



Biophysical and Biocultural Upheavals in Mesoamerica, a Conservation Perspective: Mountains, Maize-Milpa, and Globalization

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Three upheavals shaped southern Mexico to Panama (SMP) biodiversity:

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1. The Great American Interchange that allowed migrations between the Neotropical and the Nearctic biogeographic realms;
2. human colonization with the generation of Mesoamerican cultures; and
3. the Spaniards' arrival and globalization.

Tectonic events generated a narrow piece of land with steep topography and high environmental heterogeneity, demanding high levels of local adaptation. Habitat size is usually restricted and reduced by frequent disturbances. Topography imposes few options for individuals forced to displace. Thus, extinction risks should be unusually high. Humans initiated an ongoing defaunation process and introduced the maize and the milpa, an itinerant maize-based slash-and-burn polyculture, which depends on revegetation to re-establish soil fertility. Also, the milpa is a most important pre-Hispanic legacy, a biocultural and landrace reservoir actively affecting landscape configuration, succession, soil development, and the genetic architecture of the species. Unprecedented human epidemics and soil, biodiversity, and culture erosion followed behind the Spanish aftermath and the subsequent globalization. > 63 million people and ≈100 ethnic groups inhabit SMP in 2020, which, with the biota, share the same problems of climate change, disturbance, and acculturation. SMP has been the scenario of severe climate change, fastest and deadliest extinction events (amphibians), a most spectacular exotic-species invasion (Africanized honeybees), and accelerated deforestation, defaunation, and acculturation. Biocultural conflicts between native and non-native people are globalization byproducts and sources of habitat destruction and species decline. Bottom-up initiatives are likely the best option for conservation in indigenous areas, whereas honest (i.e., with truly conservation intentions) top-down initiatives are helpful if the affected people are considered subjects (no objects) of conservation plans. We suggest some unique areas requiring conservation attention and analyzed current conservation initiatives. Not a single initiative is best suited for all conservation needs in SMP. Protection of all successional stages is critical for resilience

and revegetation. Conservation of the milpa system (crop fields and subsequent fallows) is an optimal option for minimizing tradeoffs between conservation and people needs and safeguarding traditional culture and local landraces but is limited to areas with indigenous people and may not work for species with large home ranges.

Keywords: Central America, climate change, extinction, Mexico, migration, secondary succession, traditional agriculture, bottom-up conservation initiatives

INTRODUCTION

The biota is an essential and unique earth component. Human-triggered disturbances have accelerated extinction rates unprecedentedly, severely affecting human welfare. Proposing effective ways to ameliorate such effects requires a deep understanding of the abiotic, biological, and social components on a regional and historical base. Such components are very complex in Mesoamerica and have generated extremely rich biodiversity far from being wholly described. Standley and Steyermark (1946) estimated 8,000 plant species just for Guatemala. Currently, important biodiversity projects have been underway. Flora Mesoamericana is perhaps the most ambitious, aiming to describe all the vascular plants in this region (Anonymous, 2022). The available information about biodiversity confirms early statements suggesting that Mesoamerica is among the world's richest biodiversity hotspots (Gaston and Williams, 1996; Thomas, 1999; Myers et al., 2000). Nevertheless, 300 endemic species of flora and fauna are threatened with extinction, of which 107 are critically endangered (Conservation International [CI], 2007). The Mesoamerica limits are arbitrary. Aside from the Yucatan Peninsula, the landscape is shaped by mountains that play a crucial role in their peculiar biodiversity and ecology. We focus our attention mainly on Southern Mexico mountain areas south of the Trans-Mexican Volcanic Belt, essentially from Puebla, Oaxaca, and Chiapas states, in Mexico, to Panama (SMP). The Trans-Mexican Volcanic Belt and the areas north of this mountain chain are different in geographic length and climate and so populous that they deserve separate analysis. The Yucatan peninsula also deserves separate analyses due to its flat terrain, distinct geology, and rich culture. This review examines the singularities of the biodiversity and conservation strategies of SMP from a historical, biophysical, and biocultural perspective.

THE INTRICACIES OF ADAPTATION FROM SOUTHERN MEXICO TO PANAMA

Adaptation in SMP mountains is particularly challenging for many species. Adaptation is an evolutionary response driven by natural selection, allowing sufficient survival, reproductive, and dispersal capacity to persist in time. However, adaptation is environmental contingent: an improvement to a particular environment usually is achieved at the expense of adaptation losses in other environments because of constraints or trade-offs (Kassen, 2002; Agrawal et al., 2010; Poisot et al., 2011). Spatial and temporal heterogeneities are expected to

foster conflicting evolutionary responses because organisms usually have limited resources to perform their vital activities. Heterogeneous temporal or spatial environments (fine-grained environments) are commonly associated with generalist species, while specialization is expected in environments with few spatial or temporal changes (coarse-grained environments) (Kassen, 2002; Poisot et al., 2011). These trends should be calibrated by the dispersal capabilities of the organisms and the dispersal barriers that the habitat imposes, limiting the organisms' displacements (O'Neill, 2001; Poisot et al., 2011). Limited migration facilitates specialization (Lenormand, 2002).

Habitat size is also a concern for conservation because it imposes the maximum limits on population size in each place. Reduced population size increases extinction risks by inbreeding, depression, loss of genetic diversity, and Allee effects (Frankham et al., 2002). Small habitat size can be caused by a steep orography generating significant environmental changes at few distances (Rull, 2011; Rahbek et al., 2019); spatiotemporal fluctuation in environmental conditions, often unpredictable, such as earthquakes (Garwood et al., 1979); anthropogenic causes, such as habitat loss and fragmentation (Fahrig, 2003); or long-term and continuous climatic events, such as global warming (Bell and Collins, 2008). The factors mentioned above, coupled with an intricate past, limited migration, and socioeconomic conflicts, make the SMP biota prone to extinction.

Physiography

Examining Myers et al. (2000) biodiversity hotspot list, three factors are relevant. First, a significant fraction of the hotspots has or are mountain areas (e.g., Tropical Andes, Central Chile, California Floristic Province, Madagascar, Mediterranean Basin, New Guinea, New Zealand, South Central China, West African Forests). Second, most are tropical (e.g., the Tropical Andes, Amazonia, Madagascar, and West African Forests). Third, some resulted from the collision of two continents (e.g., Sundaland, Hall, 2001; Indo-Burma, Uddin and Lundberg, 2004). Mesoamerica combines these three factors in a very narrow piece of land.

Mesoamerica is a dynamic geological landscape shaped by complex Earth surface processes relevant to biodiversity (Marshall, 2007). The most relevant are the tectonic collision of South America with the North American plates along a SE-NW axis; and the SW-NE collision between the Rivera, Cocos, and Nazca plates with the North American and Caribbean plates generated a subduction zone, the Middle America Trench, on the Pacific side and a very rough relief on the continent (Marshall, 2007). We used a digital elevation model to elaborate a

topographic profile of different cuts along SMP to illustrate the complex SMP topography using the QGIS 3.2 software (QGIS Development Team, 2017; **Figure 1**). On the Atlantic side, the mountains start from an often-narrow plain coast, if any, up to 150 m wide and reaching between 70 and 100 m elevation, followed by a sharp slope change (**Figure 1**). Elevation (1,700 m on average) changes dramatically at short distances. Most areas (71.5%) are above 100 m elevation: Mountains usually rise below the sea level on the Pacific side. The Atlantic side could be less steep with a plain coast. Low-steepness piedmont areas can be found along the coast, as on the Mexico/Guatemala border (Love, 2007). Also, the SMP terrain is shaped in part by the rivers' drainage (Marshall, 2007). Finally, sites above 3,000 m elevation are present but uncommon (0.6%).

From the above information, we can advance the following conservation recommendations. First, high elevation sites (>3,000 m) should be among the most endangered in SMP because they are uncommon and have a reduced surface. Second, the abundance of river systems (see Marshall, 2007) and the complex topography in SMP suggest vicariance and endemism in the freshwater biota as detected in fishes (Smith and Bermingham, 2005). Third, the biota of crater lakes in SMP has been developed in isolation and are abundant in endemic fishes, as in the Nicaragua crater lakes (Arkonada, 2019). Fourth, riparian ecosystems alongside waterways deserve particular attention because they are biodiversity-rich and might constitute an essential refuge for mesic flora before long-term drought events, such as climate change (Meave et al., 1991). *Alnus acuminata* (Betulaceae) is an example. This tree is common in humid secondary cloud forests (Velasco-Murguía et al., 2021), but it can become established in drier climates in gallery forests (e.g., Aguilar Luna, 2018).

Fifth, flat and low-steepness areas are scarce and ideal for urbanization or farming. In such places, native biodiversity should be highly endangered. Indeed, intermontane valleys are often the first places for human settlements (e.g., El Paraíso Valley, Honduras, Canuto and Bell, 2013). High fertility, high-soil moisture, and a relatively flat area make alluvial fans convenient for farming (Bull, 1968). Also, alluvial fans may generate terraces associated with distinct vegetation types that, in turn, influence ant diversity (Tehuacán Valley, Puebla, Ríos-Casanova et al., 2006). Thus, the biodiversity of alluvial fans and flat or low-steepen areas in SMP deserves more attention and conservation actions.

Climate

Macroclimate

The interaction between global climate and regional factors generates a strong climatic spatial heterogeneity in SMP. The Pacific slope is usually drier than the Caribbean slope by the winter regimes and the Caribbean low-level jet in summer (Sáenz and Durán-Quesada, 2015). This regional trend is locally modified by the complex orography producing significant climate differences at low geographical scales (Klinges and Scheffers, 2021). Mountain passes channel low-level winds and orographic rain. On the east side of the mountains, moist winds are often

retained; humidity is concentrated and condensed as fog or rain partially blocking the summer humid wind flow from the Caribbean Sea, usually the primary rain source. On the opposite side, the leeward, the air is dry; the mountains' cooling effect makes the air descend and turn warm, reducing the probability of rain (Sáenz and Durán-Quesada, 2015). Indeed, the precipitation gradient from the Caribbean Sea to the Pacific Ocean is reflected in paleoclimatic studies using $\delta^{18}\text{O}$ isotopic records, as estimator of the surface water content, and explained by the rain shadow effect on the Pacific side (Lachniet and Patterson, 2009). Summer convective storms and mid-latitude cold fronts ("nortes") contribute to the seasonal climatic variation (Poveda et al., 2006).

The role of vegetation on climate is important. In the tropics, vegetation modulates hydrological variability and the severity of interannual climatic variations (Poveda et al., 2006). One notorious example of the role of vegetation on climate is the low-cloud interception by tree canopies in tropical montane cloud forest areas (horizontal rain), having a significant impact on the hydrological cycle (Bruijnzeel and Proctor, 1995). The water trapped from the fog by the vegetation canopy eventually drops to the soil contributing between 2.4 and 60.6% of the total water input, based on estimations performed on cloud forests areas of the Central Cordillera of Panama (Cavelier et al., 1996). Horizontal rain can be irreversible destabilized with forest degradation in cloud forest areas (Hildebrandt and Eltahir, 2008).

Forest fires and pollutants can dramatically alter weather conditions, and their consequences may take place hundreds of kilometers away from their sources. Atmospheric pollutants such as smoke particles mainly derived from forest fires in Southern Mexico, for instance, can travel long distances causing severe weather effects in the United States, such as hail and lightning (Wang et al., 2009).

Large-scale fluctuations in air pressure between the western and eastern tropical Pacific, the southern oscillation index, generates warm events (ENSO, El Niño) or cold events (La Niña), disrupting SMP climate in complex ways (Poveda et al., 2006). These events affect ecosystems, agriculture, and the people livelihoods (Cane, 2005). However, land-surface atmospheric interactions can modulate the effects of such fluctuations. Lower evapotranspiration caused by El Niño event, for instance, can be exacerbated by deforestation reducing even more cloud production contributing to increase drought severity (Poveda et al., 2006). Thus, vegetation alterations can impact climate at local and trans-regional scales, implying that locally preserving forest ecosystems can have positive impacts at multiple spatial scales.

Long-term climate change has been so widespread in Mesoamerica and their putative effects are often dramatic, devastating, and an active area of research (e.g., Comisión Económica para América Latina y el Caribe [CEPAL], 2015). Studying climate change has been mostly implemented throughout the use of models, although the complex topography makes it difficult to provide accurate projections at local scales. Nevertheless, global warming and precipitation decreases are expected particularly during the dry season

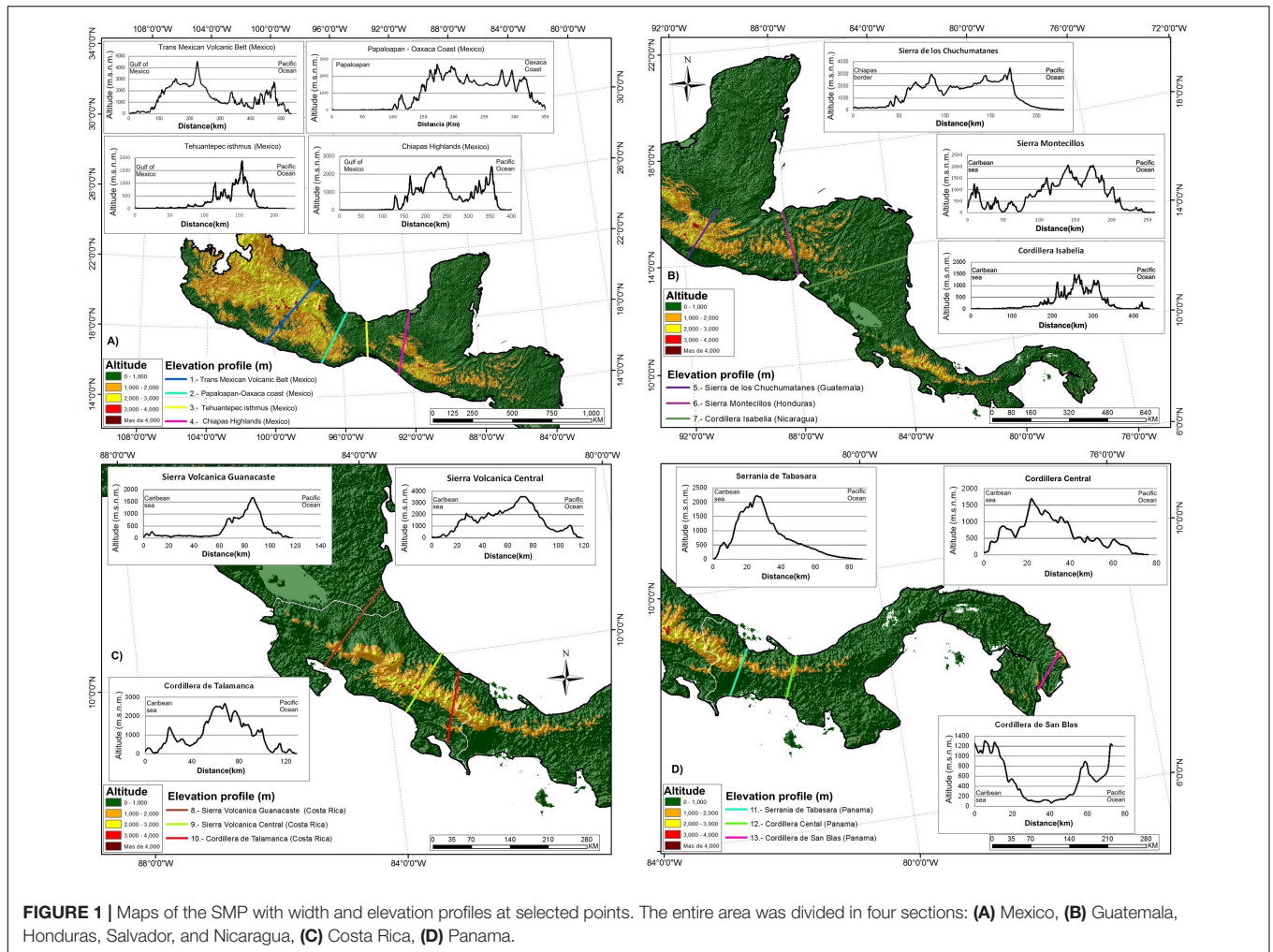


FIGURE 1 | Maps of the SMP with width and elevation profiles at selected points. The entire area was divided in four sections: **(A)** Mexico, **(B)** Guatemala, Honduras, Salvador, and Nicaragua, **(C)** Costa Rica, **(D)** Panama.

(Karmalkar et al., 2011). Climate change may interact with other climate events. The extreme 1997–1998 El Niño event caused an unusual severe drought in SMP, probably accentuated by global warming (Cai et al., 2015). In the following sections, we provide some examples of the impacts of El Niño and global warming in SMP, and their interactions with other factors.

Mesoclimate and Biodiversity

Mountain areas are tightly associated with high biodiversity, but the underlying processes are poorly known (Perrigo et al., 2020). Microclimatic variations contribute to explaining the high diversity. Slope angle, aspect, and elevation in montane areas generate tremendous spatial heterogeneity at shorter distances, affecting temperature and moisture, thus influencing species distribution, vegetation zonation, and ecosystem processes (Singh, 2018). In the tropics, such effects probably are more accentuated. Overlaps in temperature between different elevations are more reduced than in temperate areas where diurnal and seasonal variations are wider. Thus, because the tropics are less seasonal, tropical plants and animals should be adapted to a narrower temperature and elevational ranges than species living in temperate habitats (Janzen, 1967). Although not

a rule (e.g., Gadek et al., 2018), this trend is common (Smith et al., 2014; Sheldon et al., 2018). The combination of very high within-site environmental homogeneity with very high-between site heterogeneity likely fostered adaptations to only a subset of all the possible habitats in SMP. Thus, SMP species may face tradeoffs associated with climate, such as surviving moist areas or displaying drought adaptations to dry areas, or adapting to a warm environment in the lowlands or a cool climate in the highlands. Tropical plants may face these tradeoffs even at short distances favoring endemism. Indeed, the frequency of endemisms is high, as in tropical montane cloud forests (Rzedowski, 1991). Therefore, even if abundant in their habitats, species in the neotropics often do not have extended distributional ranges (e.g., Lieberman et al., 1996; Williams et al., 2010).

One consequence of this specialization is the diverse ecosystems of SMP mountains, likely climate-related, and often related to elevation (e.g., Taylor, 1963). Many vegetation classification systems have been suggested (e.g., Velázquez et al., 2016). Holdridge (1967) proposed a simple way to classify world life zones based on temperature, precipitation, and expected climax vegetation. Except for very extreme habitats, such as

tundra or desert, all world plant formations described by Holdridge (1967) are present in SMP mountains (e.g., Rzedowski, 1978; Grellier, 2000) and likely are explained by the wide climatic variation described above. Most vegetation types in SMP are tree-dominated. The height of the vegetation and the fraction of trees that lost their leaves during the dry season have been helpful for classification purposes. Evergreen tropical rain forests prevail in moist lowland areas characterized by their highest biodiversity and tallest trees. As elevation increases, sub-montane or montane cloud forests with a shorter stature are typical vegetation on the humid side of the mountains. At very high elevations, shorter alpine and paramo vegetations can be found. The deciduousness of the vegetation often increases as annual rainfall decreases. Tropical deciduous dry forests or scrublands occupy dry lowlands, and their composition is often linked to the substrate, as seen below. In contrast, pine, pine-oak forests, or shrublands are often common in less humid areas at mid-elevations (Taylor, 1963; Sawyer and Lindsey, 1971; Rzedowski, 1978). Because of the high rate of anthropogenic and natural disturbances, it is not always easy to discover what the original vegetation was.

Mountains display a high β floristic diversity between distinct elevation belts, in agreement with Janzen's (1967) statement (e.g., Lieberman et al., 1996; Zacarías-Eslava and del Castillo, 2010; Salas-Morales and Meave, 2012; Ramirez-Bautista and Williams, 2018; Martin et al., 2021).

Slope aspect effects can be significant for plants and vegetation in tropical areas, as reviewed by Singh (2018). These effects are expected to be more severe as steepness increases, and north-facing slopes are cooler and wetter in the Northern Hemisphere than south-facing slopes (Holland and Steyn, 1975). Slope aspect effects have been detected even at a low scale (10–100's of m) in a tropical dry forest in Central Valleys, Oaxaca, where succulent plants displayed the lowest floristic similarity between north and south slopes (Luis-Martínez et al., 2020). Considering slope orientation has been helpful for forest protection. For example, in Yeguaré, Honduras, the slope aspect is essential regarding fire risks, which tend to be highest on south-facing slopes (Cáceres, 2011).

High specialization in environmental conditions associated with elevation helps explain the vegetational altitudinal displacements detected by paleoclimatic studies. In the Cordillera de Talamanca, Costa Rica, the tree line displayed altitudinal shifts following the warming and cooling cycles of the last glaciations (Hooghiemstra et al., 1992). Fluctuating glacial and interglacial climates brought about changes in species ranges resulting in endemism and disjunctions (e.g., Wendt, 1987; Nixon, 2006). Such fluctuations may have left a genetic signature: reductions in population size associated with habitat cutbacks significantly reducing population genetic variation (Allendorf and Luikart, 2007). For example, *Pinus chiapensis* of Holarctic origin and endemic to southern Mexico and Guatemala (Farjon, 2018), shows an unusually low population genetic diversity compared with other pine species, including its nearest closest extant relatives: the North American white pines, *P. monticola* and *P. strobus* (Syring et al., 2007). Genetic bottlenecks derived from glacial fluctuations

and anthropogenic habitat losses may explain this result (del Castillo et al., 2011).

Quaternary climatic oscillations also affected species of Gondwana (southern hemisphere) origin. The highland *Podocarpus matudae* and *P. oleifolius* (Podocarpaceae) displayed strong evidence of population expansion during the coldest last glacial maximum; following glacial retreat, the populations contracted and became fragmented (Ornelas et al., 2019). The small population size of species whose populations declined after the last glaciation, coupled with current global warming and habitat destruction, likely put these species at higher extinction rates. Population size is correlated with genetic diversity, the raw material for adaptation (Allendorf and Luikart, 2007).

Microclimate, Microcosms, and Biodiversity

The complex three-dimensional variation observed in the mountains takes place in trees at a lower scale. The tree canopy creates multiple niches for various organisms (Ozanne et al., 2003). By being the SMP vegetation tree-dominated, the arboreal component of biodiversity is crucial. Batke et al. (2016) estimate 2,781 species of flowering plant epiphytes for Central America, likely contributing to ~20% of the vascular flora based on Cusuco National Park, Honduras, assessments. The extraordinary capacity of forest canopies to retain humidity and maintain a rich epiphyte community provides an additional reason for forest protection.

Arboreal organisms are small-scale ecosystems that may sustain multitrophic species assemblages. SMP harbors notable examples. The unusual pelage of the two-fingered (*Choloepus* spp., Choloepodidae) and three-fingered (*Bradypus* spp., Bradypodidae) sloths maintains a large community of epibionts including fungi, Cyanobacteria, algae, beetles that feed upon the algae and moths whose larvae consume the sloth dung; birds consumed some of such insects (Kaup et al., 2021). Tank epiphytes are another example: their rosette stores water and generate a micro-ecosystem. For instance, five *Tillandsia* (Bromeliaceae) species are associated with the lizard *Abronion oaxacae* (Anguidae), which feed upon insects that live in their tanks in Oaxacan temperate forests of Cruz-Ruiz et al. (2012).

Soil

Soil is essential in defining vegetation types and biodiversity. Soil properties are strongly correlated with climate variations associated with elevation, as detected in montane oak forest gradients in Costa Rica (Kappelle and van Uffelen, 2006). Even at the same elevation, soil dramatically changes. The thickness of the O horizon increased, whereas soil pH and N/P ratio decreased toward older stands in a tropical montane cloud forest area (Bautista-Cruz and del Castillo, 2005). Soil pH was found to explain species discontinuities of cloud forest species in Sierra Norte, Oaxaca (Domínguez-Yescas et al., 2020). Soil properties depend on the surface lithology, which in SMP is among the world's most complex (Marshall, 2007). For instance, pine forests in west-central Honduras are abundant on thin soils derived from ultramafic rocks (Grellier, 2000).

Igneous soils derived from volcanic activity or schists may occur close to limestone soils derived from calcium carbonate outcrops and platforms (Marshall, 2007). Limestone soils are chemically and physically different from those derived from siliceous rocks, often more acidic. First, they are more water-permeable, creating drier conditions than siliceous soils (Larcher, 1983). The edaphic aridity that generates limestone outcrops was evident by their higher proportion of xerophytic plants than that observed in adjacent vegetation growing on schist-derived soils (Nizanda, Oaxaca, Pérez-García and Meave, 2005). Second, high concentrations of CaCO₃ make calcareous soils very alkaline, imposing severe nutrient limitations for plants relative to soils derived from siliceous rocks with neutral or slightly acidic pH (Taiz et al., 2015). Litter production releases organic acids buffering the alkalinity of limestone-derived soils, thus reducing pH differences between calcareous and siliceous soils toward more humid areas. Not surprisingly, the vegetation in dry areas is very different even under the same climate when the geological substrate changes (e.g., Rzedowski, 1978).

Species' soil preference in semiarid habitats is a relatively well-known phenomenon (Goettsch and Hernández, 2006). The Tehuacán-Cuicatlán Valley (Puebla, Oaxaca) abundant in geological substrates (Mendoza-Rosales et al., 2013), endemisms, and the world richest columnar cactus diversity is an example (Dávila et al., 2002). Many of such species are endemic and edaphic specialists. *Cephalocereus columna trajani*, *Mitrocereus fulviceps*, and *Neobuxbaumia mezcalaensis* are examples of calcicolous species, whereas *Pachycereus weberi*, *Polaskia chende* grow on siliceous soils (Meyrán-García, 1973; del Castillo, 1996; Arias-Montes et al., 1997). At least 90 bird species, of which 56 are resident, have been found in columnar cactus forests in this valley (Arizmendi and de Los Monteros, 1996). Climate change and habitat destruction may severely impact the Tehuacán-Cuicatlán biota, particularly low mobility species or edaphic-specialist species. The complex orography and limited areas with similar edaphic conditions significantly reduce the opportunities for finding a similar place elsewhere.

Migration Options Are Restricted From Southern Mexico to Panama

The SMP complex orography in a very narrow piece of land and its SE-NW oriented continental main axis generates a dispersal bottleneck (Figure 1). These factors may account for the limited detected migration opportunities between North and South American landmasses, particularly the few historical human cultural contacts and diffusion of domesticated species (Diamond, 1999). For a North American species adapted to mid-elevations, migrating to South America would require passing to tropical areas with a warmer climate and few migration options.

Other geographic accidents in SMP may also function as dispersal barriers generating a phylogeographic structure, even those with flying capabilities. One example is the Nicaraguan Depression, a gene flow obstacle to the spot-crowned woodcreeper, *Lepidocolaptes affinis* (Furnariidae) (Arbelaez-Cortés et al., 2010). Limited gene flow and high spatial heterogeneity may explain SMP mountains' great diversity and

endemism. For instance, dispersal limitations could explain why the fresh-water fish species richness of small ranges exceeded large range fishes in south Mesoamerica (Smith and Bermingham, 2005). The Tehuantepec Isthmus was likely a significant source of lineage divergence and geographic discontinuity among selected plant, bird, and rodent species whose ranges are separated by this narrow piece of land (Ornelas et al., 2013). Topography complexity is not only an obstacle to migration and gene flow but also to cultural transmission as expressed in language (Cavalli-Sforza and Feldman, 1981). The given Zapotec names given to *Pinus chiapensis* (Pinaceae) in Sierra Norte, Oaxaca changes from village to village, separated a few kilometers from each other: *Suy du do*, *Ya yieri do*, *Ya guieri do*, *Ya guir do*, (approximate spelling) revealing a sort of linguistic drift akin to genetic drift (del Castillo and Acosta-Castellanos, 2002).

If species specialization is favored when the probability of a successful migration is reduced, then the frequency of specialists should increase with altitude. At high elevations, finding another similar or higher elevation place should decrease because high altitudinal belts are uncommon (Figure 1). The frequency of amphibian endemism, for instance, is higher in Mesoamerican uplands (Lips et al., 2005).

Migration is often the species' last resource before climate change. Temperature tends to decrease with both latitude and altitude. Thus, migration to higher latitudes or altitudes is a typical response for many plants and animals affected by global warming (Parmesan and Yohe, 2003; Colwell et al., 2008; Wilson and Gutiérrez, 2012). The common assumption that migration is an easy task should not take for granted. Latitudinal displacements fostered by global warming are prone to be bottlenecked by the orography and climate in SMP (Figure 1). For example, for an endemic species of the Chiapas Highlands affected by global warming, migrating to higher latitudes requires first passing to the low and warm areas of the Tehuantepec Isthmus before finding cooler northern regions. Global warming has forced the upward migration of species, such as *Pinus patula*, which displays morphological and physiological evidence of better performance at elevations higher than those at which this species is commonly distributed (del Castillo et al., 2020).

Furthermore, upslope displacement implies a higher exposure to UV-B light, which is more elevated at tropical latitudes (Caldwell et al., 1980). UV-B light induces mutagenic and cytotoxic DNA lesions (Rastogi et al., 2010). The mutagenic impact of displacements to upland areas needs to be studied but likely accelerates extinction rates. The low availability of migration routes and the lack or scarcity of better alternatives to become established reinforce the relevance of implementing conservation actions at high elevation areas.

Natural Disturbances

Disturbance events may permanently or temporarily disable the affected land to be eventually colonized by the original species, reducing the potential sites that a species can occupy. The expected distributional response to global warming based only on thermal biology overestimates the potential area that the focus species can occupy in the future (see Peterson et al., 2011).

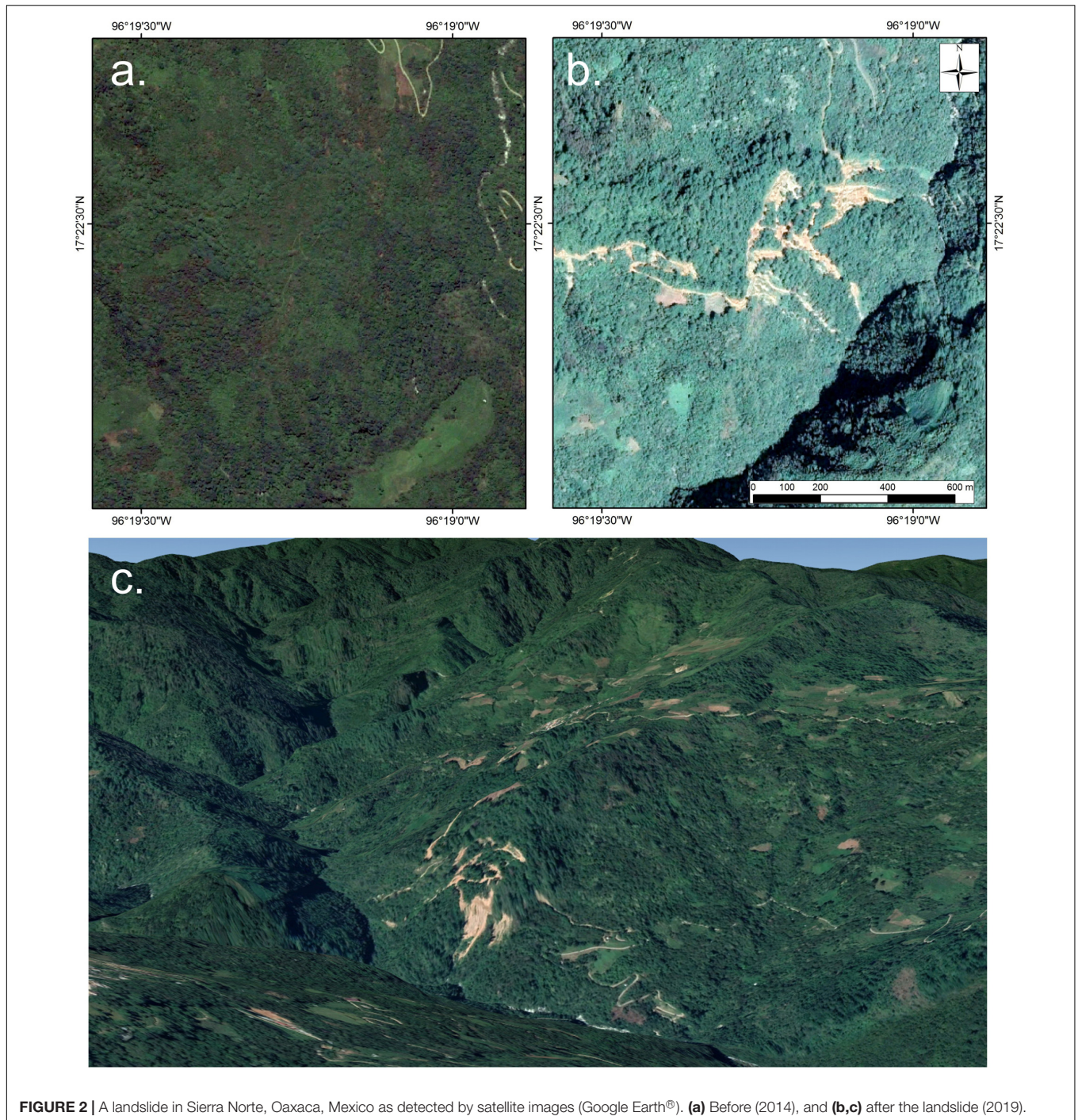


FIGURE 2 | A landslide in Sierra Norte, Oaxaca, Mexico as detected by satellite images (Google Earth®). **(a)** Before (2014), and **(b,c)** after the landslide (2019).

Considering such an overestimate is particularly relevant in SMP since disturbances are common in SMP. Regardless of their origin, human activities usually magnify disturbance effects.

Earthquakes, Hurricanes, Landslides, and Volcanoes

SMP is a seismic area. Consequently, earthquakes are common and critical stochastic events disrupting the biota. Steep slopes triggering landslides often magnify earthquake effects with disastrous consequences (Malamud et al., 2004). Land cover

change by landslides in SMP mountains is significant and challenging to estimate (Restrepo and Alvarez, 2006). In 1976, earthquake landslides denuded 54 km² of tropical areas in Panama (Garwood et al., 1979). Also, landslide effects interact with rainfall and soil type (Bommer and Rodríguez, 2002). Hurricane Mitch generated more than 500,000 landslides in Honduras, with a high death toll and economic impacts (Harp et al., 2002; Perotto-Baldivieso et al., 2004). Landslides are frequent on slopes higher than 40% (**Figure 2**); however, slope



FIGURE 3 | Poas volcano crater and plants damaged by the volcanic activity, Costa Rica (photo by R.F. del Castillo).

instability caused by deforestation magnifies landslide effects (Alcántara-Ayala et al., 2006). Landslide damages may not be permanent, but revegetation is slower than in less-steep slopes, even in humid areas (Dalling, 1994).

Eruptive activity is a common disturbance in SMP tightly linked to earthquakes. Its multiple manifestations involve lava effusions, gas-and-ash explosions, pyroclastic density currents, and lahars, as in Guatemala's Santiaguito lava-dome complex (Lamb et al., 2019). The destructive effects of lahars and pyroclastic density currents was detected by changes in the normalized difference vegetation index (NDVI) before and after the Santiaguito volcanic event; the sediment deposits affected tens of km² of land (Harris et al., 2006). Due to episodic releases of ashes, volcanic eruptions significantly decreased tree survival and growth near the Tacaná Volcano, Guatemala-Mexico border (Allende et al., 2020). The ashes and hot gases released often kill or damage the plants (e.g., Poas volcano, Costa Rica, **Figure 3**). Unusual baldness probably caused by volcanic ash ingestion was observed in the spear-nosed bat (*Phyllostomus hastatus*, Phyllostomidae) (Masca, Honduras, Divoll and Buck, 2013).

Strong winds often associated with hurricanes are common in SMP and interact with other disturbance factors such as landslides. The complex orography can locally increase wind speed (Wagenbrenner et al., 2016). The resulting power of the winds can destroy significant vegetation areas. This little-studied phenomenon in Sierra Norte, Oaxaca, Mexico, affected upper sections of the mountains' east side in 2016 (**Figure 4**).

Fires

Forest fires are frequent and often very destructive in SMP. The abundance of fire-adapted species suggests that fires are common in some semidry environments. In a frequently burned stand of *Pinus oocarpa* forest in Honduras, Clewell (1973) reported 124 species of flowering plants. High intensity fires are associated with abundant seedling density of this pine (Sola de Vega, Oaxaca, Juárez-Martínez and Rodríguez-Trejo, 2003). Furthermore, prescribed low-intensity burnings may reduce fire-hazards (Hudson et al., 1983). Nevertheless, not all semi-dry areas in SMP are rich in fire-adapted species, as the Guanacaste dry

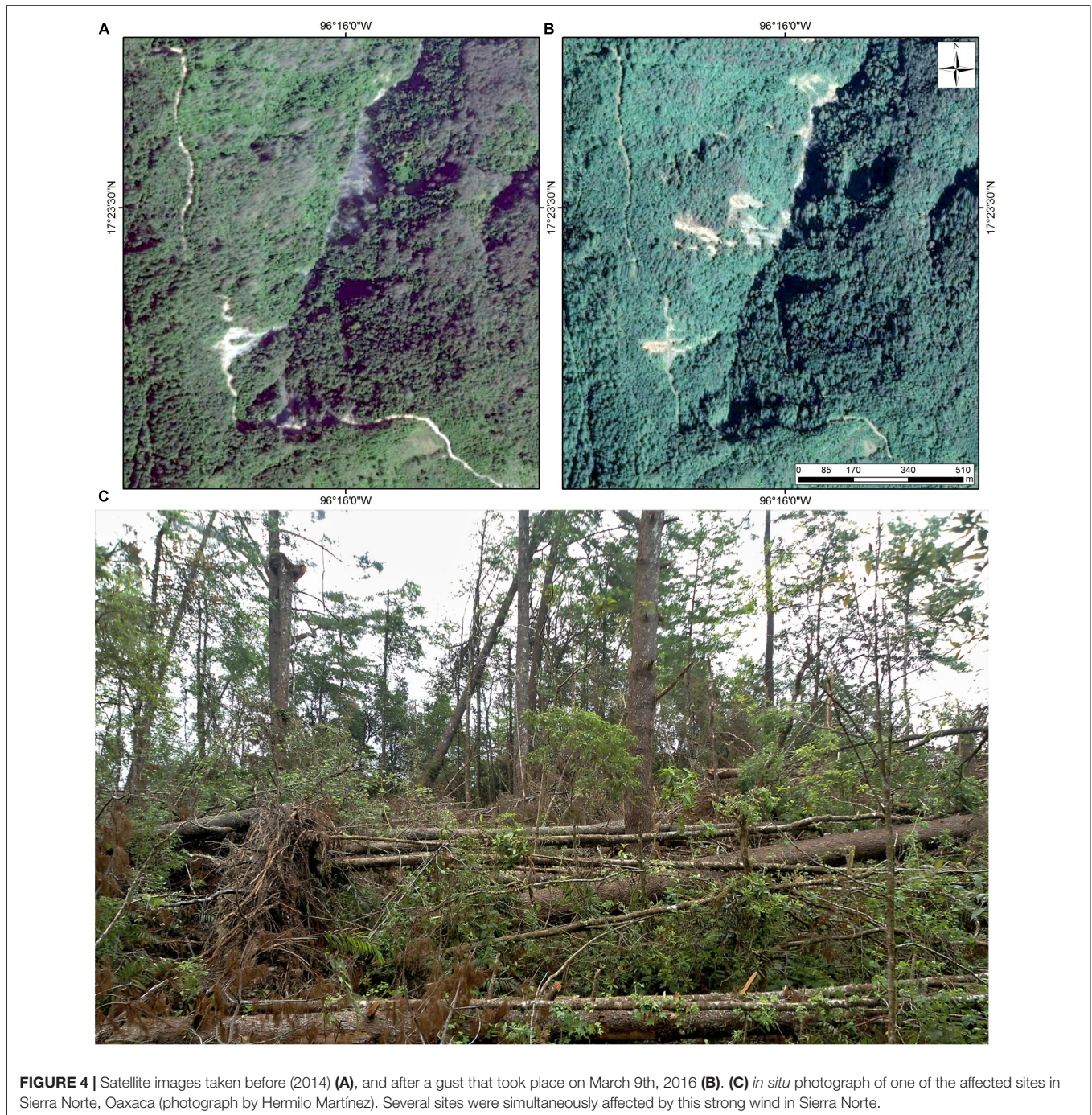
forest, in which case, fires can be disastrous. The high frequency of fires in this forest appears to be anthropogenic and linked to agricultural practices. In this case, fire controlling is essential for biodiversity conservation (Moline, 1999). Uncontrolled fires are a significant concern because of their high destructive power, outstanding aerosols, and CO₂ released into the atmosphere. Fire frequency significantly increased from 1995 to 2020 in Puebla, Oaxaca, and Chiapas (Comisión Nacional Forestal [CONAFOR] and Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT], 2021; **Figure 5**). Climate-related factors, including climate change, often exacerbated by human activities, could explain these increases.

Drought can trigger and amplify fire events. So far, the worst year in forest fires was in 1998 in northern SMP (Comisión Nacional Forestal [CONAFOR] and Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT], 2021). This year was anomalous dry owing to the 1997–98 El Niño event and is probably associated with an unusual increase in atmospheric CO₂ (Zeng et al., 2005). Under extreme climatic events, fires can be catastrophic in humid areas. Drought transformed the high amounts of litter accumulated by the slow decomposition rates in the humid forests' acid soils into a potent fuel that can become easily ignited, as detected in a tropical montane cloud forest, by Asbjornsen et al. (2005, Chimalapas, Oaxaca). The 1997–98 El Niño event likely triggered fires that destroyed 82–100% of the above-ground tree biomass in the areas they studied, being the elfin forest the most impacted. Fine-root live biomass was more affected in plants growing on the sedimentary than on metamorphic substrates (Asbjornsen et al., 2005). Thus, the effects of same disturbance event can significantly vary at local scales.

Pioneer Plants and Secondary Vegetation

Natural and anthropogenic disturbance events are inherent to SMP. Thus, preserving the biota involved in naturally restoring disturbed areas is essential for conservation. Successional ecosystems, such as landslides and lava domes, are included in the Nicaraguan FAO ecosystem classification (Arkonada, 2019). Secondary vegetation assures ecosystem recovery before disturbance events. Often, few species are common between young and old-growth stands suggesting that disturbances are a source of mortality for some species and establishment for others (Denslow, 1980). Seed germination can be accelerated after deforestation in an old forest in Costa Rica (Young et al., 1987) or in open seral stages or forest gaps in Chiapas (González-Espinosa et al., 2006).

It is easy to assume that pioneer plants have few ecological requirements owing to their capability to become established in open places. Nevertheless, climate change and habitat destruction may increase their extinction risks. Colonization potential was associated with heterozygosity, genetic diversity, and population size in the pioneer pine *Pinus chiapensis*, Pinaceae (del Castillo et al., 2011), some of whose small populations are at high extinction risk (e.g., Martínez-Carrasco, 1998). Lack of ectomycorrhizal fungi (EMF) in soil deter the establishment of pine species in open areas, requiring EMF inoculation from forest soils (e.g., Sánchez-Montalvo et al., 2005). Also, seed richness



in early successional depends on seeds dispersed from nearby stands in Costa Rica (Young et al., 1987). Chiapas highlands' late-successional stage forests may harbor remarkable diversity of EMF fungi, displaying high turnover rates between nearby sites suggesting the importance of older forests as EMF reservoirs (Pérez-López et al., 2021). Consequently, successful revegetation should depend on two factors: First, intrinsic characteristics of potential colonizers, such as their viability as influenced by genetic factors, and second, habitat configuration, through the spatial distribution of nearby sites as suppliers of essential seeds

and spores. Patches of young forests scattered in the landscape can maintain rare habitats through high stand turnover rates (Denslow, 1995).

Secondary neotropical forests have a relatively high resilience (Derroire et al., 2016; Poorter et al., 2016, 2021). Fostering early successional and old-growth forests offers the best balance between biodiversity conservation and landscape resilience. Vegetation recovery is affected by opposing factors such as disturbance frequencies, tending to decrease biodiversity and equitability, and soil seed bank inputs which tend to decrease

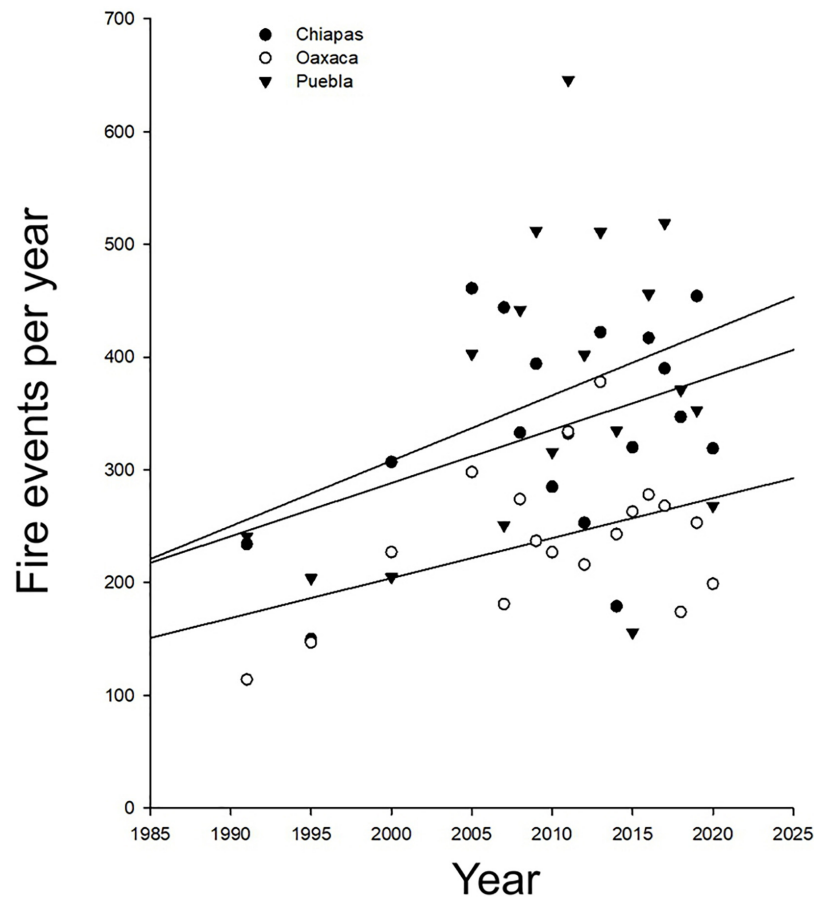


FIGURE 5 | Forest fires per year in the three mountainous states of southern Mexico: Puebla, Oaxaca, and Chiapas from 1995 to 2020. Data from Comisión Nacional Forestal [CONAFOR], and Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT] (2021). Fire frequency has significantly increased in recent decades, from 1995 to 2020, in Puebla, Oaxaca, and Chiapas [$F_{(1, 50)} = 10.26, P = 0.002$]. Fire incidence was significantly different among these states [$F_{(2, 50)} = 9.11, P = 0.0004$]. However, the non-significant state-by-year interaction suggests that common factors act in similar ways in the observed increase in fire events in these states.

with the age of successional stands (Young et al., 1987; Poorter et al., 2021). Thus, not a simple and universal method is likely effective for conserving frequently disturbed areas. Disturbance administration can be an option helping to protect biodiversity. For example, prescribed fires may reduce the intensity of other and more destructive fires and increase soil fertility (Nigh and Diemont, 2013; Alcañiz et al., 2018). A profound understanding of the successional process in SMP mountains is urgently needed, also providing an excellent opportunity for ecologists to have deep insights into such an important phenomenon.

HISTORICAL UPHEAVALS

The Great American Interchange

Several Neogene tectonic events shaped the complex biogeography of Mesoamerica and its rich biodiversity (Rull, 2011). The northward displacement of South America that eventually joined North America through the Panama Isthmus

in the Pliocene, the Great American Interchange, facilitated the encounter between the Neotropical and the Nearctic biogeographical realms, resulting in an impressive exchange of flora and fauna between the two subcontinents (Cox et al., 2019). This exchange generated an exceedingly high regional species pool (*sensu* Cornell and Harrison, 2014). The combination of high diversity in a heterogeneous habitat fosters more opportunities for species interactions and, thus, the generation of new niches, as Darwin (1859) and Wallace (1878) first noticed.

Climate change, particularly during glaciations and interglacial periods, played a significant role in the observed asymmetrical outcomes in mammalian exchanges when the land bridge was opened. During the humid interglacial period, in the late Pliocene, rainforests prevailed, facilitating south-north migrations from Amazonia into SMP. Through the following dry and cold glaciation period, savannas extended to tropical latitudes, and mammalian migration from North America outnumbered those from the south, probably because the temperate source area was larger than the south area (Webb, 1991). Also, invading North American carnivorous mammals

spread into SMP more than their South American marsupial counterparts, probably because they were more effective predators (Leigh et al., 2014). In birds, migration across the land bridge mainly was from south to north (Weir et al., 2009). In plants, ecological and phylogenetic analyses rather than paleontological records are used because of the paucity of plant fossils. Early studies suggest that plant exchanges between North American and South America were not as sharply outlined as birds and mammals (Simpson and Neff, 1985). A recent molecular phylogenetic meta-analysis revealed that angiosperms dispersed earlier than animals, before the isthmus of Panama was closed (Cody et al., 2010). Similarly, the divergence between North American and South American *Diadasia* bees (Apidae) took place before the formation of the Panama Isthmus and is consistent with that of angiosperms, based on phylogenetic studies (Wilson et al., 2014). The contrasting migration patterns detected among the studied taxa and the lack of information of many others warn about generalizing and urge more data and integrative research to explain the origin and diversification of the incomparable Neotropical biodiversity (Antonelli et al., 2018).

Human Colonization

Humans should severely impact the SMP mountain pre-Columbian environment. Early evidence of human settlements in SMP was found in Santa Martha, Chiapas ~11,340–11,280 BP, during the Pleistocene/Holocene boundary by Solís-Torres et al. (2021). The authors argue that the diversity of tropical ecosystems and species facilitated successful foraging and eventual transitions to agriculture. The same statement can be applied to most SMP, including semiarid areas (e.g., Valley of Oaxaca, Feinman and Nicholas, 2020). Many plants, including maize, squash, and beans, were poly-cultivated, as revealed by palaeoecological studies in Joya de Cerén, Salvador (Slotten et al., 2020). Still, more studies and multiple approaches are needed to provide accurate quantitative assessments of such impacts in Mesoamerica (Harvey et al., 2021a) and to understand the complex biocultural interactions that caused the rise and decline of pre-Columbian human settlements (Castanet et al., 2022).

Defaunation

Anthropogenic species extinction likely started very early after human colonization in SMP. Large animals characterized by low natality rates (small offspring number and longer time to attain reproductive maturity) are most threatened (cf., Begon et al., 1996). Radiocarbon dating studies conducted at La Estanzuela, Guatemala, suggest the possibility that the giant extinct gomphothere (*Cuvieronius hyodon*, Gomphotheriidae) coexisted with humans (Dávila et al., 2019). Also, the North-South displacements of early human colonizers through the American continent coincide with transgressive declines of the extinct megafauna consistent with Martin's (1973) overkill hypothesis (Surovell et al., 2016). The invention of agriculture might boost the megafauna extinction (Alford, 1970).

Ethnic Diversity

As of 2020, the total human population of SMP comprised > 63 million people and ~100 ethnic groups (Table 1). The ethnic

TABLE 1 | Human population and ethnic groups of SMP by country and state (Mexico).

Country/State	Total population (2020)	Ethnic groups
México, Puebla	6,583,278*	Náhuatl, Totonacos, Tepehuas, Otomí, Mixtecos, Ngiwa and Mazatecos. ****
México, Oaxaca	5,543,828*	Zapotecos, Mixtecos, Mazatecos, Mixes, Chatinos, Triquis, Cuicatecos, Huaves, Chontales de Oaxaca, Zoques de Oaxaca, Nahuas, Amuzgos, Chocholtecos, Tacuates, Ixcatecos, Afromestizos, Tzotziles ****
México, Chiapas	3,801,962*	Kaqchikeles, Jakaltecos, Mames, K'anjob'ales-Q'anjob'ales, Tojolabales, Tekos, Mochós, Tzeltales, Lacandones, Zoques, Tsotsiles, Ch'oles, Chujes, Akatecos. ****
Guatemala	14,901,286**	Achií, Akateco, Awakateco, Chalchiteco, Ch'orti', Chuj, Garifuna, Itzá, Ixil, Jakalteko (popti), Kaqchikel, K'iche', Mam, Mopan, Poqomam, Poqomchi', Q'anjob'al, Q'eqchi', Sakapulteco, Sipakapense, Tektiteko, Tz'utujil, Uspanteko, Xinka *****
El Salvador	6,453,553***	Ulúas, Lencas, Cacaopera, Chortís, Non-ualcos, Nahua-pipil y Pocomanes†
Honduras	9,904,61***	ch'orti', lenca, miskito, nahuas, pech, tawahka, tolupán, afrodescendientes, garifunas y creoles††
Nicaragua	6,518,478***	Miskitos, sumos or Mayagnas, Ramas, Garifunas, Creoles, Nahuatl, Chorotegas, Sutiabas or Hokan Sui, Matagalpa.†††
Costa Rica	5,094,114***	Huetar, Maleku, Bribri, Cabécar, Brunka, Ngábe, Bróran, Chorotega††††
Panamá	4,314,77***	Ngöbe-Buglé, Emberá-Wounaan, Naso (Teribe), Guna (Kuna), Bri Bri, Bokata†††††

*INEGI (2020), **INE-Guatemala (2021), ***Bif-aif (2021), ****SIC-MEXICO (2021), *****INE-Guatemala (2021), †Ministerio de Cultura (2021), ††EspacioHonduras (2021), †††Fedrick (2003), ††††IWGIA (2021), †††††Coba (2005).

diversity of SMP can be explained by: (a) the long occupation history; (b) the complex orography hindering migration, as migration routes were essential for agriculture dissemination (Zizumbo-Villarreal and Colunga-GarcíaMarín, 2010; González-Martín et al., 2015); and (c) habitat heterogeneity demanding local specific survival adaptations. These factors may have fostered habitat specialization by human groups in this coarse-grained environment, just as expected for any other species. Despite such a high ethnic diversity, most SMP ethnic groups have in common the maize (*Zea mays*: Poaceae) as the base of their subsistence (e.g., Boege, 2008; Hünemeier et al., 2012). By comparing modern words of related indigenous languages, Brown (2010) estimates that before 7,000 BP, maize and other managed plants became important enough to receive specific names by the speakers of Mesoamerican highlands.

Maize and the Milpa System

The Invention of Maize and Milpas

Maize cultivation in SMP has millennial roots: the eldest palaeoecological record stretches back to 6,250 BP in the Guilá-Naquitze Cave, Oaxaca (Benz, 2001; Piperno and Flannery, 2001). Also, ancient vestiges of maize cultivation have been detected throughout SMP: Panama (Piperno et al., 1985), Costa Rica and Nicaragua (Horn, 2016), Salvador (Dull, 2016), Honduras (Kennett et al., 2017), Guatemala (Castanet et al., 2022), Chiapas (Hammond, 2001; Rosenswig et al., 2015), and Puebla (Long and Fritz, 2001; Torres-Rodríguez et al., 2018). The presence of maize in palaeoecological records correlates with human genomic changes, sedentary lifestyle development, and farming techniques (Hünemeier et al., 2012). The traditional way of maize cultivation, the milpa, has been practiced by indigenous farmers till the present, giving a clue to how maize was cultivated during Pre-Columbian times (Horst, 1989; Bellon et al., 2018). Traditional milpa practices currently involve slashing and burning 1–2 Ha of forest fragments, little or null use of agrochemicals, no or few plugging, and long fallow periods (e.g., Pérez-García and del Castillo, 2016). A similar process of forest clearing and burning for maize cultivation was practiced during > 3,000 years in SMP as detected by palaeoecological studies (e.g., near Las Cruces Biological Station, Costa Rica, Clement and Horn, 2001).

The milpa is often defined as an itinerant, slash-and-burn, rainfed polyculture in which maize is cultivated with beans (*Phaseolus* spp., Fabaceae), squashes (*Cucurbita* spp., Cucurbitaceae), and other crops, with the tolerance of semi-domesticated and wild species, depending on the region (e.g., Altieri et al., 2012). It is a system of continuous improvement, locally adapted based on the conditions of the farmers' territory: sowing time and cultivated landraces depend on elevation, rainfall, and soil, even within the same mountain range (e.g., González, 2001). The farmer selects seeds from plants in their field during each cultivation cycle with the desired qualities for the next cultivation cycle (e.g., González, 2001). Since maize is an annual plant, the domestication process has been continued for several thousands of selection rounds, likely explaining the differences in the maize genome compared with those of their closest extant wild relatives, the teosinte (*Zea mays* spp.) (Tian et al., 2009). Also, genetic drift and founder events, through historical population contractions and expansions and genetic exchange between teosinte, shaped the maize genome (Wang et al., 2017). Consequently, the maize landrace diversity is enormous and distributed over a wide array of populations as this crop is broadly cultivated in highly heterogeneous Mesoamerica (Sánchez et al., 2000). However, novel techniques involving genotyping and phenotyping are needed to fully characterize the great variety of landraces (Prasanna, 2012).

Pedogenetic Processes

The milpa system generates a cycle of soil acidification during revegetation and soil de-acidification during vegetation burning (Bautista-Cruz and del Castillo, 2005). Soil acidification may contribute to the release of nutrients to the soil from the parent material, while vegetation burning makes them available to crop plants by increasing soil pH. By not relying on chemical

fertilizers, soil nutrients in milpas are often depleted after 2–4 cultivation cycles. Then, a piece of forestland is slashed and burned to initiate a new cropping cycle elsewhere (Boege, 2008; Toledo et al., 2019). The pace of soil recovery is slow and may take between ~45 and > 100 years after the cultivation phase in tropical montane cloud forest areas, depending on the soil property (Bautista-Cruz and del Castillo, 2005). Therefore, the milpa requires large areas of secondary forest stands for soil recovery (Watters, 1971).

Secondary Succession

Soil recovery is associated with long-lasting revegetation generating fragments of successional stages of different ages in the landscape. Guariguata and Ostertag (2001) provided the general patterns of secondary succession in the Neotropics, which basically are the same as those observed in post-milpa fallows. Only a few highlights are shown here. Herbs, shrubs, and tree saplings dominate the first vegetation stage, commonly called *acahual*. Traditional milpas that do not use plowing leave tree stumps from the previous fallow, enhancing a rapid revegetation (Pérez-García and del Castillo, 2017). The *acahual* is eventually replaced by pioneer heliophilous tree species, constituting the earlier forest stage, commonly dominated by pines (*Pinus* spp.) (González-Espinosa et al., 1991, 2000; Almazán-Núñez et al., 2016; Velasco-Murguía et al., 2021), probably because pines are pioneer trees distributed from the sea level to > 3,000 m elevation from dry to humid areas north of Costa Rica in SMP (Farjon, 2018). Alternatively, other tropical trees are abundant in the first arboreal successional stage, such as the balsa tree *Ochroma pyramidale* (Malvaceae) (low humid lands, Vleut et al., 2013) or *Mimosa acantholoba*: Mimosaceae, in lowland dry forest (Lebrija-Trejos et al., 2008). Pioneer species often facilitate (*sensu* Connell and Slatyer, 1977) the establishing of shade-tolerant species dominated by angiosperm trees (e.g., González-Espinosa et al., 1991, 2006; de la Luz Avendaño-Yáñez et al., 2014; Almazán-Núñez et al., 2016; Velasco-Murguía et al., 2021). Tropical ecosystems, such as dry forests, are resilient before disturbances but with a slow recovery rate in species composition (Derroire et al., 2016).

Landscape Configuration Changes

SMP landscapes appear to result from two opposing factors: common and diverse disturbance events and the subsequent revegetation. Assuming that most disturbances were localized, pre-human landscapes in SMP should be mainly composed of late-successional forests and, at a lower frequency, different fragments of early and mid-successional stages resulting from past disturbances and recently disturbed areas (Figure 6A). Two significant events altered this successional dynamic: first, the colonization and dissemination of indigenous groups into virtually all Mesoamerica; second, the Spaniards' introduction of new species and land-use methods.

Milpa itinerancy and the long-lasting successional processes required for soil recovery alter the pre-human SMP landscape in three ways: (a) introducing cropland fragments; (b) increasing early successional shrublands and forest fallow lands, and (c)

reducing old-growth forestlands (**Figure 6B**). Thus, the landscape was transformed into a checkerboard of field crops and associated fallows that constitute the milpa system (**Figure 7**). Landscape patchiness generates diverse niches for many species, as observed in other regions (e.g., Fuhlendorf et al., 2006). Indeed, the fraction of shared species among different-aged fallows is meager (e.g., González-Espinosa et al., 2006). Species of small non-flying mammals have different peaks of abundance at distinct successional stages (e.g., Santos Moreno, 2008). The species richness of shrubs, geophytes, and other low plants peaks very early during succession, in contrast to lianas and trees, which peak at later successional stages in cloud forest areas (del Castillo and Blanco-Macías, 2007).

Biotic Relationships, Domestication, and Co-domestication

The invention of the milpa fostered novel adaptations to the newcomer humans in the local biota. For instance, squash seeds were found in *Mastodon* (Mammutidae) dung deposits, suggesting that this extinct mammal was the original seed disperser. Domestication likely saved some *Cucurbita* species from extinction by humans fulfilling their dispersal needs, likely contributing to the survival of humans and squashes (Kistler et al., 2015). *Cucurbita*, milpas' common companion plants, are pollinated by specialist bees (*Peponapis* spp., Apidae). The fields where squashes are cultivated maintain a significantly different bee composition compared with adjacent non-cultivated areas (Baja Verapaz, Guatemala, Enríquez et al., 2015). As species richness increases in the maize agroecosystem, maize root colonization by arbuscular mycorrhizal fungi, AMF, and soil fertility (N, P) increases (Negrete-Yankelevich et al., 2013). The rhizospheric bacterial community associated with milpa maize changes at different cultivation stages (Rebollar et al., 2017). The huitlacoche or corn smut disease (*Ustilago maydis*, Ustilaginaceae) is an obligate and highly appreciated edible maize fungal pathogen. Molecular analyses demonstrate that domestication and early maize cultivation changed the huitlacoche population's genetic structure (Munkacsy et al., 2008). A maize landrace from Sierra Mixe, Oaxaca, displays extensive development of adventitious roots that secrete a sugar-rich mucilage that sustains nitrogen-fixing bacteria, according to Van Deynze et al. (2018). The authors estimate that 29–82% of this maize landrace nitrogen is of atmospheric origin, opening the possibility of developing nitrogen fixation for commercial maize agriculture (Sheoran et al., 2021). The roots of milpa-associated beans, such as *Phaseolus vulgaris*, host a great diversity of *Rhizobium* spp. (Rhizobiaceae) nitrogen-fixing bacteria (Martínez-Romero, 2003). Maize-bean intercropping increased *Rhizobium* nodulation, rhizosphere-soil P availability, and grain yield relative to monocultures on phosphorus-deficient soils (Latati et al., 2016). The above examples suggest that domestication in milpas have generated significant transformation in the genetic architecture of many species of different life kingdoms.

The fallows associated with the milpas are not only land pieces left idle for revegetation and pedogenesis. They are part of the milpa system in which the domestication of valuable species occurs. This process involves the forest species' manipulation

through selection processes aiming to enhance the desired properties of forest plants and, together with the entire milpa practice, constitute the co-domestication of forest and tree species (Wiersum, 1997).

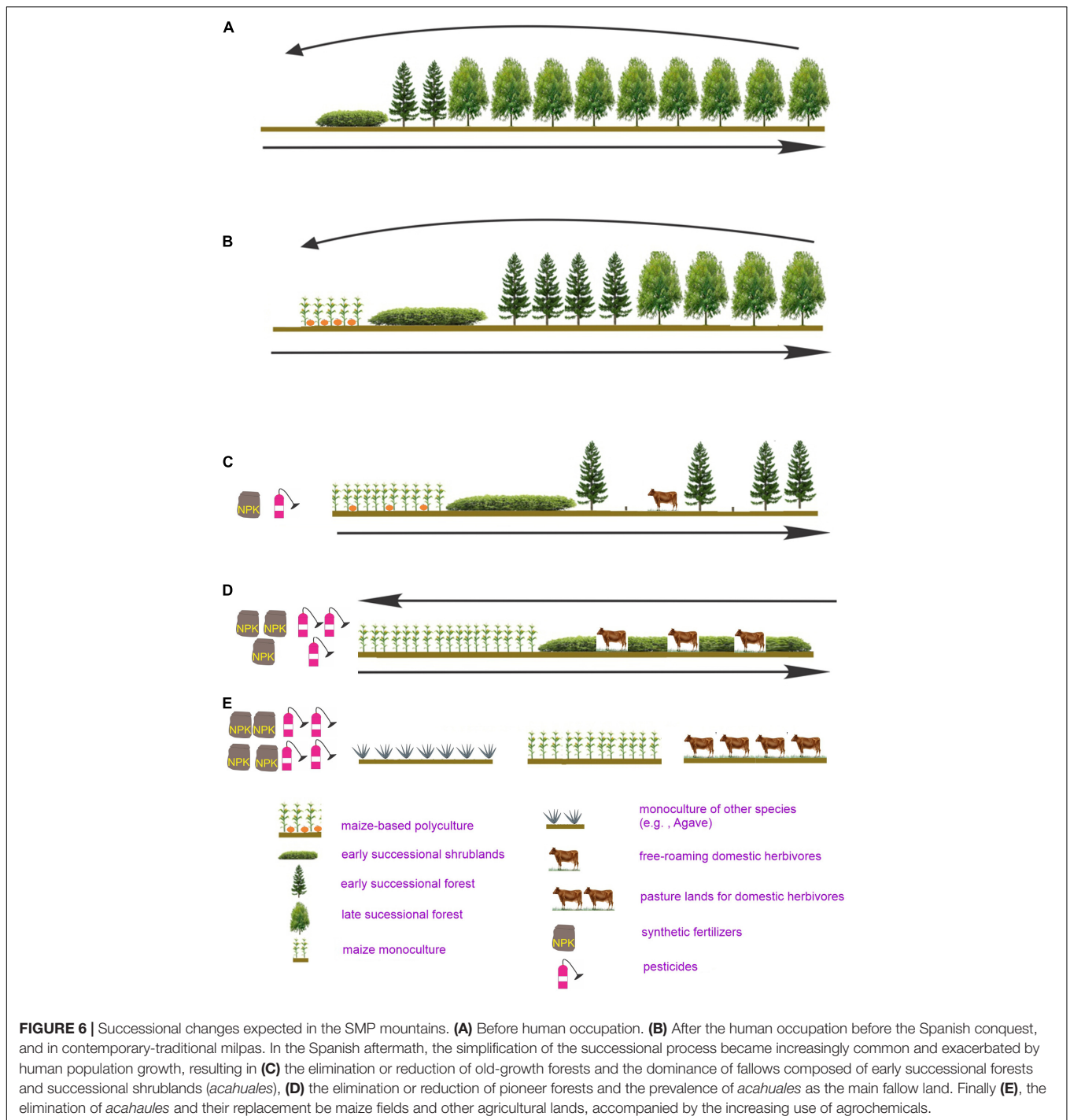
Indeed, the lands adjacent to crop areas, often fallows, were domestication scenarios of a great variety of plants in Mesoamerica, such as agave (*Agave* spp., Asparagaceae, semi-dry shrublands), avocado (*Persea americana*, Lauraceae, humid tropical forest), guava (*Psidium guajava*, Myrtaceae, warm secondary forest), tejocote (*Crataegus mexicana*: Rosaceae, temperate oak forest), and papaya (*Carica papaya*, Caricaceae, disturbed tropical rain forest) to mention few examples of the > 600 plant species domesticated in Mesoamerica (see Nieto-Angel et al., 1997; Caballero et al., 1998; Pennington and Sarukhán, 1998; Casas et al., 2007; Delgado-Lemus et al., 2014; Chávez-Pesqueira and Núñez-Farfán, 2017). In addition to the abovementioned example of *Cucurbita*, Janzen and Martin (1982) suggested other possible examples of neotropical anachronisms in plants such as avocado and cacao (*Theobroma cacao*: Malvaceae), which domestication could have helped to avoid their extinction and likely expanded their distribution ranges (Van Zonneveld et al., 2018).

Other Ecosystem Services

Many of the species' fallows are medicine, firewood, and construction material sources for the local people (Aguilar-Santelises, 2007; Diemont and Martin, 2009). Spatially altering polyculture fields within several vegetation types likely reduce pest numbers relative to a solid monoculture (Horn, 2012). Also, the movement of wind-dispersed weeds between different crop fields is likely hampered by vegetation fragments that lie between crop fields, probably reducing unwanted weeds (see Cousens et al., 2008). Properly managed milpas may contribute to soil fertility and long-term carbon sequestration (Nigh and Diemont, 2013). Milpa is also an adaptive system subject to improvement. Yield, for instance, can be improved by changing sowing density (van der Wal et al., 2006).

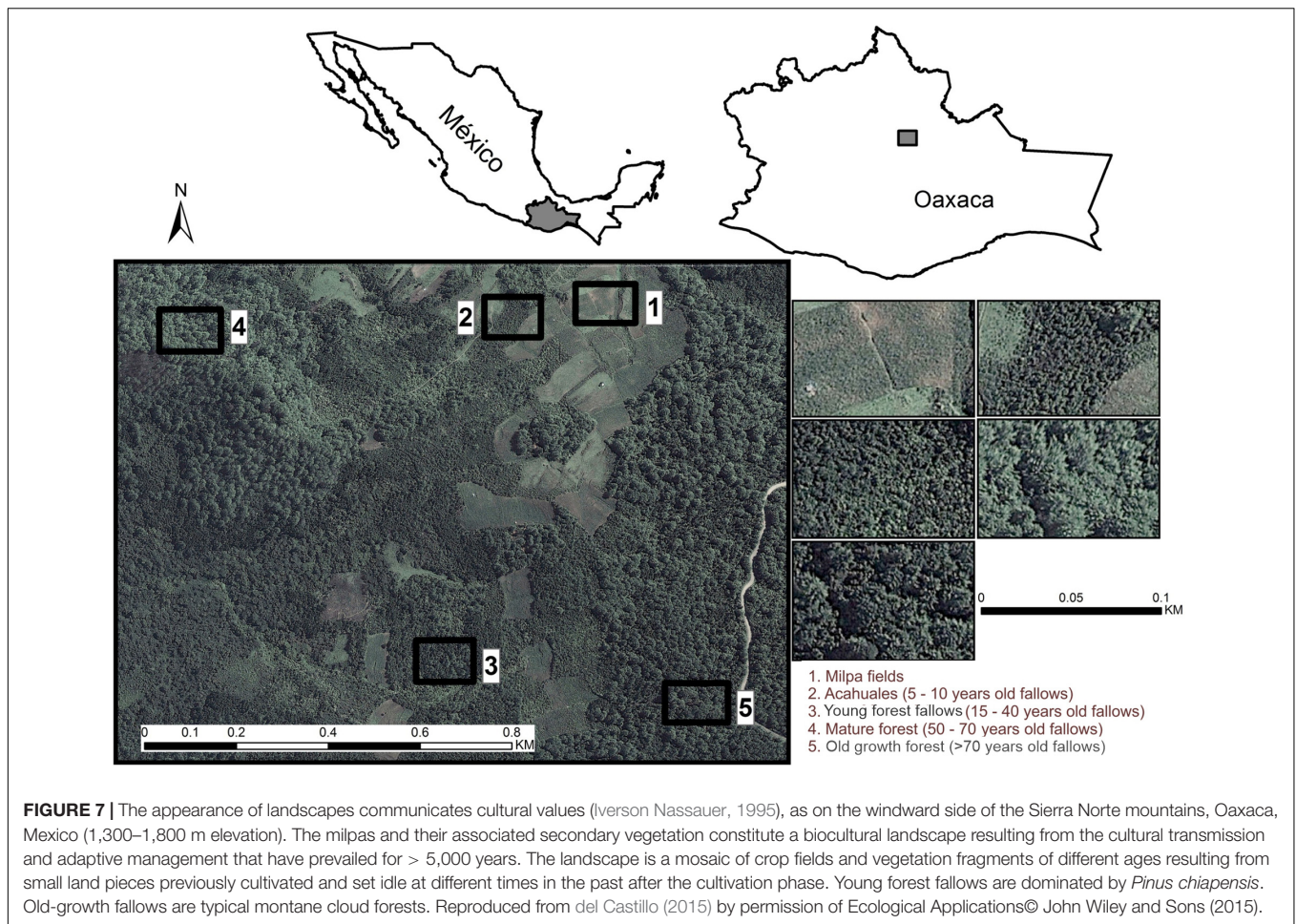
The Spanish Conquest and Globalization

The Spaniard's arrival initiated the last biological upheaval, implying a tremendous cultural supplantation through globalization. Like the other two previous upheavals, the Spaniards altered the landscape, life kingdoms, biotic relationships, and the genetic architecture of some species. In a few decades, mining, building new roads and settlements, the introduction of exotic animals, crops, and diseases started an ongoing transformation of the Americas (Challenger, 1998; Diamond, 1999). One of the fastest, earliest, and most dramatic biotic impacts was the 16th-century series of disease outbreaks that decimated the native human population, considered one of the worst and deadliest epidemics (Diamond, 1999). There are many gaps and speculations regarding these outbreaks. However, they were of continental dimensions and multifactorial (Cook and Lovell, 2001). After a 1,519–1,520 smallpox epidemic, a 1,545–1,576 outbreak followed, probably caused by a hemorrhagic fever that the Indians called *cocolitzi*, the word for pest in the Nahuatl language; these two outbreaks killed



between 12 and 25 million people in central Mexico (Acuña-Soto et al., 2002). *Salmonella enterica* (Enterobacteriaceae), a bacterium that causes enteric fever, is the most likely culprit of the 1,545 *cocolitzli* outbreak, based on a genome-wide study on pulp teeth skeletons from possible victims from the Mixteca Alta, Oaxaca (Vågene et al., 2018). Ten lesser epidemics followed, but the 1,545 severe epidemic coincided with an unusual drought after a wet period, which likely favored the proliferation of *cocolitzli*-infected rodents, and their subsequent displacements to human settlements searching

for food (Acuña-Soto et al., 2002). The decimation of the Indian populations paved the way for a fast cultural and biotic transformation, through the ongoing globalization process, with two significant stages: biocultural reduction followed by biocultural homogenization (Rozzi, 2018). Earlier effects of such changes have been documented in SMP. Severe deforestation caused by pine over-exploitation for shipbuilding wood was detected in the eighteenth century in Chimalapas, Oaxaca (De Bethencourt Massieu, 1960). Palynological records attested to the mixed hardwood forest decline in Chuchumatanes Highlands,



Guatemala, after the Spaniards' arrival (Harvey et al., 2021b). The Spanish conquest time coincides with a significant global decline in terrestrial vertebrates (Dirzo et al., 2014).

Landscape Changes: Simplification of Successional Dynamics and Ecosystem Losses

Globalization and high food demand have simplified the indigenous successional process by substituting old-growth hardwood forests with early secondary forests. This process has been referred to as “pinarization” as pines usually dominate early secondary forests north of Costa Rica (*sensu* González Espinosa, 2000; Galindo-Jaimes et al., 2002; **Figure 6C**). The litter derived from pines gives lower crop yields than old-growth forest plants (García-Barrios and González-Espinosa, 2004). This decrease would have augmented the demand for more croplands at the expense of forestlands, enhanced the use of synthetic fertilizers, or both. Increasing crop field connectivity by reducing forestlands should have boosted the dispersal of weeds and crop pests, thus increasing pesticide demand. Insecticide applications probably favor the decimation of squash bee pollinators, favoring monoculture. Eventually, forestlands might disappear, remaining *acahuales* and croplands, or only croplands, encouraging, even more, the use of agrochemicals. In the meantime, the pressure on forestlands should have increased by logging, firewood extraction, and freely roaming

domestic herbivores (**Figure 6D**). The above factors should have diminished the capability of pioneer forest plants to revegetate by reducing their effective population size, as described above, thus accelerating deforestation. Indeed, intensive agriculture and high human population density have transformed vast SMP forestlands into croplands, pasturelands, and monocultures (e.g., Chiapas Highlands, Luna, 2019; **Figure 6E**). However, estimating deforestation rates are challenging because of the complex dynamics of land use in forestlands, involving traditional land management practices, shade tree coffee, and sustainable management of forests for timber production (Noble and Dirzo, 1997; Bray, 2009).

Soil erosion could have been intensified by indigenous agriculture and aggravated by drought periods during pre-Hispanic times (Nochixtlán valley, Oaxaca, Mueller et al., 2012). This problem, however, was exacerbated by domestic animal overgrazing, deforestation, and agriculture after the Spanish conquest. For instance, El Salvador had lost more than 50% of the arable land by the end of the last century, remaining few forestlands (Leonard, 1987). Neotropical mountain forests have vanished in many places or were simplified by humans, causing a severe decline of species of which large-sized animals were the most evident cases (e.g., Figel et al., 2009), but not the only ones (e.g., Janzen and Hallwachs, 2019). Agricultural encroachment in the Bosawas Biosphere Reserve and Wawashan

Nature Reserve corridor in Nicaragua has contributed to the decline of the jaguar, the largest feline in America (*Panthera onca*, Felidae), and six large-bodied prey species, including white-lipped peccary (*Tayassu pecari*, Tayassuidae), collared peccary (*Pecari tajacu*, Tayassuidae), and red brocket deer (*Mazama americana*, Cervidae) (Petraçca et al., 2014).

Mammal defaunation, particularly of large-sized animals, has augmented since the 1970s. Nicaragua and Honduras, in the Neotropics, are the countries with the heaviest defaunation burden, according to Bogoni et al. (2020). The authors found that forest reduction, hunting, and increasing accessibility to wild areas explain this decline. Similarly, increasing secondary vegetation and croplands in Oaxaca cloud forest areas likely have enhanced the jaguar extinction risk (Briones-Salas et al., 2012). Also, old-growth forest decline should contribute to reducing epiphyte populations. Epiphyte colonization is a slow process observed in cloud forest areas in Guatemala (Catling and Lefkovitch, 1989) and Oaxaca; vascular plant epiphytes were the latest groups to colonize the tree trunks in a successional gradient (Cordova and del Castillo, 2001). Finally, old-growth forest plants and relict species probably are other essential groups deserving urgent conservation efforts.

The Complexity of Species Declining

SMP has been the scenario of accelerating species declines in the last decades, but the factors involved other than humans are unclear. The amphibian decline after the 1970s is perhaps the most dramatic (Alroy, 2015). The interactions between disturbance and pathogens might act synergistically to reduce amphibian populations (Whitfield et al., 2016). The rapid amphibians decline has been displaced from Costa Rica to Panama, becoming more severe in the mountains (Lips et al., 2006). The emergence of the fungal pathogen *Batrachochytrium dendrobatidis* (Chytridiomycota), which spread from Mexico to Costa Rica, coincides with the decline of the golden toad *Bufo periglenes* (Bufonidae) (Cheng et al., 2011). Multiple migration events and factors may account for the amphibian decline, likely transforming Mesoamerica into one of the world's worst centers of frog and squamate extinctions (Alroy, 2015).

Bark-beetle (*Dendroctonus* spp., Coleoptera) neotropical pine outbreaks exemplify how multifactorial interactions magnify species decline. Drought events may weaken and increase the vulnerability to the bark beetle in *Pinus pseudostrobus* trees (Gómez-Pineda et al., 2022). Temperature increases might account for south displacements of this insect, augmenting its distribution area (Armendáriz, 2012). In 2003, in the department of Santa Ana, El Salvador, a wildfire burned 80 Ha of *Pinus oocarpa* forest. The beetle severely affected the surviving pines the following year, whereas no affected pines were detected in adjacent unburned forests (Billings et al., 2004). Agrarian conflicts between municipalities magnify bark beetle infestation in Oaxaca by impeding the arrival of forest technicians to the affected areas; from 2010 to 2020, this plague affected 5,000 Ha of forestlands in this state (Agencia NEC, 2020).

Fire incidence increases fostered by global warming and human activities in dry forests of the Lomas Barbudal, Costa Rica, have reduced the supply of essential resources

for bees, undoubtedly impacting other species, such as the plants they pollinate (Barthell et al., 1993). Fragmentation has augmented the perimeter/area of the vegetation patches. Thus, the canopy exposure of the host trees to open areas in Sierra Norte oak forests, Oaxaca favors tree colonization by the epiphyte *Catopsis compacta* (Bromeliaceae). However, its long-term survival may be compromised by reductions in host regeneration by global warming and deforestation (del Castillo et al., 2013). Also, increasing the fragment's perimeter/area might favor the fragment shrub/tree species composition, probably because of the higher preference for shrubs to more exposed areas (Aguilar-Santelises and del Castillo, 2013). Deforestation and bat diversity decreases in Costa Rica appear to enhance male-biased parasitism in bat assemblages (Frank et al., 2016). Sex ratio bias diminishes the effective population size, increasing extinction probabilities (Frankham, 2005). Thus, disturbances affect the biota in complex ways.

Genetic Erosion in Crops

The replacement of landraces with modern cultivars causes genetic erosion and threatens food biosecurity (Van de Wouw et al., 2010). The presence of transgenes in local maize landraces is an example in SMP. Transgenic plants generated by transnational companies are common cultivars with high-added value. Transgenic maize is commonly cultivated in many countries since it is allegedly insect-resistant, herbicide-tolerant, non-allergenic, or toxic to animals and humans (Baktavachalam et al., 2015). In Mexico, its cultivation is forbidden, but transgenic maize is widely imported for consumption and inadvertently cultivated (McAfee, 2008). Since maize pollen is wind-pollinated, pollen flow between transgenic maize and local landraces is possible, mainly if cultivated in proximity (Bellon and Berthaud, 2004). However, seed flow carried out by farmers appears to be more critical (van Heerwaarden et al., 2012). Indeed, transgenes in local landraces were unequivocally detected in Sierra Norte, Oaxaca (Piñeyro-Nelson et al., 2009).

The proliferation of maize monoculture should have accelerated genetic erosion. On the humid side, at mid-elevations (1,400–1,900 m), yellow and blue maize landraces are cultivated in traditional milpas (Pérez-García and del Castillo, 2016). However, the state laws impose punishments upon anyone who, in forestlands, perform any other activity than forestry (Gobierno del Estado de Oaxaca, 2020). As such, a semi-permanent system has been implemented in the same areas. This system is characterized by fire suppression, agrochemical usage, and a monoculture using the white local landrace (Pérez-García and del Castillo, 2016). The substitution of milpas by maize monoculture may disrupt biotic interactions such as the ancient maize-microbe interactions involving bacteria of three phyla, which may benefit the plants (Aguirre-von-Wobeser et al., 2018). The risks of genetic introgression with transgenic maize could be enhanced as both the kernels of the transgenic maize and the white local landrace are similar and complex to sort out.

Exotic Species

The Spaniards' introduction of exotic mammals, mainly cattle, sheep, and goats, has two significant implications for the biota

TABLE 2 | Conservation sites of SMP that require urgent conservation and often are not considered, or conservation is logistically challenging.

	Main kind of protected species	Area	Dispersal success	Potential threatening factors	Social/Biocultural peculiarities
Alluvial fans	Endemic-non-endemic species,	+ /+++	++	Agriculture/grassing/garbage disposal/pollution	None
Crater lakes	Endemic freshwater species	+	-/+	Pollution	None
High elevation areas	Endemic species adapted to low temperatures	+	-/+	Global change	None
Low-steepness areas	Several kinds of species	+ /+++	++	Urbanization/agriculture/grazing/garbage disposal/extraction of plant material/invasive species	None
Rivers	Freshwater species, some endemic	+ /+++	++	Pollution/overfishing/invasive species/sand extraction	Require coordination between many authorities along the river
Milpa landscapes (cropfields and subsequent fallows.	Several kinds of species	+ /+++	+ (late successional) + /+++ (early successional stages)	Globalization	Very Important germplasm and biocultural reservoirs
Riparian ecosystems	Endemic/climate change sensitive species	+ /+++	+++	Agriculture/extraction of plant material/invasive species	Same as rivers
Areas of edaphic endemism	Edaphic specialists	+	+	Over collecting/grazing	Unknown

We used the following criteria. (a) Area: species inhabiting small areas are expected to be more threatened than those from large areas. (b) Dispersal success: we considered the most endangered cases in which the organisms have few opportunities to find alternative areas in the event of habitat destruction or climate change. (c) Main potential threatening factors. Finally (d), we identify some social/biocultural peculiarities that may hinder conservation plans or provide additional benefits that justify the conservation in such areas. Please note that this table is not exhaustive nor definitive, and more research and studies are needed to refine it. +, ++, +++, in the area column, is the relative expected area to protect. -, +, ++, + + +, in the dispersal success column, is the expected probability of migration if habitat destruction forces the target species to migrate to other places. from null (-) to very high probability (+++).

and the landscape. The natural vegetation or croplands are transformed into grasslands for raising these animals (Figure 7; Guevara and Laborde, 2014). This conversion implies significant organic matter losses resulting in greenhouse gas emissions (Aryal et al., 2018), likely altering the species composition of many species groups, including AMF (e.g., Alvarez-Lopez et al., 2019). Abandoned pasture lands in Panama, Costa Rica, Nicaragua, and Mexico may regenerate into the original vegetation. However, fires, long histories of forest clearance, and reduced abundance of remnant trees are limiting factors (Griscom and Ashton, 2011). Overgrazing and inadequate agriculture result in land erosion, which is challenging to lessen due to the lack of coordination between different political systems (e.g., Rio Lempa Basin, Honduras-Salvador border, Kim et al., 2005).

Second, when domestic mammals are left in natural ecosystems to roam freely, they compete with native herbivores, usually accelerating land degradation and extinction (Gillespie et al., 2000). However, domestic animals might contribute to the disperse seeds of native plants such as jicaro (*Crescentia alata*: Bignoniaceae) and guanacaste (*Enterolobium cyclocarpum*: Fabaceae) that presumably were initially dispersed by Pleistocene extinct megafauna (Janzen and Martin, 1982, but see Blanco et al., 2019).

There are many other examples of exotic species' introduction in SMP. That of honeybees (*Apis mellifera*: Apidae) is remarkable. First, they spread widely into the Americas and might

outcompete social-native stingless bees (Roubik et al., 1986). Second, an africanized variety later escaped from a Brazilian laboratory and rapidly expanded and hybridized with resident honeybees on the continent, considered "the most spectacular biological invasions yet documented" (Pinto et al., 2005). The africanized honeybees are more aggressive and adapted to tropical climates than their European counterparts, which genes were common in bees of the first invasion. Recent molecular genetics studies indicate that, after the second invasion, most genes of honeybees from Panama, Costa Rica, and Mexico are of African origin, suggesting an adaptive advantage of those genes over the original European genes (Zárate et al., 2022). Studies of the impact of such invasions on native bees are needed. Of particular importance is that non-native species introduction is another element that erode local culture (e.g., Simberloff, 2018).

Cultural Erosion and Bio-Cultural Conflicts

Landscape simplification decreases biodiversity and impacts culture and local human populations in SMP. Small indigenous landholders are frequently the most affected. For indigenous people, deforestation signifies losses of valuable species and services. A species' local extinction in an indigenous territory is of cultural impact, meaning the loss of a pedagogical element for the cultural transmission from parents to offspring, contributing to the erosion of the cultural heritage, and a loss of an ingredient to justify any attempt to preserve the ecosystem. Formal education has contributed to this erosion, as usually little or no

information provides about the peoples' local habitat. As such, the estimated traditional knowledge, for instance, tends to increase with the fraction of native-language speakers and to decrease with the level of formal education in Mixtecan municipalities, Oaxaca (Aguilar-Santelises and del Castillo, 2015). Therefore, one of the benefits of biodiversity conservation is restoring to the people what they have lost through the acculturation process (Allen, 1988).

Cultural conflicts between local people, and newcomer immigrants or non-indigenous people, are common in SMP. These conflicts increase deforestation and biodiversity losses. Illegal logging and fauna trafficking are examples (e.g., Richards et al., 2003; Honey-Rosés, 2009; Masés-García et al., 2021). In Chimalapas, indigenous people using community-based rules for forest management and conservation conflict with recent immigrants fomenting cattle rising (Payne, 2002). These examples stress the importance of the biocultural heritage for biodiversity conservation (Toledo, 2001).

Disturbances and Climate Change Impact Humans and Other Species

A recent survey across six different landscapes reveals that coffee and maize producers have noticed global warming and unpredictable rains reduce crop production (Harvey et al., 2018). As is the case of other species, migration could be an option for farmers facing climate change (see Lustgarten, 2020). In mountain areas, upslope displacements of agricultural lands are expected, probably at a higher pace than anticipated for many local species (Bush, 2002). Consequently, upslope migrating species may find reduced colonization options because of the small areas of high elevation belts and the risks that such areas could be partially or totally anthropized. Thus, humans, small landholders, and biodiversity are severely affected by common problems: disturbances and climate change. Holistic approaches seeking human welfare and biodiversity conservation can be challenging to design and apply, but their probability of success should be high (Harvey et al., 2008; Rozzi, 2018).

CONSERVATION CHALLENGES

Mesoamerican countries are officially aware of the importance of biological diversity, have ratified the Biological Diversity Convention, and implementing actions favoring conservation (Aguilar-Støen and Dhillion, 2003; Toly, 2004; Harvey et al., 2008). A deep analysis of conservation initiatives in SMP is beyond the scope of this review. However, two conservation kinds of initiatives are worth mentioning. They are entirely different, often yielding conflicting results reflecting the contrasting interests of the actors and economic sectors involved in formulating such initiatives.

Top-Down and Bottom-Up Initiatives

Top-down initiatives are mainly derived from top-level government agencies, often with the participation of foreign agencies. Perhaps the best example is the Costa Rican National Park Network, whose implementation began in the early 1970s

(Toly, 2004). This network has been recognized worldwide owing to its success in helping to protect critical biodiversity reservoirs and generating income through ecotourism (Valverde-Sánchez, 2018).

Some top-down initiatives aim to legitimize regional access to biodiversity resources and estimate their market exchange value (Brand and Görg, 2003). One of the missions of the Costa Rica National Institute of Biodiversity, established in 1992, is the production of diversity derivatives, such as genetic and biochemical resources that can be exploited by large multinational companies (Toly, 2004). Two different initiatives, the Plan Puebla-Panama, seeking regional free trade and development, and the Mesoamerican Biological Corridor with conservation goals, are additional examples aiming at the entire Mesoamerican region. These initiatives include the systematic search for biochemical and genetic information in nature to develop commercially valuable products (Toly, 2004). Such initiatives may promote biodiversity conservation, but the probability of success is low unless local people are considered the main actors and beneficiaries.

Bottom-up initiatives are based on the local people's participation and initiatives targeting biodiversity conservation, sustainability, and community benefits. Some examples include traditional (Pascual-Mendoza et al., 2020) or novel agroforestry techniques, sometimes with the involvement of academics (e.g., Rosales Adame et al., 2020); in other cases, design and maintain communal voluntary conservation reserves (Anta, 2007), perform forestry practices, balanced by processes of forest recovery, maintenance, and protection (Van Vleet et al., 2016; Pazos-Almada and Bray, 2018); or develop a network of communitarian germplasm banks (Mejía Lacayo, 2019). Most of the above-mentioned bottom-up examples are ruled by indigenous people. Bottom-up initiatives seldom are recognized outside the frontiers of the land at which they are aimed, even among the conservation scientific community (Van Vleet et al., 2016). The lack of recognizance leads to the false conclusion that the problems and threats to biodiversity are because of the dearth of conservation initiatives. Instead, most conservation problems result from conflicting perspectives and interests between the actual or potential primary users of biological resources and between the people who formulate the conservation initiatives.

Another difference between bottom-up and top-down initiatives is the conception of indigenous people's roles in conservation. For top-down initiatives, the presence of the people in areas to preserve is a nuisance. Thus, rural-urban migration, common in SMP, is considered an opportunity for forest recovery (Aide and Grau, 2004). However, urban migration of people practicing traditional forms of land management might clear the way for easy access to their lands, facilitating aggressive land uses, including intensive land exploitation and illegal logging, mining, hunting, and trafficking of species and drugs by reducing the number of local people who can safeguard the land. Holistic and more efficient conservation agendas must consider how humans should coexist with nature (Rozzi et al., 2013). Conservation policies should include the diversity's biological and cultural components since both are tightly linked (Pretty et al., 2009).

TABLE 3 | Comparative of selected conservation and management options currently applied in SMP mountains regarding their conservation potential, resilience, biocultural conservation, the potential for providing foods and other goods for human self-consumption (low, +, to very high, +++++), cash inflow (\$, low to very high \$\$\$\$), potential geographic applicability (e.g., elevation, climate), and potential applicability to be conducted by different human groups (all, local or outsiders; local, local people regardless their cultural background; indigenous, local people with local traditional backgrounds).

Selected conservation and management options currently applied in SMP mountains									
Conservation/land management options	Biodiversity conservation (old growth forest/late successional spp.)	Pioneer species/ Resilience	Biocultural conservation	Native maize landrace conservation	Food (human self-consumption)	Goods other than cash/foods (self-consumption)	Cash inflow	Geographic potential applicability	Potential applicability (human groups)
Classical reserves	++++	+	-	-	-	-	/\$\$\$\$\$	All	All
Agroforestry with maize	+	++	+	-/+	++	+	-/\$\$	All	All
Shade coffee	+ /++++	+	++	-	+	+	/\$\$\$\$	Humid-mid elevation	All
Communal forest plantations (native species)	++/++++	+	++	-	-/+	+ /++	\$\$/\$\$\$\$	All	Local people
Traditional milpa	+ ++	+++	+ ++	+++	++/++++	++/++++	-/\$	All	Indigenous people
Semi-permanent maize fields	-	+	-/+	-/+	++/++++	-	/\$\$\$	All	All
Communal reserves	++++	+ /++	++	-	-/+	-/+	-	All	Local people
Intensive agriculture	-	+	-	-	+	-	/\$\$\$\$	All	All
Induced grasslands for cattle/sheep	-/+ (*)	-/+	-/+ (*)	-	+	-/+	/\$\$\$\$	All	All

*Some grasslands in SMP have native trees as fences or for shadow. The table is preliminary and aims to induce more research.

Shade coffee plantations are another important non-traditional conservation and land management initiative practiced at mid-elevation in the humid areas of SMP mountains. This strategy may involve top-down and bottom-up initiatives, which, properly integrated, can benefit biodiversity and households (Méndez et al., 2010). Shade coffee plantations may maintain similar composition and structure to native vegetation, generating profits (Alvarez-Alvarez et al., 2021). However, the common use of *Inga* (Fabaceae) as a shade plant may decrease the proportion of native species, making it essential to fomenting the importance of these species in plantations among coffee farmers (Valencia et al., 2016). Also, the livelihood strategies and suitable types may influence the success of coffee plantations in maintaining biodiversity (Méndez et al., 2010). Coffee yield may negatively correlate with shade coffee plantations' tree diversity, thus requiring some compensation for yield losses (Perfecto et al., 1996). Furthermore, conflicts between economic revenues and conservation may transform more forests into coffee plantations (e.g., Tejeda-Cruz et al., 2010). Thus, shade coffee plantations can be a good conservation option but need careful monitoring and improvement.

Social Contradictions in Conservation Programs

In Costa Rica, laws that ban forest conversion into other land uses are valuable for conservation and are included in the conservation agenda (Harvey et al., 2008). As we mentioned above, such laws may not work in indigenous territories in SMP. For indigenous-dominated communities banning agriculture

practices in forest areas imply banning traditional milpas and is against their biocultural heritage. Such regulations favor monoculture practices, reduce the land's capacity to revegetate after cultivation (Pérez-García and del Castillo, 2017), and provide basic nutrient requirements for the people (e.g., López-Ridaura et al., 2021; Novotny et al., 2021). Please recall that in Costa Rica, 2.4% of the population is indigenous, compared to 41.0%, in Guatemala, for instance, and many dominated-indigenous communities live partially isolated in the mountains (Banco Mundial, 2015). Thus, the same conservation policies may have opposing effects depending on where and when they are applied.

Disagreements between local people and top-down initiatives often arise because local people are commonly ignored during the decision-making process (Toly, 2004). Certification politics of fair-trade initiatives such as the Fair-trade USA coffee plantations have generated economic insecurity and housing problems in Nicaragua (Raynolds and Rosty, 2021). Complex regulations against logging and institutional corruption in Nicaragua and Honduras, for instance, have fostered illegal logging. At the same time, the landowners of the affected forests, mostly indigenous groups, become the most prejudiced (Richards et al., 2003). The effects of land use regulation on biological resources may have transnational implications. More rigid and more efficient rules against logging in Costa Rica have generated timber shortfalls partially covered by illegal woods smuggled from Nicaragua (Richards et al., 2003). Furthermore, laws forbidding the commerce of threatened species may become very difficult to enforce. Some of such species have long been traditionally traded

in local markets, as is the case of some orchids in Mexico (Cruz-García et al., 2015).

At first glance, recent initiatives such as the Mesoamerican Corridor are promising. This initiative comprises establishing connectivity between ecosystems, landscapes, and the evolutionary processes from southern Mexico to Panama (DeClerck et al., 2010; Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México [CONABIO], 2021). However, the local people's participation in the planning and execution of this kind of project is crucial. This is not always the case, as shown in the Nicaraguan section of the Mesoamerican Corridor, where the participation of the local government and the impacted human groups is reduced (Finley-Brook, 2007). The main objective of such kinds of initiatives should be attending to real conservation problems and not a bureaucratic shield to mask other intentions (Grandia, 2007).

Other conservation alternatives, such as the payment for environmental services, may generate tradeoffs between people's needs and environmental goals in SMP (Kosoy et al., 2007; Calvo-Alvarado et al., 2009). Also, without considering people's needs, afforestation may increase forest cover and social marginalization (e.g., Costa Rica, Kull et al., 2007). The participation of local people in monitoring species is also an efficient alternative to protect wildlife, particularly large animals in danger of extinction, such as the jaguar in Oaxaca (Lavariéga et al., 2020). The successful establishment of reserves coupled with economic and political changes have fostered the recovery of tropical dry forest areas in Costa Rica (Hilje et al., 2015).

Local people participation in conservation initiatives likely guarantees long-lasting conservation efforts bringing genuine opportunities for involving bottom-up and top-down initiatives. The Área de Conservación Guanacaste is a promising example (Janzen and Hallwachs, 2020). Attending to local people's needs is essential in any serious attempt to protect natural environments; moreover, people practicing traditional farming have a profound ecological knowledge of their land (Altieri and Toledo, 2011). Therefore, studies of biological and cultural diversity, including traditional land management, ecological processes, and community-based social practices, are required to lay the foundations of effective conservation methods that simultaneously protect biological and cultural diversity, ameliorate disturbance events, and assure the welfare of the local people.

CONCLUSION

The biodiversity of SMP is the product of three upheavals:

1. The Great American Interchange and the subjacent tectonic events
2. Human colonization with the generation of Mesoamerican cultures and the maize-milpa system
3. The Spaniards' arrival and subsequent globalization

These events and frequent disturbances have dramatically altered the landscape spatial configuration, successional dynamics, biotic relationships, and the genetic architecture of some species. Frequent disturbances, habitat heterogeneity, poor

habitat connectivity, and habitat size likely reduce the capability to respond to environmental stresses.

The milpa system (crop fields and associated fallows) is one of the most important legacies of the pre-Hispanic human occupation in Mesoamerica. It is also an ecological and genetic engineering system actively affecting landscape configuration, successional, and pedogenetic processes, and an agent that modifies the genetic architecture of species of different life kingdoms through domestication. It is also a biocultural reservoir, a product of close links between biological and cultural diversity (Perales et al., 2005). Thus, conservation of the milpa system should positively impact food biosecurity, culture, and biodiversity. Also, preserving the milpa system is concordant with the recently promoted biocultural ethics that try to understand and foment coherent links between human habits and habitats (Rozzi et al., 2013), a challenging task in SMP.

The Spanish conquest and globalization led to unprecedented human epidemics and the erosion of soil, culture, and biodiversity. SMP has been the scenario of severe global warming, one of the fastest and deadliest extinction events (amphibians), one of the most spectacular exotic-species invasions (Afrikanized honeybees), and accelerated deforestation, defaunation, and acculturation.

Biocultural conflicts are expressed in conservation initiatives based on different perspectives and interests between the involved stakeholders, often ignoring the affected people. Local bottom-up initiatives can be the best suited for conservation in indigenous areas, whereas honest (i.e., with truly conservation intentions) top-down initiatives can be helpful if the affected people are considered subjects (no objects) of conservation plans.

We suggest some often-neglected unique habitats requiring conservation attention based on habitat size, expected probabilities of the protected species to migrate to similar habitats in the event of habitat destruction or climate change; habitat refuges, potential threatening factors; and social/biocultural peculiarities (e.g., requiring the involvement of local indigenous people or coordination between different authorities along the target area) (Table 2). We analyzed current conservation initiatives based on the target species and habitats, biocultural dimension, resilience, goods and cash generated, and applicability (Table 3).

Not a single conservation initiative is best suited for all conservation needs in SMP. Protection of all successional stages is imperative to assure enough resilience and genetic material for natural restoration. Conservation of the milpa system (crop fields and associated fallows) is an optimal option for minimizing tradeoffs between conservation and people needs and safeguarding traditional culture and local landraces but is probably limited to areas with indigenous people and may not work for species with large home ranges.

AUTHOR CONTRIBUTIONS

RC wrote the manuscript. RR-G analyzed the satellite imagery, designed the maps, and conducted documentary research. Both authors contributed to the article and approved the submitted version.

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