Richness and distribution of herbaceous angiosperms along gradients of elevation and forest disturbance in central Veracruz, Mexico

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Botanical Sciences
95 (2): 307-328, 2017

DOI: 10.17129/botsci.859

Abstract

Background: Terrestrial herbs are a significant floristic element of tropical forests; however, there is a lack of research focused on this plant group.
Question: Which are the patterns of species distribution of herbaceous angiosperms along gradients of elevation and forest disturbance at Cofre de Perote, central Veracruz, Mexico?
Studied species: Terrestrial herbaceous angiosperms.
Study site and years of study: Eastern slopes of Cofre de Perote, central Veracruz, Mexico; from 2012 until 2014.
Methods: We established an elevational transect (40 to 3,520 m), where floristic sampling in eight study sites within elevational belts of about 500 m each were realized. We recorded the occurrence of terrestrial angiosperm herbs within 135 20 × 20 m plots, distributed in old-growth, degraded forest, secondary vegetation, as well as azonal vegetation. Species richness and floristic composition was compared between the different elevational belts and forest disturbance.
Results: We recorded a total of 264 herb species, 31 endemic to Mexico and three classified as threatened. This number of species represents 5.7 % of Veracruz's herbaceous angiosperm flora. The highest species richness was recorded at 2,500 m (76) and 1,500 m (52). In most of the cases, secondary forests showed the highest species richness independently of the elevational gradient, whereas old-growth forests had fewer species.
Conclusions: The observed species richness, including endemic elements, highlights the importance for plant conservation of the area which is threatened by land use changes. Additionally, we suggest that vegetation variations formed by mature, disturbed and secondary forests is acceptable (and unavoidable) and can even increase species richness.
Keywords: conservation, disturbance gradient, floristic inventory, forest fragmentation, terrestrial herbs.

Riqueza y distribución de angiospermas herbáceas a lo largo de gradientes de elevación y perturbación del bosque en el centro de Veracruz, México

Resumen

Antecedentes: Las hierbas terrestres son un elemento florístico importante de los bosques tropicales; sin embargo, aún es escasa la investigación centrada en este grupo de plantas.
Pregunta: ¿Cuáles son los patrones de distribución de especies de angiospermas herbáceas a lo largo de gradientes de altitud y de perturbación en el Cofre de Perote, centro de Veracruz, México?
Especies de estudio: Angiospermas herbáceas terrestres.
Sitio de estudio y años de estudio: Vertiente este del Cofre de Perote, centro de Veracruz, México; desde 2012 hasta 2014.
Métodos: Establecimos un gradiente altitudinal (40 a 3,520 m), donde realizamos un muestreo florístico en ocho sitios de estudio dentro de pisos altitudinales de aproximadamente 500 m cada uno. Registramos la presencia de angiospermas herbáceas terrestres dentro de 135 parcelas de 20 × 20 m, distribuidas en bosques maduros, degradados, secundarios, así como vegetación azonal. Se analizó la riqueza de especies, la composición florística y luego comparamos los datos resultantes entre los diferentes pisos altitudinales y los grados de perturbación del bosque.
Resultados: Se registraron 264 especies de plantas, 31 endémicas de México y tres amenazadas. Esta riqueza representa 5.7 % de la flora de herbáceas angiospermas en Veracruz. Los pisos altitudinales con mayor riqueza de especies fueron 2,500 m (76) y 1,500 m (52). En la mayoría de los casos, los bosques secundarios tuvieron la mayor riqueza de especies en el gradiente altitudinal, mientras que los bosques maduros tuvieron menos especies.
Conclusiones: La riqueza de especies observada, incluyendo elementos endémicos, resalta la importancia de esta zona para la conservación de plantas, que se encuentra amenazada por el cambio de uso del suelo. Además, sugerimos que la variación de la vegetación formada por bosques maduros, perturbados y secundarios es aceptable (e inevitable) y puede incluso incrementar la riqueza de especies.
Palabras clave: conservación, gradiente de perturbación, inventario florístico, fragmentación del bosque, hierbas terrestres.

Author Contributions
Jorge A. Gómez-Díaz & César I. Carvajal-Hernández conducted fieldwork.
Jorge A. Gómez-Díaz analyzed data and wrote the paper.
All authors conceived, designed the research and reviewed drafts of the paper.

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Growing human pressure on terrestrial ecosystems represents one of the most important threats to biodiversity, especially in the tropics (Godfray *et al*. 2010, Melo *et al*. 2013, FAO 2014). Therefore, the planet is suffering rapid and dramatic changes across the majority of biomes (Foley *et al*. 2005). Considering the current high rates of deforestation in most of the tropical countries (Lindenmayer *et al*. 2006), it is projected that areas with old-growth forests will become increasingly scarce and fragmented (Köster *et al*. 2009, FAO 2014). Human population growth and the intensification of agricultural practice are the major factors that threaten old-growth forests and their associated biodiversity in the tropics (Wright 2005), due to their conversion into cropland, grassland for cattle and human settlements (Foley *et al*. 2005). Consequently, complete floristic inventories documenting which species are affected by human interference are urgently needed (DeClerck *et al*. 2010).

The Mesoamerican region including Mexico is considered as a hotspot of plant diversity, meaning that it is very rich in endemic species, but also highly threatened (Myers *et al*. 2000). The main reason is the loss of primary vegetation due to high deforestation and urbanization rates (Wright & Muller-Landau 2006). Within Mexico, the state of Veracruz is considered a priority site for national and global conservation of biodiversity due to its outstanding geographical characteristics, such as the complex topography and the transition between tropical and temperate zones (Olguín 2011). Veracruz covers an area of 72,420 km^2 of which less than 20 % consists of natural vegetation, with a high degree of habitat fragmentation (Gómez-Pompa *et al*. 2010, CONABIO 2011). Nevertheless, Veracruz hosts a large number of angiosperms (6,876 species) that represents about 31 % of the flora of Mexico (Villaseñor & Ortíz 2012), and thus it is considered as the country´s third richest state in angiosperms after Oaxaca and Chiapas (Rzedowski 1993, Villaseñor & Ortíz 2014). The state is also known for having all vegetation types registered in Mexico (Gómez-Pompa & Castillo-Campos 2010), according to the classification of Rzedowski (2006). Despite being a region with high species richness, there are still many parts of the state which lack a reliable floristic inventory (Gómez-Pompa *et al*. 2010), especially in remote montane areas, such as our study area. Until now, no floristic research along this elevational gradient has been conducted, taking into account terrestrial herbaceous angiosperms, human land use intensity and geoecological conditions.

In the last two decades studies about diversity patterns of tropical vegetation along elevational gradients have received substantial consideration (Vázquez & Givnish 1998, Colwell *et al*. 2008, Willinghöfer *et al*. 2012), but the focus considering different taxonomical plant groups is unevenly distributed because most of the research is concentrated in the most species-rich herbaceous family (*e.g*., Poaceae, Asteraceae, Araceae) of every study area (Willinghöfer *et al*. 2012). However, many other herbaceous angiosperm families, such as Orchidaceae, Zingiberaceae and Begoniaceae, are significant elements in the composition of tropical vegetation (Willinghöfer *et al*. 2012, Cicuzza *et al*. 2013).

Nevertheless, terrestrial forest herbs have been little studied from a floristic and biogeographic point of view. As a result, there is little knowledge about how herbaceous angiosperm associations change along elevational gradients, and if they exhibit similar patterns like other plant groups (Willinghöfer *et al*. 2012). Only a few relevant studies have been realized in pastures (Lira-Noriega *et al*. 2007) and coffee plantations (Ramos *et al*. 1983) or focusing on single families, such as Poaceae (Hernández *et al*. 1990, Mejía-Saulés *et al*. 2002), Orchidaceae (Sosa & Platas 1998, Salazar 1999) and Asteraceae (Villaseñor *et al*. 2006).

Further studies on the geographical distribution of the floristic elements of central Veracruz are necessary in order to better understand its complex mix of plant species (Villaseñor 2010). Inventories of specific groups of plants or particular geographic areas contribute to the completion of the national flora of Mexico and form the basis for the appropriate management of the natural resources (Martinez-Camilo *et al*. 2012). This kind of data can also provide information about the degree of endemism and endangered species in specific areas, which allows evaluating protected areas about the richness and uniqueness of their flora (Rzedowski 2006).

The objective of this study was to record the flora of herbaceous angiosperms in central Veracruz, Mexico, along gradients of elevation and human forest use intensity along the *Cofre de Perote* mountain. The study was conducted to gather information about the floristic composition, elevational ranges and geographical distribution of the species, as well as to compare species richness and similarity between elevational belts and forest types. In this way, we provide more detailed information about patterns of species richness and distribution, which presents another step towards defining priority areas for conservation of this complex vegetation mosaic.

Materials and methods

Study area. The study was conducted at eight study sites along an elevational gradient of ca. 82 km between 40 and 3,520 m a.s.l. on the eastern slopes of the Cofre de Perote, an extinct volcano of 4,282 m elevation in the central part of the state of Veracruz, Mexico (Figure 1). This region is located at the junction of the Trans-Mexican volcanic belt and the *Sierra Madre Oriental*, a mountainous area between 19° 25' 5.7'' and 19° 36' 54'' N, and 96° 22' 36'' and 97° 09' 36.9'' W. According to Lauer (1972), five climate zones can be found in the study area in combination with six forest types as classified by Miranda & Hernández-Xolocotzi (1963) (Table 1).

Tierra caliente (0-1,250 m).- In this climate zone, we selected three study sites located in two forest types (Figure 1, Table 1): the tropical semi-humid deciduous forest (TSDF) is found in

Table 1. Overview of the study sites along gradients of elevation and forest disturbance in central Veracruz, Mexico. Forest type: TSDF = tropical semi-humid deciduous forest, TOF = tropical oak forest, HMF= humid montane forest, POF = pine-oak forest, PF = pine forest, and FF = fir forest. Mean annual temperature and mean annual precipitation and number of recorded species within the four habitats with different forest use intensities (OG = old-growth, DE = degraded, SE = secondary, AZ = azonal).

Study site	Elevational range (m)	Forest type	Number of plots	Temp. (°C)	Prec. (mm)	OG	DE	SE	AZ
La Mancha	30-50	TSDF	15	26	1,221	4	6	8	-
Palmarejo	610-670	TSDF	20	23	938	12	35	11	20
Chavarrillo	900-1,010	TOF	15	21	1,552	11	13	19	-
Los Capulines	1,470-1,650	HMF	20	18	1,598	24	21	20	31
El Zapotal	2,020-2,230	HMF	15	14	3,004	16	18	20	-
El Encinal	2,470-2,600	POF	20	12	1,142	47	41	38	35
Los Pescados	3,070-3,160	PF	15	10	821	22	26	37	-
El Conejo	3,480-3,540	FF	15	8	829	9	13	10	-

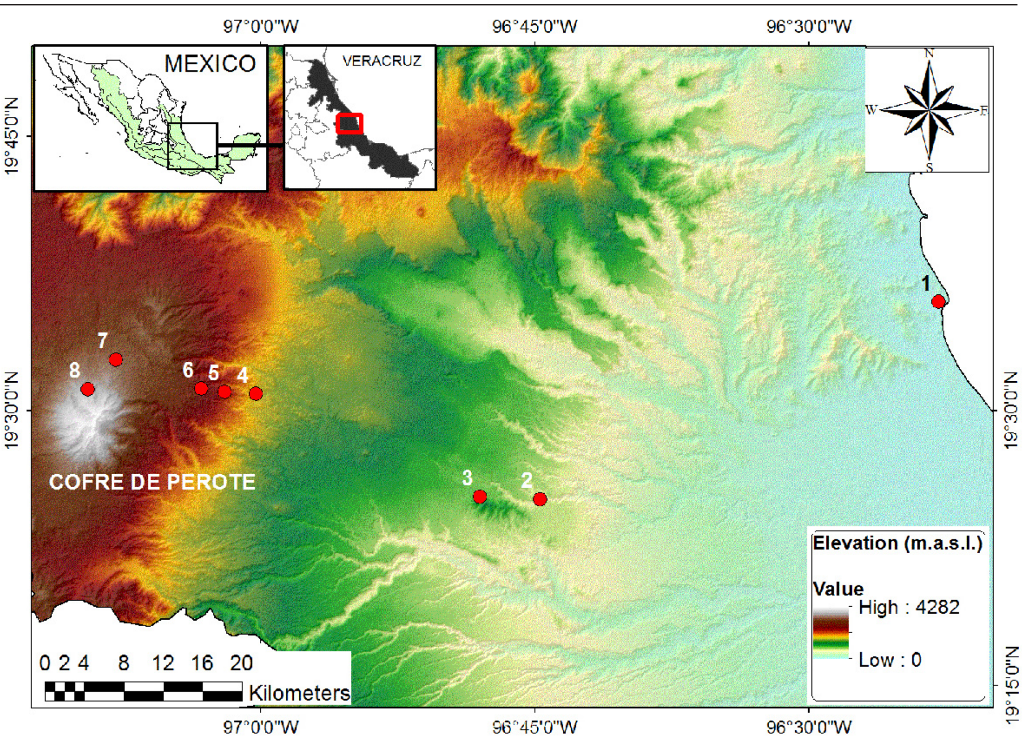

Figure 1. Location of the eight study sites along gradients of elevation and forest disturbance in central Veracruz, Mexico. Study sites: 1. La Mancha (50 m); 2. Palmarejo (650 m); 3. Chavarrillo (1,000 m); 4. Los Capulines (1,600 m); 5. El Zapotal (2,100 m); 6. El Encinal (2,500 m); 7. Los Pescados (3,100 m); 8. El Conejo (3,500 m). The limits of the Neotropics according to Löwenberg-Neto (2014) are shown in light green.

the localities of *La Mancha* at 50 m and *Palmarejo* at 650 m (Castillo-Campos & Travieso-Bello 2006) and characterized by the trees *Brosimum alicastrum* Sw., *Cedrela odorata* L., *Bursera simaruba* (L.) Sarg. and *Ficus obtusifolia* Kunth. Canopy trees lose leaves mostly during the prolonged period of drought (October to May). The tropical oak forest (TOF) in the locality of *Chavarrillo* at 1,000 m is typically dominated by one to three oak species (*Quercus oleoides* Schltdl. & Cham., *Q. laurina* Bonpl. and/or *Q. peduncularis* Née), whereas other tree species are scarce. The period of leaf fall lasts about four months and it is related with the dry season (February to May).

Tierra templada (1,250-2,200 m).- In this climate zone, two study sites within one forest type were chosen (Figure 1, Table 1): the humid montane forest (HMF), which is found in the localities of *Los Capulines* at 1,500 m and *El Zapotal* at 2,100 m. One of the most important ecological factors that characterizes this kind of forest is the frequent occurrence of fog (*bosque de niebla* or cloud forests; Zamora-Crescencio & Castillo-Campos 1997). In general, this community includes a mix of lower montane forest genera (*e.g.*, *Quercus* L. and *Liquidambar* L.) with tropical lowland forest families (Acanthaceae, Rubiaceae and Myrsinaceae). The period of leaf fall lasts about four months and is related to the dry season (February to May).

Tierra fría I (2,200-2,700 m).- In this climate zone, one study site within one forest type was chosen (Figure 1, Table 1): the pine-oak forest (POF), which is found in the locality of *El Encinal* at 2,500 m. This forest type comprises a community whose dominant trees belong to the genera *Quercus* and *Pinus* L. Typically, in the afternoons fog occurs (Narave-Flores 1985, Castillo-Campos 2011), which makes that the temperature and humidity stay constant.

Tierra fría II (2,700-3,200 m).- In this climate zone, one study site within one forest type was chosen (Figure 1, Table 1): the pine forest (PF), which is found in the locality of *Los Pescados* at 3,100 m. This forest type is dominated by several species of the genus *Pinus* L. (*P. montezumae* D. Don in Lamb., *P. patula* Schltdl. & Cham., *P. pseudostrobus* Lindl., *P. teocote* Schltdl. & Cham.) causing a high canopy openness.

Tierra helada (3,200-4,282 m).- In this climate zone, one study site within one forest type was chosen (Figure 1, Table 1): the fir forest (FF), which is found in the locality of *El Conejo* at 3,500 m. This forest type is a mono-specific *Abies religiosa* (Kunth) Schltdl. & Cham. community with sparse canopy openness.

Along the complete elevational gradient, mean annual precipitation (MAP) ranges from 813 to 3,004 mm, being highest in humid montane forest at 2,100 m and lowest in coniferous forests above 3,000 m, whereas mean average temperature (MAT) ranges from 9 to 26 °C (SMN 2016) (Table 1). The elevational vertical temperature gradient follows a negative linear pattern with MAT decreasing by 0.55 °C every 100 m ($r^2 = 0.96$, $p < 0.001$).

Sampling and botanical records. Field sampling was conducted between February 2012 and January 2014 at eight sites within elevational belts of about 500 m each (Figure 1, Table 1). In order to simplify hereafter we will refer to every site as categorical unit (50, 650, 1,000, 1,500, 2,100, 2,500, 3,100, 3,500 m).

We studied terrestrial herbaceous angiosperms (excluding epiphytes), whose life form was defined as plants that have no persistent woody stem above ground or plants that are only slightly woody, rooted on the forest floor and have short height (Moreno 1984, Poulsen 1996). Ferns were not included in this study because their diversity patterns were already described in the work of Carvajal-Hernández & Krömer (2015). Presence-absence was recorded for all species in each elevational belt within 15 to 20 plots of 20 × 20 m. The plot size of 400 m^2 was selected in order to have a representative study area of the forest fragments, which is small enough to keep abiotic factors and ecological physiognomy uniform within the plot (Kessler & Bach 1999). The total number of plots for the entire study was 135, resulting in a total study area of 54,000 m^2. For our study, we defined four types of habitat with different forest use intensities following Newbold *et al*. (2015): old-growth, degraded, secondary and azonal forest (Table 2).

To avoid edge effects, our plots were established at least 50 m away from the nearest forest edge. An equal number of plots was studied for every forest type, *i.e*. five were established in each of the following habitats with different use intensities: i) old-growth, ii) degraded and iii) secondary forest. Only in the sites of 650, 1,500 and 2,500 m we were able

Table 2. Classification of habitats with different forest use intensities according to the main physiognomic characteristic, the gap fraction in the canopy, dominance of canopy trees, percentage of shrubs and the presence of lianas (*sensu* Newbold *et al.* 2015).

Habitat	Characteristic	Gaps (%)	Forest use intensity	Canopy trees	Shrub (%)	Lianas
Old-growth	No obvious forest use, dominance of mature trees	< 10	Low	High	< 30	No
Degraded	Selective logging, grazing and understory removal	11-25	Medium	Low	30-50	Low
Secondary	Re-growth after clear-cut	> 25	High	Very low	> 50	High
Azonal	Grows in riparian forest and humid ravines	< 10	Low	High	< 30	No

to add five plots in vi) existing azonal vegetation, causing the uneven numbers of plots per elevational belt (Table 1).

Taxonomic determination. In each study site (but not in every plot), all terrestrial herbaceous angiosperms species were collected mostly in triplicate and deposited at the following herbaria: *Herbario Nacional de México, Instituto de Biología*, UNAM, (MEXU, including all unicates), *Instituto de Ecología, A.C.*, (XAL), *Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, IPN (CIIDIR)* and/or at the local herbarium of the *Facultad de Biología, Universidad Veracruzana* (XALU). Collection and processing of botanical specimens were made according to the proposal of Lot & Chiang-Cabrera (1986). Botanical determinations were realized by use of the relevant taxonomic literature (*Flora de Veracruz* and *Flora fanerogámica del Valle de México*), by comparison with specimens deposited at MEXU and XAL, and consultation of experts in different plant families (see Acknowledgements). Also, morpho-species which are clearly different were incorporated in the floristic list (Krömer *et al*. 2013). It was not possible to identify all specimens to species or genus level for two main reasons: i) most of the studied plant groups are not well known and their identification is difficult due to a lack of relevant literature, ii) some individuals were found sterile. Taxa were classified according to the classification of the Angiosperm Phylogeny Group (APG; Bremer *et al*. 2009).

Data analyses. We used the package "vegan v2.3-4" (Oksanen *et al*. 2016) in R statistical language v3.2.3 (R Core Team 2014) to calculate the number of unobserved species with the Bootstrap function, which is based on presence-absence data and takes into account rare, unique and duplicated species. This species richness estimator is reliable because it has a sensibility to species aggregation in the initial stage of the sampling when the species distribution is random.

Based on their geographical distribution area, each species was placed in one of the following categories (sensu Rzedowski 1991): i) endemic to Mexico, ii) endemic to the southern United States and Mexico (Megamexico 1), iii) endemic to Mexico and Central America (Megamexico 2), iv) endemic to the southern United States and Central America (Megamexico 3), and v) introduced species (Gómez-Pompa *et al*. 2010, Espejo-Serna 2012).

Finally, to compare our results with other studies, we calculated the taxonomic diversity index (TDI; Magurran 2004) for the total number of species and for the three most important families: Asteraceae, Poaceae and Orchidaceae, with the following equation:

$$TDI = \log\text{-}S - \log\text{-}A$$

where S is the total species number and A is the entire studied area in m^2.

Results

In 135 plots along the elevational transect, we recorded 264 (morpho-)species of terrestrial herbaceous angiosperms from 152 genera and 54 families (Appendix). Of all recorded species, 201 (76 %) were identified to species level, 42 (16 %) to genus level and 21 (8 %) to family level. Monocots contributed 45 % of the species and 28 % of the families, and dicots 55 % of the spe-

Table 3. Most representative families and genera of herbaceous angiosperms along gradients of elevation and forest disturbance in central Veracruz, Mexico.

Family	Species number	Percentage (%)	Genera	Species number	Percentage (%)
Poaceae	36	14	*Peperomia*	10	4
Asteraceae	31	12	*Salvia*	8	3
Orchidaceae	27	10	*Begonia*	6	2
Cyperaceae	17	6	*Senecio*	6	2
Lamiaceae	13	5	*Cyperus*	5	2
Araceae	12	4	*Anthurium*	5	2
Piperaceae	10	4	*Carex*	5	2
Commelinaceae	9	3	*Ageratina*	4	2
Rubiaceae	8	3	*Arenaria*	4	2
Other families	101	38	Other genera	211	80
Total	264	100	Total	264	100

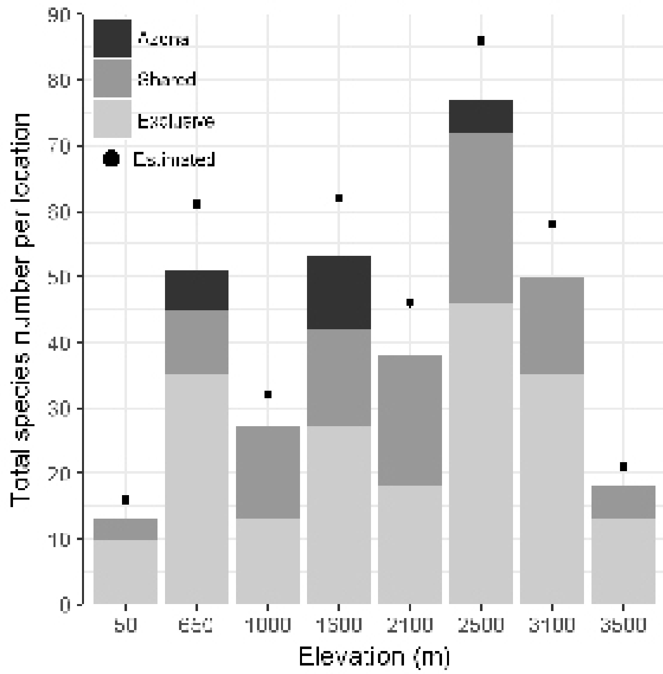

Figure 2. Observed and estimated (Bootstrap species richness estimator) species richness of all species together per elevational belt. We present the number of exclusive species at each study site, the number of species shared with other sites, and the species that are exclusive for azonal habitats.

cies and 72 % of the families. Table 3 summarizes the most species-rich taxa at family and genus level. The observed species richness varied between 79 and 90 % of the predicted values by the estimator Bootstrap at every elevational belt (Figure 2).

In order to compare overall species richness between the eight study sites, we used the values excluding and including species of azonal vegetation. In the first case, the highest number of species was found in the site of 2,500 (71), followed by 3,100 m (48) and 650 m (43); in the second case, the site with the highest number of species was 2,500 m (76), followed by 1,600 m (52) and 3,100 m (48) (Figure 2). All habitats of the 2,500 m site taken separately had the highest species richness of the elevational gradient (Table 1), whereas all habitats of 50 m had the lowest richness. The secondary forest in most of the sites had the highest number of species, whereas old-growth forests had the lowest number of species in most of the sites. In the sites with azonal vegetation, this habitat had more species than old-growth forests, and except for 2,500 m, even more than secondary forests (Table 1). TDI was 0.51 for all species and between 0.31 and 0.033 for the three most important families (Table 4).

Geographical distribution. Most of the study sites shared only low numbers of species (Figure 2). The highest number of exclusive species was found at 2,500 m, followed by 650 m

Table 4. Comparative species richness of herbaceous angiosperms along elevational gradients reported in some studies from México, Brazil and Ecuador. TDI = taxonomic diversity index (calculated for the total species number and for the most important families Ast= Asteraceae, Poa = Poaceae and Orc = Orchidaceae).

Region, Country	Elevation (m)	Latitude	Species number	Area (ha)	TDI	Ast	TDI	Poa	TDI	Orc	TDI	Authors
Manaus, Brazil	70-150	2° 37' S	24	0.09	0.47	0	-	2	0.10	0	-	Costa (2004)
Cuyabeno, Ecuador	250-300	0° 00' S	70	1.00	0.46	0	-	8	0.23	0	-	Poulsen *et al*. (2006)
Los Tuxtlas, Veracruz, Mexico	140-1,670	18° 43' N	50	2.96	0.38	0	-	0	-	17	0.28	Krömer *et al*. (2013)
Jalcomulco, Veracruz, Mexico	350-900	19° 21' N	60	0.67	0.46	2	0.08	4	0.16	2	0.08	Palacios-Wassenaar *et al*. (2014)
Central Veracruz, Mexico	1,800-2,000	19° 29' N	139	0.02	0.92	2	0.13	4	0.26	2	0.13	García-Franco *et al*. (2008)
Sierra de Manantlán, Jalisco, Mexico	1,500-2,500	19° 30' N	181	4.30	0.49	ND	ND	ND	ND	ND	ND	Vázquez & Givnish (1998)
Central Veracruz, Mexico	50-3,500	19° 31' N	264	4.80	0.52	31	0.32	36	0.33	27	0.31	This study
Central Veracruz, Mexico	400-900	19° 37' N	300	1.20	0.61	42	0.40	53	0.42	2	0.07	Castillo-Campos (2007)
Pacific coast of Mexico	400-2,860	19° 45'	1,793	140,000	0.36	333	0.28	221	0.26	181	0.25	Vázquez *et al*. (1995)
Sierra de Zapalinamé, Coahuila, Mexico	1,590-3,140	25° 25' N	171	3.30	0.49	61	0.40	27	0.32	0	-	Encina-Dominguez *et al*. (2007)

Table 5. Number of species under geographic distribution and life strategy recorded along gradients of elevation and forest disturbance in central Veracruz, Mexico. OG = old-growth forest, DE = degraded forest, SE = secondary forest, AZ = azonal forest. Total numbers of species in each category are also shown.

Distributional/life strategy category	OG	DE	SE	AZ	Total
Under special protection	1	2	2	-	3
Endemic to Veracruz	1	-	-	-	1
Endemic to Mexico	11	15	20	9	31
South of United States of America and Mexico	1	2	1	-	2
Mexico and Central America	9	12	11	9	20
Introduced	5	6	9	2	14
Ruderal	13	19	27	11	41
Generalist	65	92	73	56	152

and 3,100 m. Concerning biogeography, 70 % of the taxa showed a Neotropical affinity and we recorded 31 species endemic to Mexico, including two species (*Begonia multistaminea* Burt-Utley and *Sedum obcordatum* R.T.Clausen) endemic to Veracruz (see Appendix). Furthermore, 20 species were endemic to Mexico and Central America and two to the South of United States of America and Mexico. Three species are listed in Official Mexican Law (SEMARNAT 2010), two of these are threatened and endemic to Mexico (*Anthurium podophyllum* (Schltdl. & Cham.) Kunth and *Peperomia subblanda* C. DC.), and another was under special protection (*Monotropa hypopitys* L.). Additionally, we found 14 introduced species to Mexico that were mostly recorded in secondary and degraded forests (Table 5 and Appendix).

Discussion

General taxa richness. A comparison with previous studies on terrestrial angiosperms and other plant groups in state of Veracruz shows that we recorded a high number of species in our study.

Although our sampling area was limited (5.4 ha), the total number of species recorded was higher than those reported by Cházaro-Basáñez (1992) who focused on a floristic description of the different forest types within the upper part of the same elevational gradient. Cházaro-Basáñez reported only 12 herbs in the humid montane forest, 17 in the pine-oak forest, two in the pine forest and 14 in the fir forest. Carvajal-Hernández & Krömer (2015) found 155 species of ferns and lycophytes in the same plots of our elevational gradient of which 82 were terrestrial species. Several studies from central Veracruz reported a lower number of terrestrial herbs, *e.g.*, Palacios-Wasenaar *et al*. (2014) recorded 230 species of vascular plants of which 60 (26 %) were herbs (Table 5). García-Franco *et al*. (2008) found 258 vascular plant species in similar forests, of which 139 (54 %) were herbs. Novelo-Retana (1978) recorded 238 species of vascular plants of which 67 (28 %) were herbs. Zamora & Castillo-Campos (1997) recorded 390 species of vascular plants of which 225 (58 %) were herbs.

In contrast, a higher number of herbaceous species has been reported in some studies from central Veracruz. The relatively high number of herb species might be explained by the large environmental gradient covered in our study and will be discussed in the next paragraphs. For example, Castillo-Campos *et al*. (2007) recorded 580 species of vascular plants of which 369 (64 %) were herbs, and Narave-Flores (1985) recorded 853 species of vascular plants of which 557 (65 %) were herbs. For Southern Veracruz, Ibarra-Manríquez & Sinaca-Colin (1987) recorded 991 species of vascular plants of which 536 (54 %) were herbs. However, all these studies were realized in much bigger sampling areas than the present study.

Due to the limited number of similar transect studies in the study area we were only able to compare our results with the following studies realized in Southern Veracruz by Krömer *et al*. (2013), which however included mainly terrestrial ferns and only a few orchids and bromeliads, Western Mexico (Jalisco) by Vázquez & Givnish (1998) and Vázquez *et al*. (1995), and Northern Mexico (Coahuila) by Encina-Domínguez *et al*. (2007). Furthermore, we compared our results with the species numbers of terrestrial angiosperms found along two elevational gradients of Brazil and Ecuador (Table 4).

In most of the cases, our study site shows a higher number of species than the other locations. The TDI also shows that excluding the works from central Veracruz, our study has a higher species per area value than the other studies (Table 4). These differences among the geographical areas can be explained by environmental factors, such as latitudinal influence, precipitation, temperature, elevation and soil nutrients (Vázquez & Givnish 1998, Cicuzza *et al*. 2013). The TDI indicates different patterns for the three most important families, *e.g*., there is an increase of the values of Asteraceae with elevation (Table 4), which is different from the family pattern shown in Mexico (Villaseñor *et al*. 2005). In the case of the Poaceae, the index shows that at lower latitudes this family is an important component of the flora, whereas in central Veracruz the family has similar values than the Asteraceae, and at the highest latitude there was a decrease in the value. In the case of the Orchidaceae, our study shows the highest value compared to the other locations, which demonstrates that the forest fragments in central Veracruz harbor a high number of orchids (Castañeda-Zárate *et al*. 2012).

On the other hand, species richness in our study was much lower compared to the numbers presented by Castillo-Campos *et al*. (2007), which is due to the fact that their work was realized in tropical deciduous forest which is recognized as vegetation type with high diversity of herbaceous angiosperms, as well as a more concentrated and exhaustive sampling effort in only one vegetation type. In general, the tropical deciduous forests occur in environments with highlight incidence during the dry season (Chiarucci 1994). Besides, the limitations imposed by the bedrock, such as lack of organic matter in the soil, restrict the establishment of other plant groups (*e.g*., trees). Therefore, the herbaceous layer is facilitated by excluding competitors due to the physiological and functional traits that are characteristic for this plant group (Castillo-Campos *et al*. 2007).

Patterns of richness along the elevational gradient. We found a not very pronounced hump-shaped pattern in the overall species distribution along the elevational gradient (Figure 2), which is a pattern found in different groups of vascular plants along tropical elevational gradients, such as ferns (Salazar *et al*. 2015), terrestrial herbs (Willinghöfer *et al*. 2012) and shrubs (Chawla *et al*. 2008). Rahbek (1995) suggested that the distribution of plants in tropical areas is affected by the high variation of environmental factors that can change substantially in small regions, and this causes differences in the form of distributional patterns. We found that the sea level site was less species-rich compared with the other sites. The following sites (from 650 until 2,100 m) have an intermediate species richness (Figure 2). This is probably due to heterogeneity in their landscape in comparison to other areas of the state, such as the coastal plain, caused by the heterogeneous structure of the physiographic discontinuity generated by the union of two regions: Coastal plain of the Gulf of Mexico and Trans-Mexican Volcanic Belt (Narave-Flores 1985, Torres-Cantú 2013).

The highest species richness was found at 2,500 m, which has been also reported from Ecuador for all endemic vascular plant species, endemic species of Acanthaceae, Asteraceae, Lamiaceae, Piperaceae and Scrophulariaceae (Kessler 2002), and for liverworts in the Northern Andes (Wolf 1993). This pattern is based on a contact of different species assemblages within the transition between two climate zones (Lauer 1972, Wolf 1993) and a high level of humidity due to cloud condensation (Rahbek 1995, Hemp 2006). The richness tends to decrease at higher elevations because productivity and temperature decrease with elevation (Currie *et al*. 2004, Hawkins *et al*. 2007); both factors affect the competition and growth of plants (Vázquez & Givnish 1998). Furthermore, the kind of dominant tree species (*Pinus* spp. and *Abies religiosa*) at the highest sites (3,000 and 3,500 m) has an influence on the herbaceous community because the coniferous litter changes the soil properties (Whittaker 1975, van Wesenbeeck *et al*. 2003).

Forest use intensity effect. The degraded and secondary forests of the 50, 650, 2,100, 3,100 and 3,500 m sites had higher species richness, compared to the old-growth forests. Furthermore, we found introduced and generalist species most frequently in secondary and degraded forest due to the changes in abiotic factors, such as a drier microclimate, change in soil nutrients and higher light incidence (Köster *et al*. 2009) that allow them to outcompete native species due to specific arrangements of traits (Schultz & Dibble 2012) (Table 1, Appendix). Similarly, Firn *et al*. (2011) reported that some herbaceous angiosperms are related to human forest use intensity, which allows the establishment of ruderal species. These species increase the richness in anthropogenically influenced habitats, although native biodiversity is affected negatively by introduced plant species. This indicates that modifications in the structure of the old-growth forest affect the species composition of herbaceous angiosperms because changes in abiotic factors due to forest use intensity may increase the richness, especially of Poaceae and Orchidaceae in degraded habitats, whereas Asteraceae increase in secondary habitats. This is due to the ability of ruderal species to survive or even being favored in drier microclimates (Givnish 1995, Pons & Poorter 2014) with more light in the understory due to the more open canopy of degraded forests (Grime 1977, Lavorel *et al*. 2011). Consequently, in North American forests, a higher richness of terrestrial herbs was found in the degraded forest with open canopy gaps compared to mature forests with closed canopies (Meekins & McCarthy 2001).

However, the richness of species decreases in the degraded and secondary forests of the 1,600 and 2,500 m sites compared to the old-growth humid montane forest. This similar pattern was found for ferns (Carvajal-Hernández *et al*. 2014, Carvajal-Hernández & Krömer 2015) and in general for vascular epiphytes (Krömer & Gradstein 2003, Köster *et al*. 2009). This loss of species is due to the adaptation of many native species to temperate climate with high humidity (Parry *et al*. 2007). Furthermore, the changes in the structure of soil due to the forest use intensity leads to a loss of microbial organisms that favor the establishment of some species (Camenzind *et al*. 2014). On the other hand, it is widely documented that fragmentation has a negative effect on species richness in lowland forest, especially on understory plants (Magrach *et al*. 2014). For example, in the south of Veracruz, Zambrano *et al*. (2014) found that seeds of understory plants could be affected by altered microclimatic conditions in the fragmented landscape. These species seem to be adapted to moderate conditions of humidity and temperature which, respectively, decrease and increase with forest use intensity (Dale *et al*. 2001). *Peperomia magnoliifolia* (Jacq.) A. Dietr. serves as an example in the 650 m site, *Begonia multistaminea* and *P. cobana* C. DC. in the 1,600 m site, where these are commonly found in habitats of high humidity and shadow (old-growth forest), but probably cannot tolerate high levels of radiation and low humidity and thus are rare in degraded and secondary forests (Ali 2013, Mathieu *et al*. 2015).

It was hypothesized that intermediate forest use intensity leads to higher species richness (Connell 1978, Warren *et al*. 2007) and plantcommunity endemism (Kessler 2001). The mosaic vegetation pattern in our study area is an important shelter for the endemic flora of the region. Since the level of forest use intensity was similar in all sites, the different effects can only be attributed to feedbacks between the specific plant community and the changes in environmental factors, such as microclimate or soil nutrients.

In azonal vegetation (riparian forests), except for the 2,500 m site, the richness was higher than in old-growth forests, which might be due to stable moist environmental conditions and higher soil moisture. In the case of the 650 m site, the species richness recorded in azonal vegetation was almost twice of that observed in the old-growth tropical semi-deciduous forest. This interpretation is consistent with results found by Poulsen & Balslev (1991) in the Amazonian rain forest, who recorded the highest richness of herbs along rivers, which was explained by a mix of species from the border zone to the moist zone next to their study plot and the edaphic and topographic heterogeneity. In the case of terrestrial ferns, Carvajal-Hernández & Krömer (2015) found the same pattern suggesting that fern richness is favored in areas with the influence of water and high humidity. These results confirm the value of the azonal vegetation as reservoirs of biodiversity.

Introduced species. Within the set of introduced species, there is a subgroup known as invasive alien or invasive species, which includes those that survive, are established and reproduce uncontrollably outside their natural environment, causing serious damage to biodiversity, economy, agriculture and public health (CONABIO 2016). We found several introduced species recognized as invasive, *e.g*. *Commelina diffusa* Burm. f. is a species that can withstand flooding and infests cultivated lands, roadsides, pastures and wastelands, which is problematic primarily in young crops, but can also cause a problem in mature crops in Mexico due to its sprawling behavior (Boyette *et al*. 2015). *Oeceoclades maculata* (Lindl.) Lindl. is competing for the same microhabitat and may displace other native terrestrial orchids (Moreno-Molina & Beutelspacher 2014). *Hedychium coronarium* J. Koenig has a negative influence on the recruitment of plants from the plant community, with consequences for the biodiversity of invaded areas (de Castro *et al*. 2016). *Foeniculum vulgare* Mill. is particularly aggressive in abandoned agricultural fields and grazed areas (Power *et al*. 2014). *Rumex acetosella* L. might interfere with secondary succession processes and gap colonization dynamics of native species, and it has the ability to competitively exclude native tussock grasses (Franzese & Ghermandi 2014).

Geographical distribution. In general, the inventoried species show a phytogeographical affinity with southern latitudes, which can be seen by the high number of taxa also occurring in Central and South America. Nevertheless, many endemic taxa of central Mexico have also been encountered. In this context, Rzedowski (2006) suggests that for the flora of *Tierra caliente* (from sea level until ca. 1,400 m) the southern Neotropical affinity dominates over the boreal affinity. In addition, in *Tierra templada*, the most important elements have a southern origin with less boreal elements. In the cooler zones (*Tierra fría* and *Tierra helada*), the most important floristic elements are equally of southern and boreal affinity with some being endemic species from North America, such as *Ageratina pazcuarensis* (Kunth) R.M. King & H. and *Festuca rosei* Piper, whereas others, such as *Carex melanosperma* Liebm., *Corallorhiza maculata* (Raf.) Raf. and *Muhlenbergia macroura* (Kunth) Hitchc. are species endemic to Central America.

Our results show that species richness patterns of herbaceous angiosperms of forest vegetation in central Veracruz are determined by the large environmental gradient of the region. Moreover, degraded and secondary forests exhibit high species richness depending on the elevational belt, which is probably due to the ability of species in several families that compete better under high light conditions. The high richness and turnover of species, including many endemic elements, highlights the importance of this region for plant conservation; however, this area is also highly threatened by land use changes and shows very high deforestation rates (Ellis & Martínez 2010).

Castillo-Campos *et al*. (2008) proposed to create a system of many protected reserves distributed throughout the state in order to protect this kind of landscape and its flora under the plan of "archipelago reserves" described by Halffter (2005), where all landscape units are connected by small protected areas. In addition, we suggest that an environmental heterogeneity formed by mature, disturbed and secondary forests is acceptable (and unavoidable) and can even increase species richness. This is an opportunity to develop a sustainable management concept to protect and promote species richness and to take into account the need of the local population for forest ecosystem services, such as timber, water, landslide protection, recreation and tourism. This could be an alternative to the current concept of a protected area, such as a national park, that is only focused on protecting alpha diversity without consideration of species turnover rates (Castillo-Campos *et al*. 2008). Thus, it is necessary to create a conservation and management plan for the study area, which requires taking into account more taxonomic groups, the existing proportions of different habitat types, as well as studies on the socio-economic conditions across the elevational gradient.

Acknowledgements

We thank M. Ruiz-Gómez, F. Calixto-Benites, C. Alavez-Tadeo and V. Guzmán-Jacob for their help during fieldwork, A. Acebey (Araceae), J. Villaseñor-Rios (Asteraceae), G. Salazar-Chávez (Orchidaceae), D. Vergara-Rodriguez (*Peperomia*), J. Sánchez-Ken and M. Mejía-Saulés (Poaceae), M. Gonzalez-Elizondo (Cyperaceae) and M. Cházaro-Basáñez (other groups) for species identifications, and H. Kreft for helpful comments on this manuscript. We appreciate the working facilities provided at the *Centro de Investigaciones Tropicales* (CITRO), *Universidad Veracruzana*, Xalapa. The first author acknowledges support from the *Consejo Nacional de Ciencia y Tecnología* (CONACyT 311672) and the *Deutscher Akademischer Austauschdienst* (DAAD 91549681) for this research, which is part of his Ph.D. thesis. FH acknowledges a grant from the *Deutsche Forschungsgemeinschaft* (DFG; HE 6726/4-1). The research of TK was supported by CONACyT. The mobility of researchers was supported by the DAAD with resources of the *Bundesministerium für Bildung und Forschung* (BMBF, project-ID 57155237, "BIOVERA").

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Received:
July 11th, 2016

Accepted:
November 8th, 2016

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Appendix. Species of herbaceous angiosperms recorded along gradients of elevation and forest disturbance in central Veracruz, Mexico.
Collector: Jorge Gómez Díaz (JGD); Herbaria: MEXU = Instituto de Biología, UNAM; XAL = Instituto de Ecología, A.C., XALU = Facultad de Biología, Universidad Veracruzana, and CIIDIR = Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, IPN. Data corresponding to minimum (min) and maximum (max) observed elevational distribution range, number of plots (N) in which the species was recorded from a total of 135 plots, and conservation/distribution status: T = threatened, P = protected, V = endemic to Veracruz, Mx = endemic to Mexico, Mx1 = Megamexico 1, Mx2 = Megamexico 2, E = exotic and R = ruderal. Nomenclature follows Tropicos.org <www.tropicos.org> (accessed on 24 Mar 2016) and The International Plant Names Index <www.ipni.org> (accessed on 06 Mar 2017).

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
LILIIDAE				
Amaryllidaceae				
Hypoxis sp. 1 (JGD 212, MEXU; XAL)	1,500	1,500	1	
Hypoxis sp. 2 (JGD 260, XALU)	3,100	3,100	2	
Araceae				
Anthurium andicola Liebm. (JGD 329, MEXU)	2,100	2,100	2	Mx2
Anthurium podophyllum (Schltdl. & Cham.) Kunth (JGD 462, MEXU)	50	50	2	T, Mx
Anthurium scandens (Aubl.) Engl. (JGD 175, MEXU)	1,500	1,500	3	
Anthurium schlechtendalii Kunth (JGD 319, XAL)	650	1,000	17	
Anthurium sp. (JGD 369, XALU)	1,000	1,000	1	
Monstera acuminata K. Koch (JGD 444, MEXU)	650	650	3	
Monstera deliciosa Liebm. (JGD 170, MEXU)	1,500	1,500	6	
Philodendron radiatum Schott (JGD 315, MEXU; XAL)	650	650	13	
Spathiphyllum cochlearispathum Engl. (JGD 432, MEXU; XAL; XALU)	650	650	2	Mx2
Syngonium macrophyllum Engl. (JGD 321, MEXU)	50	50	1	
Syngonium podophyllum Schott (JGD 312, MEXU)	50	650	16	
Syngonium sagittatum G.S. Bunting (JGD 174, MEXU; XAL)	1,000	1,500	23	Mx
Arecaceae				
Chamaedorea elegans Mart. (JGD 336, XALU)	650	1,000	17	Mx2
Chamaedorea oblongata Mart. (JGD 452, XALU)	650	650	1	
Chamaedorea tepejilote Liebm. in Mart. (JGD 184, MEXU; XALU)	1,000	2,100	30	
Asparagaceae				
Maianthemum paniculatum (M. Martens & Galeotti) La Frankie (JGD 381, MEXU; XAL; XALU)	2,100	2,100	6	
Maianthemum sp. (JGD 451, XALU)	2,500	2,500	5	
Bromeliaceae				
Aechmea bracteata Mez (JGD 316, MEXU; XAL)	650	650	3	
Bromelia cf. *pinguin* L. (JGD 314, MEXU)	50	50	4	
Cf. *Pitcairnia* sp. 1 (JGD 268, MEXU)	3,100	3,100	5	
Cf. *Pitcairnia* sp. 2 (JGD 276, MEXU)	2,100	2,500	5	
Cf. *Pitcairnia* sp. 3 (JGD 328, MEXU)	650	650	1	
Greigia van-hyningii L.B. Sm. (JGD 330, MEXU)	2,100	3,100	22	Mx
Commelinaceae				
Callisia fragrans (Lindl.) Woodson (JGD 387, XALU)	650	650	3	Mx
Commelina diffusa Burm. f. (JGD 450, XALU)	650	650	1	E, R
Commelina erecta L. (JGD 454, XALU)	650	650	1	R
Gibasis geniculata (Jacq.) Rohweder (JGD 196, MEXU; XAL; XALU)	1,500	1,500	11	
Gibasis linearis (Benth.) Rohweder (JGD 320, XAL)	50	50	1	Mx
Tradescantia zanonia (L.) Sw. (JGD 383, MEXU; XAL)	2,100	2,100	5	

Appendix. Continuation.

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
Tripogandra disgrega (Kunth) Woodson (JGD 243, MEXU; XAL)	1,000	2,100	8	Mx2
Tripogandra serrulata (Vahl) Handlos (JGD 302, XAL)	2,100	2,100	12	
Tripogandra sp. (JGD 443, MEXU)	650	650	1	
Cyclanthaceae				
Asplundia sp. (JGD 318, MEXU)	650	650	1	
Cyperaceae				
Carex chordalis Liebm. (JGD 286A, CIIDIR)	2,100	2,500	2	
Carex cortesii Liebm. (JGD 247, XAL; CIIDIR)	1,500	2,500	11	Mx2
Carex melanosperma Liebm. (JGD 162, MEXU; XAL; CIIDIR)	2,500	2,500	3	Mx2
Carex sect. *longicaules* (JGD 286B, CIIDIR)	2,100	2,100	1	
Carex thurberi Dewey ex Torr. (JGD 323, XAL; CIIDIR)	1,500	1,500	7	
Cyperus articulatus L. (JGD 241, MEXU; XAL; CIIDIR)	50	50	1	R
Cyperus ligularis L. (JGD 286, XAL; CIIDIR)	2,100	3,100	12	
Cyperus manimae Kunth (JGD 185, MEXU)	3,100	3,100	2	R
Cyperus seslerioides Kunth (JGD 155, CIIDIR)	2,500	2,500	1	R
Cyperus surinamensis Rottb. (JGD 201, MEXU; CIIDIR)	1,500	1,500	1	
Cyperus virens Boeckeler var. *minarum* (Boeckeler) Denton	1,500	1,500	1	R
Eleocharis geniculata (L.) Roem. & Schult. (JGD 188, MEXU)	650	650	1	E
Eleocharis montana Roem. & Schult. (JGD 322, XAL; CIIDIR)	650	650	1	
Kyllinga pumila Michx. (JGD 166, MEXU; CIIDIR)	1,500	1,500	5	
Rhynchospora radicans H. Pfeiff. (JGD 169&460, MEXU; XAL; CIIDIR)	1,500	2,100	17	R
Rhynchospora schiedeana Hemsl. (JGD 303, XAL; CIIDIR)	2,100	2,100	3	
Scleria lithosperma (L.) Sw. (JGD 457, CIIDIR)	650	650	3	
Uncinia hamata (Sw.) Urb. (JGD 458, XAL; CIIDIR)	2,100	2,500	13	
Heliconiaceae				
Heliconia adflexa Standl. (JGD 186, MEXU)	1,500	1,500	1	Mx2
Heliconia schiedeana Klotzsch (JGD 240, XALU)	1,000	1,500	6	Mx2
Iridaceae				
Sisyrinchium scabrum Cham. & Schltdl. (JGD 326, MEXU)	2,500	2,500	1	
Juncaceae				
Luzula sp. (JGD 190, MEXU)	2,500	2,500	4	
Orchidaceae				
Beloglottis mexicana Garay & Hamer (JGD 372, MEXU)	1,000	1,000	1	Mx2
Calanthe calanthoides (A. Rich. & Galeotti) Hamer & Garay (JGD 394, MEXU)	2,500	2,500	7	
Calanthe sp. (JGD 466, MEXU)	2,100	2,100	1	
Corallorhiza maculata (Raf.) Raf. (JGD 295, MEXU)	3,500	3,500	1	
Cyclopogon elatus (Sw.) Schltr. (JGD 406, MEXU)	2,500	2,500	1	
Cyclopogon sp. 1 (JGD 337, MEXU)	650	1,000	5	
Cyclopogon sp. 2 (JGD 373, MEXU)	650	650	1	
Cyrtopodium macrobulbon (La Llave & Lex.) G.A. Romero & Carnevali (JGD 374, MEXU)	650	650	5	Mx2
Epidendrum radicans Pav. ex Lindl. (JGD 244, MEXU)	1,500	1,500	1	
Goodyera sp. 1 (JGD 391, MEXU)	2,100	2,100	1	
Goodyera sp. 2 (JGD 428, MEXU; XAL)	3,100	3,100	1	
Govenia superba (La Llave & Lex.) Lindl. (JGD 442, MEXU)	2,500	2,500	2	
Govenia sp. 1 (JGD 463, MEXU)	2,100	2,100	1	
Govenia sp. 2 (JGD 282, MEXU)	3,100	3,100	3	
Govenia sp. 3 (JGD 472, MEXU)	650	650	1	
Habenaria floribunda Lindl. (JGD 471, MEXU)	1,500	1,500	2	Mx2
Habenaria novemfida Lindl. (JGD 377, MEXU)	1,500	1,500	1	Mx2

Appendix. Continuation.

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
Malaxis excavata Kuntze (JGD 390, MEXU)	2,100	2,100	1	
Malaxis histionantha (Link, Klotzsch & Otto) Garay & Dunst. (JGD 371, MEXU; XAL)	1,000	1,000	6	
Malaxis soulei L.O. Williams (JGD 427, MEXU)	3,100	3,100	1	
Oeceoclades maculata (Lindl.) Lindl. (JGD 332, MEXU; XAL)	50	1,000	7	E
Pelexia funckiana (A. Rich. & Galeotti) Schltr. (JGD 198, MEXU)	1,500	1,500	10	
Prescottia stachyodes (Sw.) Lindl. (JGD 221, MEXU)	1,500	1,500	5	
Psilochilus macrophyllus Ames (JGD 200, MEXU)	1,500	1,500	1	
Schiedeella sp. (JGD 464, MEXU)	2,100	2,100	2	
Spiranthinae (JGD 465, MEXU)	2,100	2,100	2	
Vanilla insignis Ames (JGD 429, MEXU)	650	1,000	2	Mx2
Poaceae				
Aegopogon cenchroides Humb. & Bonpl. ex Willd. (JGD 199, XAL)	1,500	2,500	3	
Agrostis tolucensis Kunth (JGD 296, XAL)	3,500	3,500	1	
Andropogon sp. (JGD 310, XAL)	50	50	1	
Aristida sp. (JGD 311, XAL)	50	50	1	
Bouteloua gracilis (Kunth) Lag. ex Griffiths (JGD 301, XAL)	2,100	2,500	6	
Brachypodium mexicanum Link (JGD 258, XAL)	3,100	3,100	1	
Brachypodium sp. (JGD 298, XAL)	2,100	2,500	8	
Briza minor L. (JGD 299, XAL)	2,500	2,500	1	E
Bromus exaltatus Bernh. (JGD 300, XAL)	2,500	2,500	3	
Chusquea glauca L.G. Clark (JGD 362, MEXU)	2,100	2,100	6	Mx
Chusquea sp. (JGD 468, MEXU)	2,500	2,500	2	
Dichanthelium dichotomum (L.) Gould (JGD 160, MEXU)	1,500	1,500	14	
Eragrostis sp. (JGD 306, XAL)	1,000	1,000	1	
Festuca amplissima Rupr. (JGD 279, XAL)	3,100	3,100	1	
Festuca rosei Piper (JGD 269, XAL)	3,100	3,100	11	Mx1
Festuca sp. (JGD 305, XAL)	1,000	1,500	3	
Guadua sp. (JGD 307, XAL)	650	650	2	
Hordeum sp. (JGD 234, MEXU; XAL)	1,000	1,500	1	
Lasiacis sp. 1 (JGD 441, XAL)	650	650	1	
Lasiacis sp. 2 (JGD 161, MEXU)	1,500	1,500	6	
Lasiacis sp. 3 (JGD 168, MEXU)	1,500	1,500	2	
Melinis sp. (JGD 308, XAL)	650	650	2	
Muhlenbergia macroura Hitchc. (JGD 297, XAL)	3,500	3,500	10	R, Mx2
Muhlenbergia sp. (JGD 309, XAL)	650	650	2	
Oplismenus sp. (JGD 439, XAL)	650	650	1	
Oryza latifolia Desv. (JGD 440, XAL)	650	650	1	
Otatea acuminata (Munro) C.E. Calderón & Soderstr. (JGD 470, MEXU)	650	650	1	
Panicum sp. (JGD 469, MEXU)	650	650	1	
Paspalum sp. (JGD 362, XALU)	650	650	1	
Pennisetum sp. (JGD 324, XAL)	650	650	1	
Phyllostachys aurea Riviere & C. Riviere. (JGD 214, XAL)	1,500	1,500	2	
Schizachyrium condensatum Nees (JGD 304, XAL)	650	1,000	17	
Stipa ichu (Ruiz & Pav.) Kunth (JGD 467, MEXU)	3,500	3,500	10	R
Trisetum spicatum (L.) K. Richt. (JGD 254, XAL)	3,100	3,100	14	
Zeugites americanus Willd. (JGD 178, MEXU; XAL)	1,500	1,500	2	
Cf. *Zeugites* sp. (JGD 286C, XAL)	2,100	2,100	1	

Appendix. Continuation.

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
Zingiberaceae				
Hedychium coronarium J. Koenig (JGD 331, XALU)	50	50	2	E, R
MAGNOLIIDAE				
Acanthaceae				
Aphelandra scabra (Vahl) Sm. (JGD 449, XALU)	650	650	2	R
Pseuderanthemum alatum Radlk. (JGD 453, XALU)	650	650	4	
Ruellia sp.(JGD 368, MEXU; XAL; XALU)	1,000	1,000	5	
Cf. *Ruellia* sp. (JGD 405, XALU)	650	650	1	
Amaranthaceae				
Iresine diffusa Humb. & Bonpl. ex Willd. (JGD 233, MEXU; XALU)	1,500	1,500	4	R
Iresine sp. (JGD 433, MEXU; XAL)	2,500	3,100	3	
Apiaceae				
Eryngium columnare Hemsl. (JGD 228, XALU)	2,500	2,500	1	Mx
Eryngium proteiflorum F. Delaroche (JGD 267, XALU)	3,100	3,500	5	Mx
Foeniculum vulgare Mill. (JGD 287, MEXU; XALU)	3,100	3,100	2	E, R
Sanicula liberta Cham. & Schltdl. (JGD 211, MEXU; XAL; XALU)	1,500	1,500	5	
Araliaceae				
Hydrocotyle mexicana Schltdl. & Cham. (JGD 422, XALU)	2,500	2,500	4	
Hydrocotyle umbellata L. (JGD 213, XALU)	1,500	1,500	3	
Asteraceae				
Achillea millefolium L. (JGD 289, XALU)	2,500	3,100	4	E, R
Ageratina chazaroana B.L. Turner (JGD 401, MEXU)	2,500	2,500	2	Mx
Ageratina pazcuarensis (Kunth) R.M. King & H. Rob. (JGD 255, MEXU)	2,500	2,500	1	Mx1
Ageratina pichinchensis (Kunth) R.M. King & H. Rob. (JGD 403, MEXU)	2,500	2,500	2	
Ageratina sp. (JGD 434, XALU)	2,500	2,500	1	
Artemisia ludoviciana Nutt. (JGD 274, XALU)	3,100	3,100	1	R
Bidens sp. (JGD 163, MEXU)	2,500	2,500	1	
Cirsium conspicuum Sch. Bip. (JGD 351, MEXU; XALU)	2,500	2,500	1	Mx
Cirsium ehrenbergii Sch. Bip. (JGD 352, MEXU)	3,100	3,100	11	Mx
Cirsium nivale Sch. Bip. (JGD 253, XALU)	3,500	3,500	3	Mx
Conyza canadensis (L.) Cronquist (JGD 435; XALU)	650	650	5	R
Conyza coronopifolia Kunth (JGD 227, XALU)	1,500	2,500	6	R
Elephantopus mollis Kunth (JGD 205, MEXU; XALU)	1,500	1,500	5	
Hymenoxys integrifolia (Kunth) Bierner (JGD 273, 293 & 361, MEXU; XALU)	2,500	3,500	14	
Laennecia gnaphalioides Cass. (JGD 355, XALU)	2,500	2,500	4	
Pseudognaphalium liebmannii (Klatt) Anderb. (JGD 270, XALU)	3,100	3,100	8	
Roldana angulifolia (DC.) H. Rob. & Brettell. (JGD 396, XALU)	2,500	2,500	4	Mx
Roldana aschenborniana (S. Schauer) H. Rob. & Brettell (JGD 208, MEXU; XALU)	1,500	1,500	4	
Sabazia humilis Cass. (JGD 395, XALU)	2,500	2,500	4	Mx, R
Sabazia sarmentosa Less. (JGD 285, XALU)	3,100	3,100	1	
Senecio callosus Sch. Bip. (JGD 283& 359, MEXU; XAL; XALU)	2,500	3,500	16	
Senecio cinerarioides Kunth (JGD 436, MEXU; XALU)	3,500	3,500	2	Mx
Senecio deppeanus Hemsl. (JGD 206, MEXU; XALU)	1,500	1,500	1	
Senecio roseus Sch. Bip. (JGD 330A, MEXU)	3,500	3,500	1	Mx

Appendix. Continuation.

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
Senecio sp. (JGD 411, XALU)	2,500	2,500	1	
Sigesbeckia jorullensis Kunth (JGD 398, XALU)	2,500	3,100	6	R
Trixis inula Crantz (JGD 446, XALU)	650	650	3	
Verbesina robinsonii (Klatt) Fernald ex B.L. Rob. & Greenm. (JGD 445, MEXU; XALU)	3,100	3,100	2	Mx
Cf. *Verbesina* sp. 1 (JGD 171, MEXU)	1,500	1,500	1	
Cf. *Verbesina* sp. 2 (JGD 173, MEXU; XALU)	2,100	2,100	1	
Begoniaceae				
Begonia fusca Liebm. (JGD 181, MEXU)	2,100	2,100	1	
Begonia heracleifolia Schltdl. & Cham. (JGD 325, MEXU)	650	650	1	
Begonia manicata Brongn. (JGD 376, XALU)	1,000	1,000	1	
Begonia multistaminea Burt-Utley (JGD 187, MEXU)	1,500	1,500	1	V
Begonia nelumbonifolia Schltdl. & Cham. (JGD 386, MEXU; XAL; XALU)	2,100	2,100	2	
Begonia oaxacana A. DC. (JGD 191, MEXU; XALU)	1,500	2,500	6	
Boraginaceae				
Hackelia mexicana I.M. Johnst. (JGD 288 MEXU; XAL; XALU)	3,100	3,100	1	
Macromeria sp. (JGD 400, XALU)	2,500	2,500	2	
Phacelia platycarpa Spreng. (JGD 294, XALU)	3,100	3,100	4	R
Morpho unidentified 1 (JGD 456, MEXU; XAL; XALU)	3,100	3,100	2	
Morpho unidentified 2 (JGD 262, XALU)	2,500	2,500	1	
Brassicaceae				
Pennellia longifolia (Benth.) Rollins (JGD 409, XALU)	2,500	2,500	3	
Campanulaceae				
Centropogon grandidentatus (Schltdl.) Zahlbr. (JGD 249, XALU)	2,500	2,500	10	
Morpho unidentified (JGD 278, MEXU)	3,100	3,100	2	
Capparaceae				
Morpho unidentified (JGD 437, MEXU)	3,100	3,100	3	
Caryophyllaceae				
Arenaria lanuginosa (Michx.) Rohrb. (JGD 420, XALU)	1,000	1,000	1	R
Arenaria lycopodioides Willd. ex D.F.K. Schltdl. (JGD 257, XALU)	3,100	3,100	8	R
Arenaria oresbia Greenm. (JGD 417, XALU)	2,500	3,100	2	Mx
Arenaria reptans Hemsl. (JGD 423, XALU)	2,500	2,500	14	R
Cerastium arvense L. subsp. *molle* (Vill.) Arcang. (JGD 265, XALU)	3,100	3,100	1	E, R
Drymaria cordata (L.) Willd. ex Schult. (JGD 384, XAL)	2,100	2,500	3	R
Morpho unidentified (JGD 424, XALU)	3,100	3,100	2	
Crassulaceae				
Echeveria mucronata Schltdl. (JGD 272, XALU)	3,100	3,100	5	Mx
Echeveria rosea Lindl. (JGD 407, XALU)	2,500	2,500	2	Mx
Sedum obcordatum R.T. Clausen (JGD 291, XALU)	3,100	3,100	1	V
Cytinaceae				
Bdallophyton americanum (R. Br.) Eichler ex Solms. (JGD 358, XALU)	50	50	1	
Ericaceae				
Chimaphila umbellata (L.) Nutt. (JGD 290, MEXU; XAL; XALU)	3,100	3,100	4	
Monotropa hypopitys L. (JGD 410, XALU)	3,500	3,500	1	P
Monotropa uniflora L. (JGD 421, MEXU; XAL, XALU)	2,500	2,500	3	
Pernettya ciliata Small (JGD 431, XALU)	3,500	3,500	2	

Appendix. Continuation.

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
Euphorbiaceae				
Acalypha arvensis Poepp. (JGD 366, XALU)	650	650	1	R
Euphorbia cyathophora Murray (JGD 447, XALU)	1,000	1,000	1	R
Euphorbia dentata Michx. (JGD 207, MEXU; XAL; XALU)	1,500	1,500	3	R
Fabaceae				
Lupinus mexicanus Cerv. (JGD 399, XALU)	3,500	3,500	7	Mx
Lupinus montanus Kunth (JGD 354, XALU)	3,500	3,500	1	Mx2
Trifolium repens L. (JGD 292, XALU)	2,500	3,100	17	E, R
Gentianaceae				
Halenia brevicornis (Kunth) G. Don (JGD 402, XALU)	2,500	2,500	2	
Geraniaceae				
Geranium seemannii Peyr. (JGD 263, XALU)	3,100	3,100	2	R
Gesneriaceae				
Achimenes erecta (Lam.) H.P. Fuchs (JGD 339, XALU)	650	650	1	
Gunneraceae				
Morpho unidentified (JGD 397, XALU)	2,500	2,500	2	
Lamiaceae				
Asterohyptis stellulata Epling (JGD 338, XALU)	650	650	1	Mx
Marrubium vulgare L. (JGD 176, MEXU)	2,500	2,500	4	E, R
Prunella vulgaris L. (JGD 426, XALU)	2,500	2,500	1	E, R
Salvia carnea Kunth. (JGD 280, XALU)	3,100	3,100	9	R
Salvia coccinea Buc'hoz ex Etl. (JGD 412, XALU)	2,500	2,500	3	
Salvia hispanica L. (JGD 364, MEXU; XAL; XALU)	1,000	1,000	2	
Salvia iodantha Fernald (JGD 413, XALU)	2,500	2,500	6	Mx
Salvia mexicana L. (JGD 375, XALU)	1,000	1,000	4	Mx, R
Salvia microphylla Kunth (JGD 225, XALU)	1,500	1,500	1	
Salvia polystachya Cav. (JGD 414, XALU)	2,500	2,500	2	
Salvia tiliifolia Vahl (JGD 385, MEXU; XAL; XALU)	2,100	2,100	1	R
Scutellaria racemosa Pers. (JGD 367, XALU)	1,000	1,000	7	
Morpho unidentified (JGD 183, MEXU)	1,500	1,500	1	
Linaceae				
Linum sp. (JGD 197, MEXU).	1,500	1,500	1	
Lythraceae				
Cuphea aequipetala Cav. (JGD 416, XALU)	2,500	2,500	1	R
Cuphea calaminthifolia Schltdl. (JGD 425, MEXU; XAL; XALU)	2,500	2,500	1	Mx
Cuphea salicifolia Cham & Schltdl. (JGD 455, XALU)	650	650	4	Mx
Morpho unidentified (JGD 218, XALU)	1,500	1,500	1	
Malvaceae				
Morpho unidentified (JGD 229, MEXU)	1,500	1,500	1	
Moraceae				
Dorstenia contrajerva L. (JGD 340, XALU)	650	1,000	11	
Orobanchaceae				
Castilleja tenuiflora Benth. (JGD 177, MEXU)	3,100	3,100	1	R
Conopholis alpina Liebm. (JGD 408, XALU)	2,500	2,500	3	
Oxalidaceae				
Biophytum dendroides DC. (JGD 215, XAL)	1,000	1,500	2	
Phytolaccaceae				
Petiveria alliacea L. (JGD 333, MEXU; XAL; XALU)	50	50	1	R
Piperaceae				
Peperomia angustata Kunth. (JGD 392, MEXU)	2,500	2,500	1	
Peperomia arboricola C. DC. (JGD 393, MEXU)	2,100	2,500	4	Mx2

Appendix. Continuation.

Subclass/Family/Species (voucher, herbarium)	min	max	N	Status
Peperomia cobana C. DC. Ex Donn.Sm. (JGD 461, MEXU)	1,500	1,500	1	Mx2
Peperomia deppeana Schltdl. & Cham. (JGD 231, MEXU)	2,500	2,500	1	
Peperomia donaguiana C. DC. (JGD 189, MEXU; XAL)	1,500	2,500	9	Mx2
Peperomia glabella (Sw.) A. Dietr. (JGD 378, MEXU)	2,100	2,100	7	
Peperomia aff. *granulosa* (JGD 438, MEXU)	650	650	2	
Peperomia obtusifolia (L.) A. Dietr. (JGD 242& 473, MEXU; XAL)	650	1,500	13	
Peperomia peltilimba C. DC. Ex Trel. (JGD 245, MEXU)	1,500	1,500	1	Mx2
Peperomia subblanda C. DC. (JGD 380, MEXU; XAL)	650	2,100	8	
Plantaginaceae				
Digitalis purpurea L. (JGD 419, XALU)	2,500	2,500	1	E, R
Penstemon gentianoides Poir. (JGD 430, MEXU; XAL; XALU)	3,500	3,500	14	
Polemoniaceae				
Morpho unidentified (JGD 334, XALU)	50	50	1	
Polygalaceae				
Morpho unidentified (JGD 370, XALU)	1,000	1,000	2	
Polygonaceae				
Rumex acetosella L. (JGD 277, XALU)	3,100	3,100	2	E, R
Morpho unidentified (JGD 379, MEXU)	650	650	4	
Portulacaceae				
Morpho unidentified (JGD 335, MEXU)	650	650	3	
Ranunculaceae				
Ranunculus multicaulis D. Don ex G. Don (JGD 261, XALU)	3,100	3,100	2	Mx
Rosaceae				
Lachemilla orbiculata (Ruiz & Pav.) Rydb. (JGD 357, XALU)	2,500	2,500	6	
Lachemilla procumbens Rydb. (JGD 259, XAL)	3,100	3,100	12	R
Lachemilla vulcanica Rydb. (JGD 415, MEXU; XAL; XALU)	3,500	3,500	15	
Rubiaceae				
Bouvardia laevis M. Martens & Galeotti (JGD 251, MEXU; XAL; XALU)	2,500	2,500	2	
Coccocypselum hirsutum Bartl. (JGD 167, MEXU; XALU)	1,500	1,500	10	
Crusea coccinea DC. (JGD 350, XALU)	2,500	2,500	2	
Deppea grandiflora Schltdl. (JGD 271, XAL)	2,500	3,100	3	
Didymaea alsinoides (Schltdl. & Cham.) Standl. (JGD 388, XALU)	2,100	2,500	4	
Galium aschenbornii S. Schauer (JGD 256, XALU)	2,500	3,100	18	
Hedyotis sharpii (Terrell) G.L. Nesom (JGD 264, XALU)	3,100	3,500	4	Mx
Relbunium hypocarpium (L.) Hemsl. (JGD 474, MEXU)	2,500	2,500	2	
Solanaceae				
Cestrum dumetorum Schltdl. (JGD 448, XALU)	1,000	1,000	1	
Jaltomata procumbens (Cav.) J.L. Gentry (JGD 209, XALU)	1,500	2,500	8	R
Physalis campanula Standl. & Steyerm. (JGD 180, MEXU)	2,100	2,500	3	Mx2
Solanum aligerum Schltdl. (JGD 418, XALU)	2,500	2,500	3	
Solanum demissum Lindl. (JGD 281, XALU)	3,100	3,100	1	
Solanum laxum Spreng. (JGD 404, XALU)	2,500	2,500	2	
Solanum tuberosum L. (JGD 284, XALU)	3,100	3,100	1	E
Valerianaceae				
Valeriana sorbifolia Kunth (JGD 165, MEXU)	2,500	2,500	1	