spatial distribution pattern of crop wild relative taxa based on occurrence records from herbaria. (c) Hotspots of threatened (critically endangered, endangered and vulnerable) and near-threatened crop wild relatives (see Table 1 for the respective list of taxa). In both figures, the numbers correspond to the number of taxa found in the cell; the dark green colour corresponds to the lowest number of taxa, and the dark brown colour corresponds to highest number of taxa found in a 20 × 20-km cell. The study area is shown in dark grey



A high proportion (35%) (Methods S5) of the Mesoamerican CWR taxa assessed are threatened with extinction, including 7 Critically Endangered (CR), 48 Endangered (EN) and 16 Vulnerable (VU). Nine taxa were assessed as Near Threatened (NT), 125 as Least Concern (LC) and 19 as Data Deficient (DD) (Table S1). *Vanilla* has the highest proportion of threatened taxa with 100% of them (eight taxa) threatened, followed by cotton (*Gossypium*) with 92% (12 taxa), avocado (*Persea*) with 60% (9 taxa) and the relatives of maize *Zea* and *Tripsacum* with 44% (four taxa) and 33% (four taxa) threatened taxa, respectively (Figure 2).

3.2 | Patterns of diversity

The highest number of CWR taxa assessed in 20 km × 20 km grid cells are located in the Mexican states of Jalisco and Oaxaca with 31 and 28 taxa, respectively (Figure 1b). Other areas with high to medium richness, ranging from 15 to 27 taxa, are found in northern Mesoamerica, that is, in central Mexico, from the western states of Nayarit and Jalisco through to Michoacán, Mexico State, Mexico City, Puebla and Veracruz in the east (Figure 1b).

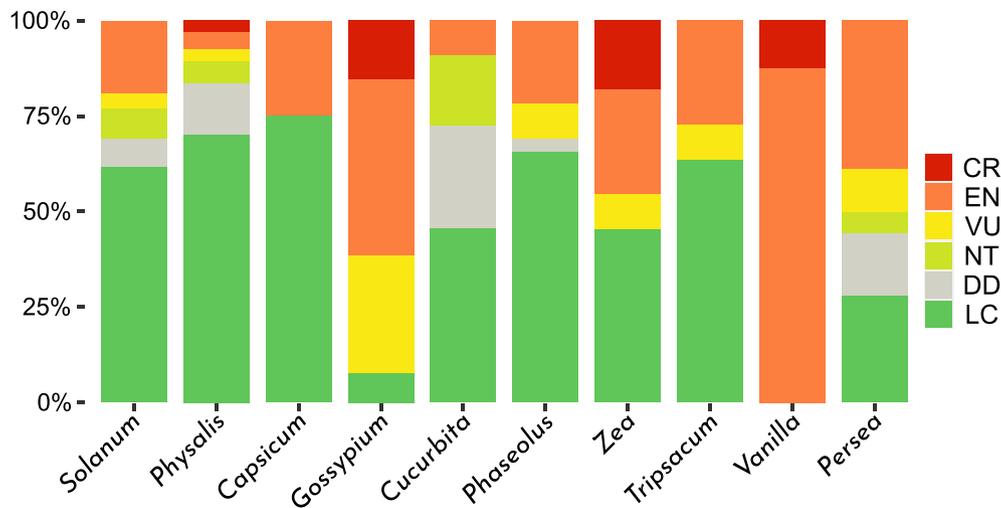


FIGURE 2 Proportion of taxa in each genus related to the selected crops by IUCN Red List category (CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, DD = data deficient, LC = least concern). *Solanum* ($n = 26$), *Physalis* ($n = 67$, 63 species and 4 subspecies), *Capsicum* ($n = 4$), *Gossypium* ($n = 13$), *Cucurbita* ($n = 11$, 9 species and 2 subspecies), *Phaseolus* ($n = 55$), *Zea* ($n = 11$, 4 species, 3 subspecies and 4 subpopulations), *Tripsacum* ($n = 11$), *Vanilla* ($n = 8$) and *Persea* ($n = 18$)

3.3 | Hotspots of threatened taxa

The highest number of threatened (CR, EN and VU) and NT taxa is found in a grid cell in the eastern Mexican state of Veracruz and includes seven threatened CWR, including four *Persea*, two *Vanilla* and one *Phaseolus* (Cell 1, Figure 1c; Table 1). Seven other areas contain six threatened and NT taxa each. Four of them are in Veracruz (Cells 3–6, Figure 1c), and together they harbour four *Persea* and two *Physalis* taxa and one taxon each of *Cucurbita* and *Capsicum* (Table 1). Another hotspot borders the state of Veracruz and Hidalgo and includes two *Persea* taxa, two *Solanum*, one *Physalis* and one *Phaseolus*, while a hotspot in Oaxaca harbours five *Persea* and one *Vanilla* (Cell 2, Table 1). Finally, an area bordering Chiapas and Guatemala has six threatened *Vanilla*. Seven more cells with five threatened taxa each (one *Capsicum*, one *Persea*, two *Phaseolus* and one *Solanum*) were found in Guatemala in parts of the departments of Chimaltenango, Sacatepéquez, Guatemala and Escuintla and in Mexico in the states of Jalisco, Puebla, Oaxaca and Veracruz (Cells 9–15, Figure 1c). Note that in all 15 cells mentioned above, only 32 taxa out 80 threatened taxa are represented and only 2 CR taxa (*Vanilla cribbiana* and *Zea perennis*) are found (Table 1). Also, taxa in different cells might represent different populations and hence genetic variability (Tobón et al. unpublished).

3.4 | Threats to Mesoamerican CWR

Threats were identified and coded according to the IUCN Threat Classification Scheme (version 3.2) for 134 taxa (60% of evaluated taxa). The most common threat process (i.e. direct human activities responsible for the degradation, destruction and/or impairment of biodiversity; Salafsky et al., 2008) affecting 65% (87) of these 134 taxa

is agriculture. In Mesoamerica agricultural production systems and their associated management intensity can vary, but smallholder agriculture and cattle ranching occupy the majority of agricultural lands. Invasive and other problematic species is the next most common threat, reported for 38% (51) of taxa with identified threats, followed by biological resource use (threats from consumptive use of “wild” biological resources, including genetic resources, organisms or parts thereof, populations, or any other biotic component of the ecosystem with actual or potential use or value for humanity, resulting from removing them from the system or destroying them) affecting 32% (43) of taxa with threats (Figure S1). Other salient threats are residential and commercial development disturbing 25% (34) of these taxa and climate change and severe weather impacting 21% (28; Figure S2).

Across all taxonomic groups, the more frequent proximate drivers of threats (i.e. the ultimate factor enabling or contributing to the threat process; Salafsky et al., 2008) varied. Smallholder agriculture affects 32% of taxa (43), and smallholder ranching affects 31% (42 taxa), possibly because of its frequency and extent, as smallholder agriculture generally has a lower impact than agro-industrial farming systems and can sometimes provide ecosystem services (Faith et al., 2010). Other threat drivers are housing and urban development (22%, 29 taxa), introduced genetic material (16%, 21 taxa), problematic native species such as pests (15%, 20 taxa), agro-industrial farming, small-scale incidental logging and climate change in the form of habitat shifting or alteration, each affecting 14% (19 taxa) (Figure 3).

The main drivers of threat differ for each taxonomic group. *Persea* (71% of taxa), *Physalis* (54%) and *Solanum* (46%) are affected by smallholder ranching, while for *Capsicum* (75%) and *Zea* (67%) the most frequent driver of threat is smallholder agriculture and for *Cucurbita* (100%) agro-industrial farming. The most common threat driver

TABLE 1 Cells in Mexico (except number 15 in Guatemala) with the highest number of threatened (IUCN category CR = critically endangered, EN = endangered and VU = vulnerable) and near-threatened (NT) taxa as shown in Figure 1c

Cell number as shown in Figure 1c	Number of threatened taxa in the cell	State/department the cell is in	Taxa found at the cell and their IUCN category in ().
1	7	Veracruz	<i>Persea chamissonis</i> (EN) <i>Persea cinerascens</i> (EN) <i>Persea longipes</i> (EN) <i>Persea schiedeana</i> (EN) <i>Phaseolus chiapasanus</i> (EN) <i>Vanilla inodora</i> (EN) <i>Vanilla pompona</i> (EN)
2	6	Puebla	<i>Persea cinerascens</i> (EN) <i>Persea schiedeana</i> (EN) <i>Phaseolus dasycarpus</i> (EN) <i>Physalis campánula</i> (NT) <i>Solanum oxycarpum</i> (EN) <i>Solanum tarnii</i> (EN)
3	6	Veracruz	<i>Capsicum lanceolatum</i> (EN) <i>Persea chamissonis</i> (EN) <i>Persea longipes</i> (EN) <i>Persea pallescens</i> (EN) <i>Persea schiedeana</i> (EN) <i>Physalis greenmanii</i> (EN)
4	6	Veracruz	<i>Capsicum lanceolatum</i> (EN) <i>Persea chamissonis</i> (EN) <i>Persea longipes</i> (EN) <i>Physalis campanula</i> (NT) <i>Physalis greenmanii</i> (EN) <i>Solanum oxycarpum</i> (EN)
5	6	Veracruz	<i>Cucurbita okeechobeensis ssp. martinezii</i> (NT) <i>Persea longipes</i> (EN) <i>Persea schiedeana</i> (EN) <i>Physalis campanula</i> (EN) <i>Physalis greenmanii</i> (EN) <i>Solanum oxycarpum</i> (EN)
6	6	Veracruz	<i>Cucurbita okeechobeensis ssp. martinezii</i> (NT) <i>Persea schiedeana</i> (EN) <i>Physalis campanula</i> (EN) <i>Physalis greenmanii</i> (EN) <i>Solanum oxycarpum</i> (EN) <i>Vanilla insignis</i> (EN)
7	6	Oaxaca	<i>Persea albida</i> (EN) <i>Persea cinerascens</i> (EN) <i>Persea longipes</i> (EN) <i>Persea pallescens</i> (EN) <i>Persea rufescens</i> (EN) <i>Vanilla planifolia</i> (EN)
8	6	Chiapas	<i>Vanilla cribbiana</i> (CR) <i>Vanilla hartii</i> (EN)

(Continues)

TABLE 1 (Continued)

Cell number as shown in Figure 1c	Number of threatened taxa in the cell	State/department the cell is in	Taxa found at the cell and their IUCN category in ().
			<i>Vanilla inodora</i> (EN) <i>Vanilla insignis</i> (EN) <i>Vanilla odorata</i> (EN) <i>Vanilla planifolia</i> (EN)
9	5	Jalisco	<i>Cucurbita radicans</i> (EN) <i>Persea hintonii</i> (VU) <i>Phaseolus albescens</i> (VU) <i>Physalis aggregata</i> (VU) <i>Solanum trifidum</i> (NT)
10	5	Jalisco	<i>Persea hintonii</i> (VU) <i>Phaseolus albescens</i> (VU) <i>Physalis lignescens</i> (EN) <i>Solanum trifidum</i> (NT) <i>Zea perennis</i> (CR)
11	5	Veracruz	<i>Cucurbita okeechobeensis</i> ssp. <i>martinezii</i> (NT) <i>Persea schiedeana</i> (EN) <i>Physalis greenmanii</i> (EN) <i>Solanum schenckii</i> (EN) <i>Vanilla insignis</i> (EN)
12	5	Veracruz	<i>Persea pallescens</i> (EN) <i>Persea schiedeana</i> (EN) <i>Physalis greenmanii</i> (EN) <i>Solanum schenckii</i> (EN) <i>Vanilla odorata</i> (EN)
13	5	Oaxaca	<i>Persea albida</i> (EN) <i>Persea chamissonis</i> (EN) <i>Persea pallescens</i> (EN) <i>Persea rufescens</i> (EN) <i>Persea schiedeana</i> (EN)
14	5	Oaxaca	<i>Persea longipes</i> (EN) <i>Persea schiedeana</i> (EN) <i>Vanilla inodora</i> (EN) <i>Vanilla planifolia</i> (EN) <i>Vanilla pompona</i> (EN)
15	5	Sacatepequez	<i>Capsicum lanceolatum</i> (EN) <i>Persea schiedeana</i> (EN) <i>Phaseolus dumosus</i> (EN) <i>Phaseolus macrolepis</i> (EN) <i>Solanum clarum</i> (VU)

Note that only 32 taxa/80 threatened taxa are represented, 24/48 (EN), 2/7 (CR), 4/16 (VU) and 2/7 (NT)

affecting *Gossypium* (46%) is development for tourism and recreation and overcollection for *Vanilla* (100%). For *Phaseolus* (50%), native pests and diseases are the main driver, while *Tripsacum* (70%) are mainly affected by nonnative invasive species (Figure 3).

For 12% (26) of taxa assessed the threats are unknown, and these corresponded to taxa categorised as DD (13 taxa), LC (10 taxa) and EN (three taxa). For 28% (62 taxa), there are no known threats or no significant threats; this is particularly true for wide-ranging taxa. In

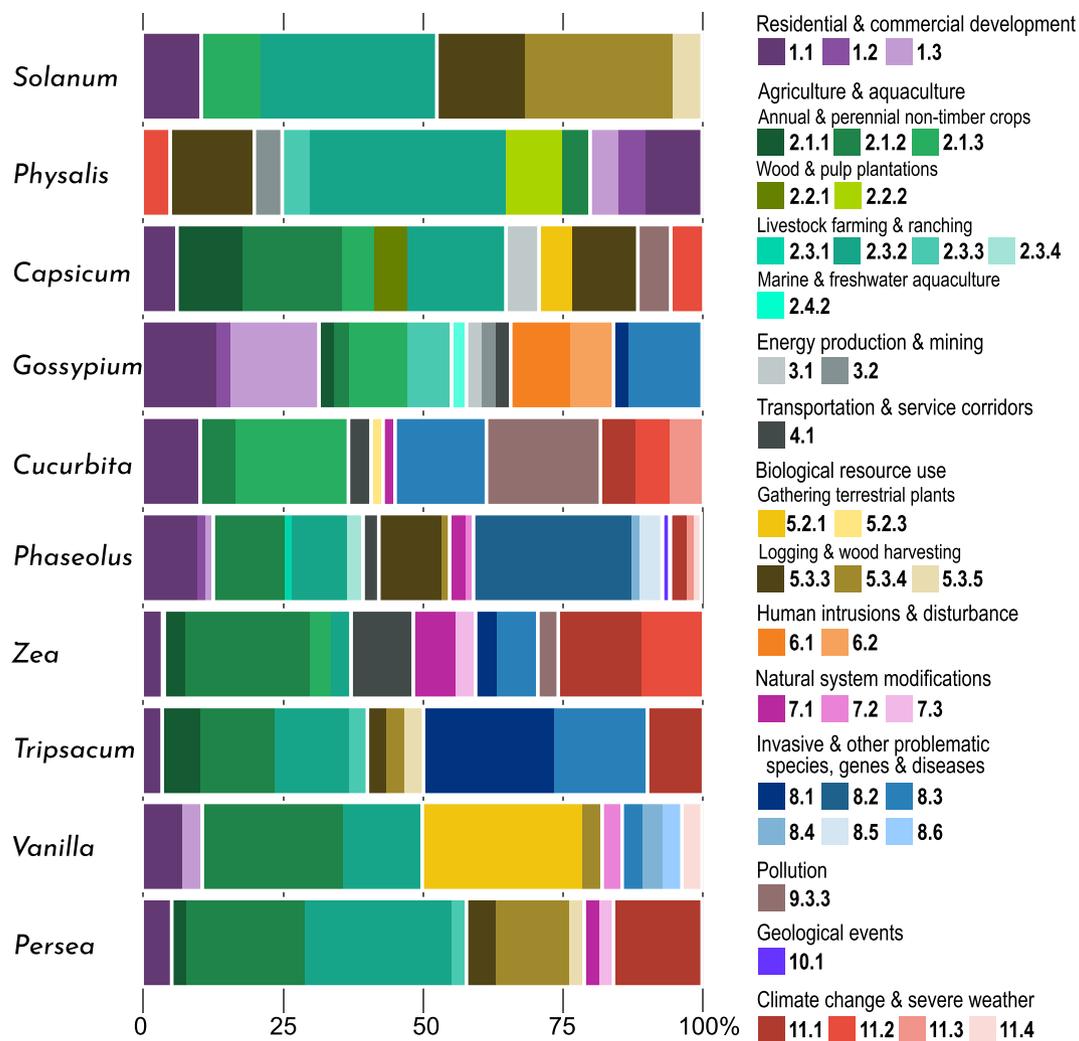


FIGURE 3 Proportion of taxa in each genus related to the selected crops affected by the different threat drivers according to the International Union for Conservation of Nature (IUCN) Threat Classification Scheme (version 3.2). Only those taxa with threat information were included ($n = 134$). 1.1 housing and urban areas, 1.2 commercial and industrial areas, 1.3 tourism and recreation areas, 2.1.1 shifting agriculture, 2.1.2 smallholder agriculture, 2.1.3 agro-industry farming, 2.2.1 smallholder plantations, 2.2.2 agro-industry plantations, 2.3.1 nomadic grazing, 2.3.2 smallholder grazing or ranching, 2.3.3 agro-industry grazing, ranching or farming, 2.3.4 scale unknown/unrecorded, 3.1 oil and gas drilling, 3.2 mining and quarrying, 4.1 roads and railroads, 5.2.1 intentional human use, 5.2.3 persecution/control, 5.3.3 unintentional effects of small scale wood harvesting, 5.3.4 unintentional effects of large scale logging, 5.3.5 motivation unknown/unrecorded, 6.1 recreational activities, 6.2 war, civil unrest and military exercises, 7.1 fire and fire suppression, 7.2 dams and water management/use, 7.3 other ecosystem modifications, 8.1 invasive alien species, 8.2 problematic native species, 8.3 introduced genetic material, 8.4 problematic species/disease of unknown origin, 8.5 viral/prion - induced diseases, 8.6 diseases of unknown cause, 9.3.3 herbicides and pesticides, 10.1 volcanoes, 11.1 habitat shifting and alteration, 11.2 drought, 11.3 temperature extremes and 11.4 storms and flooding

many cases the latter are exposed to stressors in parts of their range but no evidence linked these to significant wider population declines. Note that because threats at the subspecific level are also recorded at the species level, for those taxa assessed at the subspecific level, threats were considered for the taxon only (i.e. subspecies, varieties or subpopulations) to avoid duplication.

3.5 | Utilisation of Mesoamerican CWR

Thirty three percent of taxa assessed in this study are directly or indirectly utilised. *Cucurbita* has the highest percentage of directly utilised

taxa (91%) followed by *Vanilla* (75%) and *Solanum* (65%) (Figure S3). The most common direct end use is for human food (48%) with 31% corresponding to *Physalis*, 26% to *Solanum* and 11% to *Phaseolus* (Figure 4). Research (an indirect use), mainly for potential crop improvement, is the second most common end use (46% of taxa) with 39% of taxa being *Solanum*, 23% *Cucurbita* and 16% *Vanilla* (Figure 4). Finally, 22% of taxa have been indirectly utilised for crop improvement with *Solanum* representing 62%, *Phaseolus* 19% and 6% corresponding each to *Cucurbita*, *Persea* and *Zea* taxa. Other not so common but relevant uses are medicinal, forage and ornamental.

The genera with the highest number of taxa utilised across all different end uses were *Cucurbita* (96%), *Vanilla* (83%) and *Solanum*

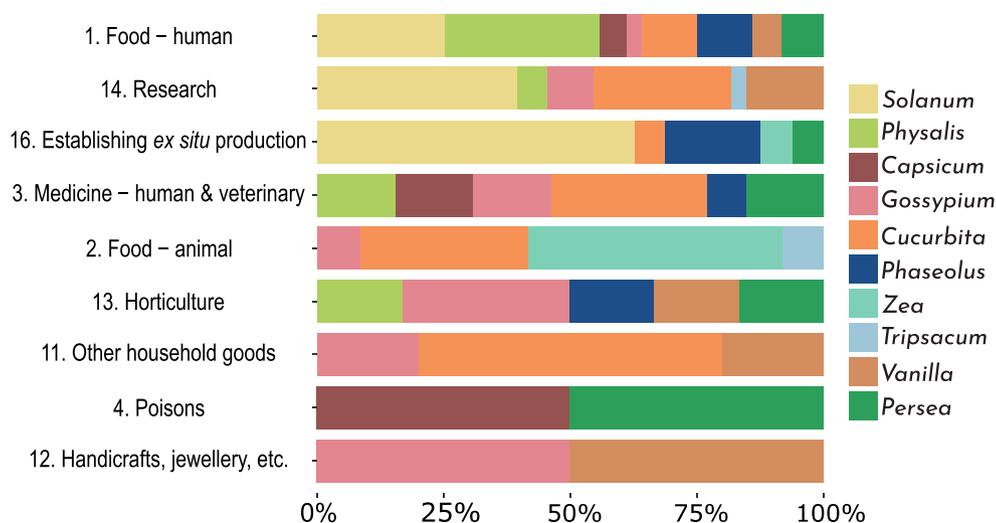


FIGURE 4 Proportion of taxa for which a direct or indirect use was recorded across the most common end use categories. Food-human ($n = 35$), research ($n = 34$), establishing ex situ production ($n = 16$), medicine-human and veterinary ($n = 12$), food - animal ($n = 7$), horticulture ($n = 6$), other household goods ($n = 5$), poisons ($n = 2$) and handicrafts, jewellery ($n = 2$). End uses according to the IUCN General Use and Trade Classification Scheme (version 1.0)

(74%) (Figure S4), while *Tripsacum*, *Phaseolus* and *Physalis* have the lowest number of utilised taxa (17%, 18% and 25%, respectively). The genera with the highest number of different uses recorded are *Gossypium*, *Persea* and *Cucurbita* with 9, 8 and 7 end uses, respectively (Figure S4).

4 | DISCUSSION

4.1 | Hotspots of threatened taxa in Mesoamerica

A high proportion of Mesoamerican CWR is threatened with extinction. With 35% of taxa being threatened (based on a best estimate; Methods S5), levels are comparable to those reported for other plant groups such as conifers (34% threatened; IUCN, 2020) and cacti (31% threatened; Goettsch et al., 2015). However, the value is more than twice as high as that reported for a regional assessment of European CWR (Bilz et al., 2011), where 16% ($n = 572$; Methods S5) of taxa were assessed as threatened.

CWR and those that are threatened are unevenly distributed across Mesoamerica. The highest values of species richness (Figure 1b) and richness of threatened taxa (Figure 1c) are found in the Mexican Transition Zone (Morrone, 2010) where the Nearctic-Neotropical biotas overlap in a region of great geological and ecological complexity (Halffter, 1978; Rzedowski, 1978). The transition zone encompasses the convergence of the Trans-Mexican Volcanic Belt in central Mexico (TMVB), Sierra Madre Oriental, Sierra Madre Occidental and Sierra Madre del Sur. The TMVB is renowned for its high plant species richness (Mastretta-Yanes et al., 2015; Rodríguez et al., 2018; Sosa et al., 2018; Villaseñor et al., 2020). The transition zone and other mountains of southern Mexico and Central America belong to a region known as the Mesoamerican forests, which contains one of the richest biotas on Earth, both in terms of species richness and endemism (Espinosa et al., 2008; Mittermeier et al., 2011).

Within the Mesoamerican mountains, threatened CWR taxa are often associated with cloud forest habitat—a naturally fragmented

plant community which, despite covering a relatively small geographical area, is renowned for its extraordinary biological diversity, divergence among lineages and complex evolutionary history (Ornelas et al., 2013; Venkatraman et al., 2019). Cloud forests are also among the most threatened habitats. In Mexico they cover only 1% of the land area, but 73% of their original vegetation has been lost or degraded (INEGI, 2003, 2016). Up to 99% of Mexican cloud forest could disappear by 2080 due to forest clearing and climate change (Ponce-Reyes et al., 2012). Cloud forests in other parts of Mesoamerica have also been disappearing at an increasing rate in recent decades (Pope et al., 2015). Protected areas in this habitat play a key role in protecting cryptic CWR (Bosland & Gonzalez, 2000); therefore, the protection of the remnants of cloud forest habitat should be a priority (CONABIO, 2010).

Critically Endangered taxa, with the exceptions of *Vanilla cribbiana* and *Zea perennis*, do not occur within hotspots of threatened taxa. Instead, they tend to occur in areas with lower taxonomic diversity and threatened taxa richness. This suggests that approaches aiming to maximise the number of threatened taxa to be conserved (e.g. by focusing on areas harbouring high numbers of threatened taxa) will only be useful in certain instances and that additional actions will be required to ensure that more narrowly distributed and threatened taxa are also accounted for. In addition, an important factor to consider in such analysis, and in particular for CWR, is the representation of genetic diversity within each taxon (Kell et al., 2012; Maxted et al., 1997; Maxted & Vincent, 2021; Riordan & Nabhan, 2019).

4.2 | Threats to Mesoamerican CWR and threat patterns

As much as for the rest of biodiversity, a large proportion of assessed taxa (65%) is affected by significant habitat loss caused by human activities and in particular agriculture and farming (Maxwell et al., 2016). Mesoamerica has lost more than 80% of its native vegetation due to intensified agriculture in the last decades, with a recent

tendency to convert diverse, traditional and smallholder agroecosystems to agro-industrial systems dependent on inorganic fertilisers, pesticides and fungicides and mechanisation (Harvey et al., 2008). In contrast to most wild species, many CWR are adapted to disturbance and can even thrive in perturbed habitats where they are tolerated and sometimes fostered, and therefore inadvertently conserved (Casas & Caballero, 1995; Delgado-Salinas et al., 2004). For example, the threatened common bean wild relative *Phaseolus dasycarpus* (EN) is tolerated and abundant at the edge of smallholder arable lands (Delgado-Salinas, 2019). Similarly, the wild squash *Cucurbita radicans* (EN), the wild relative of the scarlet runner bean *Phaseolus coccineus* and wild chilli pepper *Capsicum annuum* var. *glabriusculum* and *C. frutescens* are often found and fostered in agricultural fields (Aragón Cuevas, Sánchez de la Vega, et al., 2019). Contrastingly, other taxa are considered weeds of crops and are typically destroyed by farmers (e.g. in Mexico, wild populations of *Cucurbita argyrosperma* which correspond to *C. argyrosperma* ssp. *sororia*; Castellanos Morales et al., 2019; Aguirre Dugua et al., 2020). Switches from weed tolerant traditional agriculture to industrial agriculture, where herbicide and pesticide use is prevalent, are severely affecting wild squash (*Cucurbita* spp.), chilli pepper wild relatives (populations of *Capsicum annuum* which correspond to the variety *glabriusculum*), wild cotton (*Gossypium aridum*) and teosinte related to maize (*Zea luxurians*). Conversion of natural habitat into arable lands, including for extensive agriculture, mainly affects those wild relatives associated with more pristine areas. These include the wild relative of chilli pepper, *Capsicum lanceolatum* (EN) and the wild relative of avocado *Persea pallescens* (EN), both of which grow in the highly threatened cloud forests of Mexico (CONABIO, 2010). Similarly, much of the pine-oak forest, which is the natural habitat of the wild relative of maize, *Zea perennis* (CR), has been converted to large avocado plantations (Sánchez et al., 2019) in order to supply the high demand of international markets (de la Fuente Stevens, 2014).

Invasive and other problematic species is the second most common threat process identified affecting 38% of taxa assessed (Figures S1 and S2). Notably, 28% of *Phaseolus* taxa are impacted by pests and diseases caused by native problematic species that can potentially worsen with climate change. Invasive alien species (e.g. grasses such as *Megathyrus maximus* and *Rottboellia cochinchinensis*) are affecting 23% of *Tripsacum* taxa (Figure 3), including the EN taxa: *Tripsacum intermedium*, *T. maizar* and *T. zopilotensis* and also the CR wild relative of cotton *Gossypium armourianum*, an insular species whose habitat is affected by introduced feral goats and cats (Wegier et al., 2017). Introduced genetic material threatens taxa of the genera *Cucurbita*, *Gossypium*, *Zea* and, to a lesser extent, *Tripsacum* (Figure 3), through hybridisation of genetically modified crops with wild taxa. This facilitates genetic erosion, modifies plant-insect interactions (e.g. *Gossypium aridum*, Wegier, 2013; *G. hirsutum*, Vázquez-Barrios et al., 2021) and causes habit change (e.g. *Cucurbita argyrosperma* ssp. *sororia*; Cruz-Reyes et al., 2015). Therefore, efforts to frame the use and release of living modified organisms in Mesoamerica (Acevedo et al., 2016) and to protect the species and areas that include the genetic diversity

of CWR taxa (DOF, 2012; MAGA, 2019) are of great importance in the region.

Biological resource use is the third most prevalent threat process, affecting 32% of the CWR taxa assessed (Figure S1). Though all *Vanilla*, 75% of *Capsicum*, 53% of *Persea* and 18% of *Phaseolus* taxa are affected by biological resource use, the drivers and stresses (i.e. the impact of a threat on a taxon) vary between taxonomic groups. All *Vanilla* taxa are targeted for collection, making direct use the threat driving them to extinction in the wild. In contrast, taxa of the genera *Persea* (e.g. *P. cinerascens*), *Phaseolus* (e.g. *P. albescens*) and *Capsicum* (e.g. *C. lanceolatum*) are unintentionally affected by the use of biological resources in the form of logging and wood harvesting activities (Figure 3), which result in both species stresses (species mortality) and ecosystem stresses (i.e., habitat conversion and/or habitat degradation; Figure 5).

Although CWR may hold solutions to help adapt crops to changing climatic conditions, they are not exempt to the effects of climate change themselves (Jarvis et al., 2008; Redden et al., 2015); 21% of taxa are affected by the effects of climate change (Figure S2), mainly through shifting and altering habitats and droughts (Figure 3).

While some threats can occur across multiple taxonomic groups, others appear specific to particular crop gene pools (Figure 3). For instance, the cotton wild relatives (*Gossypium aridum*, *G. davidsonii*, *G. harkensii* and *G. hirsutum*) are threatened by social unsettlement as they occur in areas where illegal crops are grown and it is unsafe to conduct research or implement conservation actions for those populations. Here we focused on the effects of individual threats on taxa, yet in many instances taxa are affected by multiple threats (Figures S1 and 3) that, in conjunction, can result in a diverse suite of species and ecosystem stresses (Figure 5). Although our analyses provide useful, taxon-specific information, tools to map the spatial distribution of threats would be valuable for conservation planning purposes.

4.3 | Knowledge gaps and research needs

Nineteen taxa (8.5% of all assessed) grouped in *Cucurbita*, *Persea*, *Phaseolus*, *Physalis* and *Solanum* are assessed as DD (Figure 2 and Table S1), meaning information is insufficient to evaluate their extinction risk and is comparable to other plant groups (e.g. cacti 8.7%). This is relatively low and probably attributable to the high availability of plant occurrence point data required for these assessments (Goettsch et al., 2015). Such data availability is the result of enormous efforts by numerous academic, governmental and nongovernmental organisations to collect, compile and analyse data and make it available, for example, through CONABIO's National Biodiversity Information System and the Global Biodiversity Information Facility (GBIF) (Troudet et al., 2017). However, large numbers of records remain undigitised and scattered, particularly for collections in El Salvador and Honduras. A few taxa are listed as DD because of taxonomic uncertainty (e.g. *Physalis*

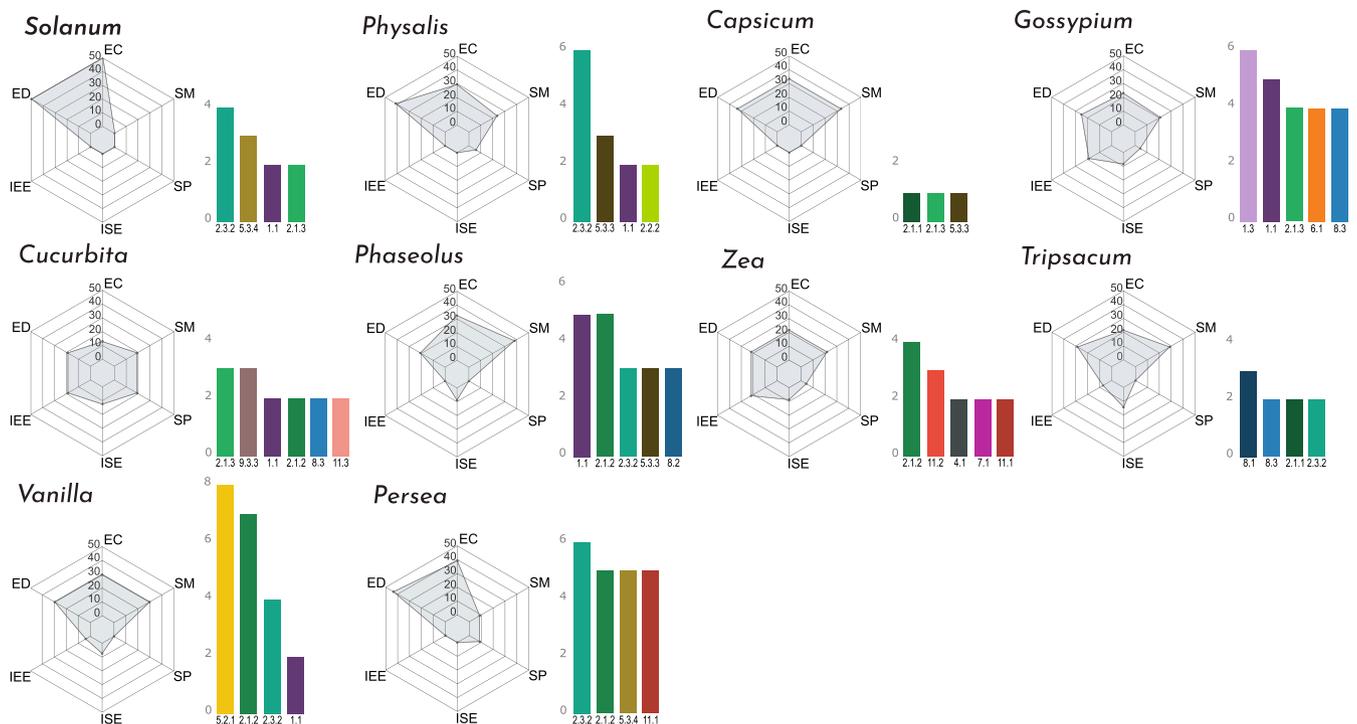


FIGURE 5 Proportion of species and ecosystem stresses caused by different threat drivers recorded for each taxon related to the selected crops. EC = ecosystem conversion, SM = species mortality, SP = species perturbation, ISE = indirect species effect, IEE = indirect ecosystem effects, and ED = ecosystem degradation. The bars correspond to the proportion of taxa impacted by the different threat drivers. Only the main threat drivers are shown. 1.1 housing and urban areas, 1.3 tourism and recreation areas, 2.1.1 shifting agriculture, 2.1.2 smallholder agriculture, 2.1.3 agro-industry farming, 2.2.2 agro-industry plantations, 2.3.2 smallholder grazing or ranching, 4.1 roads and railroads, 5.2.1 intentional human use, 5.3.3 unintentional effects of small scale wood harvesting, 5.3.4 unintentional effects of large scale logging, 6.1 recreational activities, 7.1 fire and fire suppression, 8.1 invasive alien species, 8.2 problematic native species, 8.3 introduce genetic material, 11.1 habitat shifting and alteration and 11.3 temperature extremes

longicaulis). However, for 17 taxa categorised as DD, the main constraint was the lack of accurate information on their distribution, population status and trend and on threats and their effects. Some of these taxa (e.g. *Persea sessilis* and *Solanum guerreroense*) were last collected over 78 years ago, while others are only known from their type localities (e.g. *Phaseolus leptophyllus*, *Physalis latecorollata*, *P. parvianthera* and *Persea sessilis*). Some taxa (e.g. *Cucurbita palmata*, *Persea rufescens* and *Solanum lesteri*) are reportedly known only from small areas or from a few specimens and are therefore likely to be threatened. For all these taxa, research to generate information on their distributions, threats and population sizes/trends is a priority (Figure 6) to assess their extinction risk. Field research to locate any remaining individuals or populations is also urgently needed for *Gossypium armourianum* and *Physalis tehuacanensis*, which have been identified as Critically Endangered and Possibly Extinct.

Given their importance for food security and adaptation to climate change and the level of threat they face reported here, there is a need to complete floristic inventories, identify CWR and assess their extinction risk, also including other countries in the region. Equally important is to promote research on their genetic diversity to inform in situ and ex situ conservation and to establish

their gene pool and characterize them to make these genetic resources more readily available for use in breeding programs (FAO, 2017). In addition, we need to identify those plants that are used along the domestication gradient, as occurs in Mesoamerica (Carrillo-Galván et al., 2020, and references therein). The most frequent research needs identified across all taxa and for threatened taxa were the generation of more information on the population size, distribution range and trend, followed by research/monitoring of threats and their effects on future population trends (Figure 6), which is also seen as a priority for European CWR (Bilz et al., 2011). For example, research is needed on the potential risk and monitoring of the laurel wilt pathogen (*Rafaella lauricola*) introduced by the redbay ambrosia beetle (*Xyleborus glabratus*), originally from Asia, which has caused vascular wilt disease and major mortality of redbay (*Persea borbonia*) and other species of Lauraceae in the United States (Harrington et al., 2008; Harrington et al., 2011). The most suitable areas for the introduction of *X. glabratus* into Mexico correspond to the tropical humid, tropical subhumid and some temperate regions, which will impact avocado production (Lira-Noriega et al., 2018) and also its CWR. Therefore, studies of synergic effects under global change scenarios and monitoring programs are important to design tailored CWR conservation actions.



FIGURE 6 Number of taxa in each International Union for Conservation of Nature (IUCN) Red List Category for which a research need was recorded in terms of (a) research, (b) conservation planning and/or (c) monitoring. Research needs are arranged in order of frequency. CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, DD = data deficient, LC = least concern

4.4 | Red listing CWR

There are at least three aspects that need to be considered when assessing the extinction risk of CWR following the IUCN Red List Categories and Criteria (IUCN, 2012), (1) taxonomic understanding of the taxa assessed—it is common that the taxon described at the species level belongs to the cultivated form and the CWR can be the same species, a subspecies or a variety. This depends on the evolutionary history of crop domestication; which can be complex processes in species that conform to wild-to-domesticated continuums (e.g. *Gossypium hirsutum*, Velázquez-López et al., 2018; *Capsicum annum*, de Luna-Ruiz et al., 2018) often resulting in different human modifications due to cultural diversity and management heterogeneity, which can hinder the identification of CWR. The IUCN Red List only includes assessments of wild species (i.e. excludes cultivated species), and in order to evaluate a subspecies, variety or subpopulation, the species as a whole needs to be assessed first. Therefore, a clear understanding of which taxa or populations are cultivated and which are wild is essential. (2) The generation of the native distribution maps of taxa is one of the most important steps for assessing their extinction risk. In this process, a critical step is data cleansing, for example, elimination of misidentifications, historical records and cultivated populations (Castañeda-Álvarez et al., 2016). Compared

with other components of biodiversity, this process is particularly challenging for CWR because they are often directly utilised by humans and thus purposefully transported and moved, making it common to encounter records of specimens outside their natural distribution. Furthermore, records may belong to taxa that have escaped from cultivation and present traits of the wild specimens without being strictly wild (e.g. *Phaseolus coccineus*; *Gossypium hirsutum*); these are known as ‘feral crops’ and when possible should not be mapped within the taxon’s natural range (d’Eeckenbrugge & Lacape, 2014; Guerra-García et al., 2017; Wegier et al., 2011). Records of hybrid taxa between cultivated and wild specimens should also be excluded when possible. Lastly, (3) participation of experts from the biological sciences, including botanists and conservationists, as well as from the agronomical sciences proved to be essential to gain a comprehensive view from biological, conservation, agricultural production and social perspectives.

4.5 | Indirect and direct uses of Mesoamerican CWR

Given the genetic proximity to crops, all taxa included in the present study have the potential to donate genes and therefore have indirect

utilisation potential. However, the taxa in the primary (i.e. same species as the crop) and secondary gene pools are those most closely related to crops and thus are more likely to be used as gene donors because of the relative ease of trait transfer to the crop and their conservation is commonly prioritised (Maxted et al., 2020). Having stressed this point, although taxa in the tertiary gene pool are generally more difficult to cross with the crop, they are also used by breeders if the CWR contains known and required adaptive traits. Sixteen taxa included in this study are already utilised in crop improvement, conferring crops resistance to viruses and pests (e.g. *Cucurbita lundelliana*, *Solanum bulbocastanum*, *S. stoloniferum*), drought tolerance (e.g. *Solanum pinnatisectum*, *S. stoloniferum*) or yield improvement (*Zea diploperennis*; Table S1 and also see taxa assessments on the IUCN Red List), and at least 34 taxa are being researched for this purpose (Figure 4).

Moreover, many Mesoamerican CWR are utilised directly for traditional uses such as food, fodder and as medicine (Figure S4). These taxa are collected from the wild (e.g. *Capsicum* spp., *Physalis* spp.) or are fostered in agricultural fields or their edges and are left to grow in home gardens (e.g. *Cucurbita* spp., wild *Phaseolus coccineus*, *Physalis* spp.). The direct uses of CWR present an opportunity to promote their conservation through the recovery of the knowledge around their traditional and sustainable use, including the acknowledgment of their importance for communities.

4.6 | CWR conservation needs in Mesoamerica

Ex situ conservation in gene banks is the most common conservation need identified across all assessed taxa, followed by site or area protection and habitat protection (Figure 7), especially for threatened taxa as 46% do not occur inside protected areas (Figure 8). Both of these conservation actions are of notable urgency for Critically Endangered taxa, especially for *Gossypium turneri*, *Zea perennis* and *Z.*

mays ssp. *mexicana* ‘Nobogame’ subpopulation and the EN *Zea mays* ssp. *huehuetenanguensis*. Given that at least part of the geographic range of a high proportion of Mesoamerican CWR taxa (60%) occurs within protected areas (Figure 8), there is a need to develop or adapt existing management plans specifically to actively monitor and manage CWR populations, as well as to raise awareness (Figure 7) among the general public and particularly protected area managers, about what CWR are and their importance (Holness et al., 2019). As stressed before, conservation of CWR presents different challenges and opportunities, which demand creative approaches for planning in situ or circa *situm* conservation. For many CWR, protected areas are not necessarily the best means of protection. Many taxa are adapted to disturbed areas where they are tolerated and often fostered; meaning that alternative conservation approaches are necessary. An extreme case is the EN *Zea diploperennis* which has an intricate relationship with fire cycles associated with slash-burn agriculture. Managing fire within the Sierra de Manantlán Biosphere Reserve, where the majority of the remaining populations occur, is challenging, and existing management plans are difficult to implement (Aragón Cuevas, Contreras, et al., 2019; Sánchez-Velásquez et al., 2002). *Cucurbita lundelliana* and *C. okeechobeensis* ssp. *martinezii* are rarely found within protected areas but thrive in nearby rural human settlements where people allow them to grow in home-gardens and along fences and on road sides (Sánchez de la Vega et al., 2019). The genetic diversity of *Capsicum annuum* var. *glabriusculum* in home-gardens in Guatemala was found to be as high as that found in gene banks (Guzmán et al., 2005). Therefore, in situ and circa *situm* conservation approaches for CWR should, where applicable, integrate the direct sustainable uses of taxa and expand beyond protected areas. Recently, the active in situ conservation of CWR outside protected areas by farmers within traditional farming systems has been reviewed alongside the level of public good financing that might be attached to reward the farmers for their CWR population management activities (Wainwright et al., 2019).

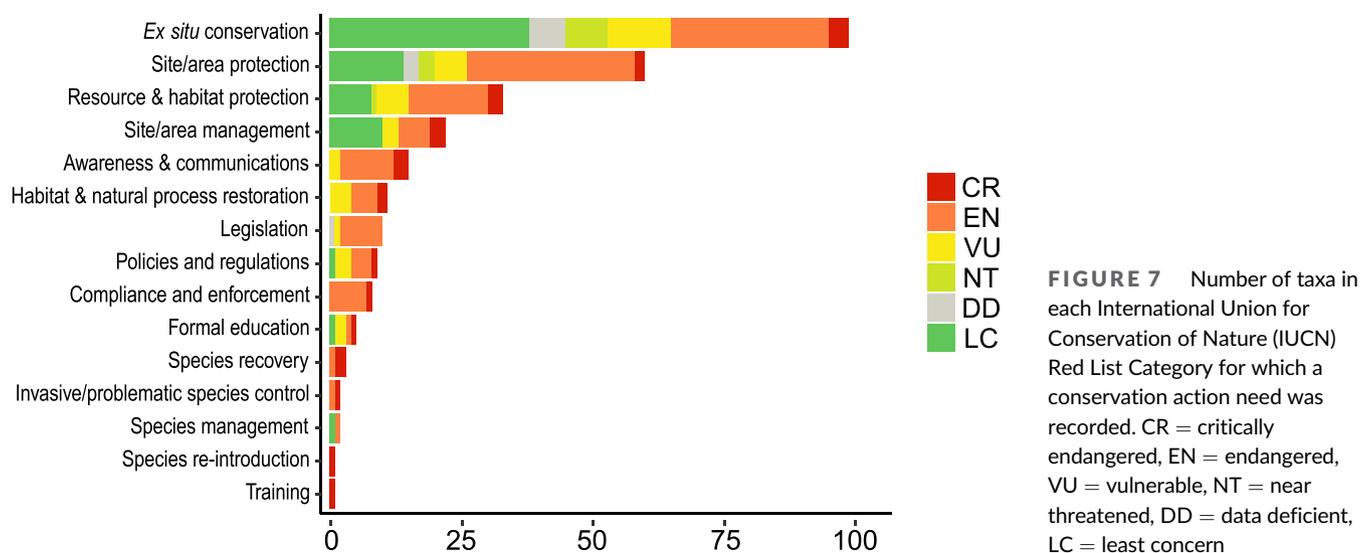
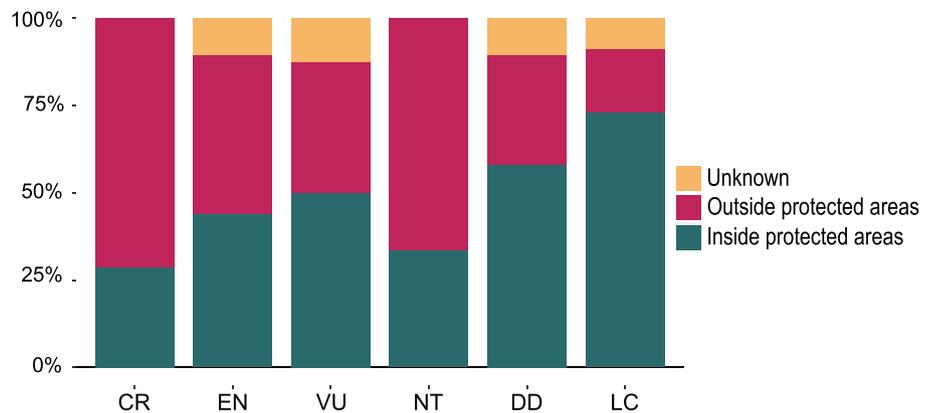


FIGURE 7 Number of taxa in each International Union for Conservation of Nature (IUCN) Red List Category for which a conservation action need was recorded. CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, DD = data deficient, LC = least concern

FIGURE 8 Proportion of taxa across all taxonomic groups that were recorded as occurring within protected areas, not occurring in protected areas or as unknown. CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, DD = data deficient, LC = least concern



4.7 | Final considerations

Conservation actions for Mesoamerican CWR are urgent given their high levels of threat and their importance in maintaining the genetic diversity that provide important resources for our diverse global food systems. The genetic complexes present in centres of origin like Mesoamerica are crucial to humankind's future well-being. Policies setting targets for plant species and specifically for CWR conservation (FAO Second GPA, GSPC, ITPGRFA, Aichi target 13, SDG Target 2) have helped align efforts, and continuation in post-2020 targets will be key to secure genetic resources.

Gains in biodiversity protection could be maximised if actions are implemented in areas with high concentrations of CWR and that ideally also contain taxa in more urgent need of conservation and that are threatened with extinction. However, special attention should be placed on Critically Endangered taxa given the limited overlap with areas with high numbers of EN and VU taxa. Conserving habitats such as cloud forests and seasonally dry forests should be a priority, and different types of policies to halt forest cover change or to foster natural regeneration could be promoted (CONABIO et al., 2019a, 2019b). These should include community-based forest management, carefully designed payments for ecosystem services programmes (Tyack et al., 2020), elimination of perverse agricultural subsidies (Whetstone, 1999) and holistic land use planning, among others initiatives that support rural economies and livelihoods (Chazdon et al., 2020; Min-Venditti et al., 2017; Wainwright et al., 2019).

The development of a multiscale and stakeholder approach is imperative to ensure that CWR species and their genetic diversity are well represented and preserved in herbaria, botanical gardens and gene banks and to strengthen knowledge and in situ conservation through the implementation of different policies and measures across landscapes (Estrada-Carmona et al., 2014; Hunter & Heywood, 2011). Efforts should take place especially within priority areas recently identified for Mesoamerica (Tobón et al., unpublished). This should aim at, for example, transforming agriculture into more sustainable food systems (see <http://teebweb.org/agrifood/>). Efforts to understand how staple foods (e.g. maize) and their genetic diversity depend on and/or are impacted by traditional production systems (CONABIO, 2017)

could prove valuable for the region, given that it harbours the totality of the genetic diversity of many crop gene pools. Conservation and knowledge of CWR can be significantly improved by developing programs to strengthen the collaboration between agencies dealing with species and habitat conservation, agricultural policy, breeding programs, conservation of genetic resources and indispensably with the communities that utilise them.

Mesoamerican people have been managing wild and cultivated plants for thousands of years using a diverse range of agricultural and in situ vegetation management techniques (Casas et al., 2007; Clement et al., 2021). One of the best documented examples is the ancient Mayans, who expanded and intensified agricultural production to sustain very large populations that altered most of the landscape (DeClerck et al., 2010, and references therein). Evidence indicates no apparent decrease in floristic biodiversity in the last 5000–6000 years, which can possibly be explained by the management of complex forest-agriculture mosaics such as those found today (e.g. less managed forests, agroforestry systems and abandoned agricultural land; Gómez-Pompa & Kaus, 1999; Correa-Cano, 2004; Dalle et al., 2006; Dalle et al., 2011). If agricultural sustainability and food security are to be attained in Mesoamerica, innovation has to involve the return to and maximisation of traditional and more diverse and sustainable production systems (CONANP, 2019). This must include the improvement of smallholder yields, supported through policies oriented to improve economic and social mechanisms (Godfray et al., 2010; Ibarrola-Rivas & Galicia, 2017) as well as gaining better understanding of their multicrop food production systems, such as the milpa. It is also necessary to develop systematic and novel ways of measuring productivity considering all the elements of these complex systems and the many ecosystem services and the benefits they provide in both the short term and long term (Bellon et al., 2018; González, 2012; Lopez-Ridaura et al., 2021).

This analysis has identified, within the selected taxa of Mesoamerican CWR, those most at threat. It also provides an in-depth understanding of the diversity of threats they face that should be expanded to other taxa and countries in the region. The collated occurrence point data and identified conservation and research needs can facilitate both in situ and ex situ conservation planning. We hope

that this will set the basis upon which national and regional multistakeholder conservation strategies of these vital resources can be developed.

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CONFLICT OF INTEREST

The authors declare they have no competing interests.

AUTHOR CONTRIBUTIONS

BG, TU-H, PK, FAG, ARC, RKB, NM, MMG and AJMH jointly created, developed and led the project. FAG, AA-M, VA, GA-I, FAC, CAP, JAC, GC-M, GC, ARC-T, LDL, DGD, AD-S, EPG-R, MG-L, EG-P, MH-A, BEH-C, MJ, SK, RL-S, FL-H, MM, AM-Y, JM, OO-G, MAO-R, MQ-C, AR, JARC, JJS, GSD, MS, WTN, MFT, OV-P, MV, AW and PZT contributed to the species assessment process. BG, TU, MECC and CMP conducted the analyses. BG, TU-H and PK drafted the manuscript and all authors commented and agreed on it.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are published in the supplementary material and The IUCN Red List <https://www.iucnredlist.org/>.

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