The role of frugivorous birds and bats in the colonization of cloud forest plant species in burned areas in western Mexico

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Abstract

The role of frugivorous birds and bats in the colonization of cloud forest plant species in burned areas in western Mexico.— The extension of montane cloud forests in western Mexico is threatened by several disturbances that limit their extension. In this study we aimed to assess the contribution of birds and bats in the dispersal and colonization of cloud–forest plants in contiguous surface–burned pine forests. We sampled seed rain and sapling establishment over one year in two surface–burned sites, which differed in the size of their closest cloud forest patch. A total of 17 plant species were found, most of which were late–successional trees, shrubs and climbers. Distance influenced the seed rain of only one dispersed taxon (*Solanum* sp.) and had no effect on the sapling distribution of this or other plants. In turn, marked differences were found between sites, with more seeds dispersed and higher sapling density in the site that was next to the larger cloud forest patch. The role of long–distance dispersers and the existence of seed banks before fire could explain the little importance of distance from seed source on seed dispersal and sapling distribution. Nevertheless, dispersal by birds and bats before or after fire facilitates the regeneration and conservation of cloud forests in disturbed areas formerly occupied by other habitats.

Key words: Cloud forest, Colonization, Disturbance, Fire, Seed dispersal, Seed rain, Succession

Resumen

La función de las aves y los murciélagos frugívoros en la colonización de las especies vegetales del bosque nuboso en zonas afectadas por incendios en el occidente de México.— La extensión de los bosques nubosos de montaña (o bosques mesófilos) del oeste de México se ve limitada por diversos factores. En el presente estudio se pretende evaluar la contribución de las aves y los murciélagos a la dispersión y colonización de las plantas del bosque nuboso en pinares contiguos afectados por incendios de superficie. Se muestreó la lluvia de semillas y el establecimiento de plántulas durante un año en dos sitios afectados por incendios de superficie, que diferían en el tamaño del fragmento de bosque nuboso más cercano. Se encontró un total de 17 especies vegetales, la mayoría de las cuales eran árboles, arbustos y lianas propios de estados avanzados de sucesión. La distancia respecto a la fuente de semillas influyó solamente en la lluvia de semillas de un taxón (*Solanum* sp.), pero no tuvo efectos en la distribución de las plántulas de esta especie ni de otras. En cambio, se encontraron importantes diferencias entre los sitios, con más semillas dispersadas y una mayor densidad de plántulas en el que estaba situado junto al fragmento más extenso de bosque nuboso. La función de los vectores de dispersión a larga distancia y la existencia de bancos de semillas previos al incendio podrían explicar la escasa importancia de la distancia desde la fuente de semillas para la lluvia de semillas y la distribución de las plántulas. En todo caso, la dispersión mediante las aves y los murciélagos antes o después del incendio facilita la regeneración y la conservación del bosque nuboso en zonas perturbadas que anteriormente hubieran estado ocupadas por otros hábitats.

Palabras clave: Bosque nuboso, Colonización, Perturbación, Incendio, Dispersión de semillas, Lluvia de semillas, Sucesión

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Introduction

Vegetation recovery after natural or human–caused disturbances such as wildfires, hurricanes, floods, grazing or logging depends on disturbance characteristics and on the regeneration capability of plants (Runkle, 1985). Regeneration is possible by several strategies, such as on–site regeneration, *e.g.,* by resprouting from undamaged tissues or germinating from a seed bank, and colonization, by seeds newly dispersed from other areas (Turner et al., 1998; Keeley & Fotheringham, 2000; Norden et al., 2009). To interpret vegetation succession and dynamics in disturbed areas, it is therefore crucial to fully understand the way different plant species can regenerate after an adverse event and the mechanisms and factors that interact with such regeneration at different scales (from disturbance severity, frequency and spatial heterogenity to specific seed facilitation, tolerance and inhibition) (Pickett et al., 1987; Reed et al., 2000; Chazdon, 2003; Balke et al., 2014).

Montane forest ecosystems in western Mexico are characterized by a complex landscape mosaic, resulting from environmental gradients related to climate, soil and geomorphological conditions, historical disturbance regimes, and a long history of human use (Jardel et al., 2004a). During the 20th century, most forested areas in Mexico were affected by the impact of logging, cattle grazing and disruption of the natural frequent–fire fire regimes (Heyerdahl & Alvarado, 2003), factors that contributed to shaping the current landscape of the region. After severe disturbances such as stand–replacement fires and clearcutting, the new forest gaps are mainly colonized by pines, which are later replaced by shade–tolerant cloud–forest species in advanced successional stages (González–Espinoza et al., 1991; Jardel, 1991). In absence of disturbances such as surface fires, these pine–dominated forests can turn into pine–oak forests in dry hilltops or into cloud forests in concave landforms and humid slopes (Jardel et al., 2004b). This process is specially interesting because cloud forests are a conservation priority in Mexico (Challenger, 1998) as they share plant species of both Holarctic and Neotropical biogeographic origins and host high levels of biodiversity (Miranda & Sharp, 1950; Rzedowski, 2006). Fire recurrence is expected to decrease in the short–tem in certain parts of western Mexico due to the human depopulation in recent decades (Jardel et al., 2004b). Therefore, if fire is currently the most important factor limiting the expansion of cloud forest in such areas, in the near future cloud forests could expand significantly from their current range (restricted to hollows) to other suitable areas, such as mountain slopes.

Colonization of open habitats such as abandoned pastures and farmlands by cloud–forest species is mainly possible due to wind and vertebrate (endozoochory) seed dispersal, and to seed banks of propagules that could have arrived previously by these mechanisms (Del Castillo & Pérez–Ríos, 2008; Muñiz–Castro et al., 2006; Zuloaga–Aguilar et al., 2010). The importance of endozoochorous dispersal is suggested by the high number of plants that show this type of dispersal strategy in cloud forests in western Mexico (up to 87 species; Orozco, 1999), and the high number of birds, bats and terrestrial mammals that feed on fleshy fruits in this habitat (Hernández–Conrique et al., 1997; Santana, 2000). Apart from diet specialization, seed shadow, *i.e.*, the spatial distribution of dispersed seeds, depends on several factors that influence the spatial signature of the dispersal vector in the landscape (Howe & Smallwood, 1982; Schupp et al., 2002). The abundance of these birds and mammals, their feeding behaviour, roosting habits, habitat preferences, mobility and speed of their digestion process will affect the seed shadow, the quantity of seeds dispersed, and the quality of the area where seeds are dispersed. All these factors have crucial implications for plant populations (Clark et al., 2005; Jordano, 1986; Schupp et al., 2002). In this regard, different frugivores can disperse seeds at different distances from the seed source (Jordano et al., 2006), and distance from this source is an important constraint in the regeneration of tropical forests in disturbed areas (Chazdon, 2003; Souza, 2014).

In this study we aimed to assess the influence of distance on the endozoochorous seed rain and shadow —mediated by flying vertebrates (birds and bats)— of plant species being dispersed from cloud forests into surface–burned pine forests in montane ecosystems of western Mexico. In particular, we analyzed whether: (1) frugivorous bats and birds can contribute to cloud–forest regeneration in a disturbed habitat; and (2) whether distance from undisturbed primary forest can affect the seed dispersal carried out by these frugivores and plant establishment.

Material and methods

Study area

The study was carried out in the 1,250–ha Las Joyas Research Station, located in the Sierra de Manantlán Biosphere Reserve, in the state of Jalisco, Mexico (19º 36' N, 104º 16' W). Las Joyas features a mean annual temperature of 15ºC and mean annual rainfall of 1,800 mm. The area has a rugged relief with an altitudinal gradient ranging from 1,500 to 2,242 m a.s.l. The vegetation in the area is basically composed by pine–hardwood and pine–oak forests, with stands of cloud forest in hollow areas, ravines and along streams, as well as patches of secondary vegetation (Jardel et al., 2004a).

We chose two study sites within the research station (at approximately 2,000 m a.s.l.), consisting of two pine–forest stands aged between 40 and 50 years old, both located within an area of 303 ha that burned in a surface wildfire in May 2003. These study sites were located adjacent to two streams. One stream acted as a barrier to the fire spread, and consequently separates the burned area from the undisturbed cloud forest. The other stream was completely surrounded by burned vegetation, except for a narrow strip of about 10–30 m wide at each flank, composed of unburned cloud forest vegetation (fig. 1). The abundance of fruits and dispersers could therefore be expected to be higher in the first area than in the second. The post–fire vegetation was

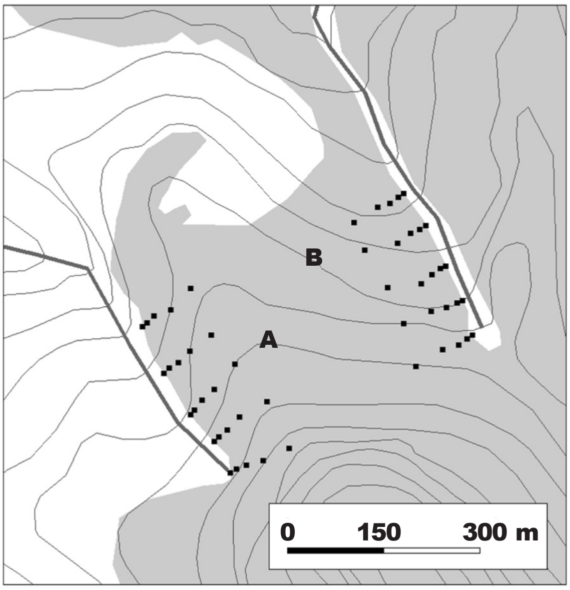

Fig. 1. Spatial distribution of the seed traps (dots) in the two study sites (A and B). Thin lines show elevation curves, bold grey lines represent water courses, and the grey area shows the surface–burned area.

Fig. 1. Distribución espacial de las trampas de semillas (puntos) en los dos sitios de estudio (A y B). Las líneas delgadas muestran las curvas de elevación, las líneas gruesas grises representan los cursos de agua y la superficie gris muestra el área afectada por un incendio de superficie.

composed of charred but live pines (which conserved the canopy intact), a minority of dead burned pines (< 5%), and regenerating shrubs in the understory.

In these study sites, several frugivorous birds and bats were observed (through 23 point counts, lasting for 10–min, surveyed in September and October) and/or trapped by mist–netting (thirteen 12–m long mist–nets were used for three days in October, from dawn to 8 h later). However, accurate monitoring to estimate their occurrence or relative abundance throughout the year was not possible. The detected frugivorous birds were *Penelope purpurascens, Trogon mexicanus, Piranga flava, Myadestes occidentalis, Turdus assimilis, Catharus occidentalis, Catharus guttatus, Piranga erythrocephala, Melanotis caerulescens* and *Icterus pustulatus.* In addition, Santana (2000) found up to 31 frugivore and 28 omnivore birds that could potentially be seed dispersers in the same area. Regarding bats, we were only able to detect (by mist–netting on two nights in October, from dusk to 5 h later) the presence of two species, *Sturnira ludovici* and *Dermanura tolteca.*

Seed rain and sapling establishment

We sampled seed rain of fleshy–fruited plant species that occur in the cloud forest (Cuevas–Guzmán et al., 2004) using seed traps. We set up five trap transects separated 50 m from each other in each study site, placing one seed trap at every selected distance (10, 25, 50, and 100 m) from the fire border (40 seed traps in total; fig. 1). Traps consisted of 1 × 1 m squares made with a permeable cloth that retained all solid material but not water. The cloth was tied to four poles at 1 m high above the forest ground. The traps were covered with a 1–cm wire mesh to keep rodents and granivorous birds out of the collected material and thus avoid seed predation. We gathered the material collected by the seed traps monthly, from September 2008 to August 2009. This material was later analyzed in the laboratory, where seeds were separated from any other debris. Seeds were identified to the most precise taxonomic level possible, using a reference collection and available literature on local and Mexican flora (Carranza, 1992; González–Villareal, 1996; Lozada, 2000; Ramírez, 1999). Only those seeds of cloud forest plants that undoubtedly came from undisturbed areas were considered for the analysis. Therefore, seeds of cloud–forest plants that occurred and bore fruits in the disturbed area were discarded, in order to avoid counting seeds of uncertain origin. On the other hand, saplings were sampled in the same study sites and distance categories used for seed traps. Sapling density was sampled in ten 1 x 2 m^2 randomly located along the four distance categories, in each site (*i.e.*, 80 squares). During seed rain and sapling surveys, we also looked for the presence of scats from medium–sized mammals between traps or quadrats, but none were found.

Data analysis

We used Generalized Linear Models (GLM) to test for a possible effect of distance in the dispersal of seeds

Table 1. Cloud–forest fleshy–fruited plants whose seeds were dispersed by birds or bats in surface–burned pine forests adjacent to cloud forest patches. The mean density of seeds (seeds/m^2) for each distance category (± SE) is shown. We also give information on the type of life form (LF) each species belongs to (H. Herb; S. Shrub; T. Tree; C. Climber), and the frequency of appearance of each species in the seed traps (number of traps with presence divided by total number of traps).

Tabla 1. Plantas de frutos carnosos de los bosques nubosos cuyas semillas se dispersaron mediante aves o murciélagos en pinares afectados por un incendio de superficie y adyacentes a fragmentos de bosques nubosos. Se muestra la densidad media de semillas (semillas/m^2) para cada categoría de distancia (± EE). También se proporciona información sobre el tipo de forma de vida (LF) al que pertenece cada especie (H. Hierba; S. Arbusto; T. Árbol; C. Liana), así como la frecuencia de aparición de cada especie en las trampas de semillas (el número de trampas con presencia dividido por el número total de trampas).

			Mean density (seeds/m^2)			
Species	LF	Frequency	10 m	25 m	50 m	100 m
Solanum spp.	H, S, T	0.34	2.3 ± 1.3	0.9 ± 0.9	0.0 ± 0.0	0.3 ± 0.3
Phytolacca spp.	H, S	0.24	1.3 ± 0.5	0.1 ± 0.1	0.9 ± 0.4	0.1 ± 0.1
Cornus disciflora DC.	T	0.17	0.3 ± 0.2	0.4 ± 0.2	0.1 ± 0.1	0.9 ± 0.6
Rhamnus hintonii M. C. Johnst & L. A. Johnst	T	0.09	0.1 ± 0.1	0.0 ± 0.0	0.4 ± 0.4	0.4 ± 0.3
Magnolia iltisana A. Vázquez	T	0.04	0.2 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.1
Persea hintonii C. K. Allen	T	0.04	0.0 ± 0.0	0.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0
Vitis blancoi Munson	C	0.04	0.2 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0
Cornus excelsa Humb. Bonpl. & Kunth	T	0.03	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.0 ± 0.0
Ilex brandegeana Loes	T	0.01	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Myrsine jurgensenii Mez.	T	0.01	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Total			4.6 ± 1.4	1.8 ± 1.0	2.0 ± 0.6	1.8 ± 0.8

of fleshy–fruited cloud–forest plants. We tested the effect of distance (as fixed effect factor) on the total number of seeds and total number of saplings. In order to consider the differences between the two study sites, we also included site as a fixed effect factor, and we also tested the interaction between site and distance. Moreover, we analyzed the effect of distance and site on the number of seeds and saplings of those species present in at least 5% of the samples. We used Poisson or quasipoisson error distributions (depending on whether the model presented overdispersion or not) and log link. The significance of the effects was tested using likelihood ratio tests, with chi–square tests in the case of Poisson–distributed models and *F*–tests in the case of quasipoisson models. Statistical significance level was set at $P < 0.05$. These analyses were carried out using R 3.1.3 software.

Results

The traps collected 102 seeds belonging to 10 species of cloud–forest fleshy–fruited plants in seed traps (table 1), confirming the hypothesis that frugivorous birds and bats contribute to seed rain from cloud–forest patches into disturbed pine forests. Moreover, we found 163 saplings of 12 plant species of the same kind as those established in the surface–burned pine forest (table 2). Five species were found in both samplings (*Solanum* spp., *Cornus disciflora*, *Magnolia iltisana*, *Persea hintonii* and *Ilex brandegeana*). The most frequent plant species was *Solanum* spp. in both cases.

Distance from undisturbed cloud forest had no significant effect on the overall seed number, but there were more dispersed seeds in site A ($F_{1;\,38}$ = 5.11, P = 0.030; fig. 2). However, significantly more seeds of *Solanum* spp. were found at 10 m than at further distances from the undisturbed area ($F_{1;\,35}$ = 5.61, P = 0.024). No effects of site or distance were observed in *Phytolacca* sp. propagules. Finally, more seeds were found at site A for *Cornus disciflora* ($F_{1;\,38}$ = 5.25, P = 0.028) and *Rhamnus hintonii* ($\chi^2_{1;\,38}$ = 12.48, $P < 0.001$), but seed distribution was not affected by distance in these species. In the case of saplings, there were no differences in their total abundance between distances, but site A held a significantly higher sapling density than B ($F_{1;\,78}$ = 4.56, P = 0.036). The same result was found in *Solanum* sp saplings

Table 2. Cloud forest fleshy–fruited plants with established saplings in surface–burned pine forests adjacent to cloud forest patches. The mean density of saplings (saplings/10 m^2) for each distance category (± SE) is shown. We also give information on the type of life form (LF) each species belongs to (H. Herb; S. Shrub; T. Tree; C. Climber), and the frequency of appearance of each species in the seed traps.

Tabla 2. Plantas de frutos carnosos de los bosques nubosos con plántulas en pinares afectados por un incendio de superficie y adyacentes a fragmentos de bosques nubosos. Se muestra la densidad media de plántulas (plántulas/10 m^2) para cada categoría de distancia (± EE). También se proporciona información sobre el tipo de forma de vida (LF) al que pertenece cada especie (H. Hierba; S. Arbusto; T. Árbol; C. Liana), así como la frecuencia de aparición de cada especie en las trampas de semillas.

			Mean density (saplings/10 m^2)			
Species	LF	Frequency	10 m	25 m	50 m	100 m
Solanum sp.	H, S, T	0.48	4.3 ± 2.3	7.8 ± 2.3	4.5 ± 1.4	3.3 ± 1.6
Viburnum hartwegii Benth.	T	0.21	1.3 ± 0.7	3.3 ± 1.2	1.0 ± 0.5	3.3 ± 1.3
Persea hintonii C. K. Allen	T	0.13	0.5 ± 0.5	1.5 ± 0.6	3.0 ± 0.7	0.3 ± 0.3
Magnolia iltisana A. Vázquez	T	0.05	0.5 ± 0.3	0.3 ± 0.3	1.0 ± 0.6	0.3 ± 0.3
Cestrum sp.	S, T	0.03	1.0 ± 0.6	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0
Cornus disciflora DC.	T	0.02	0.3 ± 0.3	0.0 ± 0.0	0.3 ± 0.3	0.3 ± 0.3
Ilex brandegeana Loes	T	0.02	0.8 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
Symplococarpon purpusii (Brandegee) Kobuski	T	0.02	0.5 ± 0.5	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0
Miconia sp.	S	0.01	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Smilax sp.	C	0.01	0.3 ± 0.3	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Parahtesis villosa Lundell	S	0.01	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Prunus serotina Ehrh.	T	0.01	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Total			9.3 ± 3.0	13.8 ± 2.7	10.3 ± 1.8	7.5 ± 2.3

($F_{1;\,78}$ = 5.48, P = 0.019). The interaction of distance and site was significant in *Viburnum hartwegii*, whose saplings were more abundant at 100 m in site A but at 25 m in site B ($\chi^2_{3;\,38}$ = 9.09, P = 0.003). No effects of distance and site were observed in *Persea hintonii*, and finally, *Magnolia iltisana* showed significantly more saplings in site A ($\chi^2_{1;\,38}$ = 11.09, P = 0.001).

Discussion

Our results show that frugivorous vertebrates play an important role in the recovery of cloud forests in montane areas of WM affected by surface fires. These vertebrates disperse the seeds of a variety of fleshy–fruited broadleaf species from undisturbed cloud forest patches into burned areas located nearby these patches. This action could promote the regeneration of this threatened ecosystem and allow the colonization of new areas.

Comparing the list of plant species found in seed rain and sapling surveys, we observed that only five plant species were found in both. The absence as saplings of plant species whose seeds had been dispersed could be due to unsuitable conditions for germination (Schupp, 1993). For instance, pokeweeds (*Phytolacca* sp.) are early–successional plants that germinate abundantly from seed banks (Hyatt & Casper, 2000) but are displaced by more shade–tolerant species under shade conditions (Elliott et al., 1998). Moreover, the plant functional group can also determine establishment success: climbers may find it difficult to establish themselves because of the lack of an adequate substrate (*Vitis blancoi* was only present as seed, and *Smilax* spp. presence was incidental). On the contrary, the absence of seeds of species found as saplings could be caused by interannual variation in the fruit production of some plants (Herrera, 1998); these saplings may have grown from seeds dispersed in previous years or dispersed before the fire and occurring in the seed bank.

Overall seed dispersal in the burned habitat did not depend on the distance from the edge of undisturbed forests. This finding may contrast with findings from other studies that found little seed dispersal out of natural forest and into altered habitats, such as early–successional forests or cultivated lands (Ingle, 2003; Estrada–Villegas et al., 2007; Del Castillo &

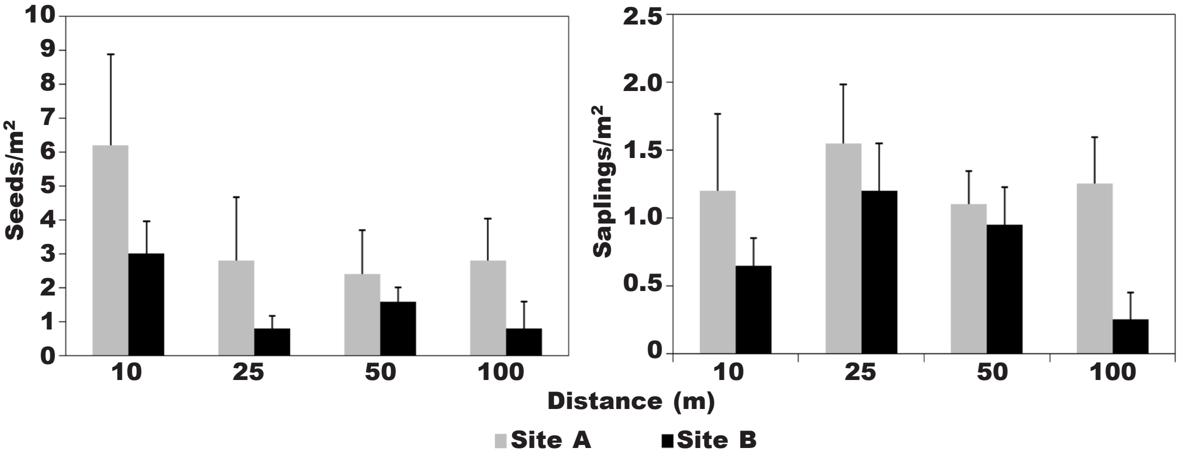

Fig. 2. Differences in seed rain and sapling density between distances from the nearest cloud forest patch and between study sites.

Fig. 2. Diferencias de lluvia de semillas y densidad de plántulas en función de la distancia del área de bosque nuboso más cercana y entre los sitios del estudio.

Pérez–Ríos, 2008). However, in our study sites, the surface fire did not change the availability of tall perches (most pines survived fire) needed by many arboreal dispersers, such as birds (Shiels & Walker, 2003). This habitat feature could thus enhance colonization of cloud forest plant species into such areas. Besides, medium–sized and large birds can disperse seeds to great distances, up to hundreds of meters from the mother plant (Jordano et al., 2006; Weir & Corlett, 2007). That could be the case of birds that would disperse large seeds like those of *Cornus disciflora* and *Rhamnus hintonii* (whose dispersal was not distance–dependent) since larger frugivores, with a higher gape width, can disperse fruits with larger seeds (Wheelwhright, 1983; Jordano, 1986). Medium–sized mammals could have also contributed to this long–distance seed transport (Willson, 1993), although we did not find scats from mammals in the study sites, probably because the high cover of low vegetation (up to 50 m) made them difficult to find. In turn, this does not seem to apply to bats, which are usually not abundant beyond natural forest edges, even when perches are available (Shields & Walker, 2003). Moreover, small bats like those we found in the study area usually have short seed retention times, and this may prevent them from dispersing seeds over long distances (Shilton et al., 1999). These causes could also explain why we found more seeds of *Solanum* near the forest edge, since their fruits are one of the few consumed by frugivorous bats in the montane forests of western Mexico (Hernández–Conrique et al., 1997; Íñiguez–Dávalos, 2005). However, *Solanum* saplings were distributed irrespectively to distance from undisturbed forest, which seems to contradict this explanation. Yet Zuloaga–Aguilar et al. (2010) found that *Solanum aphyodendron* —which would probably be one of the *Solanum* species found as seed or sapling in our study although identity of this genus could not be confirmed with certainty to species level— can tolerate high temperatures (*e.g.*, a fire episode), and that heat shocks induce its germination. Therefore, in the case of *Solanum*, an already existing seed bank before the fire could be a feasible explanation.

Our study also revealed that the habitat configuration at a higher scale has a significant role in the numbers of dispersed seeds and sapling density found in the surface–burned area. The study site that was close to the fire perimeter (A), and therefore to a large patch of cloud forest, showed a higher seed rain and higher sapling densities than the site whose closer seed source was a narrow strip surrounded by the burned area. This site (B) probably showed a much lower amount of fruits and dispersers than the other site. The specific case of *Viburnum hartwegii*, which showed higher sapling densities at different distances in the two areas, could be explained by the particularly high concentration of seed dispersal in such locations, due to the activity of some dispersal vector. This effect of site on seed rain and shadow means that cloud forest regeneration can be also influenced by the sizes and fragmentation of natural habitat patches after disturbances (Del Castillo & Pérez–Ríos, 2008).

Fire has been a historical component of the dynamics of Mexican montane forest ecosystems (Jardel et al., 2004b), but there is now a growing concern about the disruption of the fire regimes due to land–use change, fire suppression and the effects of global climate change (Rodríguez–Trejo, 2008; Flannigan et al., 2009; Liu et al., 2010). In such a scenario, the conservation of cloud forests surrounded by a matrix of fire–prone pine–oak forests emerges as a priority in western Mexico mountains. As we have shown, regeneration of this threatened forest can be enhanced by the activity of frugivorous birds and bats; this can be either after fire, when they can disperse seeds to long distances from undisturbed seed sources, or before fire, by creating seed banks. Other endozoochorous dispersers (*e.g.,* terrestrial mammals) may also play a role but were not investigated in this study. However, since regeneration can be hampered in disturbed areas that are less connected to large cloud forest patches, we encourage managers to actively preserve these patches from activities that could degrade, fragment or isolate them (*e.g.*, farming and cattle grazing) so as to favour cloud forest colonization of adjacent areas after disturbances such as surface fires.

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