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Microclimate and seeding predation as drivers of tree recruitment in human-disturbed oak forests

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ABSTRACT

Forest conservation and restoration are global priorities because of the wide variety of environmental services that these ecosystems provide, but achieving these goals depends on our knowledge about the factors driving tree recruitment. Tree establishment within forests is promoted by favorable microclimatic conditions, but seedlings in this habitat can be subjected to elevated consumer pressure by vertebrates. Conversely, while predation is usually reduced in neighboring human matrices, severe microclimatic conditions can reduce seedling survival in these habitats. Unfavorable microclimatic conditions can be ameliorated at forest edges and this may increase tree establishment rates, as compared to those in human matrices. However, seedlings at forest edges are exposed to predators from both habitats and consumer pressure may be even higher than within the forest. Thus, tree establishment in human-disturbed forests seems to depend on tradeoffs between microclimate and predation. This study focused on these issues in an oak forest from Mexico where extensive forested areas have been replaced by plantations of the exotic tree *Eucalyptus camaldulensis*. For this, two experiments were conducted by transplanting oak seedlings within the forest, at the forest edge and in a neighboring plantation. Temperature, air humidity and light intensity were measured in all habitats during the experiments. The first experiment assessed the effect of microclimate on seedling survival and, therefore, transplants were protected with wire cages to prevent predation by vertebrates. Survival of seedlings was monitored during a year and their physiological responses to microclimate were assessed by measuring their photosynthetic efficiency. In the second experiment, seedlings were not protected from herbivores and these survival data were used to discriminate between the effects of microclimate and predation. Temperature and light intensity decreased from the *Eucalyptus* plantation toward the forest interior, while relative humidity increased in that direction. The physiological performance and survival rates of protected seedlings increased from the plantation toward the forest, suggesting that local microclimate largely influences oak recruitment across these habitat types. Nevertheless, predation rates also increased from the plantation to the forest, suggesting that seedling consumers strongly reduce oak recruitment both within the forest and its edge. These results indicate that the relative importance of physical stress and seedling predation vary across the environmental gradients that compose human-disturbed forests. Thus, restoration and conservation actions should implement specific protection mechanisms addressed to reduce the impact of the main sources of seedling mortality at each particular habitat of these landscapes.

1. Introduction

Deforestation rates reached alarming levels during the 20th century because of the explosive growth of the human population and the consequent increase in the demand of lands to produce food and raw materials (Shvidenko et al., 2005). This ecological footprint is so widespread and deep that the key environmental services that forest provide are currently threatened. For this reason, conserving and restoring these ecosystems have become global priorities (Rudel et al., 2005). The achievement of these goals, however, will mainly depend on our knowledge about the factors driving tree seedling establishment in the remaining forests, as well as in human-disturbed areas.

Microclimate is perhaps the main factor that regulates forest maintenance. The establishment of late successional tree species commonly depend upon specific conditions of light, temperature and humidity that occur in the forest understory (Clinton, 2003). Any change in these environmental variables may prevent the recruitment of new individuals (Borchert et al., 1989;

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Gómez-Aparicio et al., 2008). Thus, forest regeneration may be hampered in human matrices due to adverse microclimatic conditions for juvenile stages of trees (Duncan and Duncan, 2000; Gómez-Aparicio et al., 2008; Badano et al., 2009; González-Salvatierra et al., 2013). However, forest edges can ameliorate these unfavorable microclimatic conditions and provide more suitable microhabitats than human matrices for the establishment of tree species (Laurance et al., 1998; Davies-Colley et al., 2000; Asbjornsen et al., 2004; López-Barrera and Newton, 2005; Guzmán-Guzmán and Williams-Linera, 2006).

Herbivory is another important factor that regulates seedling establishment and, consequently, tree recruitment in forest ecosystems. Most forest-dwelling vertebrates that consume tree seedlings commonly concentrate their activities in the understory because food resources and refuge opportunities are more abundant than in human matrices. This behavior of herbivores can strongly reduce the establishment rates of tree species beneath the forest canopy (Nystrand and Granström, 2000; Gómez et al., 2003; Rizkalla and Swihart, 2007). Seedling predation by vertebrates is also likely to occur in human matrices, but its impact on tree recruitment is usually less severe than within the forest because most species inhabiting these areas are opportunistic-generalist species that consume a wide variety of resources (Gill and Marks, 1991; Tellería et al., 1991; Riege and Del Moral, 2004). Nevertheless, seedling predation may increase at edges between forests and human matrices because they are exposed to herbivores from both habitats and this may preclude the establishment of late successional tree species (Ostfeld et al., 1997; Cadenasso and Pickett, 2000; Manson et al., 2001).

Both microclimate and seedling predation are important drivers of tree recruitment in human-disturbed forests. In most cases, however, the influence of these two factors has been evaluated separately or without taking into account the environmental gradients that occur from the interior of forests toward human matrices (e.g., Ostfeld et al., 1997; Laurance et al., 1998; Cadenasso and Pickett, 2000; Manson et al., 2001; López-Barrera et al., 2005; Guzmán-Guzmán and Williams-Linera, 2006; Montes-Hernández and López-Barrera, 2013). However, seedling survival in the different habitat types that compose these landscapes seems to be regulated by tradeoffs between microclimate and predation. On this issue, it could be proposed that favorable microclimatic conditions that occur within the forest promote seedling establishment in the understory, but elevated consumer pressure is likely to reduce tree seedling establishment in this habitat. Conversely, while seedling predation would be of less concern in human matrices, harsh microclimatic conditions would constrain tree recruitment in this habitat. Finally, tree establishment at edge habitats would depend on both, the magnitude with which the forest ameliorate unfavorable microclimatic conditions and the intensity with which herbivores consume seedlings.

The main objective of this study was to determine how these habitat-dependent filters affect tree seedling establishment on the environmental gradients occurring from the interior of the forest toward the neighboring human matrices. For this, we focused on a temperate oak forest (*Quercus* spp., Fagaceae) from Mexico because, although oaks are conspicuous elements in most temperate forests of the northern hemisphere, this country harbors the greatest diversity of oaks in the world, with 161 species (Nixon, 1993; Valencia-Ávalos, 2004). In Mexico, oaks have played a central role in the local culture since pre-Hispanic times (Luna-José et al., 2003) and their forests currently cover the recharge areas of most aquifers that provide freshwater to the central portion of the country (García-Coll et al., 2004). However, more than 60% of these woodlands have been replaced by productive matrices during the last four centuries (Palacio-Prieto et al., 2000) and little is yet know about the factors that influence oak recruitment dynamics in the remaining forests and abandoned fields.

2. Materials and methods

2.1. Study area

This study was conducted in an oak forest relic (19°01′N, 98°20′W, 2100–25,000 m) located in Amozoc de Mota, State of Puebla, west-central Mexico. Mean annual temperature is 16.33 °C (±3.21) and annual precipitation ranges between 750 and 950 mm (García, 1973). Rainfalls are concentrated in summer (July–October), while a markedly dry season occurs during the rest of the year (García, 1973). All this region was originally covered by oak forests, but these woodlands were extensively logged and replaced by farming fields. These lands were abandoned during the first half of the 20th century because of their low productivity. Later, local policies were applied to reconvert these abandoned fields into plantations of *Eucalyptus camaldulensis* Dehnh. (Myrtaceae) and hence promote silvicultural practices in rural people. However, plantations were never managed and this leads to a mosaic landscape composed by oak forest remnants, abandoned *Eucalyptus* plantations and sparse urban developments that have recently been set throughout the area (Badano et al., 2012).

The forest relic covers 374 ha and it is a protected natural area since 1985 (Escobar-Maravillas et al., 2001). Up to 83% of trees in this forest are oaks, where the dominant species are *Quercus laurina* Bonpl., *Quercus castanea* Nee., *Quercus laeta* Liebm and *Quercus glabrescens* Benth. (Badano et al., 2012). The forest understory is mainly covered by leaf litter, but sparse shrubs of the families Asteraceae, Rhamnaceae and Fabaceae can be found together with oak saplings. Adjoining to this forest relic there is an *Eucalyptus* plantation of 40 ha. The understory of the plantation is composed by grasses and some juvenile *Eucalyptus*, but no recruiting oaks occur in this area (Badano et al., 2012). There is a sharp boundary line between these two vegetation types (Fig. 1A), where some juvenile oaks and *Eucalyptus* individuals can be found.

2.2. Microclimate assessment

To assess microclimate in the forest, the plantation and the edge between these habitats we measured air temperature and relative humidity with dual dataloggers (HOBO U23, Onset Computer Corporation, USA). We also measured the photosynthetic photon flux density (PPFD) with light probes (S-LIA-M003, Onset Computer Corporation, USA) connected to micro-stations (HOBO H21, Onset Computer Corporation, USA). At each habitat type, three dataloggers were distributed every 30 m on 90-m line transects. In the oak forest and the plantation, transects were located 50 m away from the edge habitat. Climatic sensors of dataloggers were located 1.2 m above the ground by fixing them to wood stakes and they were programed to record climatic variables every hour during the entire period of study, which comprised from July 6th 2009 to July 7th 2010 (366 days). Temperature (average, maximum and minimum) relative humidity and PPFD during daytime (8:00–18:00 h) recorded by each datalogger were averaged for each month of study. By treating data in this way we were able to conduct proper comparisons of microclimate among habitat types, while it also allowed to assess whether observed differences in microclimate were sustained across the entire study period. These data were compared among habitat types with repeated measures ANOVA, where months were considered the repeated measures and the dataloggers the replicates (n = 3 per habitat type).