The importance of environmental and disturbance conditions in different growth stages of plants of temperate forest in the Sierra Norte of Oaxaca, Mexico

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Abstract

Environmental conditions and disturbances are important factors that could influence ecological processes. For this reason, it is essential to know the relationship between them. The objective of this study was to analyze the effect of environmental conditions and disturbance on three growth stages (adults, germinated individuals, and seeds) of conifers, oaks, and other broadleaf species that compose the temperate forests of the highlands of the Sierra Norte of Oaxaca, Mexico. For this purpose, we established 0.1 ha plots along an altitudinal gradient ranging from 1950 m to 3250 m asl where we sampled vegetation, placed traps for seed rain, and quantified seed germination. We recorded climatic, edaphic, topographic, light, and disturbance conditions. We recorded a positive influence of anthropogenic disturbances on conifers in all their growth stages analyzed. For oaks and other broadleaf species, climatic variables such as temperature and precipitation showed a negative effect on adults and seeds, while disturbance showed no effect. Our results indicate that environmental conditions and anthropogenic disturbances have a differential effect on the biological groups that compose these forests and depending on the growth stage of the biological groups.

Introduction

All organisms have unique ecological requirements in which they can carry out their life cycle (Bewley and Krochko 1982). It is essential to understand each aspect of the life cycle, as they may present particular ecological strategies (Bonte et al. 2012) such as dispersal (Nathan and Muller-Landau 2000), germination (Pearson et al. 2002; Martínez-Villegas et al. 2018), regeneration (Quiroz et al. 2019), or distribution (Gomez et al. 2011). Knowledge of environmental preferences in the different stages of plant growth becomes relevant if this information applies to conservation, restoration, or resource management issues (Wahid et al. 2007).

One of the ecological processes that is fundamental for the natural regeneration of plants is dispersal, which refers to the unidirectional movement of propagules from the mother plant to their deposition on the soil (Levin et al. 2003; Nathan et al. 2008*)* . It is one of the growth stages that control the dynamics and persistence of a plant community and can control the response of vegetation to different changes, since dispersed seeds could potentially colonize open spaces, as long as these places fulfill the germination requirements (Clark et al. 1999; Levin et al. 2003; Howe and Miriti 2004). This is because plants germinate in places that have specific environmental conditions of temperature, humidity and light (Vandelook et al. 2008).

In addition to environmental conditions, disturbances are important factors that may influence ecological processes. Disturbance is considered to be any event occurring in a defined time and space, which is capable of partially or totally destroying plant biomass and altering environmental conditions (Grime 1977; Pickett and White 1985; Ł aska 2001). If the history of disturbances that have occurred at any site is considered, it leads to the term "disturbance regime" which refers to the temporal and spatial dynamics of disturbances in a given period of time (Pickett et al. 1999; Turner 2010). The disturbance regime can be described from several attributes such as its type, intensity and frequency (Pickett and White 1985; Pickett et al. 1999; Ł aska 2001). It has been reported that disturbances influence the process of plant regeneration, being those of anthropogenic origin such as management practices or harvesting practices that can negatively affect forests (Nakagawa and Kurahashi 2005; Toledo-Aceves et al. 2009; Soriano et al. 2012; Karsten et al. 2013).

The Sierra Norte of Oaxaca is part of the biogeographic province of the Sierra Madre del Sur, characterized by a very rugged mountainous terrain (Ortiz-Martínez et al. 2005; Álvarez-Arteaga et al. 2013). The vegetation of the highlands of Sierra Norte is composed of coniferous forests, oak forests, mixed forests, mountain mesophyll forests, and riparian vegetation (Ortiz-Martínez et al. 2005; Ramírez-Ponce et al. 2009; Piña and Trejo 2014). This region is of great relevance from a floristic point of view, as it presents a high species richness attributed to its heterogeneity of habitats, coming from a complex geological history (Gómez-Mendoza et al. 2008; Ramírez-Ponce et al. 2009; Zacarías-Eslava and Castillo 2010).

Most of the human populations that inhabit the Sierra Norte of Oaxaca depend on the forests. Through ecotourism activities or the use of forest resources (Zacarías-Eslava and Castillo 2010). It is essential to have data on the ecological requirements of the plants that inhabit each region, information that is fundamental to implementing successful forest management, restoration, or conservation practices (Guitérrez and Trejo 2014; Fournier et al. 2015).

The current study is based on Hutchinson's ecological niche hypothesis, which establishes that organisms have a series of thresholds of environmental conditions where they can carry out their life cycle (Hutchinson 1957). For this reason, it is fundamental to know the essential conditions in the different stages of growth of organisms. Considering the above, the main objective of this study was to analyze the relationship between the abundance of adult individuals, the abundance of dispersed seeds and the abundance of germinated seeds of the arboreal and shrub component (conifers, oaks and other broadleaf species) with the environmental and disturbance conditions in temperate forests established in the highlands of the Sierra Norte of Oaxaca, Mexico.

This study tested the hypothesis that environmental and disturbance conditions have a differential influence on the abundance of individuals in various growth stages (adults, seeds, and germinated individuals) of arboreal and shrubby organisms. Therefore, we expect that climatic variables have a greater influence than the rest of the environmental variables and that disturbance shows a negative relationship with the different growth stages of different plant groups.

Materials and Method

Study area

The study was conducted in the municipalities of Santa Catarina Lachatao (latitude 17.26°, longitude -96.47°) and Santa María Yavesía (latitude 17.23°, longitude -96.43°) located in the highlands of the Sierra Norte in the state of Oaxaca, Mexico (Fig. 1). The area is located in an altitudinal range from 1581-3361 m asl (meters above sea level) and has temperate and sub-humid climates (Piña and Trejo 2014).

Several environmental disturbances have occurred in the region, the ones that have affected the most are harvesting practices and forest pest management. Harvesting practices in the Sierra Norte region increased in the 1950's when the federal government granted concessions for forest harvesting to forestry companies. Forest harvesting was related to the extraction of trees with wood diameter for commercial purposes ([?] 30 cm normal diameter, ND). In the study area, this type of practice is based on selective extraction, as trees of the *Pinus* genus are felled and cut in situ and then extracted (Gasca 2014).

Between 2004 and 2009, the area's forests were affected by the bark beetle *Dendroctonus adjunctus* Blandford, which mainly attacks conifers and has one generation per year. Forest pest management refers to the techniques of felling, dragging, cutting, and removal of trees with evidence of forest pests. Infested trees are usually more than 10 cm in diameter and show reddish resin clumps on their stems, and change the color of their foliage from green to yellowish-reddish. In the study area, two of the pest control methods stipulated in Mexican legislation were performed, the method of felling, cutting, and abandonment, and the method of felling, cutting, and immediate extraction (Mathews et al. 2009; Carrasco and Morales 2012; Gasca 2014; Diario Oficial de la Federacion 2018).

Data collection

We established 14 sampling sites in the study area along the altitudinal gradient from 1950 m to 3250 m asl (Fig. 1), we focused on this altitudinal range because these were the lowest and highest altitude areas to which we could have access. We conducted the fieldwork from January 2015 to March 2016.

Abundance of adults and species composition

To know the number of adult individuals, as well as the species composition at each site, we considered a circular plot of 0.1 ha (1 000 m^2) in which we recorded the data of all arboreal or shrubby individuals [?] 2.5 cm of normalized diameter (ND). We made plant collections for subsequent determination, which we conducted by comparison with specimens from the National Herbarium of Mexico (MEXU) and with the help of experts of each taxonomic group. We grouped the species into conifers, oaks, and other broadleafs for statistical analysis.

Dispersal

We placed three 1.85 m x 1.85 m plastic meshes with a 35% opening (< 1.5 mm) at a height of 1 m from the ground in each sampling plot in January 2015, this opening allowed retaining seeds of tree and shrub communities. At each of the sites, the meshes were positioned at a distance of 8.7 meters from the center of the sampling site and with a separation width of 60 degrees between each mesh.

From January 2015 to March 2016 (425 days in total), we collected all seeds deposited in each mesh for subsequent identification and counting. The collection we conducted in six time periods: from January to February 2015 (t1), from March to April 2015 (t2), from May to July 2015 (t3), from August to October 2015 (t4), from November 2015 to January 2016 (t5), and from February to March 2016 (t6). We grouped seeds into three categories: seeds of conifers, oaks, and other broadleaf species.

Germination

To determine whether dispersed seeds can potentially germinate and whether germination is related to environmental conditions and disturbances, we first determined the germination percentage of the biological groups analyzed (conifers, oaks and other broadleaf species). We placed the seeds collected in the time period t1 (January-February 2015) and t2 (March-April 2015) in germination trays of 5 cm x 5 cm with a depth of 10 cm, without any germination treatment. The substrate used was collected at each of the sites where the seeds came from and was filtered through a sieve with an opening of 1.3 mm before being used, to ensure that it did not contain other seeds. We collected the substrate in April 2015 (t2). The seeds were under constant irrigation every third day in a greenhouse where the temperature was dependent on the environmental conditions of the site and located at an altitude of 2200 m asl in the municipality of Santa Catarina Lachatao. We performed two records of germinated individuals, the first one in July 2015 (50 days after planting) and the second one in October 2015 (146 days after planting). The germinated seeds are those that could potentially germinate in each of the sites under natural conditions.

Environmental and disturbance conditions

Topography variables: we recorded altitude, slope, and slope orientation in January 2015. We recorded the altitude with a GARMIN(r) GPS model GPSMAP 64s. We measured the slope with a clinometer and the orientation with a compass.

Climatic variables : we consider temperature, relative humidity and precipitation. For temperature and relative humidity we use HOBO(r) Pro V2 model sensors, for precipitation we use HOBO(r) Data Logger rain gauges of 200 cm2 of collection surface. We placed one sensor and one data logger in the center of each sampling site. The sensors collected data from January 2015 to March 2016. We calculated their average values, in the case of precipitation we determined the amount of precipitation (in mm per day) and calculated the intensity of precipitation events in millimeters per hour (mm h^{-1}).

Edaphic variables: we considered humus depth, soil temperature and soil moisture. We measured these variables on seven occasions (January 2015, February 2015, April 2015, July 2015, October 2015, January 2016, and March 2016). We measured humus depth with a flexometer, recorded temperature with a HANNA(r) brand soil thermometer model HI 98331, and used an EXTECH(r) brand soil moisture meter model Mo750 for moisture soil. We recorded data at a depth of 5 cm for temperature and moisture, with three replicates at each sampling site at random locations within each plot.

Light variables: we calculated canopy openness (% openness) and solar radiation (mols/m2/d) from the analysis of hemispheric photographs taken with a digital camera coupled to a fisheye lens. We took six photographs per site, three photos representing the dry season taken in April 2015, and three photos representing the rainy season taken in October 2015. In the study area, the rainy season runs from May to October, and the dry season runs from November to April. We took the photographs at the same position of the seed collecting nets at the sampling sites. We analyzed the photographs with the Gap Light Analyzer program (Frazer et al. 1999) that calculates average canopy openness and solar radiation.

Disturbance variables: we considered the intensity of disturbance according to the number of tree stumps present at each sampling site. We counted the number of stumps in January 2015. Stumps are evidence of disturbance at each site, so a higher number of stumps represents a higher disturbance intensity, the opposite case with a lower number of stumps representing a lower disturbance intensity.

Statistical analysis

We performed Generalized Linear Models (GLM) to evaluate the importance of environmental and disturbance variables on the abundance of different growth stages of conifers, oaks, and other broadleaves. The variables used showed collinearity, so we performed a selection of the variables to be used later in the GLM analysis. We calculated the VIF (Variance inflation factor) with the *vif.cca* function of the vegan package of R (Oksanen et al. 2013). The variables selected were disturbance intensity (Din), orientation (Ori), slope (Slo), canopy openness (Cop), humus depth (Hde), soil moisture (Mois), soil temperature (Ste), ambient temperature (Tem), relative humidity (Hum), precipitation (Pre) and precipitation intensity (Pin).

In the GLM analysis we developed different models with the selected environmental variables to test the importance of each parameter, we used the *glmulti* function of the glmulti package of R (Calcagno and de Mazancourt 2010). We selected the best model using the Aikake information corrected criterion (AICc). Finally, we evaluated the best models with the *glm* function of the vegan package (Oksanen et al. 2013).

We performed Pearson's correlation analysis (r) in R program (R Core Team 2019) to determine whether the abundance of seeds of each biological group was related to the abundance of adults (abundance of adult individuals of conifers, oaks and other broadleaves).

Finally, we performed a PCA ordination analysis to characterize changes in environmental variables between sampling sites. PCA is an unconstrained ordination technique that allows representing the information of a multivariate data matrix in a reduced space of orthogonal axes in which the main trends in the variation of the database are synthesized (Borcard et al. 2011). We elaborate a matrix with the selected environmental variables (matrix of explanatory variables). We performed the PCA using the *rda* function of the vegan package (Oksanen et al. 2013).

Results

Abundance of adults and species composition

We recorded the lowest number of adult individuals at Site 9 at an altitude of 2750 m, while site 10 (at an altitude of 2850 m) was where we observed the highest number of individuals. Conifer abundance values were higher at altitudes above 3050 m (S12, S13, S14), while the abundance of oak individuals was higher at altitudes below 2050 m (S1 and S2). The other broadleaf species presented a higher abundance at site 11

(2950 m), on the other hand we did not obtain records of the presence of this type of plants at site 1 (1950 m) (Fig. 2).

We recorded 29 species of trees and shrubs (nine species of the genus *Pinus* , one species of the genus *Abies* , ten species of the genus *Quercus* and nine species of other broadleaf species). Conifers distributed along the entire altitudinal gradient (1950-3250 m asl). We did not record oaks at altitudes above 3150 m, while at altitudes below 2450 m we observed a high species richness of oaks. We identified altitudinal preferences for the different species, for example *Pinus lawsonii* Roezl ex Gordon and *Quercus conzattii* Trel. recorded at altitudes lower than 2450 m. On the other hand, species such as *Abies hickelii* Flous & Gaussen, *Pinus ayacahuite* Ehrenb. ex Schltdl. and *Pinus hartwegii* Lindl. distributed at altitudes above 2850 m. We found only one species that occurred in most of the altitudinal gradient studied, *Arbutus xalapensis* Kunth distributed from 2250 m to 3250 m (Table 1).

According to the GLM (Table 2) for conifer abundance, precipitation intensity (Pin) had a negative effect and disturbance intensity (Din) a positive effect. On the other hand, for oaks relative humidity (Hum) and precipitation (Pre) had a negative effect. Something similar occurred with the abundance of the other broadleaf species, which also showed negative effects of the climatic variables, in this case temperature (Tem) and precipitation (Pre).

Dispersal

At the altitude of 2550 m (site 7) we recorded the highest number of seeds (4760 seeds/ha), while at the highest altitude studied (site 14, 3250 m) we observed a total of 190 seeds/ha, being the site with the lowest number of seeds recorded. Regarding the biological groups, the abundance of conifer seeds was higher with 23 070 seeds/ha being the most abundant group, followed by oaks with 2840 seeds/ha which was most abundant at altitudes lower than 2050 m (site 1 and 2), and finally the other broadleaves with 610 seeds/ha (Fig. 3).

The analyses indicated that for conifers, the intensity of disturbance (Din) had a positive effect on the abundance of dispersed seeds, as did the humus depth (Hde). For oaks, soil moisture (Mois) had a negative effect while precipitation intensity (Pin) had a positive effect. Finally, for the other hardwoods, temperature (Tem) and precipitation (Pre) had a negative effect (Table 2).

We recorded positive and significant correlations ($p < 0.05$) between seed abundance and abundance of adult individuals for oaks (r = 0.6) and for the other hardwoods (0.9). The correlation between seed abundance and conifer adults was low (r = 0.3) and not significant ($p > 0.05$).

Germination

Only some seeds of the conifers germinated; we did not record germination of the other biological groups evaluated. For the altitude of 3150 m (site 13) there was a germination percentage of 50%, followed by site 3 with an altitude of 2150 m with 45% germination, both from the period t2 corresponding to the period March-April. While the January-February period obtained lower germination percentages (Fig. 4). According to the GLM (Table 2) for conifers, disturbance intensity (Din) had a positive effect on germination while soil temperature (Ste) had a negative but not significant effect ($p = 0.10$).

Variation in environmental conditions

According to the analyses (Fig. 5) first two ordination axes explained 59.1% of the environmental variation in the sampling sites. The first axis was positively correlated with ambient temperature (Tem, r = 0.93) and rainfall intensity (Pin, r = 0.82), negatively related to atmospheric humidity (Hum, r = -0.91). The second ordination axis was positively correlated with canopy openness (Cop, r = 0.64) and negatively correlated with orientation (Ori, r = -0.87). Sites at lower altitudes (sites 1 to 6 lying between 1950-2450 m asl) had the highest temperatures (Tem and Ste) and the highest rainfall intensity (Pin) but lower precipitation (Pre). Sites 1 and 3 differed from the rest of the sites in this altitudinal range (1950-2450 m asl) by having the lowest values of atmospheric humidity (Hum). The higher altitude sites (sites 7 to 14 between 2550-3250 m asl) had lower atmospheric temperatures (Tem) than the lower altitude sites. However, for the rest of the environmental variables that were important for the ordination (Pin, Hum, Cop and Ori) they show more variation than the sites of lower altitudes.

Discussion

We observed that there is an altitudinal distribution preference for tree species, an example of this is what we recorded for *P. ayacahuite* and *P. hartwegii* , which in the study area commonly occur at altitudes above 2850 m, or the case of *Q. conzattii* , which occurs at altitudes below 2450 m. This is in agreement with other studies where altitudinal preferences of tree species are recorded (Valencia 2004).

Regarding the relationship between environmental and disturbance conditions on the abundance of adult individuals, we observed that the abundance of conifers registered a positive effect of the intensity of the disturbance, because the sites with the highest number of stumps were those that registered the highest abundance of adult individuals (sites 3 and 10). This makes sense considering that disturbances can generate spaces with greater incidence of light, which can favor the growth of other plants (Zhou et al. 2023). Regarding the abundance of adult oaks, relative humidity and precipitation had a negative effect, because most of the oaks distributed in the lowlands thrive in low humidity conditions (Sabas-Rosales et al. 2015).

According to the results obtained for oaks and other broadleaf species, we observed that the abundance of seeds was related to the abundance of adult individuals, so that for these biological groups, the number of seeds is proportional to the number of adult individuals present. In the case of conifers, we did not observe this relationship, so the abundance of seeds does not depend on the abundance of adults for this biological group. This may be due to the fact that conifer seeds are smaller and their dispersal is favored by the wind, so they can reach greater distances, $>$ 33 km (Williams et al. 2006). Contrary to the case of oak seeds, which due to their morphology do not disperse over long distances, $<$ 1 km (Gomez 2003).

We recorded that disturbance intensity and humus depth showed a positive effect on seed abundance of conifers, this may be due to the fact that disturbances can cause stress on organisms by producing changes in environmental conditions, so when stressed plants produce a greater number of seeds (Lauder et al. 2019). Regarding oak trees, we observed that humidity had a negative effect on seed abundance, as already mentioned, most of the oak trees present in the study area show an affinity for low humidity conditions, on the other hand precipitation intensity showed a positive effect, this may be due to the fact that precipitation causes a higher seed fall in situ (Li et al. 2012).

In the case of germination of conifers, we recorded that the intensity of the disturbance has a positive effect, this may be because at the sites where intense disturbances occurred canopy opening is greater, so that the entry of light and water by precipitation increases (Fernandez and Trejo 2020), since sites that showed precipitation intervals of 435-530 mm presented a higher percentage of germination. This agrees with previous studies where they report that water availability is a determining factor in germination, as has been recorded for species such as *Pinus nigra* J.F.Arnold (Topacoglu et al. 2016), or what reported for *Pinus sylvestris* where they observed that the years with the highest germination corresponded to the years with the most precipitation (Castro et al. 2005). Although in this study, ambient temperature did not influence the germination of conifers, previous studies report that for species such as *Pinus douglasiana*Martinez and *Pinus maximinoi* H. E. Moore, temperature plays a significant role in germination, showing ideal temperatures from 9.4degC to 10degC (Ordonez-Salanueva et al. 2021).

The biological group of conifers was the only one for which the intensity of the disturbance was an important variable in all growth stages. This is due to the fact that the environmental conditions after the disturbance occurred were optimal for the growth stages analyzed, since the disturbances caused spaces with loss of canopy cover where temperatures and the amount of water from precipitation was higher than in places with greater canopy cover (Fernandez and Trejo 2020). This is in agreement with previous studies that also report an influence of environmental conditions on dispersal, such as that obtained for*Pinus pinaster* Aiton and *Pinus sylvestris* in which precipitation and high temperatures promote seed dispersal (Hannerz et al. 2002; Juez et al. 2014).

Environmental conditions are fundamental to analyze, since according to the type or intensity of the disturbance, the conditions prevailing at the site after the event may not be suitable for the ecological processes that were taking place. On the contrary, they may generate new conditions that are optimal for plants, as in the case of organisms that require large amounts of light to germinate and grow (Klopčič et al. 2015; Derroire et al. 2016), or in the best scenario may have no effect on biological systems. Particularly in the study region, more research focused on determining how disturbances modify environmental conditions is needed so that such information can be used in ecological studies.

According to the results obtained and the hypothesis initially proposed, we observed that the abundance of adult individuals, seed dispersal, and germination of arboreal and shrub organisms are influenced differentially by environmental and disturbance conditions. We find that climatic variables are more related to the abundances of the analyzed plants. On the other hand, we did not observe the assumption that environmental disturbances negatively affect growth stages since we recorded a positive impact on conifers (adults, seeds, and germination) and a null effect on the other biological groups.

Conclusions

Conifers in all growth stages analyzed (adults, dispersal, and germination) were positively influenced by environmental disturbances. In the case of oaks and other broadleaf species evaluated, climatic variables such as temperature and precipitation influenced these biological groups.

We found that environmental conditions and anthropogenic disturbances are fundamental factors influencing the different growth stages such as dispersal, germination, and the abundance of adults of the biological groups analyzed.

The information obtained from this study can be applied by the inhabitants of the study area in making decisions regarding the conservation and management of their forests. An example of this is in the collection of conifer seeds, since in the sites where the intensity of the disturbance was greater, it would be expected to obtain a greater number of seeds, and thus propagate local plants that can be used to reforest disturbed areas. This is especially relevant given the current scenario of accelerated loss of vegetation cover.

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Figures

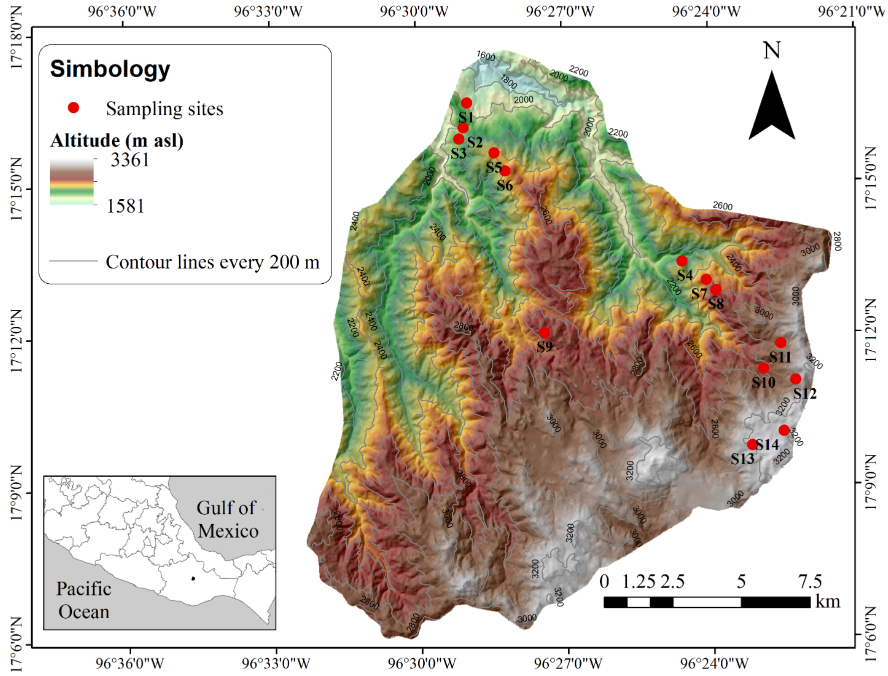

Fig. 1 Location of the study area within the Sierra Norte de Oaxaca, Mexico and location of sampling sites

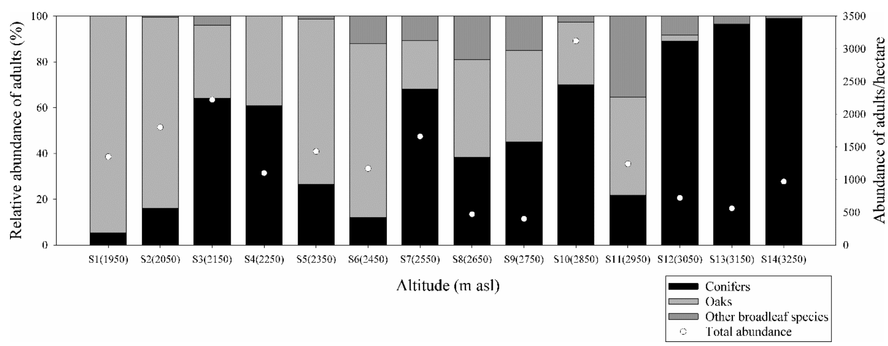

Fig. 2 Relative and total abundance of adult individuals ([?] 2.5 cm ND) per hectare according to altitudinal gradient

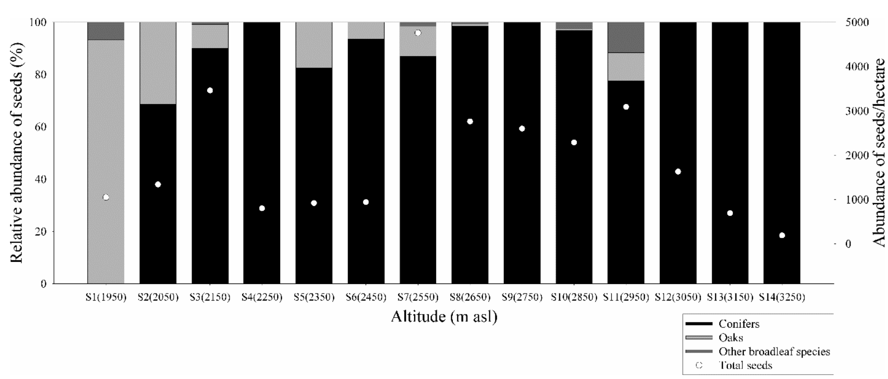

Fig. 3 Relative abundance and seed production totals per hectare according to altitudinal gradient

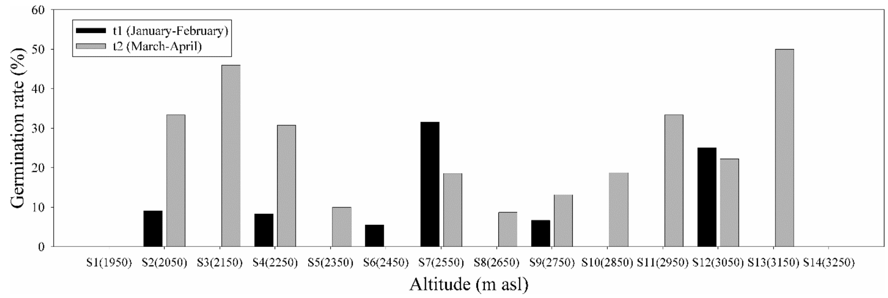

Fig. 4 Germination rate of conifers

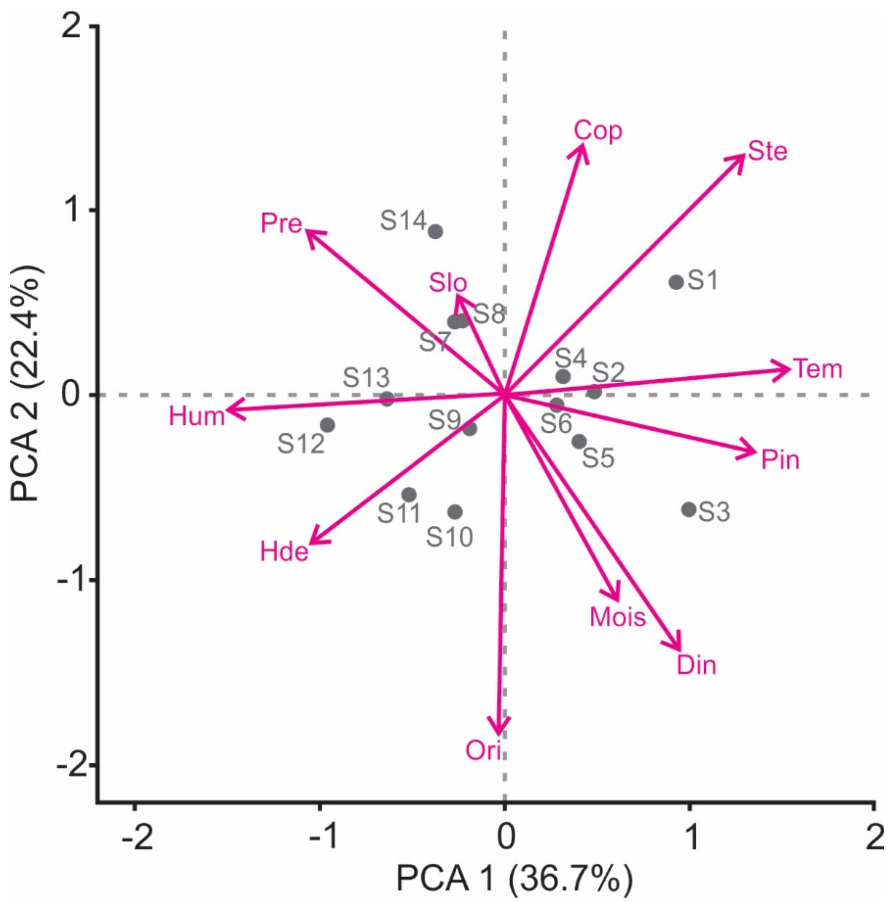

Fig. 5 Ordering based on principal component analysis of the different environmental variables in the altitudinal gradient (Din, disturbance intensity; Ori, orientation; Slo, slope; Cop, canopy opening; Hde, humus depth; Mois, moisture; Ste, soil temperature; Tem, temperature; Hum, humidity; Pre, precipitation; Pin, precipitation intensity)

Tables

Table 1 Tree and shrub species recorded in the study area

Site	Altitude (m asl)	Species	Species	Species	Species
		Conifers	**Oaks**	**Other broadleaf species**	**Other broadleaf species**
S1	1950	*Pinus lawsonii* Roezl ex Gordon	*Quercus calophylla* Schltdl. & Cham., *Quercus castanea* Née, *Quercus conzattii* Trel.		
S2	2050	*Pinus teocote* Schied. ex Schltdl. & Cham.	*Quercus conzattii* Trel., *Quercus laeta* Liebm.	*Comarostaphylis discolor* (Hook.) Diggs	*Comarostaphylis discolor* (Hook.) Diggs
S3	2150	*Pinus lawsonii* Roezl ex Gordon	*Quercus conzattii* Trel.	*Quercus conzattii* Trel.	
S4	2250	*Pinus lawsonii* Roezl ex Gordon, *Pinus patula* var. *longipedunculata* Loock ex Martínez, *Pinus pseudostrobus* var. *apulcensis* (Lindl.) Shaw, *Pinus pseudostrobus* Lindl.	*Quercus crassifolia* Bonpl., *Quercus glabrescens* Benth., *Quercus obtusata* Bonpl.	*Alnus jorullensis* Kunth, *Arbutus xalapensis* Kunth	*Alnus jorullensis* Kunth, *Arbutus xalapensis* Kunth
S5	2350	*Pinus lawsonii* Roezl ex Gordon, *Pinus pseudostrobus* var. *apulcensis* (Lindl.) Shaw,	*Quercus castanea* Née, *Quercus crasssifolia* Bonpl., *Quercus glabrescens* Benth., *Quercus obtusata* Bonpl.	*Arbutus xalapensis* Kunth	*Arbutus xalapensis* Kunth

Site	Altitude (m asl)	Species	Species	Species	Species
S6	2450	*Pinus lawsonii* Roezl ex Gordon, *Pinus pseudostrobus* var. *apulcensis* (Lindl.) Shaw	*Quercus castanea* Née, *Quercus conzattii* Trel., *Quercus obtusata* Bonpl.	*Arbutus xalapensis* Kunth, *Baccharis heterophylla* Kunth	*Arbutus xalapensis* Kunth, *Baccharis heterophylla* Kunth
S7	2550	*Pinus patula* var. *longipedunculata* Loock ex Martínez, *Pinus pseudostrobus* var. *apulcensis* (Lindl.) Shaw	*Quercus crassifolia* Bonpl., *Quercus rugosa* Née	*Alnus jorullensis* Kunth, *Arbutus xalapensis* Kunth, *Litsea glaucenscens* Kunth, *Prunus serotina* Ehrh.	*Alnus jorullensis* Kunth, *Arbutus xalapensis* Kunth, *Litsea glaucenscens* Kunth, *Prunus serotina* Ehrh.
S8	2650	*Pinus herrerae* Martínez, *Pinus maximinoi* H. E. Moore, *Pinus patula* var. *longipedunculata* Loock ex Martínez		*Alnus jorullensis* Kunth, *Arbutus xalapensis* Kunth, *Baccharis heterophylla* Kunth, *Prunus serotina* Ehrh.	*Alnus jorullensis* Kunth, *Arbutus xalapensis* Kunth, *Baccharis heterophylla* Kunth, *Prunus serotina* Ehrh.
S9	2750	*Pinus douglasiana* Martínez, *Pinus patula* var. *longipedunculata* Loock ex Martínez, *Pinus pseudostrobus* var. *apulcensis* (Lindl.) Shaw	*Quercus crassifolia* Bonpl., *Quercus rugosa* Née	*Arbutus xalapensis* Kunth, *Prunus serotina* Ehrh.	*Arbutus xalapensis* Kunth, *Prunus serotina* Ehrh.

Site	Altitude (m asl)	Species	Species	Species	Species
S10	2850	*Abies hickelii* Flous & Gaussen, *Pinus ayacahuite* Ehrenb. ex Schltdl., *Pinus patula* var. *longipedunculata* Loock ex Martínez, *Pinus pseudostrobus* Lindl.	*Quercus crassifolia* Bonpl., *Quercus ocoteifolia* Liebm.	*Comarostaphylis discolor* (Hook.) Diggs	*Comarostaphylis discolor* (Hook.) Diggs
S11	2950	*Abies hickelii* Flous & Gaussen, *Pinus ayacahuite* Ehrenb. ex Schltdl., *Pinus pseudostrobus* Lindl.	*Quercus crassifolia* Bonpl., *Quercus glabrescens* Benth.	*Comarostaphylis discolor* (Hook.) Diggs, *Litsea glaucenscens* Kunth, *Lonicera mexicana* (Kunth) Rehder, *Oreopanax xalapensis* (Kunth) Decne. & Planch., *Prunus serotina* Ehrh., *Senecio andrieuxii* DC.	*Comarostaphylis discolor* (Hook.) Diggs, *Litsea glaucenscens* Kunth, *Lonicera mexicana* (Kunth) Rehder, *Oreopanax xalapensis* (Kunth) Decne. & Planch., *Prunus serotina* Ehrh., *Senecio andrieuxii* DC.
S12	3050	*Abies hickelii* Flous & Gaussen, *Pinus ayacahuite* Ehrenb. ex Schltdl.	*Quercus laurina* Bonpl., *Quercus ocoteifolia* Liebm.	*Comarostaphylis discolor* (Hook.) Diggs, *Senecio andrieuxii* DC.	*Comarostaphylis discolor* (Hook.) Diggs, *Senecio andrieuxii* DC.

Site	Altitude (m asl)	Species	Species	Species	Species
S13	3150	*Abies hickelii* Flous & Gaussen, *Pinus ayacahuite* Ehrenb. ex Schltdl.		*Arbutus xalapensis* Kunth	*Arbutus xalapensis* Kunth
1S4	3250	*Pinus hartwegii* Lindl.		*Arbutus xalapensis* Kunth	*Arbutus xalapensis* Kunth

Table 2 Results of generalized linear models of the association of the different developmental stages of plant groups with environmental variables. (*) Significant effects, S.E. = standard error, Est. = estimated value of the effect of the environmental variable (slope of the curve), z = statistical value

Stage	**Environmental variable**	**Est.**	**S. E.**	z	p
Conifer seeds	Din	0.14	<0.01	15.16	<0.01*
	Hde	0.16	<0.01	22.23	<0.01*
Oaks seeds	Mois	-0.11	0.01	-8.36	<0.01*
	Pin	0.11	<0.01	13.88	<0.01*
Other broadleaf species seeds	Tem	-0.27	0.05	-5.78	<0.01*
	Pre	-0.02	<0.01	-5.96	<0.01*
Conifer germination	Din	3.58	1.43	2.50	0.03*
	Ste	-2.58	1.44	-1.78	0.10
Conifer adults	Din	0.30	0.02	17.84	<0.01*
	Pin	-0.12	<0.01	-16	<0.01*
Oaks adults	Hum	-0.02	<0.01	-8.84	<0.01*
	Pre	< -0.01	<0.01	-12.54	<0.01*
Other broadleaf species adults	Tem	-0.23	0.03	-7	<0.01*
	Pre	< -0.01	<0.01	-6.35	<0.01*