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RESEARCH ARTICLE

Does disturbance determines the prevalence of dwarf mistletoe (*Arceuthobium*, Santalales: Viscaceae) in Central Mexico?

¿El disturbio determina la prevalencia del muérdago enano (*Arceuthobium*, Santalales: Viscaceae) en el centro de México?

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ABSTRACT

Large vegetation disturbance rates have been reported in the "Zoquiapan y Anexas" Protected Natural Area in Central Mexico. *Arceuthobium globosum* and *A. vaginatum* coexist within this area and have a deleterious impact on *Pinus hartwegii*. This study seeks to understand the relationship between this disturbance and the two dwarf mistletoe species prevalent in this zone. Twenty-four plots measuring 60 × 55 m containing *P. hartwegii* trees were selected. Within these plots, the physical features of the land, the density of host and non-host trees, the prevalence of each mistletoe species, and six disturbance indicators were recorded. We found that *A. vaginatum* infests up to 47 % of *P. hartwegii* trees and that its prevalence is affected positively by the slope, non-host tree density, and the proportion of stump and dead trees, but is negatively affected by the prevalence of *A. globosum*, fire incidence, waste deposit, and the distance to the nearest disturbance. *Arceuthobium globosum* infests up to 37 % of the trees and is affected positively by altitude, the density of non-host trees, waste deposit and the distance to the nearest disturbance, but is negatively affected by the prevalence of *A. vaginatum* and the proportion of dead trees. The prevalence of both mistletoe species within the study area is governed by the physical environment, the anthropogenic disturbance and the negative interaction between these mistletoe species. Disturbance has an important impact on mistletoe populations, modifying their prevalence; so it is primordial to understand this relationship in order to propose control methods.

Key words: disturbance indicators, interactions, logging, parasitic plants, *Pinus hartwegii*.

RESUMEN

Altas tasas de disturbio han sido reportadas en el Área Natural Protegida "Zoquiapan y Anexas" en el Centro de México. *Arceuthobium globosum* y *A. vaginatum* coexisten en esta área y tienen un impacto negativo sobre *Pinus hartwegii*. Este estudio busca entender la relación entre el disturbio y las dos especies de muérdago enano que prevalecen en esta zona. Se seleccionaron 24 parcelas de 60 × 55 m con presencia de *P. hartwegii*. Dentro de estas parcelas, las características físicas del terreno, la densidad de árboles hospederos y no hospederos, la prevalencia de cada especie de muérdago y seis indicadores de disturbio fueron registrados. Se encontró que *A. vaginatum* infesta hasta 47 % de los árboles de *P. hartwegii* y que su prevalencia está afectada positivamente por la pendiente, la densidad de árboles no hospederos, y la proporción de árboles muertos y de tocones; pero es negativamente afectado por la presencia de *A. globosum*, el área quemada, los tiraderos de basura y la distancia al disturbio más cercano. *Arceuthobium globosum* infesta hasta 37 % de los árboles y es afectado positivamente por la altitud, la densidad de árboles no hospederos, los tiraderos de basura y la distancia a los disturbios; pero es negativamente afectado por la presencia de *A. vaginatum* y la proporción de árboles muertos. La prevalencia de ambas especies de muérdago en el área de estudio está dada por el ambiente físico, el disturbio antropogénico y la interacción negativa entre estas especies de muérdago. El disturbio tiene un impacto importante sobre las poblaciones de muérdago, modificando su prevalencia; por lo que resulta primordial entender esta relación para poder proponer métodos de control.

Palabras clave: indicadores de disturbio, interacciones, *Pinus hartwegii*, plantas parásitas, tala.

INTRODUCTION

Disturbance is a significant process because of its influence on community composition and structure. Although disturbance is recognized as an important issue, little is known about the effect of disturbance on some important guilds, such as parasites. Parasitic plants are a common component of many terrestrial communities, and they are of significant ecological and economic importance because of their worldwide distribution (Musselman & Press 1995, Press & Phoenix 2005, Agrios 2005, Mathiasen et al. 2008). In North America, *Arceuthobium* (Viscaceae) is the most extensive genus, and in Mexico, it represents the second most serious cause of forest damage, after fire (Hawksworth 1983, Hawksworth & Wiens 1996, Hawksworth et al. 2002).

Dwarf mistletoes (*Arceuthobium* spp.) are hemiparasitic shrubby plants of conifer trees; their seeds are attached to a viscin coat and have a ballistic dispersion (Mathiasen et al. 2008). The effect of dwarf mistletoes over the host can range from a negligible impact to the death of the host (Manion 1991, Butin 1995, Hawksworth & Wiens 1996, Agrios 2005, Mathiasen et al. 2008), and thus, dwarf mistletoes are capable of inducing changes in the population structure because of the mortality of the infested hosts (Godfree et al. 2003). The host selection depends of the quality of the resources that the host can provide, and thus, taller trees with wide crowns are more likely to be selected by mistletoes (Arriaga et al. 1988, Donohue 1995, Overton 1994, Hernández-Benítez et al. 2005). The mortality of dwarf mistletoes depends mainly upon the elevation and latitude in which they are distributed because of the temperature and humidity conditions that they can tolerate (Hawksworth & Wiens 1996).

Parasitic relationships, particularly the host response, can be modified by disturbance and are likely to be beneficial to the mistletoe (Manion 1991, Hobbs & Huenneke 1992, Norton et al. 1997). Most studies that have evaluated anthropogenic disturbance and fragmentation processes have focused on the effect of the disturbance in terms of species richness, but only a few studies have considered the effect in terms of parasitic plant populations. These studies tend to report a significant increment in the mistletoes abundance with increased disturbances (Burguess et al. 2006, Kelly et al. 2008, Bowen et al. 2009, MacRaild et al. 2010). Furthermore, the temperate forests of Central Mexico suffer from several types of disturbance, such as fires, logging, and cattle grazing (Landa et al. 1997), and the presence of dwarf mistletoes is recurrent. These mistletoes have increased their incidence noticeably (Queijeiro-Bolaños unpublished data). In a zone in Central Mexico, 76 % of the trees above 2 m height were reported to be infested with *A. globosum*, while less than 2 % of the trees below this height were infested (Hernández-Benítez et al. 2005). This species coexists with *A. vaginatum* in several parts of the Mexican temperate forests, where they share the same host tree species (Queijeiro-Bolaños et al. 2011).

The aim of this study was to evaluate the ecological impact of this parasitism and to assess the effect of forest disturbance upon it. Specifically, the objective was to fully investigate (1) the effect of disturbance on the prevalence of *A. vaginatum* and *A. globosum*, (2) the distribution pattern of both species and their relationship with the physical properties of the location, and (3) the association between the two species.

METHODS

Study area

The "Zoquiapan y Anexas" Natural Protected Area (19400 ha), located in Central Mexico, is part of the Popocatepetl-Iztaccíhuatl biological corridor (Rojas 1983, Arriaga et al. 2000). This study is limited to the Southeast zone of the park at the Zoquiapan Experimental Station and the adjacent areas (19°12'30" to 19°20'00" north and 98°42'30" to 98°30'00" west, 3200 to 3450 masl). The mean annual temperature is 9.7°C, and the annual precipitation is 941 mm, with rain concentrated between June and September and a sub-humid temperate climate with summer rain (Obieta & Sarukhán 1981, Rojas 1983, Arriaga et al. 2000).

The vegetation types in this area are *Pinus*, *Abies* and *Quercus* forests (Obieta & Sarukhán 1981, Rojas 1983). The flora is mainly composed of *Pinus hartwegii,* although others *Pinus, Cupressus, Quercus*, and *Abies* species are present. The understory is mainly represented by *Muhlenbergia macroura* and *Festuca tolucencis* grasses (Obieta & Sarukhán 1981). The main disturbance factors investigated are natural and induced fires, unsustainable logging, human waste dumping, and grazing by introduced cattle (Obieta & Sarukhán 1981, Arriaga et al. 2000).

Study species

Arceuthobium globosum subsp. *grandicaule* (Hawksw. and Wiens), according to Hawksworth & Wiens (1996) and Hawksworth et al. (2002), is a yellow-greenish shrub measuring 18 to 50 cm tall with flabellate shoots. The basal diameter of its dominant shoots ranges from 10 to 48 mm. *Arceuthobium globosum* is the most abundant mistletoe in Central Mexico and is very common in Guatemala and Honduras. Its altitudinal range is from 2450 to 4000 m.

Arceuthobium vaginatum subsp. *vaginatum* (Willd.), according to Hawksworth & Wiens (1996), is a blackish shrub measuring 20 to 30 cm tall from the principal shoot, with very dense, flabellate, erect, and, at times, pendulum-shaped ramifications. The basal diameter of the main shoot ranges from 4 to 20 mm. *Arceuthobium vaginatum* is widely distributed from Northern to Central Mexico, where it has been considered the most damaging species for forestry (Cibrián et al. 2007). The altitudinal range of distribution is from 2100 to 3900 m.

Disturbance and dwarf mistletoe prevalence

Twenty-four plots containing considerable stands of *P. hartwegii* were selected inside the park. Four transects measuring 60 × 10 m and 5 m apart were established in each plot (Fig. 1). The number of trees (live, dead, and stumps) of any species, the number of *P. hartwegii* individuals over 1.5 m in height, the number of pines infested by *A. globosum* and the number of pines infested by *A. vaginatum* were recorded along the length of each transect. We calculated the percentage of trees infested (PTI) by each mistletoe species per plot. *Pinus hartwegii* individuals below 1.5 m in height were excluded because of their low probability of being infested (Hernández-Benítez et al. 2005).

Three 60-m Canfield lines (line-intercept method; Krebs 1978) were made in each plot (Fig. 1). This method measures cover with only one dimension: the length of a horizontal line along the course of a meter tape. This method is designed to measure the amount of cover of a plant species where the tape was laid down and is suited for estimating species composition (Mueller-Dombois & Ellenberg 1974). With these lines, covers (fraction of the line) with the following indicators of disturbance were registered: (1) burned zones; (2) cow feces, as a measure to denote grazing intensity and stepping of cattle; and (3) inorganic human waste. In addition, the distance from the edge of the plot to the nearest disturbed zone (roads, burned areas, waste dumping areas, and logged areas) was recorded in meters. With these measurements, the disturbance indicators per plot are defined as the dead tree ratio (number of dead trees recorded between the total of trees), the stump ratio (number of stumps recorded between the total of trees), burned coverage (total fraction of burned coverage), waste deposit coverage (fraction of waste coverage), distance to the nearest disturbance (meters), and cow feces coverage (fraction of feces coverage).

Horizontal distribution

The following characteristics were registered for each of the 24 plots described above: (1) geo-referential location, (2) altitude, (3) slope, and (4) orientation. In addition, the geographical coordinates of the sites where both species were observed throughout the park were recorded, and the limits for their distributions were determined within the research area.

Statistical analysis

An association coefficient (ν; Krebs 1978) was calculated between both mistletoe species for the 24 plots together. This step was performed by using a 2 × 2 contingency table that shows four categories of observations: plots where both species were present; plots where both species were absent and plots where each species was present alone. The strength of the association can be estimated through a coefficient that varies from - 1 (a negative association) to + 1 (a positive association), where zero represents no association (Krebs 1978). Because *A. vaginatum* is 100 % present in plots, we arbitrarily performed a 2 × 2 contingency table, considering plots above and below 24 % of the trees infested (half of the largest percentage of trees infested-PTI) by *A. vaginatum*.

In addition, a ν for each plot where the two species were present was computed, where we used tree numbers as a unit.

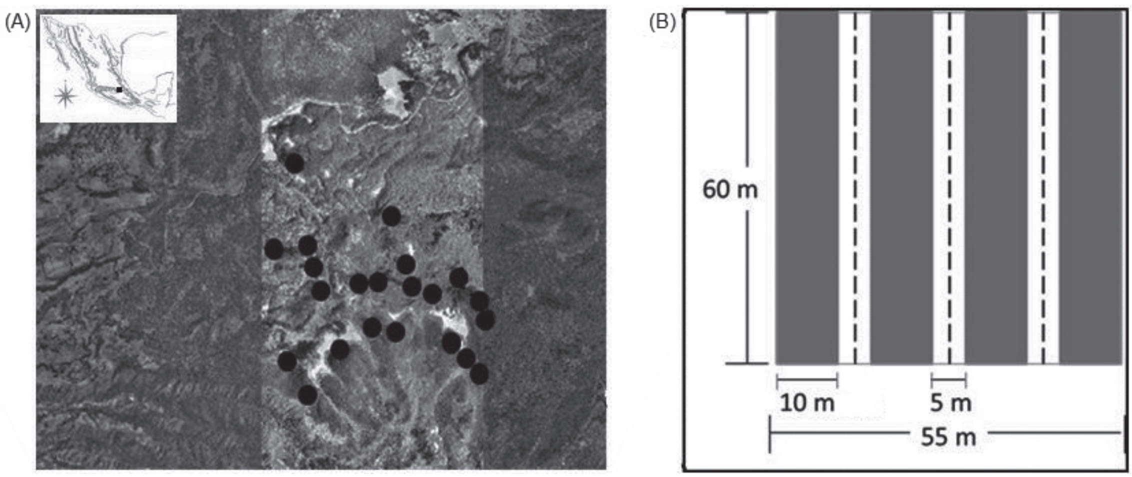

Fig. 1: (A) Spatial arrangement of plots; the black circles represent the 24 plots inside the "Zoquiapan y Anexas" Natural Protected Area. (B) Transect (grey rectangles) and intercept line (dashed lines) arrangement inside each plot.

(A) Disposición espacial de las parcelas; los círculos negros representan a las 24 parcelas dentro del Área Natural Protegida "Zoquiapan y Anexas". (b) Disposición de los transectos (rectángulos grises) y las líneas de intercepto (líneas discontinuas) dentro de cada parcela.

To test the hypothesis of an association between the two species, a χ^2 test were performed with the Yates correction for continuity (χ^2_c) for contingency tables of one degree of freedom (Zar 2010).

A generalized linear model (glm, family=binomial, link=logit) was made for each mistletoe species. For the response variable, we constructed a matrix, for each mistletoe species, of infested and uninfested trees. The predictor variables included in the model were: altitude (masl), slope (%), host-density, non-host density, dead tree proportion, stumps proportion, burned area, waste deposit, cow feces, distance to the nearest disturbance and the percentage of trees infested (PIT) by the second mistletoe species. The development of the model proceeded in the following steps: first, we assessed the existence of multicollinearity among the predictor variables through the performance of a Spearman correlation matrix of all the factors. After detecting which predictors were correlated, we performed the glm by removing these predictors one by one to identify which predictors explained redundant variation and could be deleted of the model-like a "manual" stepwise procedure. The variable selection was made with the Akaike Information Criterion (AIC), where the lowest AIC indicates the best-fitted model (Bolker 2007). The correlation analyses were performed with Statistica 8.0 (StatSoft Inc. 2007) and the glm with R (R Development Core Team, 2011).

RESULTS

We registered 6659 individuals of *Pinus hartwegii* on 24 plots; from these, 1192 pine trees (i.e. 17.9 %) were infested by *A. vaginatum* and 348 pine trees (i.e. 5.22 %) by *A. globosum*. Fifty five (0.83 %) of the 6659 pines were infested by both mistletoe species. *Arceuthobium vaginatum* was present in all 24 plots, while *A. globosum* was recorded at only 10 sites. The PTI by *A. vaginatum* varied between plots from 0.36 to 47.5 %, while the PTI by *A. globosum* varied from 0 to 37 % (Table 1). The predictors varied considerably from plot to plot (Table 1), reflecting the heterogeneity of the study area.

Because of the well-known correlation between altitude and slope, we had to choose only one of these predictors for each species model (Table 2). Besides, slope is correlated with pine density and cow feces coverage, therefore, cannot be part of the same model. The models show that for *A vaginatum* the important physical feature is the slope steepness (Table 3 model 2; all the predictors were significant); whereas for *A. globosum*, the important physical feature is the altitude (Table 3 model 1; model 3 shows only the significant predictors after a stepwise procedure to model 1).

TABLE 1

Range of the measured variables in the plots. PTI = percentage of trees infested, D_t = total tree density, $D_{P.hartwegii}$ = *Pinus hartwegii* density, D_{nh} = non-host tree density, D_e = dead trees, S = stumps, D_d = distance from the nearest disturbance.

Intervalo de las variables medidas en las parcelas. PTI = porcentaje de árboles infectados, D_t = densidad total de árboles, $D_{P.hartwegii}$ = densidad de *Pinus hartwegii*, D_{nh} = densidad de árboles no hospederos, D_e = árboles muertos, S = tocones, D_d = distancia al disturbio más cercano.

Variable	Range
PTI by *A. globosum* (%)	0-37
PTI by *A. vaginatum* (%)	0.36-47.5
Altitude (m)	3204-3429
Slope (°)	0-40
$D_{P.hartwegii}$ (trees/plot)	51-636
D_{nh} (trees/plot)	0-23
D_e/D_t	0-33
S/D_t	0-55
Burned coverage (m)	0-0.4412
Waste deposit (m)	0-0.013
Cow feces (m)	0-0.0238
D_d (m)	0.50-28.00

Of the six disturbance indicators measured, dead trees and stump proportion have a positive effect over *A. vaginatum* prevalence; while the distance from the nearest disturbance, burned coverage, and waste deposit have a negative effect on their prevalence. On the other hand, for the *A. globosum* prevalence, there is a positive effect of the distance to the nearest disturbance and the waste deposit, and a negative effect of the dead trees (Table 4). The performance of a glm considering only the effect of the disturbance factors over both species' PTI produced the same results. For both species there is a positive effect of the non-host density.

The prevalence of the two mistletoe species were negatively associated (ν= -0.41, χ^2 = 4.03, P = 0.04), although the association was non-significant when the Yates correction was

TABLE 2

Spearman correlation matrix between all the predictor variables. *P < 0.05, **P < 0.01, ***P < 0.001

Matriz de correlación de Spearman entre todas las variables predictoras. *P < 0.05, **P < 0.01, ***P < 0.001

	D_{nh}	$D_{P.hartwegii}$	Slope (%)	D_e/D_t	S/D_t	Burned area	Waste deposit	D_d	Cow feces
Altitude	-0.011	0.357	-0.786***	-0.095	0.026	-0.200	0.141	-0.077	0.241
D_{nh}		-0.069	-0.027	-0.223	-0.397	-0.237	0.149	-0.018	0.391
$D_{P.hartwegii}$			-0.484*	-0.236	-0.325	-0.077	-0.121	-0.132	0.171
Slope (%)				0.188	0.089	0.306	-0.269	0.177	-0.436*
D_e/D_t					0.215	0.241	-0.100	-0.097	-0.166
S/D_t						-0.131	0.321	0.023	-0.177
Burned area							-0.114	0.257	0.071
Waste deposit								-0.138	0.121
D_d									-0.057

TABLE 3

Generalized linear models tested for *A. globosum* and *A. vaginatum*, and their AIC values. Model 1 includes all predictors, except slope. Model 2 includes slope but excludes altitude, pine density and cow feces. Model 3 shows only the significant variables for *A. globosum*, after the stepwise procedure.

Modelos lineales generalizados probados para *A. globosum* y *A. vaginatum*, y su valor de AIC. El modelo 1 incluye todos los predictores, excepto la pendiente. El modelo 2 incluye la pendiente pero excluye la altitud, la densidad de pinos y las heces de vaca. El modelo 3 muestra sólo las variables significativas para *A. globosum* después del procedimiento paso a paso.

Model		AIC	
		A .globosum	*A .vaginatum*
1	$PTI_{Sp1} = \beta_0 + \beta_1 PTI_{Sp2} + \beta_2 D_{P.hartwegii} + \beta_3 D_{nh} + \beta_4 Altitude + \beta_5 {}^{S}/_{D_t} + \beta_6 {}^{D_e}/_{D_t} + \beta_7 Burned + \beta_8 Waste + \beta_9 feces + \beta_{10} D_d$	300.7	481.0
2	$PTI_{Sp1} = \beta_0 + \beta_1 PTI_{Sp2} + \beta_2 Slope + \beta_3 D_{nh} + \beta_4 {}^{S}/_{D_t} + \beta_5 {}^{D_e}/_{D_t} + \beta_6 Burned + \beta_7 Waste + \beta_8 D_d$	302.8	457.8
3	$PTI_{Sp1} = \beta_0 + \beta_1 PTI_{Sp2} + \beta_2 D_{P.hartwegii} + \beta_3 D_{nh} + \beta_4 Altitude + \beta_5 {}^{S}/_{D_t} + \beta_6 {}^{D_e}/_{D_t} + \beta_7 Burned + \beta_8 Waste +$	295.82	-

used (χ^2 χ= 2.54, P = 0.11). Considering each individual tree as a sampling unit, four out of the ten plots where both mistletoe species coexisted presented a negative association, while the other six plots presented a positive association (Table 5). However, only two of the ten coefficients were significant. Because of the unevenness of these associations, several Spearman correlations were performed for the ten association coefficients versus all the measured predictors to assess whether there were some factors influencing the association value between both mistletoe species. None of the correlations were significant.

TABLE 4

Generalized linear models of the factors affecting the prevalence of *A. globosum* and *A. vaginatum*.

Modelos lineales generalizados de los factores que afectan la prevalencia de *A. globosum* y A. *vaginatum*.

	Factor		SE	Z	P
A. globosum	PTI by *A. vaginatum*	-0.02586	0.004	-7.164	<0.0001
	D_{nh}	0.1029	0.014	7.126	<0.0001
	Altitude	0.01009	0.003	3.371	0.0008
	D_e/D_t	-0.2565	0.064	-3.993	<0.0001
	Waste deposit	54.74	13.9	3.939	<0.0001
	D_d	$4.373{\times}10^{-4}$	$9.040{\times}10^{-5}$	4.836	<0.0001
A. vaginatum	PTI by *A. globosum*	-0.014	0.002	-5.615	<0.0001
	D_{nh}	0.028	0.008	3.435	0.0006
	Slope (%)	0.026	0.002	10.604	<0.0001
	S/D_t	0.024	0.003	6.891	<0.0001
	D_e/D_t	0.057	0.008	7.395	<0.0001
	Burned area	-3.644	0.555	-6.565	<0.0001
	Waste deposit	-134.9	57.41	-2.35	0.0188
	D_d	$-2.218{\times}10^{-4}$	$5.789{\times}10^{-5}$	-3.831	0.0001

TABLE 5

Association coefficient (ν) between trees inside each plot in which the coexistence of *A. globosum* and *A. vaginatum* was registered. N = number of pine trees. ***P < 0.001

Coeficiente de asociación (ν) entre árboles dentro de las parcelas en donde coexisten *A. globosum* y *A. vaginatum*. N = número de pinos. ***P < 0.001

Plot	N	ν	$\chi^2\chi$
2	257	0.46	52.04***
3	260	-0.048	0.18
4	274	-0.043	0.12
5	359	-0.039	0.46
6	364	-0.055	0.61
7	267	0.089	0.42
15	209	0.085	0.17
17	291	0.078	0.18
18	231	0.074	0.26
24	585	0.193	18.37***

DISCUSSION

The role of disturbance

The two dwarf mistletoe species have a differential response to disturbance. Of the measured indicators of disturbance, the proportion of dead trees, waste deposit, and the distance to the nearest disturbance had an influence, either positive or negative, on the prevalence of both mistletoe species; while the proportion of stumps and burned area only had an impact on the prevalence of *A. vaginatum*, where the first one had a positive effect and the second one a negative effect. The lower prevalence of *A. globosum* with higher proportion of dead trees is logical because these parasites need living hosts to survive. In contrast, dead trees and stump proportion positively influence the PTI by *A. vaginatum* suggesting that this species thrives with anthropogenic disturbance, such as logging, and that disturbance can promote their overabundance on the remaining trees. This pattern is clear in bird-dispersed mistletoes because the trees represent the only perching place and the main source of fruits (some bird species have a preference for mistletoe's fruits), thus promoting a patchy distribution (van Ommeren & Whitham 2002, Aukema 2003). However, dwarf mistletoes have an unassisted, explosive discharge of their seed, so a different process may lead to the dwarf mistletoe increment when the host availability is low because of logging. Bickford & Kolb (2005) reported that forestry practices, such as thinning, stimulate the growth of *A. vaginatum* subsp. *cryptopodum* because it is benefited by greater sunlight irradiance and the host trees have less competitive pressure from their neighbors. So, *A. vaginatum* can be benefited by the effect of the greater sunlight caused by logging.

The prevalence of *A. globosum* is positively correlated with the distance to the nearest disturbance, i.e., the farther the disturbance the greater the PTI. Hence, it prefers to live far from source of disturbance such as cleared areas or roads. In other studies have been demonstrated that mistletoes are negatively impacted for fragmentation and extreme logging because of the disruption of the interactions with other organisms, such as dispersion vectors, and the host and the parasite itself are sensitive to deterioration (Norton et al. 1995, Rodríguez-Cabal et al. 2007). On the contrary, *A. vaginatum* negatively correlated to the distance to the nearest disturbance, which means that higher prevalence is presented when the disturbance is closer. Therefore, the closer presence of some disturbances (such as logged areas) favors this species. Coincidently, this is the species with the largest extension on the study area, which indicates that *A. vaginatum* can have a bias toward demographic explosion promoted by disturbance.

Arceuthobium vaginatum prevalence is negatively correlated with fire occurrence. The forests dominated by *Pinus hartwegii* exhibit important adaptations toward regular fires (Rodríguez-Trejo et al. 2004); although the host have several features to resist the damage, such as the bark thickness, it appears that the mistletoes do not survive to intense fires, as it seems to be the case of *A. vaginatum*. Dwarf mistletoes can be eliminated by fires and its recovery rate sometimes is slower than the hosts' rate, so the prescribed fire can help to control the mistletoe populations (Alexander & Hawksworth 1976, Manion 1991, Kipfmueller & Baker 1998). Nevertheless, the prescribed fires should be treated carefully as it can weaken the host, thus promoting the mistletoe regrowth (Knight 1987, Conklin & Armstrong 2001).

Inorganic waste dumping is an indicator of human activities, which can lead to contaminant accumulation on the soil (thus, reducing the trees vigor and quality of tree population) and also act as fuel material for fires (Führer 1985, Freedman 1995). For *A. globosum*, these seem to be beneficial as it has a positive relation with waste dumping; but, *A. vaginatum* is un-favored by the waste deposit. It is likely that this last mistletoe is favored by positive host vigor - as discussed above, the thinning and logging reduces intraspecific competition among pines improving the host performance - and that it gets affected by the poor performance of the host due to the effect of the garbage accumulation . Even though the role of landfills on forest deterioration has been a recurrent topic, few works center its efforts on the effect of this over parasites outbreaks (see per example Führer 1985). The relationship of landfills and dwarf mistletoes needs a further and deeply investigation.

Horizontal distribution pattern and dwarf mistletoe association

Arceuthobium vaginatum is the mistletoe species with the largest distribution observed inside the park; conversely, *A. globosum* had a more limited distribution. Likewise, the PTI of *A. vaginatum* was greater than that of *A. globosum*. *Arceuthobium globosum* and *A. vaginatum* only coexisted in ten plots; thus, the species may have a differential arrangement within the park, and there may be a low probability of finding them together.

The presence of one mistletoe species is an important factor that affects the presence of the other species, as is shown in the correlation analysis and the glm. Thus, although the interaction between the mistletoes is relevant, there are other important variables affecting the distribution of the dwarf mistletoes, such as slope, altitude, and density of non-host trees, where the last one could be working as a dispersal barrier because mistletoes would not infect these trees. Parasitic plants are known to have an aggregated distribution and a bias toward concentrating infection within a host and its nearest neighbors (Donohue 1995, Aukema 2003, Rist et al. 2011). Thus, if there are a low number of hosts, the mistletoes will tend to aggregate toward the few trees that exist. For example, Donohue (1995) reports that high host density is associated with a low proportion of infested trees and vice versa, which in turn is associated with the density of the non-host trees positively affecting the PTI of both mistletoes because these species are competitors of *P. hartwegii*. Therefore, the presence of these other species reduces the vigor of the host species, thus facilitating the mistletoe infection and assisting in the creation of infection centers (Bickford & Kolb, 2005).

As for the mistletoe associations and physical characteristics, two ideas are proposed to explain these results, and the following evidence is offered as support: (a) For interactions. The general association index between the two species is negative, although the Yates correction indicates that it is non-significant. The uncorrected chi-square shows the contrary, thus pointing to a sample size problem for the chi-square computation. Nevertheless, we believe that there is enough evidence of the negative association, like the glm (Table 4) and posterior studies (Queijeiro-Bolaños unpublished data), where the PTI of one mistletoe species is significantly affected by that of the other species. Therefore, where one species is present, the second is reduced or even absent, and it is unlikely that, once one is present, another will create a new infection (Hoffmann et al. 1986, Hawksworth & Wiens 1996, Norton et al. 1997). In addition, there is evidence that mistletoes are distributed in a differential fashion over the host to avoid competition (Norton et al. 1997, Queijeiro-Bolaños et al. 2011).

However, two plots have a positive and significant association index, which can indicate that a process of facilitation occurs, where an interaction shift between negative and positive interactions could be happening. In this scenario, one species facilitates the emergence of the second species, which, by competition, excludes the first. This idea matches with the theory that plant interactions change depending on the level of disturbances that exist (Brooker & Callahan 1998): when the conditions are more stressful or the level of disturbance is large, the dominant interactions are positive; while in less stressful or disturbed systems, these interactions are less noticeable because of the strong effect of competition. Experimental research and long-term observations are necessary to verify the type and intensity of the interactions between mistletoe species in order to fully understand the dynamics of infestation and deduce whether greater disturbance favors a positive association. (b) For differential habitats. There is some evidence of differential habitats, aside from the interaction hypothesis, because the glm gives important weight to other factors. Certain physical features of the terrain were significant variables: for *A. vaginatum*, the slope was the significant positive variable; for *A. globosum*, the related variable was altitude, which was also positive. Thus, both species have a differential habitat requirement. The distribution of *A. globosum* occurs between 2450 to 4000 masl. (Hawksworth & Wiens 1996). The slope has a very strong and negative correlation with altitude, which is why *A. globosum* is distributed in zones with low inclination. In contrast, *A.*

vaginatum is distributed from 2100 to 3900 masl over steep sites. According to Hawksworth & Wiens (1996), topography has a great influence on mistletoe distribution because weather conditions determine the success of its survival and reproduction mechanisms. *Arceuthobium globosum* is generally distributed in higher altitude sites, which suggests that it can tolerate lower temperatures (Hawksworth & Wiens 1996). In contrast, *A. vaginatum* is more frequently found at lower altitudes; thus, this species is assumed to be less tolerant of low temperatures than *A. globosum* (Hawksworth & Wiens 1996). However, the process by which the dynamics for these abiotic interactions develop is unknown.

Disturbance has been reported to have a significant influence on the abundance of parasitic plants, as is the case for *A. vaginatum* and *A. globosum* in Central Mexico. Most of the responses of parasitic plants toward disturbance have been described for plants that have a close interaction with fruit and seed dispersers. For dwarf mistletoes, this pattern is not relevant because of their ballistic dispersion. Nonetheless, these mistletoes have a significant and differential response toward anthropogenic disturbance, such as logging, fires, and landfills. This study brings an exploration of the effect of disturbance on the incidence of important parasitic plants, and a wide perspective is derived from these results; such as investigating more deeply the effect of tree logging and landfills, and the role of fire as a control method.

Long-term experimental studies with an appropriate experimental design are recommended to determine whether the physical and biotic interactions or habitat differentiation can explain the observed differential distribution of these species.

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