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Effect of habitat and grazing on the regeneration of wild *Agave cupreata* in Guerrero, Mexico

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ABSTRACT

Agave cupreata is harvested from tropical dry forests, oak forests, and other habitats by rural communities in the Chilapa region of Guerrero, Mexico to make mescal, a traditional and culturally important liquor. Local management systems use various techniques to regulate *Agave* harvest and encourage regeneration, including the exclusion of cattle. This study examines the impacts of cattle exclusion and of the different habitat types on the population structure and density of *A. cupreata*. Sampling was conducted in pastures, oak forest, tropical dry forest, and mixed oak-tropical dry forest using 54 transects of 1000 m^2, where *Agave* was counted by size-class and measurements were taken of the vegetation and physical environment. Transects were divided between areas with cattle present and cattle excluded in all four habitats except for oak forest, where all areas were open to cattle. *Agave* density per 1000 m^2 was highest in pasture (148 ± 5, mean ± SE), followed by oak forest (100 ± 4), tropical dry forest (88 ± 5) and mixed oak-dry forest (81 ± 2). The size-class structures of *Agave* populations were also significantly different between vegetation types, with oak forest supporting higher seedling densities but lower numbers of juveniles. A regression subset selection algorithm showed that one of the most important factors influencing *Agave* populations was the presence of cattle, which can reduce densities by trampling and grazing on seedlings and floral stalks. Cattle presence significantly lowered *Agave* densities in the smaller size classes in all vegetation types but did not significantly alter size-class structure. Total *Agave* density per 1000 m^2 was significantly higher in transects where cattle were absent (148 ± 4) than where cattle were present (81 ± 1). In all areas sampled, the high number of juveniles relative to other size-classes suggests that *Agave* populations are successfully regenerating in the Chilapa region, and the higher *Agave* densities in fenced areas suggest that local management techniques are effectively increasing *Agave* yields. These results highlight the potential for sustainable management of *Agave* to conserve forest habitats while also providing important income from mescal to local communities in the region.

1. Introduction

The *Agave* plant is an important economic and cultural resource in Mexico, yet overharvesting and habitat destruction threaten many *Agave* populations. There is a long pre-Columbian history of *Agave* use in the dry regions of Mexico and Central America, and today *Agave* use continues to be widespread (Bahre and Bradbury, 1980; Colunga-GarcíaMarín and Zizumbo-Villarreal, 2006). A recent survey found that 74 species of *Agave* are used in Mexico for food, fermented or distilled beverages, fiber and forage; of these, 42 species are used for mescal production in 26 states in Mexico (Colunga-GarcíaMarín et al., 2007). Mescal is a traditional liquor made by distilling fermented *Agave* and is an essential part of religious celebrations, weddings, and other cultural events (Bahre and Bradbury, 1980; Burwell, 1995; Colunga-GarcíaMarín et al., 2007). Because there is a constant cultural demand, the production of mescal can provide a reliable source of income to local communities. For example, in the state of Sonora, mescal making provides the third largest income from a natural resource to many rural subsistence households (Burwell, 1995).

To produce mescal, the *Agave* plant must be harvested before flowering to insure that the leaf bases, which are used for fermentation, have the highest possible concentration of sugars (Bahre and Bradbury, 1980; Illsley et al., 2005). While many *Agave* species reproduce clonally, some do not, and mescal harvesting can drastically reduce the number of *Agave* seedlings recruited into the population each year (Jiménez-Valdes et al., 2010). A study of mescal production in Sonora, Mexico, for example, has documented the

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depletion of wild populations of *Agave angustifolia*, *Agave palmeri*, and *Agave shrevei* on communal land due to chronic over-harvesting (Burwell, 1995).

Many rural communities harvest wild *Agave* from tropical dry forests and other habitats (Burwell, 1995; Illsley et al., 2005; Colunga-GarcíaMarín et al., 2007). Tropical dry forests are among the most species-rich ecosystems in Mexico, yet these forests are being cleared at an alarming rate for agriculture, cattle ranching, and timber extraction (Murphy and Lugo, 1986; Ceballos and Garcia, 1995; Trejo and Dirzo, 2000). Although a few tropical dry forest reserves exist in Mexico, these protected areas alone are not sufficient to maintain all of the species and habitats of the original dry forest ecosystem (Ceballos and Garcia, 1995). To expand protection of these habitats and the natural resources they contain, tropical dry forests throughout Mexico could be managed for the sustainable production of forest products (Ceballos and Garcia, 1995). The sustainable harvest of wild *Agave* could be an example of this conservation strategy to preserve the forest habitat while providing local communities with much-needed income.

For mescal production to successfully drive tropical dry forest conservation the *Agave* must be harvested in a sustainable fashion such that the species continues to regenerate. In the region of Chilapa, Guerrero there exist strong traditional management systems for *Agave cupreata* Trel. & Berger (Agavaceae), the primary *Agave* species in the area, that could offer a model for sustainable harvest (Illsley et al., 2007). *A. cupreata* is only found on mountain slopes of the Rio Balsas basin in the Mexican states of Michoacan and Guerrero at elevations of 1200–1800 m (Gentry, 1982). Communities in the mountains of Guerrero harvest and make mescal out of *A. cupreata*, and in an area where 46–80% of the indigenous population older than 15 has essentially no income, the production of mescal can represent an important source of revenue (SIPAZ, 2008; Illsley et al., 2007).

A. cupreata is a long-lived plant with mature leaves reaching between 40 and 80 cm in length and a flowering stalk of 4–7 m (Gentry, 1982). The age of maturity for *A. cupreata* is variable, but generally occurs at any time between 7 and 15 years (Meneses, 2004; Illsley et al., 2007). A monocarpic perennial that does not reproduce clonally, *A. cupreata* allocates its accumulated resources toward the production of a single inflorescence and dies following the production of seeds (Nobel, 1988).

Because the *mescalero* communities near Chilapa already have a variety of different management systems in place for *A. cupreata*, they provide a unique opportunity to investigate the potential for sustainable *Agave* harvest. Illsley et al.'s (2007) study found that *Agave* populations in the region are declining slightly, but their study also suggests that restricting harvest to mature plants, as required by some forms of traditional management in the area, is less damaging to the rate of population growth. Illsley et al. (2007) collected data on the diameter growth rate of *Agave* individuals, but did not discuss population density. The present study expands upon the work of Illsley et al. (2007) by examining the effects of management and environmental conditions on the population structure and density of wild *Agave* in the region of Chilapa in Guerrero, Mexico. The objectives of the study are to (1) characterize the habitats in which the *Agave* grows, (2) examine the effects of these habitats on *A. cupreata* population structure and density, and (3) examine the effects of cattle exclusion on *A. cupreata* populations.

2. Methods

2.1. Study area

The study was conducted in the state of Guerrero, Mexico in the municipalities of Chilapa and Ahuacuotzingo (Fig. 1). The region around Chilapa is mountainous, and the majority of sampling sites are located on sloped terrain between 1460 and 2114 m above sea level. Seven properties were sampled, including three private-properties, two community-owned locales, and two *ejido* lands. *Ejidos* are communal lands owned by the Mexican government with certain cultivation, land use, and governing rights granted to the e*jido* members indefinitely. Illsley et al. (2007) described the three common management systems for *A. cupreata* in the Chilapa region as (1) extensive management, (2) traditional intensive management, and (3) modernized intensive management. The extensive management system is used in many ejidos and communal lands, and is controlled primarily by regulations prohibiting the harvest of immature plants and the use of flowers for feeding cattle, encouraging the spread of seeds if a floral stalk is cut for construction, ensuring that some mature plants are left to flower, and rotating harvested areas. The traditional intensive management system is more common on private properties, and includes the exclusion of cattle, and the active dispersal of seeds and care for seedlings. The modernized intensive management system uses enrichment planting of transplanted seedlings from local nurseries. The present study focuses on the extensive management and traditional intensive management systems.

A. cupreata is found in four main vegetation types: oak forest, tropical dry forest, mixed oak forest-tropical dry forest, and regenerating pasture. These are classifications given by local organizations and are consistent with the units of tropical dry forest, pasture, and temperate forest identified in the tropical dry forest in the Chamela Region of Mexico (Maass et al., 2005). The tropical dry forests are dominated by tree species from the Burseraceae and Fabaceae and have a canopy height of about 7 m (Becerra, 2005; Martinez-Yrizar et al., 1992). Common species in this tropical dry forest include: *Bursera glabrifolia*, *Leucaena esculenta*, *Acacia* spp., *Pseudosmodingium* spp., *Brickellia* spp., *Tecoma sans*, *Byrsonima crassifolia*, *Brahea dulcis*, and *Quercus* spp. The temperate oak forests have a canopy of up to 15 m (Olvera-Vargas et al., 2006), and are dominated by *Quercus magnoliifolia*, *Quercus glaucoides*, *Acacia* spp., *Eysenhardtia polystachya*, and *Pinus oocarpa*. The pasture is usually found in areas that were cleared for agriculture but no longer farmed, and often contains *B. dulcis* palms and *A. cupreata* managed by the local community.

2.2. Sampling

Sampling was conducted using 10 × 100 m (1000 m^2) transects divided into five 10 × 20 m (200 m^2) plots. These plots were used to facilitate data collection, while the whole transects were considered the replicates in analyses. A total of 54 transects including all four vegetation types were sampled from six different properties. In pasture, five transects with cattle present and 10 transects with cattle excluded were sampled; in tropical dry forest, eight transects with cattle present and four with cattle excluded were sampled; in mixed oak-tropical dry forest, 12 transects with cattle present and five with cattle excluded were sampled; and in oak forest, all 10 transects had cattle present.

Within each transect, every *Agave* encountered was tallied and assigned to one of five size classes, with a sixth category for harvested individuals (Fig. 2). The size-classes were defined as: seedlings (five leaves or fewer), juvenile I (less than 10 cm tall and more than five leaves), juvenile II (between 10 and 50 cm tall), juvenile III (greater than 50 cm but without bud scales), mature (bud scales of the inflorescence are developed), flowering (inflorescence present), and harvested (flower stalk has been cut). The flowering and the mature plants are combined under the mature size-class in analyses. These size classes were defined based on discussions with local *mescaleros* and researchers, and were agreed to be both easily distinguishable and representative of life stages. Tree

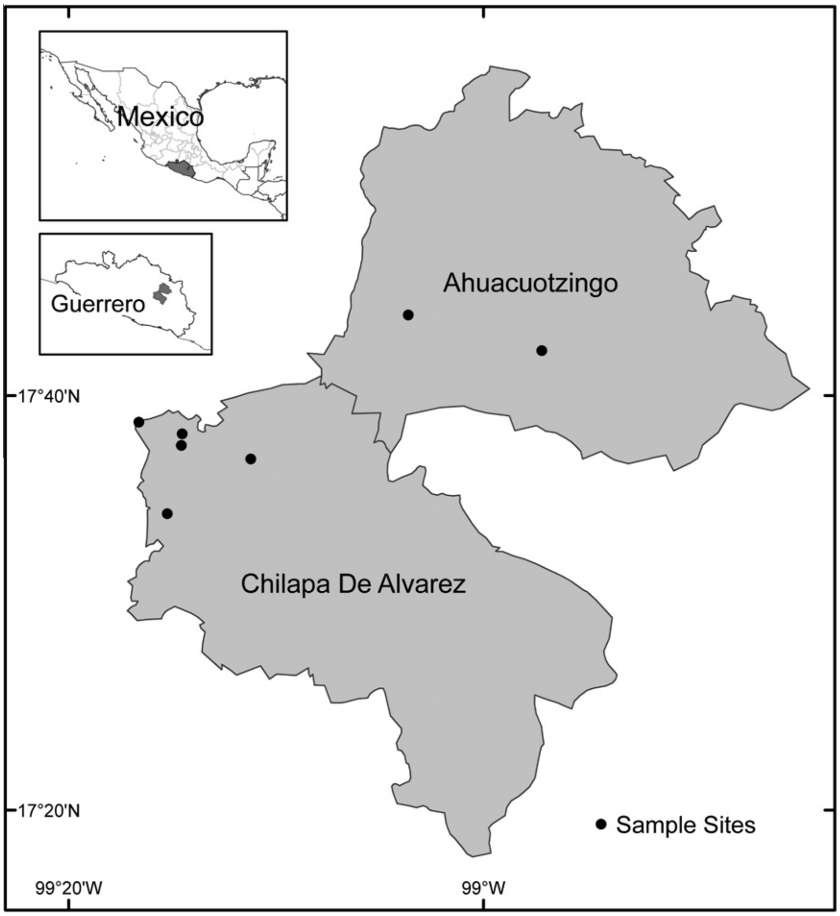

Fig. 1. Map of the seven sample sites in the municipalities of Ahuacuotzingo and Chilapa de Alvarez in the state of Guerrero, Mexico.

and shrub species ⩾1.3 m tall within the transect were counted and identified; and data on slope, canopy cover, rockiness, altitude and soil depth were collected for each transect. Canopy cover was measured with a spherical densiometer, slope was measured with a clinometer, altitude was calculated using a GPS, soil depth was measured with a soil probe, and rockiness was visually estimated by the percent of terrain under the 20 m rope used to measure each plot that was dominated by rocks. These physical data were collected in the center points of the first, third, and fifth plots in each transect to find average values for each transect. Local guides and land owners provided a history of land use and management at each sampling location. These factors included type of land ownership (private property or community/*ejido*), recent uses of the site (such as for cattle grazing or as an abandoned maize field), and whether management included exclusion of cattle, planting of seedlings or any other activities. Sampling occurred from June to August of 2008, 5 years after Illsley et al. (2007) conducted a study in the same region.

2.3. Data analysis

The densities of *Agave* plants of all size classes were compared using a two-way ANOVA with vegetation type and the presence of cattle as factors. Although data on land tenure was also collected, this factor overlapped with livestock exclusion and was not significant in a three-way ANOVA. To analyze the structure of the *Agave* size-class distributions we performed three *G*-tests with a Williams correction to compare the differences in distributions between vegetation types, between private and communal land, and between land with cattle present and absent (Sokal and Rohlf, 1995). We also ran three *G*-tests to compare differences in distributions between open and fenced areas within pasture, tropical dry forest, and mixed oak-tropical dry forest habitats. The *G*-test is a goodness of fit test of frequency distributions, and has been recommended on theoretical grounds by Sokal and Rohlf (1995). The Williams' correction reduces the value of *G*, and results in a more conservative test. For all analyses, the mature and the flowering plant categories were combined because counts were generally below three individuals. All statistical analyses were conducted using R (R, 2006).

To determine those factors which most influence total *Agave* density, we used the model selection algorithm "leaps" in R. Leaps performs an exhaustive search for the best subsets of the environmental and management variables for predicting *Agave* density in linear regression using a branch-and-bound algorithm (Lumley, 2008). The leaps function is a generalization of the stepwise regression methods that are more widely known, but, unlike stepwise regression, is not limited to operating with a single variable at each iteration and instead examines all possible subsets of × variables. Leaps has been used in subsets regression model building in a variety of analyses, from models of carbon sequestration using satellite imagery (Bricklemyer et al., 2007), to predicting species richness (Algar et al., 2009), to selecting explanatory variables for understanding herbaceous and shrubby understorey layers (Gazol and Ibáñez, 2009). We first ran leaps including only the main effects of rockiness, altitude, canopy cover, soil depth, slope, number of tree stems, number of tree species, vegetation type, cattle access, and land tenure. We then ran a second model-simplification process using the main effects retained in the best-fit model and the interactions between these retained factors. Because some of the

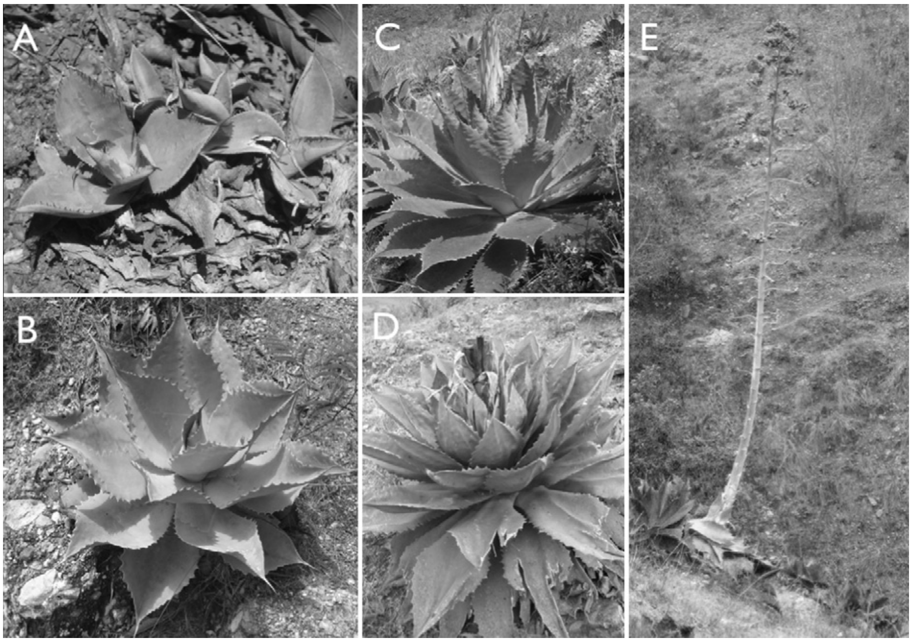

Fig. 2. Size-classes used in *A. cupreata* study. (A) Seedling (five leaves or fewer). (B) Juveniles. Juveniles were divided into three classes: juvenile I (less than 10 cm and more than five leaves), juvenile II (between 10 and 50 cm), and juvenile III (greater than 50 cm but without bud scales). (C) Mature (bud scales of the inflorescence are developed). (D) Harvested (flower stalk has been cut). (E) Flowering (inflorescence present). The flowering and the mature plants are combined under the mature size-class in analyses.

factors were recorded at the transect level (e.g. vegetation type, cattle access, land tenure and altitude) and others were recorded at the plot level (e.g. rockiness, canopy cover, soil depth, slope, number of tree stems, and number of tree species), we tested a hierarchical linear model with the factors and interaction effects chosen by the leaps algorithm, and compared this to the best-fit linear model. We also ran a separate model selection with all pasture transects removed, as this habitat is artificially maintained through intensive human influence.

3. Results

Agave densities were significantly different based on vegetation type, cattle access, and the interaction of these effects (two-way ANOVA, $F_{47} > 3.0$, $p < 0.04$). Mean total *Agave* density per 1000 m^2 ± SE was significantly different between vegetation categories, with the highest density in pasture (148 ± 5), followed by oak forest (100 ± 4), tropical dry forest (88 ± 5) and mixed oak-tropical dry forest (81 ± 2) (ANOVA, $F_{3,53} = 4.18$, $p = 0.01$). The size-class distributions were significantly different between vegetation types (*G*-test, $G_{15} = 41.69$, $p = 0.002$; Fig. 3). The size-class structure of oak forest was clearly different from those of the other three vegetation types, with seedlings as the largest size-class and a relatively even distribution of all three juvenile classes in oak forest. In contrast, *Agave* population structure in pasture, tropical dry forest, and mixed forest transects showed a greater relative abundance of the juvenile I size class, with decreased abundance in larger juvenile II and III classes (Fig. 4).

Total *Agave* density per 1000 m^2 was significantly higher in transects where cattle were absent (148 ± 4) than where cattle were present (81 ± 1) (ANOVA, $F_{3,53} = 19.2$, $p < 0.0001$). The size-class structures were not significantly affected by the presence of cattle when transects across vegetation types were considered together (*G*-test, $G_5 = 2.2$, $p > 0.05$). Total *Agave* density was significantly higher in both pasture and tropical dry forest when cattle were excluded, but could not be analyzed in oak forest where all transects were open to cattle (ANOVA, $F_{1,45} = 5.10$, $p = 0.02$; Fig. 4). When presence of cattle was analyzed within each habitat type, there was a significant difference in size-class structure between open and fenced areas of pasture (*G*-test, $G_5 = 24.4$, $p = 0.0002$). These differences in density and in size-class structure were primarily due to increases in seedlings and juveniles in the fenced areas. With cattle excluded, the highest densities were found in pasture (194 ± 12), followed by tropical dry forest (125 ± 18), followed by mixed oak-tropical dry forest (90 ± 8, Fig. 4). With cattle present, the highest densities were in oak forest (101 ± 5), followed by mixed oak-tropical dry forest (78 ± 4), followed by tropical dry forest (71 ± 5), followed by pasture (70 ± 5; Fig. 4). Pasture contained the highest density when cattle were excluded, but the lowest when cattle were allowed access.

The best-fit model produced by leaps was a linear model including significant main effects of canopy density, altitude, oak forest, and cattle presence, and significant interaction effects between canopy density:cattle, altitude:tree stem density, and altitude:cattle (Table 1, AIC = 2260). Of the main effects, the canopy density and altitude had weakly negative effects on total *Agave* density, the presence of cattle had a strongly negative effect on *Agave* density, and the presence of oak forest had a positive effect ($p < 0.01$). Of the interaction effects, the presence of cattle mitigated the negative effect of canopy density (i.e. increased canopy density had a less negative effect on *Agave* densities when cattle were present). The same effect was seen in the interaction between cattle and altitude, where the presence of cattle reduced the change in density as altitude increased.

With all transects in pasture removed, the best-fit model was a linear model with main effects of altitude and cattle presence, and significant interaction effects between altitude and cattle, and rockiness and tree density (Table 2, AIC = 1514). Both main effects of altitude and cattle presence had a significant, negative effect on *Agave* density. The interaction between cattle presence and altitude had the same effect as in the first model, where the presence of cattle decreased the rate of change in *Agave* density as altitude increased.

Analysis of the physical and biological characteristics between habitat types showed some significant differences in canopy den-

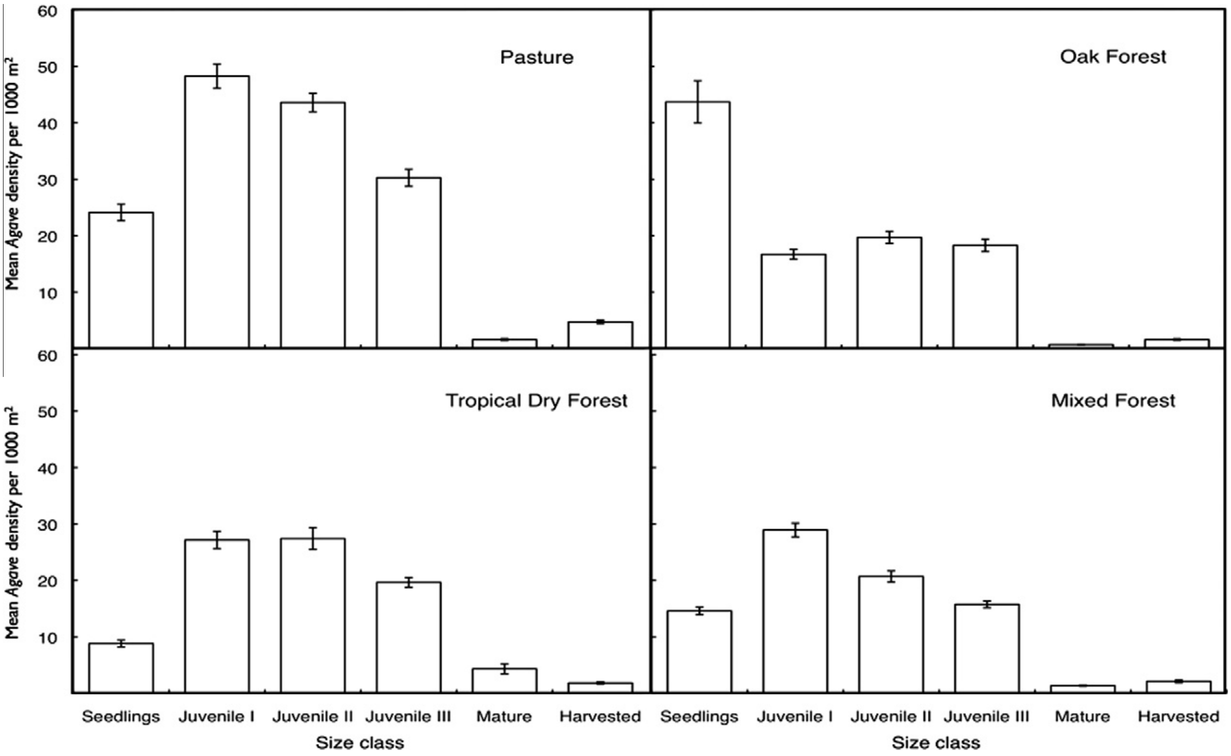

Fig. 3. Size-class distributions by vegetation type with ±1 standard error. The y-axis shows the mean abundance of *Agave* per 1000 m^2 transect of each size class in each vegetation type.

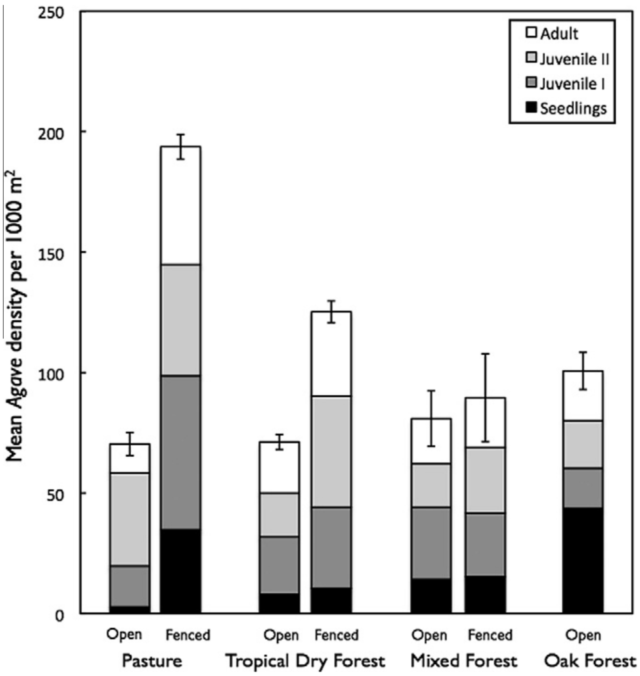

Fig. 4. *Agave* densities per transect (1000 m^2) with ±1 standard error for the total *Agave* density by habitat type in areas open to cattle and fenced off. In the oak forest all transects were open to cattle. The seedling, juvenile I and juvenile II size-classes are represented within the total by shading, and the adult class consists of the juvenile III and mature classes combined.

sity, rockiness, slope inclination, and number of tree species (Tukey's HSD test with Bonferroni correction, $p < 0.0085$; Table 3). As expected given the nature of pasture, canopy density was significantly lower compared to all forest habitats and number of tree species was significantly lower compared to the tropical dry and the mixed oak-tropical dry forests; additionally, rockiness was significantly higher in tropical dry forest compared to oak forest and pasture; and slope inclination was significantly steeper in oak forest than in pasture or mixed oak-tropical dry forest (Tukey's HSD test with Bonferroni correction, $p < 0.0085$; Table 3).

4. Discussion

4.1. Are A. cupreata populations declining?

The populations of *A. cupreata* in the Chilapa region showed high densities in the juvenile size-classes relative to the mature and harvested *Agave* size-classes, indicating regeneration of the population. The high densities of juveniles may be due to the success of current management strategies in encouraging population regeneration. However, Illsley et al. (2007) found that *A. cupreata* populations were declining at a rate of 2% per year in the Chilapa region based on sampling in three sites between 2001 and 2003. Their study focused on the diameter growth of selected plants and the rate at which individuals moved from one size-class to the next, but did not provide information on the size-class distributions themselves or on changes in population density over time, making direct comparisons to their data difficult. The *Agave* populations are not consistent in density and structure throughout the region, as seen in the differences found between habitat types and between fenced and open areas. Thus the growth of some populations may be declining, while others may be effectively regenerating.

The regeneration of an *Agave* population is largely dependent on the management and harvest systems employed (Jiménez-Valdes et al., 2010). A study of population dynamics of *Agave marmorata* in Puebla, Mexico found that the harvesting practices in the region had negative effects on population dynamics, and that harvesting for mescal decreased individual survival and growth (Jiménez-

Table 1
Summary of the best fit model with intensively managed transects excluded. Residual $SE_{257} = 15.47$, multiple R-Squared = 0.3224, adjusted R-Squared = 0.2907, $F_{12,257} = 10.19$, $p = 2.376\text{e-}16$. Significance codes: $^{***}p < 0.001$, $^{**}p < 0.01$, and $^{*}p < 0.05$.

	Estimate	Standard error	t Value	Pr(>|t|)
Intercept	104.5	21.22	4.924	1.52e-06***
Canopy density	−0.2875	0.0928	−3.1	0.002176**
Altitude	−0.0371	0.0124	−2.99	0.003089**
Oak forest	14.63	5.741	2.548	0.011426*
Cattle presence	−95.45	27.87	−3.42	0.000717***
Canopy density: tree stem density	0.0037	0.0024	1.527	0.127928
Canopy density: oak forest	−0.1491	0.0997	−1.5	0.135834
Canopy density: cattle presence	0.2439	0.0869	2.807	0.005384**
Altitude: tree stem density	−0.0002	0.0004	−0.39	0.698628
Altitude: cattle presence	0.0436	0.0166	2.63	0.009061**
Tree stem density: number of species	0.0176	0.0195	0.904	0.366756

Table 2
Summary of the best fit model with pasture and intensively managed transects excluded. Residual $SE_{179} = 11.25$, multiple R-Squared = 0.3189, adjusted R-Squared = 0.2618, $F_{15,179} = 5.586$, $p = 2.81\text{e-}09$. Significance codes: $^{***}p < 0.001$, $^{**}p < 0.01$, and $^{*}p < 0.05$.

	Estimate	Standard error	t Value	Pr(>|t|)
Intercept	122.3	42.65	2.867	0.004647**
Altitude	−0.0510	0.0234	−2.18	0.030286*
Cattle presence	−134.6	37.35	−3.6	0.000405***
Altitude: canopy density	−0.0002	0.0002	−1.11	0.267122
Rockiness: tree stem density	0.0059	0.0026	2.3	0.022624*
Altitude: tree stem density	−0.0004	0.0005	−0.9	0.369854
Altitude: oak forest	−0.0007	0.0566	−0.01	0.990458
Altitude: cattle presence	0.0728	0.0207	3.518	0.000550***
Tree stem density: number of species	0.0363	0.0211	1.722	0.086871
Number of species: tropical dry forest	−0.6819	1.0710	−0.64	0.525111

Table 3
Summary of canopy density, altitude, rockiness, slope inclination, soil depth, number of tree stems, and number of trees per transect in each habitat type with standard error. Factors with a '*' showed significant difference between habitats (Tukey's HSD pair-wise comparison with Bonferroni correction, $p < 0.0085$).

	Oak forest	Tropical dry forest	Mixed forest	Pasture
Transects	10	12	17	15
Canopy density*	57 ± 1.7	44 ± 1.2	39 ± 1.3	4 ± 0.4
Rockiness*	11 ± 0.3	35 ± 1.4	29 ± 1	13 ± 0.7
Altitude (m)	1673 ± 3.3	1561 ± 11	1715 ± 13	1673 ± 8.8
Slope inclination*	31 ± 0.3	25 ± 0.6	21 ± 0.5	21 ± 0.2
Number of tree stems	83 ± 4.4	97 ± 6.1	103 ± 4.4	37 ± 2.3
Number of tree species*	6 ± 0.1	14 ± 0.6	9 ± 0.2	3 ± 0.1
Soil depth (cm)	8 ± 0.1	8 ± 0.3	11 ± 0.2	10 ± 0.2

Valdes et al., 2010). In the state of Sonora, Burwell (1995) witnessed a "tragedy of the commons" situation where populations of *A. angustifolia*, *A. palmeri*, and *A. shrevei* were being rapidly depleted due a lack of means to restrict or regulate *Agave* harvest on communal lands. Burwell (1995) found that the lack of communal regulation of the resource was partially due to a strong emphasis on family autonomy, and to a belief that *mescalero* actions are not responsible for, and cannot control, the degradation of the *Agave* resource. The *mescaleros* interviewed claimed that it was impossible for them to follow the traditional harvest method of cutting the budding flower stalk and leaving the plant to accumulate sugars, as another *mescalero* would take the *Agave* (Burwell, 1995). Because of this, *Agave* was being harvested based on size rather than maturity, meaning more individuals were needed per liter of mescal because of the lower sugar content in each harvested plant. Without regulations over land use, intensive livestock grazing and repeated burning of communal rangelands can also contribute to *Agave* population declines, especially when in conjunction with harvesting for mescal (Martinez-Morales and Meyer, 1985).

In Zacatecas, Mexico, Martínez-Salvador et al. (2005) reported that the use of *Agave salmiana* as forage for livestock and for the production of mescal contributed to a decline in the number of *Agave* individuals that reach full maturity. Unlike *A. cupreata and A. salmiana* can also reproduce clonally so the population structure and dynamics will likely differ between these species. Even with the more limited reproductive strategy, the range of *A. cupreata* density in Chilapa was within that of *A. salmiana*. The areas of lowest density of *A. cupreata* (tropical dry forest with cattle present) contained 700 ± 49 *A. cupreata*/ha, compared to the low density category of 652 *A. salmiana*/ha (Martínez-Salvador et al., 2005). The areas of medium density of *A. cupreata* ranged from 790 to 1250 *A. cupreata*/ha, compared to the medium category of 788 *A. salmiana*/ha in Zacatecas. The areas of highest density of *A. cupreata* (pasture with cattle excluded) contained 1940 *A. cupreata*/ha compared to the 3125 *A. salmiana*/ha found in only 2% of the range in Zacatecas (Martínez-Salvador et al., 2005). It is likely that the high densities of *A. cupreata* did not reach those of *A. salmiana* in Zacatecas due to the inability of *A. cupreata* to reproduce clonally, and possibly to differences in site conditions. While these studies are not directly comparable, many of the sites sampled for *A. cupreata* contained densities greater than the medium and low ranges that Martínez-Salvador et al. (2005) considered to be a sign of overexploitation. In Zacatecas, the deterioration of local plant populations is due to a lack of appropriate management and increased exploitation of *A. salmiana* (Martínez-Salvador et al., 2007). In Chilapa, *A. cupreata* populations may be more successfully regenerating under the communal management systems employed.

4.2. The effect of cattle

In contrast to the examples of over-exploitation and lack of control over *Agave* harvest in other regions of Mexico, strong traditional management systems are used in the Chilapa region (Illsley et al., 2007). The two systems employed in areas sampled by this study were the extensive management system and the traditional intensive management system (Illsley et al., 2007). The extensive management system prohibits the harvest of immature *Agave* and regulates the harvest intensity, and usually is found on communal lands (Illsley et al., 2007). The traditional intensive management system is more common on private lands, and includes fencing areas to exclude cattle, dispersal of collected seeds, and occasional care for seedlings (such as transplanting to better sites) (Illsley et al., 2007). Because of these management practices, the factor of land tenure overlapped with that of cattle presence in our data. The exclusion of cattle represents the use of the more intensive management system.

The exclusion of cattle dramatically increased *Agave* density in both pasture and tropical dry forest, indicating that the traditional intensive management strategies being used by local communities in the Chilapa region are effectively increasing *Agave* density. The presence of cattle exerted a strong negative influence on *Agave* density, and was highly significant in both of the best-fit models. Cattle will eat the seedlings and budding flower stalk, and will trample plants (Burwell, 1995). Unlike the rest of the *Agave* plant, these parts are not defended by spines and are therefore susceptible to herbivory. Therefore the presence of cattle may not alter the growth rate of plants (Illsley et al., 2007), but may lower density by preventing regeneration and establishment of seedlings. Thus the areas in pasture and tropical dry forest fenced off from cattle showed the largest increases in the seedling and juvenile size classes (Fig. 4).

While Illsley et al. (2007) found that the exclusion of livestock had no influence on the growth rate of *A. cupreata* in this same region, their study was based on individual plant growth rather than the density of *Agave* populations. They used this data to model population growth rates and to make projections for three different harvest regimes based on the size-classes harvested. Their finding, that the enclosed and the open areas showed equivalent growth rates, implies that cattle may not impact the growth of plants already established, but does not speak to the effect of cattle on the density or regeneration of the population as a whole. Although seemingly contradictory in results, our study complements Illsley et al.'s (2007) work on *Agave* plant growth rates by examining the effects of cattle on population structure and density. Since cattle seem to have the greatest impact on seedling and juvenile densities, their negative effects may not be seen in the growth rates of larger size-classes.

In a comparable study of barrel cactus populations in Mexico, Jiménez-Sierra et al. (2007) found that because the adults could persist for many years, no relationship between habitat disturbance and population growth was seen even though suitable micro-habitats for the establishment of new individuals were lost. The cacti populations were severely damaged by intense grazing, but the study found that exclusion of herbivores did not immediately lead to cactus regeneration, as negative effects of grazing persisted (Jiménez-Sierra et al., 2007). Illsley et al.'s (2007) findings of population decline in both open and enclosed sites may reflect long lasting impacts of cattle grazing in the now enclosed areas.

Cattle have been reported to play an influential role in the population dynamics of several other species of monocarpic perennials besides *Agave*. Jiménez-Sierra and Eguiarte (2010) found that the most important disturbance factors for the cacti populations used to make the candy *acitrón* were human activity, habitat deterioration, and livestock. A study of *Heracleum mantegazzianum* found that management practices allowing for cattle grazing have greater effects on population development than climatic differences (Pergl et al., 2006). Cattle browsing on the inflorescences of *Yucca elata* was found to significantly affect the reproduction and population structure of this species (Kerley et al., 1993).

The local communities in the Chilapa region are already well aware of the negative impact of cattle, and have responded by fencing off areas under the traditional intensive management system. The exclusion of cattle from an area represents an investment of time, energy, and money in the creation and upkeep of fences, and therefore represents significant management effort. The fact that these areas supported significantly higher *Agave* densities in juvenile size-classes indicates that this is an effective management strategy.

The areas with cattle were not evenly distributed among vegetation types, however, and in oak forest all areas were open to livestock. Although cattle were present in all the oak forest transects, oak forests showed a strongly positive influence on *Agave* density in the best-fit models. The implication is that there is some characteristic of oak forests that increases *Agave* densities enough to overcome the negative impact of cattle. This characteristic may not be the presence of the oak trees themselves, but could be some physical feature which promotes both oak and *Agave*. The oak forest habitat is threatened in this region due to high rates of fuel wood harvest, especially because of the large quantity of oak wood needed in the production of mescal, favored for of the distinctive flavor it imparts. More information about the effect of this vegetation on *Agave* populations is therefore particularly important.

4.3. The effect of vegetation type

In oak forest, the greatest abundance of *A. cupreata* plants was in the seedling size-class, while there was a relative abundance of juveniles in pasture, tropical dry forests, and mixed oak-dry forest, creating significantly different population structures between habitat types (Fig. 3). With the exception of oak forest, the size-class distributions of the populations were unusual in that there were fewer seedlings than juveniles. The observed population structure is likely due to seasonal dynamics, as sampling occurred in June and July before seedlings germinated in August and September. Therefore the seedlings counted in this study were those that either germinated early or had germinated the previous year and had not yet been recruited into the juvenile I size-class.

The difference in seedling densities between habitats may also be due to variation in seedling growth rates. The oak forest had the densest canopy, so high seedling density in oak forest vegetation could be due to a slower seedling growth rates under low light conditions. The large number of seedlings in oak forest may be attributed to individuals that germinated the previous year and had not yet been recruited into the juvenile I size-class. Conversely, the high density of the juvenile I size-class and lower density of seedlings in pasture land could result from faster seedling growth in the high light levels, with many of the seedlings from the previous year having grown into juveniles.

The oak forest vegetation type was one of the significant factors in the best-fit model, and exerted a strong positive effect on total *Agave* density. The oak forest may be subject to reduced drought stress due to the larger amount of leaf litter and relatively closed canopy. Water availability was not measured here, but is likely an important factor for *Agave* growth and survival in this arid habitat.

4.4. Agave in pasture

Although all lands in the region are impacted by human-use of some form, the pasture vegetation type is the most human-dominated. These areas are generally the result of forest cleared for crop agriculture and then left fallow. The pasture contained the highest density of *Agave* of the four vegetation types in areas of cattle exclusion, but the lowest in areas open to cattle, highlighting the impact of human management in this habitat. These fallow pastures may be more depleted in nutrients than other habitat types which have not been cultivated, so they may support lower densities of *Agave* when not intensively managed. The lower number of species and the open nature of the pasture vegetation may also make the *Agave* more susceptible to grazing and trampling by cattle. However, when cattle are excluded and the pasture is more intensively managed, *Agave* densities are dramatically higher than in any other habitat, especially in the juvenile size-classes.

The management of these fallow pastures varies between properties, but generally involves a continual process of maintaining fencing and supporting *Agave* population regeneration through the spread of collected seed and the occasional transplanting of seedlings, as described by Illsley et al. (2007) as the traditional intensive management system. Locals often refer to this management as "reforestation," where the successional development of the land is enriched with *Agave*, *B. dulcis* palm, and other useful species. Seeds collected from individuals that were left to flower are spread in open areas, resulting is dense clusters of *Agave* of different sizes. Care for seedlings in this system can include their transplant into better micro-site conditions (Illsley et al., 2007). In a few areas, the "reforestation" of these fallow pastures follows the modernized intensive management system described by Illsley et al. (2007). These areas were not included in this study, though, as they are more akin to plantation systems where seedlings from local nurseries are planted in rows.

Because the pasture is a habitat necessarily modified by human use, we ran a model with pasture transects excluded to try to isolate environmental impacts in other vegetation types less dominated by human management. The resultant best-fit model included only altitude and cattle as main effects, with significant interaction effects between altitude and cattle, and between rockiness and number of tree stems (Table 3). Altitude showed a small negative effect on total *Agave* density, probably because there is more erosion and less water retention at higher levels on a slope. The region is very dry, so with water availability as a limiting factor on plant population sizes, higher altitudes with lower moisture levels would support lower *Agave* densities.

4.5. Management strategies and sustainability

Although size-class distributions are dynamic, they can give an indication of the future structure and density of a plant population (Peters, 1995; Condit et al., 1998). The high numbers of juveniles in these populations could, therefore, imply the effective regeneration of *Agave* populations in the Chilapa region. The increased density of *Agave* in areas with cattle excluded suggests that the active management of *A. cupreata* is particularly effective at increasing population sizes. Although Illsley et al. (2007) did not find differences in growth rate in fenced areas, they did report that the intensive management method seems to be sustainable and seems to provide a continuous harvest based on interviews. In fact, based on the density of juveniles recorded in fenced areas of pasture, these populations may continue to grow in the future, further increasing the number of *Agave* plants available for harvest.

In contrast to the studies of mescal production in Sonora, Mexico, in Chilapa and Ahuacuotzingo there are strong regulations imposed by community and *ejido* governing bodies controlling harvest intensity in communal lands and, rather than a "tragedy of the commons" situation, the local *Agave* populations in this region appear to be regenerating and thriving under communal control. According to the models of Illsley et al. (2007), harvest of the largest size-class will not lower the population growth rate. Therefore the regulations on harvesting only mature individuals already imposed by many *ejido* and community governing bodies in the extensive management system provide a means to maintain sustainable yields of *Agave* in these areas. Through careful monitoring, these communities could adjust their harvest levels in the future in response to the current density and regeneration of *A. cupreata*, thereby avoiding the over-exploitation and population depletion experienced by *mescalero* communities in other areas. In addition to regulating the harvest of *Agave*, attention should be devoted to the impacts of mescal production on other species. Further studies analyzing the impacts of these management systems on the other species, especially the oak and tree species harvested for fuel wood, are particularly important for the management of these habitats and for the sustainable production of mescal.

Efforts are being made by the local *campesino* organization Sansekan Tinemi to market the mescal produced in these communities as a local and sustainably harvested forest product to patrons of the upscale bars and restaurants in Mexico City and Acapulco. It is hoped that this recognition and revenue will create additional incentives for communities to maintain their traditional management practices. The sustainable harvest of *A. cupreata* for making mescal could provide a strong economic incentive to conserve tropical dry forests, and would also contribute to the well-being and cultural traditions of the local communities.

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