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# TREE MORTALITY AND RECRUITMENT IN HETEROGENEOUS STANDS OF SUB-TROPICAL MIXED-OAK FORESTS IN WEST-CENTRAL MEXICO

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## SUMMARY

We studied how patterns of tree mortality and recruitment are associated with forest structure, species diversity and physiographic differentiation in sub-tropical mixed-oak forests. We used non-metric multidimensional scaling and generalized additive models. Tree mortality and recruitment were present in nearly fifty percent of the species recorded in the study plots. Proportions of tree mortality were greatest in the small-

est diameter classes while only sixteen out of the twenty-six species recorded in our study plots had recruitment. Variables explaining patterns of tree mortality and recruitment were: the number of species, density and mean diameter by plot. Stands with low density are not supporting oak recruitment while individuals in the suppressed category showed the highest mortality rates.

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**T**ree mortality and recruitment patterns are among the most important natural processes structuring forest ecosystems. Interspecific differences in tree mortality play a crucial role in determining plant community structure, successional dynamics as well as in the maintenance of species diversity (Shimatani *et al.*, 2008). It has been emphasized that mechanisms driving tree death reflect both taxon- and individual-level properties, which in turns have an important impact on changes in demographic rates and computed over time, can alter forest structure, species composition and functioning (Chao *et al.*, 2008). For example, van Mantgem *et al.* (2009) argue that persistent doubling of background mortality rate (such as from 1 to 2%/year)

ultimately would cause a >50% reduction on average tree age in a forest, and hence potential reduction in average tree size. Thus, quantifying tree mortality is important for the prediction of forest dynamics and for a better understanding of the species ecological characteristics as a foundation for forest management. However, the question of when and why trees eventually die is largely unsolved; tree mortality appears to be context-dependent and species-specific, it is highly stochastic, and one of the greatest challenges of forest ecology (Holzwarth *et al.*, 2013). Recent studies stress that slow-acting and cumulative natural causes of tree mortality are not well understood, mainly due to the difficulties involved in collecting long-term data. Ecological studies of tropical tree dynamics often consider

mortality but not recruitment (Lewis *et al.*, 2004), even when patterns of tree recruitment play an important role in the dynamics of most forest ecosystems. Spatially extensive analyses of long-term changes in tree demographic rates have been limited to tropical forests, where tree mortality and recruitment rates have increased over the past several decades (van Mantgem *et al.*, 2009). But for temperate and sub-tropical forests comparably extensive analyses have not been conducted and there is a need of comparative information for tree mortality and recruitment (Bin *et al.*, 2011).

*Quercus* is the most diverse genus in *Quercus*-dominated sub-tropical forests in west-central Mexico, where *Quercus* species coexist with an important number of coniferous and broad-leaved

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**KEYWORDS / NMDS / *Quercus* / Recruitment / Stand Structure / Tree Mortality /**

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species of similar ecological requirements {Olvera-Vargas, 1998 #97@@author-year; Olvera-Vargas, 2010 #1}. These ecosystems are second-growth forests that have remained unmanaged for over the last ~25 years; they constitute young to mature forest stands of variable densities with mean diameters ~ 20 cm where tree mortality and recruitment seems to be key processes influencing succession and the future composition of the community.

## Materials and Methods

### Study site

The study was conducted in sub-tropical, mixed-oak forests located on a mountain chain (19°24'32"-19°31'02"N and 103°57'44"-104°01'09"W) between the Nearctic-Neotropic realms along the western portion of the Trans-Mexican Volcanic Belt. Elevations range from ~2000 to 2450masl. The physiography is exceptionally irregular, characterized by a series of disconnected sandy ridges in which the underlying soil is often exposed. The slopes differ in steepness from 10 to 60%, although steep-sided ravines of more than 90% can occur. The sub-humid climate typically has warm summers and mean annual temperatures between 12 and 18°C (Martínez-Rivera *et al.*, 1992). Over the past 4000 years forest fires have shaped the structure and functioning of the vegetation in the study area (Figueroa-Rangel *et al.*, 2008); present-day small-scale fires occur almost every year, predominantly as a result of uncontrolled burnings from agricultural systems. Most of the forest stands seems to be prone-fire adapted; a revision of ecological research concerning the effects of frequent fires on the local flora suggests that forest fires occur between 5 and 14 years (Jardel-Pelaez *et al.*, 2003).

*Quercus*-dominated sub-tropical forests are young to mature second-growth stands with ages between 60 to 90 years (Olvera 2006) that resemble a stand exclusion stage (*sensu* Oliver and Larson (1996)); thus, these ecosystems are undergoing secondary succession as a result of intra and interspecific competition (Olvera *et al.*, 2010; Olvera *et al.*, 2014). These circumstances led to the replacement of the former vegetation and to the development of highly fragmented secondary forest with ecologically complex stands, variable structure and species composition.

### Sampling procedure

We used data from 60 circular permanent plots (500m<sup>2</sup> each)

collected over an 8-year period (1994; t<sub>1</sub> to 2002; t<sub>2</sub>). These plots were established in *Quercus*-dominated forest stands of varying maturity randomly located along a 10km floristic gradient. In each permanent plot all live trees (diameter at breast height (dbh) ≥5cm) were individually measured and marked with numbered aluminium tags, and botanically identified to species. Following Kraft's classification (Smith 1986), we evaluated crown position considering each tree's relative position to its adjacent trees as D: dominant, Cd: codominant, I: intermediate, and S: suppressed. This classification was used as a surrogate of tolerance to light. We recorded slope, angle aspect and catena for each plot to account for the effect of physiographic factors on the dynamics of the forest. Catena was determined by visual classification of physiographic positions categories following Olvera-Vargas *et al.* (1996) as Cat0: flat terrain; Cat1: ridge slope; Cat2: upper slope; Cat3: middle slope; Cat4: lower slope; Cat5: base slope; Cat6: gully/ditch.

### Tree mortality and recruitment records

Mortality rates were based on stem counts of dead tagged trees on each plot at the end of the 8-year period. Within the 8-year period, no catastrophic disturbances, such as severe forest fires, insect outbreaks, blow-downs, severe droughts or silvicultural interventions (e.g. logging or thinning operations) had occurred in or near any of the permanent plots. Therefore, intra- or inter-specific competition was assumed the main cause of tree mortality. Recruitment was estimated from ingrowth of untagged trees into the plot over the 8-year period.

### Data analyses

We estimated annual tree mortality and recruitment separately using logarithmic models that assume a constant probability of mortality and recruitment (Phillips *et al.*, 2004). Hence, annualized estimates of tree mortality and recruitment rates for each species were generated according to Condit *et al.* (1999): for Mortality,  $m = (\ln n_0 - \ln S_t)/t$  and for Recruitment,  $r = (\ln n_t - \ln S_t)/t$ . Where:  $n_0$  is the population size at time 0 (permanent plot establishment),  $n_t$  is the population size at the end of the 8-year period, and  $t$  is the census interval (8 years).  $S_t$  is the number of survivors at the end of the 8-year period. We calculated the upper and lower confidence limits (95%) for tree mortality and recruitment rates using binomial probabilities (Zar, 1999). We used non-metric

multidimensional scaling (NMDS) available in the R package 'vegan' (Oksanen *et al.*, 2010) to analyze patterns of variation in tree mortality and recruitment among permanent plots using ordinations of a mortality matrix and a recruitment matrix. Bray-Curtis dissimilarity distance was used to compute the resemblance matrix among plots. We used stress values to assess power of ordinations taking stress values between 0.05 and 0.10 to indicate little danger of drawing false inferences (Oksanen *et al.*, 2010). We only incorporated species that occurred in ≥10 plots and had ≥30 individuals in the total sample; this was an arbitrary cut-off to remove species for which tree mortality and recruitment estimates would be unreliable due to small sample size. Eleven species met these criteria and were included in the analysis. We used number of species by plot for analysis of diversity patterns, and tree density and mean diameter by plot for analysis of forest structure. In order to interpret the ordination axes we fitted linear vectors (using density, number of species, mean diameter, aspect, slope and catena by plot) onto ordination results, by the function *envfit* implemented by the R package 'vegan' (Oksanen *et al.*, 2010).

We then generated smooth surfaces for those significant quantitative variables by fitting thin plate splines using general additive models and interpolating the fitted values on the unconstrained ordination diagram implemented by the R package 'vegan' (Oksanen *et al.*, 2010). To test for differences in diameter distributions over the 8-year period for the 11 species, we used the non-parametric Wilcoxon paired-sample test. We did not compensate for increases in recruitment and losses due to tree mortality. In order to assess changes in population structure we calculated tree species frequency distributions per 5cm-dbh intervals for each time period. Similarly, to relate tree mortality with diameter size, we estimated inequality using the Gini coefficient (G). This is an index based on the Lorenz curve that ranges from 0 to 1, where 0 represents perfect equality and 1 total inequality. G was calculated using individual tree diameter data (Dixon, 2001) as

$$G = \frac{\sum_{i=1}^n (2i - n - 1) X_i}{(n-1) \sum_{i=1}^n X_i}$$

where  $n$ : number of individual trees in the sample;  $X_i$ : size (diameter) of the  $i$ th tree,

when trees are sorted from smallest to largest,  $X_1 \leq X_2 \leq \dots \leq X_n$ ; and  $i$ : diameter of an individual tree. The  $G$  was estimated for each time period (1994- $t_1$ - to 2002- $t_2$ -).

## Results

### Patterns of tree mortality

Fifteen out of the 26 species recorded in the sixty plots experienced mortality during the 8-year period. Although the number of individuals by species was highly variable among species and confidence limits for mortality rates were very broad for those species with small sample sizes (e.g. *Acacia farnesiana* and *Xylosma flexuosa*), mortality rates varied from 0 to 8.66% (Table I) with an average value of 1.31% for all species. *Quercus laurina* and *Q. obtusata* had no dead individuals during the 8-year period; however, the highest mortality rate was for *Quercus crassipes* (N= 855; 95% CI= 2.22-2.91) and the lowest for *Q. rugosa* (N= 66; 95% CI= 0.004-1.01). Most taxa experienced mortality mainly over the smallest diameter classes (e.g. 5-10cm dbh). However, dbh range for dead trees was greater (Table II) for *Quercus crassipes* (5-50cm dbh), *Q. castanea* (5-40cm dbh) and *Alnus jorullensis* (5-30 cm dbh). NMDS ordinations distinguished three

groups of plots (stress of 0.07) based on patterns of variation in tree mortality (Figure 1). One group (right side of the ordination diagram) contained plots mostly dominated by *Quercus crassipes*, *Pinus leiophylla*, *Prunus serotina* and *A. jorullensis*. The second group (center of the ordination diagram) included plots dominated by *Q. candicans* and *Q. castanea*. The third group (left side) was dominated by *Ternstroemia lineata*, *Symplocos citrea*, *Garrya laurifolia*, *Cornus excelsa* and *Q. rugosa* (Figure 1).

Linear vector fitting showed that patterns of variation in tree mortality were significantly related to number of species ( $r^2= 0.50$ ,  $p=0.001$ ) and mean diameter ( $r^2= 0.16$ ,  $p=0.027$ ). None of the physiographic variables (catena, slope or aspect) were significantly related to mortality patterns. When fitting thin plate splines using general additive models, the main gradient along axis 1, from left to right, corresponded to a decreasing number of species; for axis 2, a gradient with differences in mean diameter was evident from the bottom (from 18 cm) to the top (~26cm). *A. jorullensis* and *Quercus crassipes*, with two of the greatest mortality rates, were associated to the lowest number of species (4) and mean diameters of 18-20cm. Plots with the highest number of species (9) but

small diameters (~17cm) were dominated by *G. laurifolia* (Figure 1).

### Patterns of recruitment

Sixteen out of the 26 recorded species had recruitment. Excluding *Xylosma flexuosa* whose sample size was too small for comparison, recruitment rates varied from 0 to 2.35%; however, only *P. serotina*, *Q. castanea*, *Quercus crassipes* and *T. lineata*, had more than 6 recruits (Table I). Recruitment ordinations with NMDS provided evidence of three groups of plots (Stress of 0.06). One major group (lower right side, Figure 2) contained species such as *Quercus crassipes*, *P. serotina*, *G. laurifolia*, *A. jorullensis* and *P. leiophylla*. A second group (left side) was typified by *T. lineata* and *C. excelsa*. A final central group was dominated by oak species, *Q. candicans*, *Q. castanea* and *Q. rugosa*. When fitting linear vectors onto ordination results, again physiographic variables such as catena, slope and aspect were unimportant; significant variables related to patterns of recruitment were number of species ( $r^2= 0.52$ ,  $p=0.001$ ) and density ( $r^2= 0.43$ ,  $p=0.001$ ). The surface fitting procedure revealed two main gradients; those plots with the highest number of species at the left and those with low number of species at the right of the ordination diagram. From

TABLE I  
MORTALITY AND RECRUITMENT RATES FOR TREE SPECIES IN SUB-TROPICAL MIXED-OAK FORESTS

| Species  | Code  | N   | D   | R  | Mortality rate (%) | 95% confidence limits | Recruitment rate (%) | 95% confidence limits |
|--|-------|-----|-----|----|--------------------|-----------------------|----------------------|-----------------------|
| <i>Alnus jorullensis</i> Kunth subsp. <i>lutea</i> Furlow            | Ajor  | 117 | 42  | 3  | 5.55               | 3.4 5.6               | 0.31                 | 0.06 0.91             |
| <i>Arbutus xalapensis</i> Kunth                                      | Axal  | 19  | 4   | 2  | 2.95               | 0.75 5.69             | 1.25                 | 0.16 4.14             |
| <i>Cornus excelsa</i> Kunth  | Cexc  | 32  | 5   | 2  | 2.12               | 0.69 4.09             | 0.75                 | 0.09 2.6              |
| <i>Garrya laurifolia</i> Hartweg ex Benth.                           | Glau  | 36  | 2   | 1  | 0.71               | 0.08 2.33             | 0.34                 | 0.008 1.81            |
| <i>Pinus leiophylla</i> Schiede ex Schltdl. & Cham.                  | Pleio | 54  | 5   | 3  | 1.21               | 0.38 2.53             | 0.67                 | 0.14 1.92             |
| <i>Prunus serotina</i> Ehrh. subsp. <i>capuli</i> (Cav.) McVaugh     | Pser  | 169 | 4   | 35 | 0.29               | 0.08 0.74             | 2.35                 | 1.85 3.45             |
| <i>Quercus candicans</i> Née   | Qcan  | 104 | 4   | 3  | 0.61               | 0.13 1.19             | 0.35                 | 0.07 1.02             |
| <i>Quercus castanea</i> Née  | Qcas  | 176 | 18  | 11 | 1.34               | 0.77 1.96             | 0.75                 | 0.38 1.34             |
| <i>Quercus crassipes</i> Humb. & Bonpl.                              | Qcra  | 855 | 175 | 35 | 2.88               | 2.22 2.91             | 0.5                  | 0.35 0.70             |
| <i>Quercus rugosa</i> Née  | Qrug  | 66  | 1   | 6  | 0.19               | 0.004 1.01            | 1.08                 | 0.42 2.34             |
| <i>Styrax ramirezii</i> Greenm.                                      | Sram  | 45  | 1   | 1  | 0.28               | 0.007 1.47            | 0.27                 | 0.007 1.47            |
| <i>Symplocos citrea</i> Lex.   | Scit  | 41  | 12  | 4  | 4.32               | 2.01 5.69             | 1.16                 | 0.34 2.89             |
| <i>Ternstroemia lineata</i> DC. subsp. <i>lineata</i>                | Tlin  | 431 | 28  | 62 | 0.41               | 0.54 1.15             | 1.68                 | 1.4 2.25              |
| <i>Xylosma flexuosa</i> (Kunth) Hemsl.                               | Xfle  | 5   | 1   | 1  | 2.78               | 0.06 8.95             | 2.27                 | 0.06 8.9              |
| <i>Quercus laurina</i> Humb. & Bonpl.                                | Qlau  | 67  | 0   | 2  | 0                  | 0 0                   | 0.36                 | 0.04 1.29             |
| <i>Quercus obtusata</i> Humb. & Bonpl.                               | Qobt  | 15  | 0   | 2  | 0                  | 0 0                   | 1.56                 | 0.20 5.05             |
| <i>Acacia farnesiana</i> (L.) Willd                                  | Afar  | 6   | 3   | 0  | 8.66               | 1.47 11.02            | 0                    | 0 0                   |
| <i>Abies religiosa</i> (Kunth) Schltdl. & Cham var. <i>religiosa</i> | Arel  | 2   | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Carpinus tropicalis</i> (Donn. Sm.) Lundell.                      | Ctro  | 1   | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Comarostaphylis discolor</i> (Hook.) subsp. <i>discolor</i> Diggs | Cdis  | 7   | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Fraxinus uhdei</i> (Wenzig) Lingelsh.                             | Fuhd  | 9   | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Ilex toluca</i> Hemsl.  | Itol  | 34  | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Lippia umbellata</i> Cav.   | Lumb  | 2   | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Oreopanax xalapensis</i> (Kunth) Decne. & Planch.                 | Oxal  | 7   | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Pinus pseudostrobus</i> Lindl.                                    | Ppseu | 16  | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |
| <i>Zinowiewia concinna</i> Lundell.                                  | Zcon  | 3   | 0   | 0  | 0                  | 0 0                   | 0                    | 0 0                   |

N: total number of individuals in the sample, D: number of dead trees, R: number of recruited trees, Code: species abbreviations for use in graphs. Nomenclature for species followed Vázquez-García *et al.* (1995) and Tropicos.org (2013).

TABLE II  
NUMBER OF DEAD INDIVIDUALS BY DIAMETER CLASS\*

| Species  | Diameter class (cm) |    |    |    |    |    |    |    |    |    |
|--|---------------------|----|----|----|----|----|----|----|----|----|
|  | 5                   | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 50 |
| <i>Alnus jorullensis</i> Kunth subsp. <i>lutea</i> Furlow        | 16                  | 9  | 9  | 5  | 2  | 1  |    |    |    |    |
| <i>Cornus excelsa</i> Kunth                                      |                     | 4  | 1  |    |    |    |    |    |    |    |
| <i>Garrya laurifolia</i> Hartweg ex Benth.                       |                     |    | 1  | 1  |    |    |    |    |    |    |
| <i>Pinus leiophylla</i> Schiede ex Schltdl. & Cham.              | 4                   | 1  |    |    |    |    |    |    |    |    |
| <i>Prunus serotina</i> Ehrh. subsp. <i>capuli</i> (Cav.) McVaugh | 2                   | 2  |    |    |    |    |    |    |    |    |
| <i>Quercus candicans</i> Née                                     |                     |    |    |    | 2  |    |    |    |    | 2  |
| <i>Quercus castanea</i> Née                                      | 4                   | 4  | 2  | 3  | 2  | 1  |    | 2  |    |    |
| <i>Quercus crassipes</i> Humb. & Bonpl.                          | 128                 | 34 | 5  | 4  | 1  | 1  |    | 1  |    | 1  |
| <i>Quercus rugosa</i> Née  |                     | 1  |    |    |    |    |    |    |    |    |
| <i>Symplocos citrea</i> Lex.                                     | 7                   | 5  |    |    |    |    |    |    |    |    |
| <i>Ternstroemia lineata</i> DC. subsp. <i>lineata</i>            | 19                  | 5  | 4  |    |    |    |    |    |    |    |

\* Only species with  $\geq 30$  individuals in the sample and present in  $\geq 10$  plots are included.

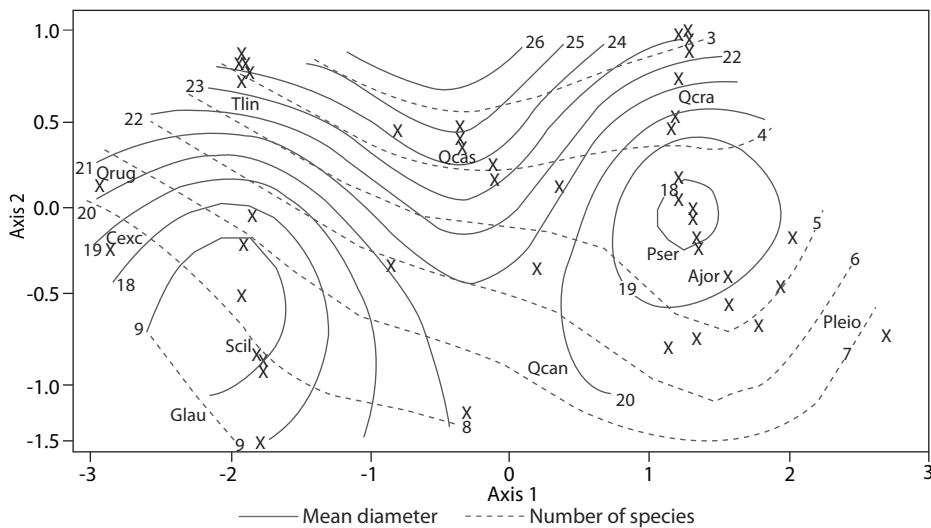


Figure 1. Non-metric multidimensional scaling ordination of mortality using the number of dead individuals per species per plot; only those species with  $\geq 30$  individuals in the sample and present in  $\geq 10$  plots were considered. Plot scores represented by x; species scores represented by species abbreviations as in Table I. Contour lines show smoothed surface of mean diameter (continued lines) and number of species (dashed lines).

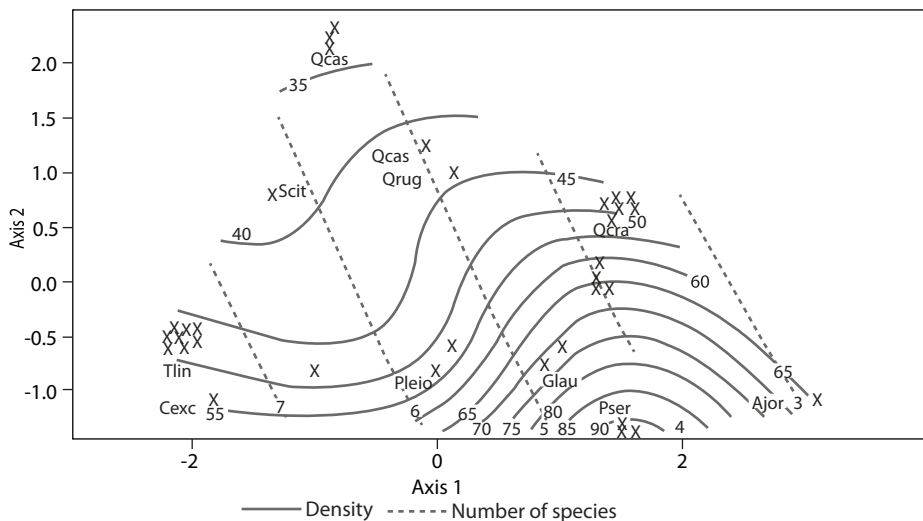


Figure 2. Non-metric multidimensional scaling ordination of recruitment using the number of recruits per species per plot; only those species with  $\geq 30$  individuals in the sample and present in  $\geq 10$  plots were considered. Plot scores represented by x; species scores represented by species abbreviations as in Table I. Contour lines show smoothed surface of density (continued lines) and number of species (dashed lines).

bottom to top, the diagram showed a decrease in plot density. *T. lineata*, the species with the highest number of recruits, was present in plots with intermediate density ( $\sim 50$  individuals by plot) and high number of species ( $\sim 8$ ); excepting *Quercus crassipes*, the rest oak species, with few to intermediate number of recruits, were in plots with low density (Figure 2).

### Structural differentiation

Structural differentiation based on comparison of mean diameters among the 26 species showed a 5-90cm dbh range. *Quercus* species had the largest diameters, followed by *P. leiophylla* (up to 65cm), while the rest of the species were  $< 45$ cm dbh (Figure 3). *C. excelsa* had the smallest diameters whilst *Q. candicans*, *Q. castanea* and *Q. rugosa* had the largest diameters. Diameter distribution for *Quercus crassipes*, *T. lineata*, *C. excelsa* and *P. serotina* resembles a reverse J-shape (Figure 3). According to the Wilcoxon test, differences in diameters during the 8-year period were statistically significant at  $p < 0.05$  for *G. laurifolia* and, at  $p < 0.0001$ , for *A. jorullensis*, *P. serotina*, *P. leiophylla*, *T. lineata*, *Q. candicans*, *Q. castanea*, *Quercus crassipes* and *Q. rugosa*. As a general pattern, tree density of small diameter categories decreased while density of large diameter trees somewhat increased with time. *C. excelsa* ( $p = 0.180$ ) and *S. citrea* ( $p = 0.06$ ) were not statistically significant. Results of the Gini coefficient showed that diameter distributions were relatively uniform for all species including those of *Quercus* (Gini's from 0.35-0.43). *Q. castanea* and *Q. rugosa* showed the highest inequality while *G. laurifolia*, *C. excelsa* and *P. serotina* had the highest equality. The Gini coefficient in the two time periods showed small differences in most of the species, but *S. citrea*, *P. leiophylla* and *A. jorullensis* had the highest positive differences over time, with decreasing Gini values among size-classes (Figure 3). As we were expecting, species regarded as shade-intolerant or light-demanding such as *Abies religiosa*, and *Pinus pseudostrobus* respectively, contain most of their individuals in the codominant category while most of the *Quercus* species, regarded as shade-tolerant or intermediate, share individuals between the codominant and the intermediate crown position (Table III).

### Discussion

Based on the present mortality results, the three different

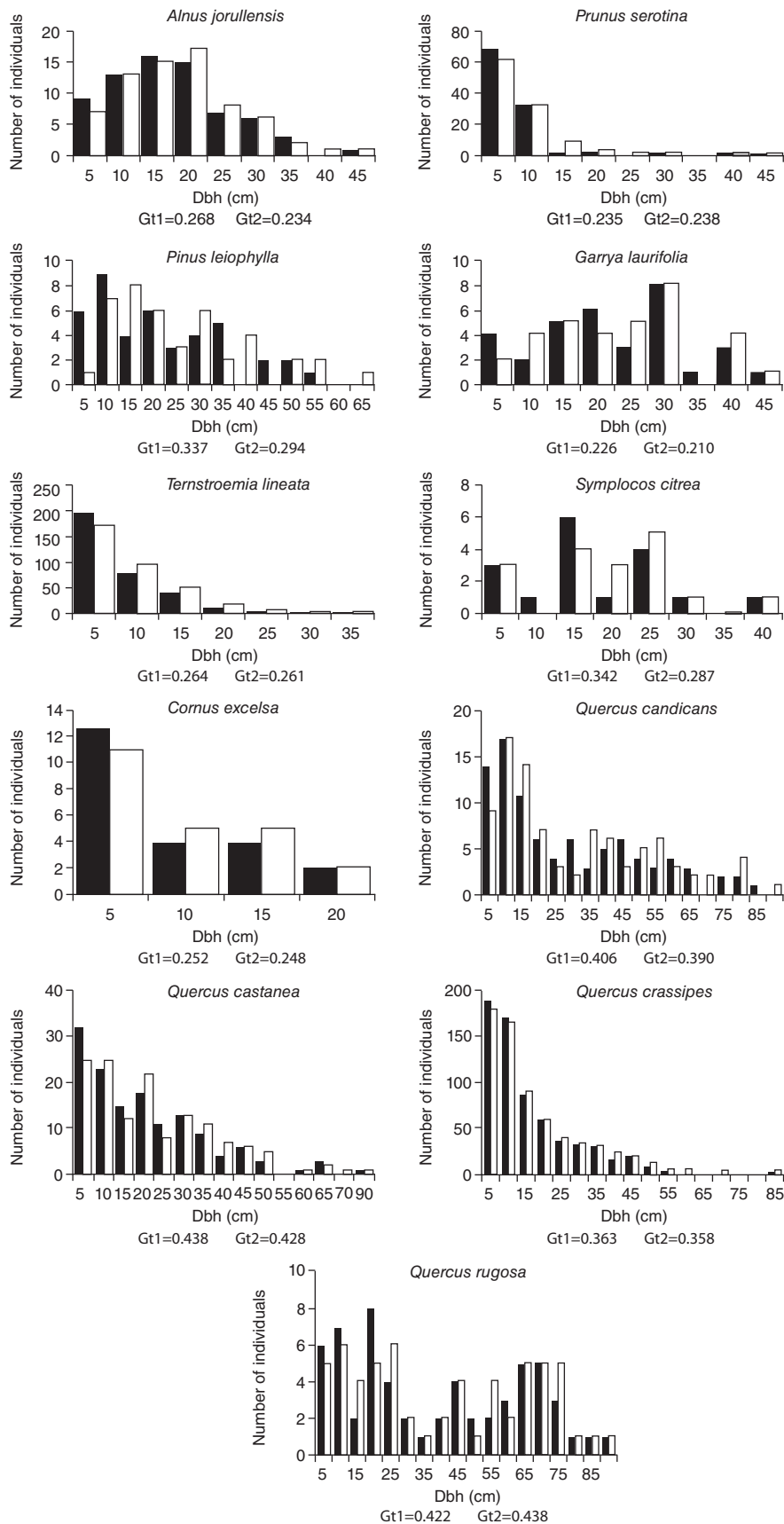


Figure 3. Diameter distribution for species with  $\geq 30$  individuals in the sample and present in  $\geq 10$  plots. Gt1: Gini coefficient for the year of the plots establishment (black rectangles), Gt2: Gini coefficient for the year of re-measurement (white rectangles).

groups of plots along axis 1 of the NMDS diagram seem to be leading by indicator species (*T. lineata*, *Q. castanea* and *Quercus crassipes*) whose number of dead individuals was the maximum in each plot. Concerning recruitment patterns, the same three species (*T. lineata*, *Q. castanea* and *Quercus crassipes*) demarcated the groups.

Most taxa were closely related to those found in Nearctic ecosystems; nevertheless the dominant species in the canopy have closer affinity to temperate associations. Thus, we were expecting similarities in mortality and recruitment rates with those reported for temperate forests. In particular, our results showed that average annual mortality rates for all the species (1.31%) roughly approximates to those annual mortality rates reported for temperate forests ( $< 1.2\%$ ) (Laarmann *et al.*, 2009) and fall behind those for different tropical forest ecosystems ( $< 2\%$ ), e.g. in Amazonia (Phillips *et al.*, 2004), Panama (Condit *et al.*, 1995), Dominican Republic (Sherman *et al.*, 2012) and French Guiana (Madelaine *et al.*, 2007). Taking into account oak species only, tree mortality ranged from 0 to 2.88% per year while the average rate for oaks in natural regenerated temperate forests in Europe is around 1% (Drobyshev *et al.* 2009). Excluding *Quercus crassipes*, oak species experienced intermediate to low mortality rates that may be related to the slow-growth behavior reported for oaks (Bréda *et al.*, 1995). The same seems to apply for oaks in our study area whose relative annual growth rate (RGR) was estimated at  $< 0.025\text{cm}^{-1}/\text{year}$  (Ibarra Cerdeña, 2001). Comparatively, *Q. castanea* mortality rate (1.34%) in our study plots was near to the European average, but *Q. rugosa* and *Q. candicans* mortality rates values were below it. In studies of North America, oak mortality rates varied according to diameter size ranging as high as 6% for 5cm dbh individuals whereas for 15cm dbh trees the average is 1% (Johnson *et al.* 2002). The higher mortality rate for *Quercus crassipes* was affected by mortality in the 5cm dbh class. *Q. candicans* and *Q. rugosa* mortality occurred in the 10-15cm dbh class. In contrast, *Q. castanea* had mortality over a broad range of diameters, i.e. 5-45cm dbh. Mortality rates estimated by Johnson *et al.* (2002) were based on trees  $> 10\text{cm}$  diameter cut-off, whereas our findings were based on trees  $> 5\text{cm}$  dbh. Inclusion of small-diameter trees in our sampling could be a factor influencing the results, i.e., a higher mortality rate was found in those species that had high densities in the smaller diameter classes. As Luo and

TABLE III  
PERCENTAGES OF SPECIES ACCORDING TO CROWN POSITION  
USING KRAFT'S CLASSIFICATION (SMITH, 1986)

| Species  | D    | Cd   | I    | S    | St |
|--|------|------|------|------|----|
| <i>Abies religiosa</i> (Kunth) Schtdl. & Cham var. <i>religiosa</i>  | 1.2  | 78.0 | 20.8 |      | t  |
| <i>Acacia farnesiana</i> (L.) Willd                                  |      |      | 100  |      | ld |
| <i>Alnus jorullensis</i> Kunth subsp. <i>lutea</i> Furlow*           |      | 43.9 | 46.3 | 9.8  | ld |
| <i>Arbutus xalapensis</i> Kunth                                      | 5.9  | 23.5 | 47.1 | 23.5 | t  |
| <i>Carpinus tropicalis</i> (Donn. Sm.) Lundell.                      |      | 100  |      |      | t  |
| <i>Comarostaphylis discolor</i> (Hook.) subsp. <i>discolor</i> Diggs |      | 14.7 | 64.7 | 20.6 | t  |
| <i>Cornus excelsa</i> Kunth*   |      |      | 50.0 | 50.0 | t  |
| <i>Fraxinus uhdei</i> (Wenzig) Lingelsh.                             |      | 100  |      |      | t  |
| <i>Garrya laurifolia</i> Hartweg ex Benth.*                          |      | 2.6  | 63.2 | 34.2 | t  |
| <i>Ilex toluicana</i> Hemsl.   |      | 29.5 | 59.1 | 11.4 | t  |
| <i>Lippia umbellata</i> Cav.   |      |      |      | 100  | t  |
| <i>Oreopanax xalapensis</i> (Kunth) Decne. & Planch.                 | 4.9  | 61.0 | 34.1 |      | t  |
| <i>Pinus leiophylla</i> Schiede ex Schtdl. & Cham.*                  |      | 20.0 | 50.0 | 30.0 | ld |
| <i>Pinus pseudostrubus</i> Lindl.                                    |      | 100  |      |      | ld |
| <i>Prunus serotina</i> Ehrh. subsp. <i>capuli</i> (Cav.) McVaugh*    |      | 25.0 | 75.0 |      | ld |
| <i>Quercus candicans</i> Née*  | 6.6  | 46.7 | 38.7 | 8.0  | t  |
| <i>Quercus castanea</i> Née*   | 1.0  | 37.0 | 48.0 | 14.0 | i  |
| <i>Quercus crassipes</i> Humb. & Bonpl.*                             | 1.0  | 33.0 | 40.5 | 25.5 | i  |
| <i>Quercus laurina</i> Humb. & Bonpl.                                | 2.5  | 28.7 | 51.0 | 17.8 | t  |
| <i>Quercus obtusata</i> Humb. & Bonpl.                               | 13.4 | 13.4 | 26.6 | 46.6 | t  |
| <i>Quercus rugosa</i> Née*   | 11.0 | 63.0 | 13.0 | 13.0 | t  |
| <i>Styrax ramirezii</i> Greenm.                                      |      | 3.1  | 62.8 | 34.1 | t  |
| <i>Symplocos citrea</i> Lex.*  |      | 17.2 | 61.4 | 21.4 | t  |
| <i>Ternstroemia lineata</i> DC. subsp. <i>lineata</i> *              |      | 1.0  | 51.4 | 47.6 | i  |
| <i>Xylosma flexuosa</i> (Kunth) Hemsl.                               |      |      | 75.0 | 25.0 | ld |
| <i>Zinowiewia concinna</i> Lundell.                                  |      | 50.0 | 50.0 |      | t  |

D: dominant, Cd: codominant, I: intermediate, and S: suppressed. St: shade-tolerance according to Olvera-Vargas (2006); ld: light-demanding, t: shade-tolerant, and i: intermediate.

\* Species with  $\geq 30$  individuals in the sample and present in  $\geq 10$  plots.

Chen (2011) claim, the effect of the relative dbh-size on mortality may be explained by the size-dependent resources uptake ability, resource availability, external-stress susceptibility and their interactions. Recruitment rate data from both temperate and tropical forests is relatively scarce but records from tropical forests average 2-3% (Phillips *et al.*, 2004, Sherman *et al.*, 2012), which is in agreement with our records (<3%). Recruitment rates for *Quercus* species ranged from 0.35 to 1.56%, which is fairly similar to the range (0.63-1.36%) reported for North American oak species (Graney and Murphy 1991).

#### Factors contributing to tree mortality and recruitment patterns

Endogenous factors were the main drivers of tree mortality and recruitment in sub-tropical forests in west-central Mexico. Previous studies (Olvera-Vargas *et al.*, 2010) emphasized that physiography, in particular catena, is one of the main variables explaining patterns of floristic composition. As a result, we expected differences in patterns of recruitment according to differences in physiography; nonetheless, recruitment was more related to density and number

of species, while patterns of tree mortality were related to the number of species and diameter sizes. Therefore, for dense stands we were expecting that inter- and intra-specific competition lead to the mortality of the less competitive individuals, mainly by suppression (Das *et al.*, 2011). This was the case for *Quercus crassipes*, one of the most dynamic species in terms of tree mortality and, coincidentally, the most abundant species in our study plots. Conversely, its recruitment rate was six times lower than any other species. Regeneration strategies in oak species can be playing a decisive role in the recruitment process; personal observations in our study plots revealed that oak saplings are very scarce in the understory. Moreover, the seedling to sapling stage has been observed to be a critical bottleneck in the demographic dynamics of this community (Olvera-Vargas *et al.*, 2014). To explain differences in mortality rates among co-occurring species, Stephenson *et al.* (2011) offered several hypotheses related to life-history traits such as shade tolerance and the proportion of tolerant versus intolerant species, with shade-intolerants showing higher mortality rates in overcrowded stands. In our study, we observed inconsistent results in mortality patterns among light-demanding or

shade-intolerant species. For example, *A. jorullensis* had high mortality rate while *Pinus* species and *Prunus serotina* exhibited low levels. Therefore the highest mortality rates were not always correlated with light-demanding species. We then found that species such as *Quercus crassipes*, *Q. castanea*, *A. jorullensis* and *C. excelsa*, with higher proportions of individuals in the intermediate crown position, showed high mortality rates. The number of species and density were most strongly related to recruitment, with the highest recruitment rate occurring at intermediate densities. For example, recruitment was relatively high for *T. lineata* and *Quercus crassipes* when plot density ranged from 45 to 50 individuals. In contrast, *Q. candicans*, *Q. castanea* and *Q. rugosa* species, with low recruitment rates, were mainly located in plots of low density (35-40 individuals) while *A. jorullensis* had low recruitment when plot density was relatively high, e.g. 85-90 individuals per plot.

#### Diameter sizes, mortality and recruitment

Results of the Wilcoxon test revealed significant changes in diameter size distribution for most of the species with the highest mortality and recruitment rates, except for *C. excelsa* and *S. citrea*. This finding suggests that these two species are experiencing an apparent compensating process between mortality and recruitment. Results of the Gini coefficient showed that most of the species pointed to a decrease in the coefficient values during the 8-year period, which indicates a tendency to size equality. For oak species, the highest inequality corresponded to *Q. castanea*, with mortality in different diameter sizes as well. This confirms that, as trees grow larger along time, the competition become asymmetric as larger trees obstruct light for smaller ones. According to Weiner (1990), asymmetric competition is synonymous with terms such as dominance and suppression. In this study, *Q. castanea* and *Quercus crassipes* had higher proportions of trees in the intermediate crown position and higher mortality rates. Gould *et al.* (2011) reported similar results for *Quercus garryana* in northwest USA, where higher mortality was predicted for trees in less favourable competitive positions. Trees in the understory have reduced growth due to shading and competition for other resources. Therefore, they are small in diameter due to suppression. If light levels are low enough then seedlings are unable to produce enough food to meet basic respiration and to produce extra energy for growth. After a

sufficiently long suppression period, not only growth is low, and trees remain small in diameter, but also mortality processes are prompted to occur.

## Conclusion

We observed different tree mortality and recruitment rates in sub-tropical mixed oak forests across species depending on diameter, density, crown position and plot diversity. The importance of this research was to improve our ability to discriminate the particular causes of tree mortality and recruitment occurring in these relatively unknown forest ecosystems. The determination of endogenous and exogenous factors driving tree mortality and recruitment in these communities is crucial to understand. As a definite example we could see that species such as *T. lineata*, *Q. castanea* and *Quercus crassipes*, whose number of dead as well as recruited individuals were the maximum of the group of species present in each plot, belong to intermediate category regarding shade-tolerance; they had correspondingly the highest percentages of their individuals in intermediate category concerning crown position.

They were also the same species leading the groupings in the ordination results; they appeared segregated into three different groups because they were present in plots with differences in density, mean diameter and number of species. Therefore we conclude that species life-traits are not the only component to investigate when studying demographic processes but also the conditions of the stand where every species is growing.

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## MORTALIDAD Y RECLUTAMIENTO ARBÓREO EN RODALES HETEROGÉNEOS DE BOSQUES SUB-TROPICALES MIXTOS DE ENCINO EN EL CENTRO-OCCIDENTE DE MÉXICO

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### RESUMEN

*Estudiamos como los patrones de mortalidad y reclutamiento de especies arbóreas se encuentran asociados a la estructura, diversidad de especies y diferencias en fisiografía en bosques sub-tropicales mixtos de encino. Para ello se utilizó escalamiento multidimensional no-métrico y modelos aditivos generalizados. La mortalidad, así como el reclutamiento se presentaron en ~50% de las especies registradas en los sitios. La proporción de la mortalidad arbórea fue mayor en las ca-*

*tegorías diamétricas más pequeñas, mientras que solo 16 de las 26 especies registradas en los sitios, presentaron reclutamiento. El número de especies, la densidad y el diámetro medio fueron las variables que mejor explicaron los patrones de mortalidad y reclutamiento en los sitios de estudio. Sitios con menor densidad no presentaron reclutamiento mientras que los individuos en categorías suprimidas mostraron las mayores tasas de mortalidad.*

## MORTALIDADE E RECRUTAMENTO ARBÓREOS EM AGRUPAMENTOS HETEROGÊNEOS DE BOSQUES SUBTROPICAIS MISTOS DE CARVALHO NO CENTRO-OESTE DO MEXICO.

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### RESUMO

*Estudamos a forma em que os padrões de mortalidade e recrutamento de espécies arbóreas se encontram associados à estrutura, diversidade de espécies e diferenças na fisiografia nos bosques subtropicais mistos de carvalho. Para isto utilizamos escalamento multidimensional não-métrico e modelos aditivos generalizados. A mortalidade, assim como o recrutamento, se apresentaram em ~50% das espécies registradas nos locais. A proporção da mortalidade arbórea foi maior nas*

*categorias diamétricas menores enquanto que, somente 16 das 26 espécies registradas nos locais, apresentaram recrutamento. O número de espécies, a densidade e o diâmetro médio foram as variáveis que melhor explicaram os padrões de mortalidade e recrutamento nos lugares de estudo. Lugares com menor densidade não apresentaram recrutamento enquanto que os indivíduos em categorias suprimidas mostraram as maiores taxas de mortalidade.*