



Remnant sugar maple (*Acer saccharum* subsp. *skutchii*) populations at their range edge: Characteristics, environmental constraints and conservation implications in tropical America

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ABSTRACT

Relationships between environmental conditions and persistence of populations at edges of ranges should be useful for predicting consequences of climate change. We characterized environmental conditions of six disjunct sites in Mexico and Guatemala that contain all known relict populations of the most southern subspecies of sugar maple, cloud forest sugar maple (*Acer saccharum* subsp. *skutchii*). We also sampled abundance and basal area of all tree species, recording 164 species, 92 genera (61% tropical), and 54 families at these sites. Temperate genera decreased in number from north to south, but mixtures of temperate and tropical species were co-dominant with cloud forest sugar maple at all sites. For all species, basal area was 24–52 m² ha⁻¹ and density was 990–2986 trees/ha at the six sites. Cloud forest sugar maple comprised 7–43% of total basal area and 1–16% of total densities at each site. Populations of cloud forest sugar maple currently are vulnerable to environmental change. Anthropogenic disturbance is negatively affecting four populations, and regeneration is successfully occurring in only two sites. As a result, densities and basal area are much reduced compared to more northern temperate populations. NMS-ordination indicated that elevation and hurricane frequency are major environmental constraints related to abundance. Maple recruitment is associated with short hurricane return intervals that maintain higher elevation cloud forests in states conducive for regeneration. We establish the conservation status of cloud forest sugar maple at the southern end of its range relative to expected climate change and propose this subspecies be included in the IUCN-Red List.

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1. Introduction

Climate change can influence ranges of widely distributed species. For example, woody genera in North America were widely distributed throughout the boreal zone in the Miocene and Pliocene epochs (Graham, 1999a). Southward shifts in the ranges into Central America were associated with cooling of the climate during later part of the Pliocene (Graham, 1999b). More recent climate changes have reversed such shifts, causing poleward advances and upslope shifts to higher elevations along low-latitude margins of the range of temperate species (Colwell et al., 2008; Parmesan, 2006).

Currently, many temperate hardwood species that persisted at lower latitudes during glacial periods have fragmented populations at low-latitudes. Southernmost populations of temperate tree genera have become isolated and have diverged from more continuously distributed northern populations. Locally endemic species

and subspecies of broadly distributed temperate genera now occur scattered across a large region in Mexico and Central America (Rzedowski, 1996; Williams-Linera et al., 2003). One exemplary tree species with such a distribution at the southern end of its range is sugar maple, *Acer saccharum* (Sapindaceae, subfamily Aceroideae). *Acer saccharum* subsp. *skutchii* (hereafter designated cloud forest sugar maple) is the most southern representative of sugar maples in America. This subspecies has historically been considered a separate species (*A. skutchii*), but more recently has been recognized as a subspecies of *A. saccharum* (Murray, 1975, 1980). It now occurs as disjunct populations in widely separated cloud forests of small size, often only a few hectares in sheltered ravines on isolated mountain slopes in Mexico and Guatemala (Vargas-Rodriguez, 2005).

Populations at the low-latitude edge of the range of a species are likely to be environmentally constrained. Edge populations potentially experience environmental stresses such as droughts and extreme temperatures as a result of changing climate (Jump et al., 2010). These changing-toward-less-favorable habitats can negatively affect growth and fitness of individuals (Hampe and Petit, 2005; Pulido et al., 2008). Modifications in precipitation,

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cloudiness, and increases in evapotranspiration as a result of global climate change could affect the hydrologic cycle and the persistence of cloud cover in cloud forests (Foster, 2001; Nair et al., 2010). Such constraints are likely to occur in cloud forests inhabited by sugar maples. The abiotic environments, disturbance regimes, and plant community composition of cloud forests with maple at their range edge in tropical America are not known.

Shifts in local distributions of populations of cloud forest sugar maple to more suitable conditions along elevation gradients with ongoing climate change are likely to be hampered by human threats. Any environmental changes are likely to be exacerbated by diminution of suitable habitat. For example, less than 1% of the land in Mexico contains cloud forests, and approximately 50% of such habitat has already been replaced by other land uses (Chalenger, 1998). Additional major threats for Mexican cloud forests include illegal logging and conversion to pasture land and agricultural crops (Barradas et al., 2010). Cloud forest habitats containing cloud forest sugar maple, already fragmented and isolated, thus are likely at risk from human actions.

In this study we explored the composition, structure and conservation status of all known populations of *A. saccharum* subsp. *skutchii* in tropical America. We: (1) updated distribution records of the subspecies, (2) explored associations between local environmental conditions and cloud forest sugar maple populations, as well as co-occurring tree species, (3) characterized tree species composition of the forests, (4) determined the physiognomic structure and size class composition of each cloud forest sugar maple population, and (5) related natural and anthropogenic disturbances to current characteristics of cloud forest sugar maple populations. Using these field data, we explored the association of sugar maple with other disjunct temperate genera in cloud forests at the southern ends of the ranges of these species. We also assessed the threat of extinction of the subspecies using IUCN Red List Criteria and used these data to propose conservation measures for relict populations at their range edge in tropical America.

2. Methods

2.1. Field sites

We identified known populations of *A. saccharum* subsp. *skutchii* using the scientific literature, online databases, herbarium records, and field explorations (Murray, 1980; Jardel et al., 1996; Vázquez-García et al., 2000). We located all six sites where cloud forest sugar maple has been recorded using maps (1:50,000) produced by the Instituto Nacional de Estadística, Geografía e Informática (Mexico) and the Instituto Geográfico Nacional (Guatemala).

2.2. Field sampling methods

We compiled characteristics for all six sites containing cloud forest sugar maple. Location, latitude, longitude, elevation, slope aspect, mean annual temperature, mean annual precipitation, substrate, and whether sites occurred in a protected area are presented for each site in Table 1. The size of the area containing each stand sampled was estimated from field exploration during sampling and information provided by local inhabitants.

We sampled cloud forests at five sites during 2003 and one in 2006. Each forest occurred within areas ranging from 0.10 to 3 ha (Table 1). We used a stratified random design (Greig-Smith, 1983) to establish circular plots with an area of 100 m² in Ojo de Agua del Cuervo and Sierra de Manantlán sites and with 314 m² in the other sites. We sampled 3–30 plots comprising areas of 0.094–0.3 ha at the sites (Table 1). Their number, area and location

of plots depended on the size of the forest remnants; we sampled almost all of the extant populations of sugar maples at most sites.

We assessed local conditions at each site. Topography, physiographic unit, and rockiness data were gathered using categories from Olvera-Vargas et al. (1996) and Figueroa-Rangel and Olvera-Vargas (2000). Canopy cover was measured in the center of each circular plot using a spherical densiometer. Near the center of each circular plot, we removed the litter layer and took a soil sample (30 cm depth). Each sample was later spread in an aluminium tray, air-dried at room temperature, and sieved for laboratory analysis. The pH, electrical conductivity, texture, organic matter, nutrients (NO₃, NO₄, P, K, Ca, Mg, Mn, Fe, Zn, sulfates), cation exchange capacity, and moisture were analyzed quantitatively. Soil nutrients were measured using a Mehlich III extraction method, NH₄ with Kjendhal, NH₃ with Cadmium reduction, pH with a potentiometer, soil moisture with gravimetric method, organic matter with Walkley-Black, and texture with Bouyoucos methods (AOAC International, 1990; APHA-AWWA-WPCF, 1992; Agricultural Experiment Stations, 1998). Details of data are presented in Vargas-Rodriguez (2005).

We measured the extent of disturbance at each site. We recorded number of tree stumps, fallen trees, and standing dead trees. The extent of cattle grazing and damage from forest fires were assessed using five quantitative categories (none, low, moderate, high and severe) based on Olvera-Vargas et al. (1996) and Figueroa-Rangel and Olvera-Vargas (2000). Hurricane and tropical storm frequency for each site were compiled from US National Oceanic and Atmospheric Administration (NOAA) records (<http://www.nhc.noaa.gov/>). Using the number of hurricanes crossing the region and the time interval during which hurricanes were recorded, we calculated an average return interval between successive hurricanes for each site.

We measured, tagged, and mapped all cloud forest sugar maples in each plot. Abundance and basal area of maples was obtained by measuring tree individuals (≥ 1 cm diameter at breast height (dbh) at 130 cm above ground). Heights of juveniles (individuals <130 cm height) and saplings (dbh <1 cm and ≥ 130 cm height) were recorded in the 100 m² plot or in a similar-sized subplot concentric within each 314 m² plot. We also measured and recorded the species of all trees (≥ 1 cm dbh at 130 cm above ground) rooted in each plot.

We collected at least one voucher specimen of each tree species in the plots at each site. Species identifications were performed by the authors, as well as specialists. Nomenclature follows the Gray Card Index International Plant Name Index (IPNI). Herbarium specimens were deposited in the herbarium at Louisiana State University (LSU) and the Mexican National Herbarium (MEXU).

2.3. Data analysis

We obtained densities and basal area for species within plots using the field data. Both density and basal area were normally distributed (Shapiro–Wilks *W* test, $P < 0.0001$). Therefore, untransformed basal area and stem density were used to examine differences among sites using ANOVA. The Tukey–Kramer multiple comparison post-hoc procedure was used to identify significant differences between means. All tests were performed using SAS v8.02 statistical software (SAS Institute, 1999–2001).

We estimated the relative ecological importance of cloud forest sugar maple and other tree species at each site. We calculated the relative basal area and stem density (Curtis and McIntosh, 1951) and used them to estimate importance value indices (IVIs) (Kent and Coker, 1992) (Appendix A). Data summed over plots to estimate densities and basal areas of each species at each site are presented in Appendix A. We excluded frequency calculations from

Table 1
Characteristics of each site containing a cloud forest sugar maple population.

Site #	Country, State, Municipality, Site	Latitude Longitude	Elevation (m)	Aspect	Mean annual T (°C)	Mean annual precipitation (mm)	Substrate	Included in protected area	References	Total sampled area (ha)/ number of plots	Approximate area of cloud forest patch (ha)
1	MX, Tamaulipas, Gómez Farías La Colmena-Agua Escondida-Agua del Indio	23°03'N 99°12'W	1481	NE, S	16.3	927.7	Sedimentary rocks. Lithosol, Rendzina	Yes: El Cielo Biosphere Reserve (144,530 ha)	Puig and Bracho, 1987; SMN, 1995	0.188/6 plots	3
2	MX, Jalisco, Talpa de Allende Ojo de Agua del Cuervo	20°12'N 104°45'W	1798	N, NE, NW, S, SW	18.3	1294.6	Cretaceous, Plio-Quaternary, acid extrusive rocks. Dystric Regosol, haplic Phaeozem, dystric Cambisol	No	Vázquez-García et al., 2000; INEGI, 1974a, 1974b; SMN, 1995	0.3/30 plots	2
3	MX, Jalisco, Autlán de Navarro Sierra de Manantlán	19°36'N 104°17'W	1850	N, NW, W	18.5	1257.6	Intermediate extrusive rocks. Ferric Cambisol	Yes: Sierra de Manantlán Biosphere Reserve (139,577 ha)	Jardel et al., 1996; CETENAL, 1975, 1976; SMN, 1995	0.1/10 plots	1
4	MX, Guerrero, Coahuayutla de José María Izazaga Barranca El Silencio	18°11'N 101°24'W	2300	N, S	18	1090	Tertiary, extrusive igneous rocks. Eutric Regosol, chromic Luvisol	No	Vargas-Rodriguez, 2011; INEGI, 1983, 2001; SMN, 1995	0.126/4 plots	1
5	MX, Chiapas, Tenejapa Cañada Grande	16°49'N 92°30'W	2209	N, NE, E	13.4	1011.7	Cretaceous, Tertiary, and sedimentary rocks. Humic Acrisol, chromic Luvisol, and chromic Cambisol	No	Breedlove, 1986; Vargas-Rodriguez, 2005; INEGI, 1993, 1999; SMN, 1995	0.126/4 plots	0.15
6	GUAT, El Progreso, San Agustín Acasaguastlán El Balsamal	15°03'N 89°56'W	1750	S, SE, SW	-	-	Paleozoic rocks, lime and clay soils present in Sierra de las Minas Biosphere Reserve	Yes: Sierra de las Minas Biosphere Reserve (242,642 ha)	Vargas-Rodriguez, 2005; Fundación Defensores de la Naturaleza, 2002	0.094/3 plots	0.10

the IVI to prevent inaccurate estimation resulting from small numbers of plots in localities with small surface area.

We compiled size-class distributions for cloud forest sugar maple and all species combined at each site. We used 5 cm intervals to construct size categories for diameter or height. We calculated the proportions of maples and trees ≥ 1 cm dbh by dbh categories and the proportions of juvenal and sapling maple by height categories at each of six cloud forests studied. We then analyzed whether or not the size-class distributions of cloud forest sugar maple and co-occurring trees resembled an inverted-J distribution, which we assumed would indicate regeneration (Lorimer, 1980).

We identified generic affinities and species protection status using literature. We obtained affinities from Graham (1999a), Luna-Vega et al. (1988), Qian and Ricklefs (2004), and Rzedowski (1996). To determine species under legal protection, we used the Mexican and Guatemalan Endangered Species Act (CONAP, 2001; SEMARNAT, 2010), the International Union for Conservation of Nature-Red List of Threatened Species (IUCN, 2001), and the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2005).

We explored relationships of cloud forest sugar maple populations and co-occurring vegetation with environmental variables. We used Non-metric Multidimensional Scaling (NMS) ordination, an indirect analysis that does not involve assumptions of linear relationships among variables. We constructed two matrices: one for density of trees (164 species, 57 plots) and one for values of environmental and biotic variables (elevation, aspect, slope, topography, physiography, soil characteristics, natural, anthropogenic disturbance, species richness, and basal area) (44 variables, 57 plots). We recognized that variable numbers of plots at each site and interrelationships among some environmental variables might bias the ordination. We performed preliminary runs to determine appropriate dimensionality using a configuration of six dimensions, an instability criterion of 0.00001, 40 runs with real data, 50 runs with randomized data, and 100 iterations. Based on results, we selected a three-dimensional solution because additional dimensions resulted in only small reductions in stress. Then, a three-dimensional configuration with 1500 runs with real data was employed to evaluate stability. The probability that a three dimensional ordination would achieve lower final stress than

would be expected by chance was assessed with a Monte Carlo test with 1500 runs of real data, 900 runs of randomized data, a stability criterion of 0.00001, and 500 iterations. We used Sørensen's distance measure. We used Pearson correlation coefficients to evaluate the relationship between the identified axes of the ordination and the environmental variables. Only variables with scores on either axis larger than a 0.250 cutoff value were plotted to overlay only a few most relevant vectors. We used PC-ORD v4.27 software for the analysis (McCune and Mefford, 1999).

We further examined significant correlations obtained in the NMS ordination using a direct analysis. We evaluated the hypothesis that soil, disturbance, climatic and geographic conditions were associated with density and basal area of cloud forest sugar maples and co-occurring trees. We examined the strength of relationships between density and basal area in all forests with the environmental variables identified with NMS, as likely to be important, using ANOVA. Only significant correlations are presented.

3. Results

All six populations of *A. saccharum* subsp. *skutchii* occurred in cloud forest that ranged between 15°–23°N and 89°–104°W in six different sites. Five populations occur in four states in Mexico: Tamaulipas (north, site 1), Jalisco and Guerrero (central, sites 2, 3, 4), Chiapas (south, site 5). Another occurs in one department in Guatemala (El Progreso) (south, site 6). Northern and central Mexican populations were separated by 800 km and central and southern by 1100 km (Table 1).

3.1. Basal area and density

Density and basal area of cloud forest sugar maple was low at all six sites. The density of maples averaged 130 ± 35 (s.e) trees/ha, ranging from 32 (Cañada Grande) to 237 (Ojo de Agua del Cuervo) trees/ha (Table 2). Plots within sites contained variable densities, and thus overall density did not differ significantly among sites (one-way ANOVA, $F = 1.6$, $P = 0.19$). Mean densities of maples constituted 1–16% of the total mean tree density at each site (Table 2). Mean basal area of cloud forest sugar maple averaged 7.5 ± 1.3 (s.e.) $\text{m}^2 \text{ha}^{-1}$, ranging from 2.5 (Cañada Grande) to $11 \text{m}^2 \text{ha}^{-1}$ (El Balsamal). Variation among plots within sites resulted in basal area of maples not differing significantly among sites (one-way ANOVA, $F = 1.36$, $P = 0.27$). Mean basal area comprised 7–43% of the total basal area at the different sites (Table 2).

Density and basal area were much greater for all trees ≥ 1 cm dbh than for cloud forest sugar maple (Table 2). The density of all trees at sites averaged 2120 ± 330 (s.e.) trees/ha, ranging from 990 (Sierra de Manantlán) to 2986 (Barranca El Silencio) trees/ha (Table 2), but differences among sites were not significant (one-way ANOVA, $F = 2.21$, $P < 0.08$). Density of trees tended to vary within and among sites, with the highest densities occurring in the most southern sites. Mean basal area of all trees averaged 35.6 ± 4.3 (s.e.) $\text{m}^2 \text{ha}^{-1}$, ranging from 24 (Barranca El Silencio) to

$52 \text{m}^2 \text{ha}^{-1}$ (Ojo de Agua del Cuervo), but did not differ significantly among sites (one-way ANOVA, $F = 0.75$, $P = 0.56$).

3.2. Tree size class distributions

Size-class distributions of cloud forest sugar maple trees differed among sites. An inverted-J diameter distribution of maples was observed at two sites, La Colmena–Agua Escondida–Agua del Indio and Ojo de Agua del Cuervo. At these two sites, large percentages occurred in the smallest diameter categories, but there also were individuals as large as 109 cm dbh. In contrast, in El Balsamal (southernmost site), no trees >65 cm dbh were present (Fig. 1). All cloud forest sugar maple populations contained saplings and juveniles. La Colmena–Agua Escondida–Agua del Indio had the highest densities of saplings. Ojo de Agua del Cuervo was the only site where the frequency of saplings and juveniles was uniformly distributed across all height classes (Fig. 1). Ojo de Agua del Cuervo and Sierra de Manantlán had the largest number of juvenile and sapling maples (Table 2). The southern most populations had the fewest juveniles and saplings (Table 2). Densities were slightly higher in sites with shorter hurricane return intervals (ANOVA, $F = 4.10$, $P \leq 0.11$). Environmental effects on regeneration patterns might not be expressed as a result of cattle grazing and logging.

Based on IVI, cloud forest sugar maple was a dominant or co-dominant tree species at all sites. It was the dominant tree in the Guatemalan forest (Appendix A). Maple was co-dominant in Mexican forests with *Alnus acuminata* Kunth subsp. *arguta* (Schltdl.) Furlow, *Carpinus caroliniana*, *Cornus excelsa* Kunth, *Liquidambar styraciflua* L., *Podocarpus reichei* Buchholz & A. Gray, and *Zinowiewia concinna* Lundell (Appendix A).

3.3. Cloud forest trees indirect ordination

Ordination using NMS and a Monte Carlo test indicated a best fit using a three dimensional model. The final stress was 20.09. Axes accounted for a reduction in stress of 0.0011 and instability of 0.01819 with 1500 iterations. Most of the stress was reduced after 38 iterations. Elevation, latitude, and hurricane frequency were the variables with scores on axes larger than the 0.250 cutoff values and are shown in the ordination diagram (Fig. 2).

In the NMS ordination, variance in the first axis was correlated with one soil variable, three disturbance variables and four geographic and climatic variables (Table 3). Variance in axis 2 was explained by one soil variables, hurricane frequency, elevation, and latitude variables. Variance in axis 3 was explained by a disturbance variable, three soil variables and three geographic and climatic variables (Table 3). Along axis 1, Ojo de Agua del Cuervo was located in the extreme position (Fig. 2). Sites from La Colmena–Agua Escondida–Agua del Indio and Cañada Grande were at the extreme along axis 2 (Fig. 2).

Highest correlations between tree densities and environmental variables were with geographic/climatic and soil characteristics. Most correlations occurred with axis 2 (Table 4). Densities of 23

Table 2
Characteristics of trees in cloud forests at each site. Basal area and density of maples and all trees ≥ 1 cm dbh, and density of juveniles and saplings ≤ 1 cm dbh are presented for cloud forest sugar maple at each site.

Site #	Site name	Maple basal area ($\text{m}^2 \text{ha}^{-1}$)	Maple density (number of trees/ha)	Maple juveniles and saplings abundance	Total tree basal area ($\text{m}^2 \text{ha}^{-1}$)	Total tree density (number of trees/ha)
1	La Colmena–Agua Escondida–Agua del Indio	8	234	355	33	1417
2	Ojo de Agua del Cuervo	7	237	558	52	2070
3	Sierra de Manantlán	11	90	916	43	990
4	Barranca El Silencio	7	111	235	24	2986
5	Cañada Grande	2	32	40	34	2930
6	El Balsamal	11	85	28	26	2346

species increased with increasing elevation and soil Fe, while only two species decreased (Table 3 and 4). Some of these 23 species were light-demanding shrubs (*Cestrum*, *Montanoa*) (Table 4). The strongest correlation occurred between the 23 species and eleva-

tion, with increasing densities associated with increases in elevation (Table 3). In addition, correlations with axis 2 indicated that increasing densities of the 23 species were associated with decreases in hurricane frequency (Table 3). Correlations with axes 1

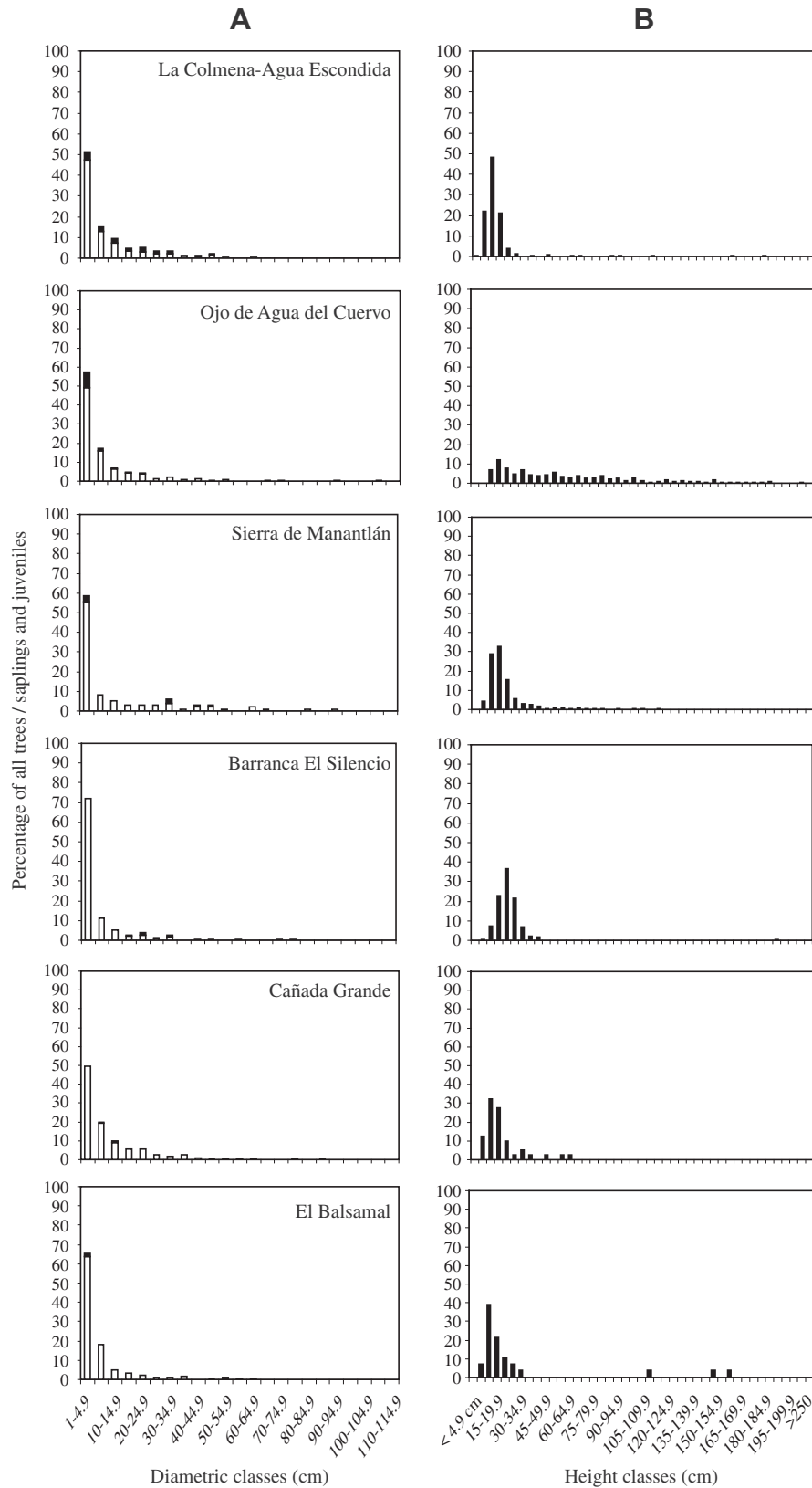


Fig. 1. (A) Proportion of all trees at each site in successive 5 cm dbh size categories. The black portion in each bar indicates proportion comprised of cloud forest sugar maple. (B) Proportion of cloud forest sugar maples at each site, 5 cm height categories.

and 3 were with densities of 12 species and disturbance and latitude, as well as soils and mean annual precipitation and temperature; the highest correlation was with mean annual precipitation (Table 3). Along these axes, increases in the density of *A. saccharum* subsp. *skutchii* as well as in the densities of *C. caroliniana*, *Quercus* spp., *L. styraciflua*, among others, were associated with decreases in logging, canopy gaps, and cattle grazing (Table 3). ANOVA results also showed significant relationships of tree species densities with elevation and hurricane frequency, as recovered in the NMS ordination.

3.4. Cloud forest trees direct analysis

Densities of cloud forest sugar maple negatively correlated with differences in hurricane return intervals. Densities were significantly higher in sites with shorter hurricane return intervals (ANOVA, $F = 7.29$, $P \leq 0.05$) (Fig. 3). In contrast, basal area showed no relationship to differences in mean return intervals of hurricanes (ANOVA, $F = 0.20$, $P \leq 0.67$). Differences in densities of maples at sites with similar return intervals, such as Ojo de Agua del Cuervo and Sierra de Manantlán (Table 5), may have been related to differences in the intensity of cattle grazing among sites.

Densities of all trees ≥ 1 cm dbh were positively correlated with differences in hurricane return intervals. Densities of all trees were higher in sites with longer hurricane return intervals (ANOVA, $F = 4.61$, $P \leq 0.09$). Basal area of all trees was not correlated (ANOVA, $F = 1.31$, $P \leq 0.31$). Densities also were positively related to elevation (ANOVA, $F = 4.97$, $P \leq 0.08$). Nonetheless, elevation and mean hurricane return intervals were not correlated (ANOVA, $F = 1.9$, $P \leq 0.23$).

3.5. Forests composition and species richness

A total of 164 tree species representing 92 genera and 54 families were recorded in the six sites. The most species rich families

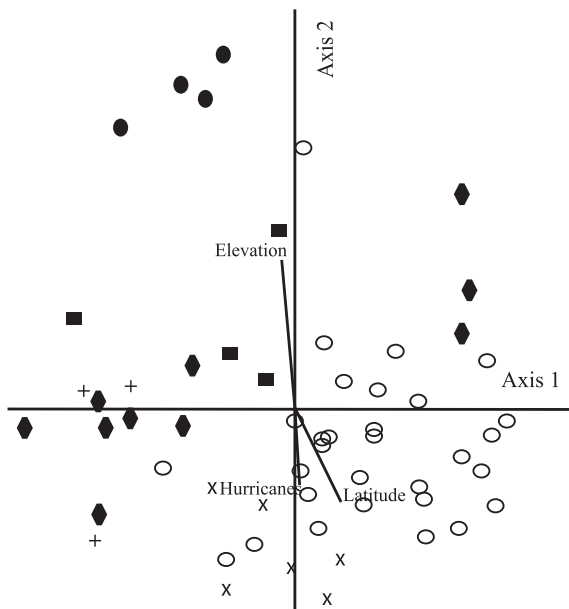


Fig. 2. Ordination diagram for axes 1 and 2 derived from Non-metric Multidimensional Scaling using plots at each site, and density of all trees ≥ 1 cm dbh. Correlation values of three variables (latitude, elevation, hurricane return frequency) with the two axes reported in Table 4 are indicated by lines extending from origin. Symbols of localities are as follow: X, La Colmena–Agua Escondida–Agua del Indio (Tamaulipas); O, Ojo de Agua del Cuervo (Jalisco); ◆, Sierra de Manantlán (Jalisco); ■, Barranca El Silencio (Guerrero); ●, Cañada Grande (Chiapas); +, El Balsamal (Guatemala).

Table 3

Pearson correlation coefficients (r) of environmental variables and ordination axes using density data of woody plants ≥ 1 cm dbh from the six cloud forest sugar maple populations. Only correlations with an absolute value >0.35 are shown ($df = 55$, $P < 0.01$).

Variable	Density data		
	Axis 1	Axis 2	Axis 3
Soil	Fe	0.495	
	Ion exchange capacity	−0.409	0.514
	Na		−0.418
	NO ₃		−0.444
Disturbance	Anthropogenic (logging)	−0.417	
	Canopy gaps	−0.385	
	Cattle grazing	−0.408	0.411
Geographic, climatic	Elevation		0.742
	Hurricane frequency		−0.542
	Latitude	0.410	−0.583
	Longitude	0.494	
	Mean annual prep. (mm)	0.465	−0.536
	Mean annual temp. (°C)	0.495	−0.410

were Fagaceae (13), Lauraceae (13), and Asteraceae (12). The temperate genera *Carpinus*, *Clethra*, *Cornus*, and *Quercus* were the only ones present in more than 80% of the sites; other temperate and tropical genera, *Dendropanax*, *Ilex*, *Magnolia*, *Ostrya*, *Pinus*, and *Symplocos* occurred in more than 66% of the sites. Species richness varied from 19 in Sierra de Manantlán to 43 in Ojo de Agua del

Table 4

Significant Pearson correlations (r) between density of all trees of each species from the six sites, and NMS ordination axes. Only correlations with an absolute value >0.35 are shown ($df = 55$, $P < 0.01$).

Species	Axis 1	Axis 2	Axis 3
<i>Acer saccharum</i> subsp. <i>skutchii</i>	−0.393		0.388
<i>Alnus acuminata</i> subsp. <i>arguta</i>		0.381	
<i>Ardisia verapazensis</i>			0.378
<i>Buddleja skutchii</i>		0.545	
<i>Carpinus caroliniana</i>			0.359
<i>Cestrum elegantissimum</i>		0.449	
<i>Cestrum luteo-virescens</i>		0.559	
<i>Clethra nicaraguensis</i>		0.424	
<i>Cleyera integrifolia</i>	0.395		
<i>Clusia salvinii</i>	0.425		
<i>Cornus disciflora</i>		0.453	
<i>Cornus excelsa</i>		0.672	
<i>Deppea flava</i>		0.378	
<i>Fuchsia arborescens</i>		0.417	
<i>Koanophyllon</i> sp.		0.378	
<i>Liquidambar styraciflua</i>			0.369
<i>Litsea acuminatissima</i>		0.576	
<i>Miconia glaberrima</i>		0.498	
<i>Montanoa hexagona</i>		0.429	
<i>Myrica cerifera</i>		0.467	
<i>Myrsine coriacea</i> subsp. <i>coriacea</i>		0.513	
<i>Oreopanax xalapense</i>		0.630	
<i>Parathesis villosa</i>	−0.368		
<i>Persea chrysobalanoides</i>		0.596	
<i>Phoebe</i> aff. <i>saxchanalensis</i>		0.443	
<i>Pinus patula</i> subsp. <i>tecunumanii</i>		0.515	
<i>Piper amalago</i>			0.362
<i>Prunus brachybotrya</i>		0.557	
<i>Podocarpus reichei</i>		−0.426	
<i>Prunus serotina</i> subsp. <i>serotina</i>		0.509	
<i>Quercus germana</i>		−0.362	
<i>Quercus salicifolia</i>	0.393		
<i>Quercus skinneri</i>			0.378
<i>Symplocos</i> sp.		0.378	
<i>Styrax argenteus</i>			0.430
<i>Trichilia havanensis</i>			0.373
<i>Viburnum jucundum</i> subsp. <i>jucundum</i>		0.582	

Cuervo and 44 in Barranca El Silencio (Table 6). An important contribution to species richness at the last two forests was made by species with tropical affinities. These two sites and El Balsamal had the highest number of species under legal protection (Table 6).

Generic composition of cloud forest sugar maple sites indicated both temperate and tropical affinities. Based on species floristic information available, we identified 61 genera in cloud forest sugar maple sites with tropical affinities. Seventy-two percent of these tree genera had Pan-tropical or Neotropical affinities. The number of temperate genera decreased from 15 in northern Mexico to six in Guatemala (Table 6, Appendix A). Temperate genera with disjunct distributions in Mexico and Guatemala comprised 20% of the total generic composition in the six sites studied. Only *Cornus* co-occurred with cloud forest sugar maple at all sites. *Cornus*, *Carpinus*, and *Liquidambar* extended to the southernmost cloud forests containing *Acer* in Guatemala. Among the tropical genera, 17 were disjunct with Asia, the Antilles, Africa, and Central-South America.

3.6. Conservation status and disturbance of the sites

The subspecies has been designated as endangered by Mexican Endangered Species Act (SEMARNAT, 2010) and it is only considered as restricted to cloud forest in the Guatemalan Species Red List (CONAP, 2001). Ojo de Agua del Cuervo, with the highest number of species under legal protection, was not within a protected area (Table 6).

We found evidence of anthropogenic disturbance at all sites. Common disturbances were cattle grazing, fire, wood collection,

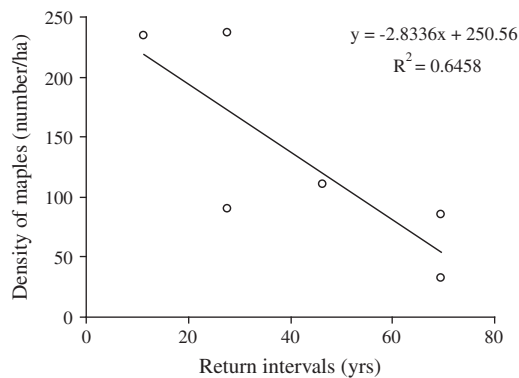


Fig. 3. Densities of cloud forest sugar maples (all sizes combined) at the six sites were negatively correlated with average return intervals of hurricanes (ANOVA, $F = 7.29$, $P \leq 0.05$).

Table 5

Disturbances at each site containing a cloud forest sugar maple population. Numbers of hurricanes during the period of time for which there were records were used to estimate return intervals. Disturbances were recorded as number of tree stumps, fallen trees, and standing dead trees in each site. Livestock grazing was indicated by presence of cattle or dung, and fires by scars and heights above ground.

Site #	Site name	Hurricane frequency (no./years)	Return times (yr)	Tree stumps	Fallen trees	Standing dead trees	Livestock presence	Fire
1	La Colmena–Agua Escondida–Agua del Indio	13 (146)	11.2	13	12	29	Cattle/low dung	No fire scars
2	Ojo de Agua del Cuervo	5 (139)	27.8	2	26	12	No cattle/dung or occasional in low numbers	Moderate intensity: Fire scars <1 m
3	Sierra de Manantlán	5 (139)	27.8	4	13	16	Cattle/low dung	Moderate intensity: Fire scars <1 m
4	Barranca El Silencio	3 (139)	46.3	1	4	8	No cattle/dung	High intensity: Fire scars >1 m
5	Cañada Grande	2 (139)	69.5	33	4	36	Cattle/moderate dung	No fire scars
6	El Balsamal	2 (139)	69.5	29	21	4	Cattle/high dung	High intensity: Fire scars >1 m

and timber harvesting. Excepting Barranca El Silencio, all sites had cattle grazing; the most southern sites (Cañada Grande and El Balsamal) had the most extensive wood extraction. Signs of past fires (fire scars in the bark) were also common in Ojo de Agua del Cuervo, Sierra de Manantlán and El Balsamal (Table 5), but there were no documented records of fire intensity, frequency, or area burned for the sites. At Barranca El Silencio, a high intensity fire occurred during the dry season (April–May) in 2005. Scars extended 1.5 m along the barks of trees. No documented records for previous fires exist for the site. The Cañada Grande site was clearly endangered: intensive timber harvesting and firewood collection were common in the area. Only eight maple trees were observed at this site.

4. Discussion

Acer saccharum subsp. *skutchii* is the most southerly distributed sugar maple in America (at 15°N). It has a disjunct distribution that ranges across 10° latitude from northern Mexico to Guatemala. This study corroborates and describes for the first time populations in southern Mexico (Cañada Grande) and Guatemala (El Balsamal).

Our data support the idea that distribution boundaries are constrained by environmental conditions associated with elevation (Sexton et al., 2009). Cloud forest sugar maple is constrained to a range of elevations that varies with geographic location. Cloud forests occur most commonly between 1200 and 2000 m in northern Mexico and from 2400 to 2800 m in southern Mexico (Alcántara et al., 2002). Cloud forests with sugar maple closely follow this pattern of elevational distribution, indicating that elevation constraints for cloud forest sugar maple increase as latitude decreases. In addition, temperatures suitable for maple germination occur only at higher elevations in southern regions (McCarragher et al., 2011).

Constraints that occur toward range edges at low-latitudes are present in other temperate trees. Abundance of *Fagus sylvatica* in northeast Spain decreases near the lower latitudinal limit, probably as a consequence of higher temperatures (Peñuelas et al., 2007). The same variable could be responsible for population declines along the southern range margins of tree species in the European Alps (Pauli et al., 2007). As with sugar maples, range contractions for these European trees are exacerbated by human land use.

Local site conditions could affect establishment and persistence of cloud forest sugar maple within our hypothesized elevational constraints. Soil nutrient concentrations do appear to be associated with cloud forest sugar maple densities, consistent with studies suggesting that declines in maple density are related to decreases

Table 6
Tree species richness and genera at each site and number of species under legal protection according to IUCN, CITES, or Guatemalan and Mexican Endangered Species Act.

Site #	Site name	Total tree species richness	Families with most genera (number of genera present)	Genera with most species (number of species)	Genera with temperate affinity	Number of species under legal protection
1	La Colmena–Agua Escondida–Agua del Indio	28	Betulaceae (2), Fagaceae (2), Juglandaceae (2)	<i>Quercus</i> (3), <i>Ternstroemia</i> (2)	15	7
2	Ojo de Agua del Cuervo	43	Lauraceae (4), Melastomataceae (3), Ternstroemiaceae (3)	<i>Ilex</i> (3), <i>Quercus</i> (3)	12	12
3	Sierra de Manantlán	19	Betulaceae (2), Celastraceae (2), Myrsinaceae (2), Ternstroemiaceae (2)	<i>Quercus</i> (2)	8	6
4	Barranca El Silencio	44	Asteraceae (4), Leguminosae (3)	<i>Quercus</i> (3)	9	9
5	Cañada Grande	36	Asteraceae (3), Lauraceae (3)	<i>Quercus</i> (3)	10	6
6	El Balsamal	41	Rubiaceae (4), Myrsinaceae (3)	<i>Parathesis</i> (3), <i>Senecio</i> (3)	6	9

in soil nutrients (Bailey et al., 2004; Drohan et al., 2002; Horsley et al., 2000; Modry et al., 2004). In addition, nitrates could influence differences in species composition across soil gradients, determining community organization and structure, as has been observed in cloud forests soils as well as soils from other sugar maple sites with high nitrates (Bigelow and Canham, 2007; Lovett and Mitchell, 2004; Roman et al., 2010). Thus, soil conditions can be considered internal gradients, nested within primary climatic conditions that restrict geographic range (Gaston, 2003; Sexton et al., 2009).

Hurricanes and resulting gap dynamics appear to influence populations of cloud forest sugar maple and other cloud forest tree species. Higher densities of cloud forest sugar maple in La Colmena–Agua Escondida–Agua del Indio and Ojo de Agua del Cuervo might result from more frequent non-catastrophic hurricane disturbance (Arriaga, 1988, 2000; Batista and Platt, 2003; Foster et al., 1997). Thus, differences in densities at the studied sites might be related to some forests being in areas where hurricanes occur more frequently (Quigley and Platt, 2003). Nonetheless, recruitment of other tree species, such as *Cornus disciflora* (ANOVA, $F = 28.12$, $P \leq 0.01$), is associated with longer return intervals for large-scale disturbance like hurricanes. These differences among species suggest that there is interspecific variation in resistance and resilience to natural disturbance regimes (Bellingham et al., 1995; Batista and Platt, 2003). Such variation in responses could influence the differences in community composition in forests at different latitudes as a result of differences in hurricane disturbance (Canham et al., 2001, 2010). Thus, low likelihoods of hurricanes at the southern end of the range could result in small sizes of cloud forest sugar maple populations because conditions favoring regeneration do not often occur.

Acer saccharum subsp. *skutchii* occurs with other disjunct temperate genera in cloud forests. Floristic composition changes, however, with latitude. Temperate genera decrease in numbers as latitude decreases and become progressively more restricted to dominant or co-dominant trees. Both understory and overstory plants with tropical affinities increase from northern to southern sites (Luna-Vega et al., 1999, 2001a, 2001b; Phillips and Miller, 2002; Ramírez-Marcial, 2001). Total numbers of woody species in seasonal forests have been shown to increase as latitude decreases from 40° to 20°N in the Americas (Quigley and Platt, 2003). Shrubs and subcanopy trees in tropical families tended to increase, while those in temperate families progressively decreased from 30° to 20° and 10°N. Some species, however, persisted across this zone of transition from temperate to tropical floras where environmental conditions remained favorable. As a result, forests at intermediate latitudes appeared heterogeneous in composition (Quigley and Platt, 2003).

We suggest that distributions of temperate species near their southern range limits are likely to fragment and contract further

in response to human-induced climate change. Our study suggests variables that should be included in predictions to responses to climate change. These variables should include latitude and elevation, soil conditions, and hurricane frequencies. Such habitat models potentially could be used to predict future distribution of remnant populations of temperate trees at their tropical range edge (Thuiller et al., 2008). Nonetheless, we expect local population extinctions near latitudinal limits of temperate trees as a result of warmer temperatures, decreases in ground-level clouds and reduced precipitation (i.e., loss of cloud forest environments). These extinctions may be exacerbated by human actions that threaten regeneration, as we noted and has been observed in other marginal populations of temperate trees (Todaro et al., 2007; Vaxevanidou et al., 2006). This pattern of change is suggested by the state of cloud forest sugar maple at the most southern end of its range.

Indeed, our results further suggest that anthropogenic disturbances may well be the most important influence, overriding all other variables near range limits. Anthropogenic disturbance is evident in four of the six cloud forest sugar maple populations, and it is directly threatening persistence of the subspecies at the two most southern sites. Cañada Grande and El Balsamal populations contain very few trees and might experience reductions in genetic variation if low densities continue. Cattle grazing is producing negative effects on regeneration of cloud forest sugar maple, especially at El Balsamal (despite its inclusion in a protected area); reduction of cattle grazing to increase seedling establishment is urgently needed. In addition, regeneration in southernmost sites is negatively affected by fire and by increased soil compactation. Timber harvesting and fuelwood collection also are the major threats in the most southern populations in Mexico and Guatemala. Moreover, conversion of surrounding forests to farm lands is also common, decreasing the size of forest patches and increasing edge effects, similar to conversions described elsewhere (Laurence et al., 1997; Lovejoy et al., 1986). An increase in land area used for coffee plantations is currently a major threat for the population in El Balsamal; both logging and establishment of coffee plantations should be dramatically reduced at this site. The site is in the buffer zone of a Biosphere Reserve, which can facilitate the reduction of these activities in the maple zone. Landowners of this area, as well as owners from Cañada Grande, are eligible for federal or international payments for ecosystem services, defraying possible economic losses from reduction of cattle raising, logging, and farming. Tree planting in all remnant adjacent cloud forest patches should be done together with the introduction of light tolerant native species, such as *L. styraciflua* (Williams-Linera et al., 2010). Soil conservation, enhancement of floristic and structural diversity, as well as cloud forest sugar maple recruitment can be improved with such conservation practices.

Two sites in Mexico have already some protection. Habitat protection measures, including bans on cattle grazing and timber harvesting have been implemented recently in La Colmena–Agua Escondida–Agua del Indio, the most northern site in Mexico. Thus, this population of cloud forest sugar maple should likely persist. Similar protective measures have been implemented in Sierra de Manantlán site, where the maple forest was fenced in 1993. Sporadic cattle grazing, however, still occur in both sites.

Nature reserves containing cloud forest are urgently needed. Formation of a protected area in Ojo de Agua del Cuervo would help to meet this need (Vargas-Rodríguez et al., 2010). A protected area could enhance preservation of local environmental conditions, such as ground-level clouds that reduce water stress (Anthelme et al., 2011). In addition, reserves should maintain the current vegetation surface, reducing soil erosion. Soil conservation in cloud forests is important because they occur along steep mountainsides, which limits availability of organic matter and exchangeable nutrients (Roman et al., 2010). The inclusion of higher elevation zones in protected areas should likely facilitate migration of cloud forest trees upslope to sites where suitable elevation temperatures still occur as climate changes (Altamirano et al., 2010). Finally, coordination and effective communication between local communities and government will increase the effectiveness of any management program (Heller and Zavaleta, 2009).

5. Conclusions

We propose three legal statuses for the conservation of cloud forest sugar maple. First, given that the distribution is less than 20,000 km², and consists of fragmented populations in no more than 10 locations (IUCN, 2001), *A. saccharum* subsp. *skutchii* merits “Vulnerable status” (VU B1 ab (i, ii, iii, iv, v), IUCN Red List Criteria). We thus update the status category proposed by Gibbs and Chen (2009) (EN B2 ab (ii, iii, iv)), which erroneously listed the number and location of the populations, as well as the extent of the distribution. Second, the Guatemalan Species Red List should include the species as “Endangered”. Third, the Ojo de Agua del Cuervo forest contains the most resilient of all the disjunct populations and it should be included in the Mexican National System of Natural Protected Areas (SINAP) (Vargas-Rodríguez et al., 2010). In addition, we urge that the restoration and management practices suggested here be applied without delay to Cañada Grande and El Balsamal. All these sites are within in the Mesoamerican Biodiversity Hotspot and thus deserve priority for conservation purposes (Myers et al., 2000). The conservation value of these forests with cloud forest sugar maple is high, and their genetic and evolutionary features might be different from populations more central to the range of sugar maple (Hampe and Petit, 2005).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2012.03.006>.

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