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Pollen movement of the endemic *Agave cupreata* by bats and birds in western Mexico

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Short Communication

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Abstract

We quantified the amount of pollen carried by bats and birds visiting the flowers of cultivated and wild individuals of the endemic *Agave cupreata* in western Mexico and estimated the distance to which pollen was moved using diurnal/nocturnal inflorescence exclusions and fluorescent powders. There were no differences in the amount of pollen transported by bats and birds near cultivated and wild agaves, but overall, bats transported greater loads than birds. Nocturnal pollen movement was more frequent, and the maximum distance recorded was 630 m (diurnal and nocturnal), with no transfer between cultivated and wild plants. Bats seem to provide a greater pollination service than birds in our focal anthropized landscape. It is necessary to incorporate management practices into mezcal production that ensure enough food for the wide array of animal species using this resource, which in turn will help to maintain the pollination service.

Introduction

Most flowering plants depend on animal vectors for reproduction (IPBES, 2016). Even self-pollinated species benefit from animal visitation due to its favourable effect on genetic interchange (Potts *et al.* 2010). The amount of pollen transported and the distance to which it is deposited are critical factors affecting the reproductive success of plants due to their role in connecting plant populations, reducing endogamy, and, therefore, inbreeding depression (Allison, 1990, García Cruzatty *et al.* 2017, Young *et al.* 1996). Pollen movement becomes a particularly relevant process in anthropized landscapes where the sizes of plant populations decrease, and isolation increases due to habitat fragmentation (Breed *et al.* 2015). The degree to which pollen movement is affected in anthropized landscapes is most likely related to animal vector characteristics, such as body size, mobility, behaviour, and susceptibility to habitat perturbation (Breed *et al.* 2015, Laforge *et al.* 2021). However, limited information on the characteristics of pollen movement by animals greatly hinders broadening the understanding of anthropic habitat perturbation's impacts on plant pollination and population connectivity (Nora *et al.* 2011).

Mexico is a diversification centre of plants in the genus *Agave* (locally known as 'magueyes' or 'agaves'). Of a worldwide total of 210 species, as many as 159 (75%) occur in Mexico, and 126 (61%) are endemic (García-Mendoza *et al.* 2019). The plants in the genus *Agave* have special ecological, cultural, and economic relevance in Mexico (Colunga-García Marín *et al.* 2007, Eguiarte *et al.* 2021, Torres-García *et al.* 2019). Since prehispanic times, agaves have been used as raw material to produce distilled beverages; however, growing demand for tequila and mezcal has fuelled an increase in agave harvest, which is having several negative environmental and social impacts, such as depletion of wild populations, pollution by agrochemicals, loss of natural habitats, displacement of subsistence crops, and marginalisation of small-scale agave farmers (Martínez Castro *et al.* 2015, Tetreault *et al.* 2021).

Bats are the primary pollinators of agaves (Arizaga *et al.* 2000, Rocha *et al.* 2005, Trejo-Salazar *et al.* 2015). However, many bird species (e.g., orioles, hummingbirds, warblers, and woodpeckers) are also common visitors of these plants (Sutherland, 1987, Slauson, 2000, Ornelas *et al.* 2002). Bat and bird species can differ in their capacities to move pollen and in their response to the anthropogenic modification of the landscape (Muchhala and Thomson, 2010, Laforge *et al.* 2021, Paxton *et al.* 2023). In this study, we assess whether bats outperform birds in their capacity to move the pollen of endemic *Agave cupreata* (locally known as 'Maguey chino') in an anthropized landscape in western Mexico.

Materials and methods

We conducted this study in the locality of Las Azucenas within the municipality of Madero, Michoacan in western Mexico. The municipality of Madero has an average temperature range of 12°C to 26°C, an annual precipitation of between 800 and 1,300 mm, and an altitude of between

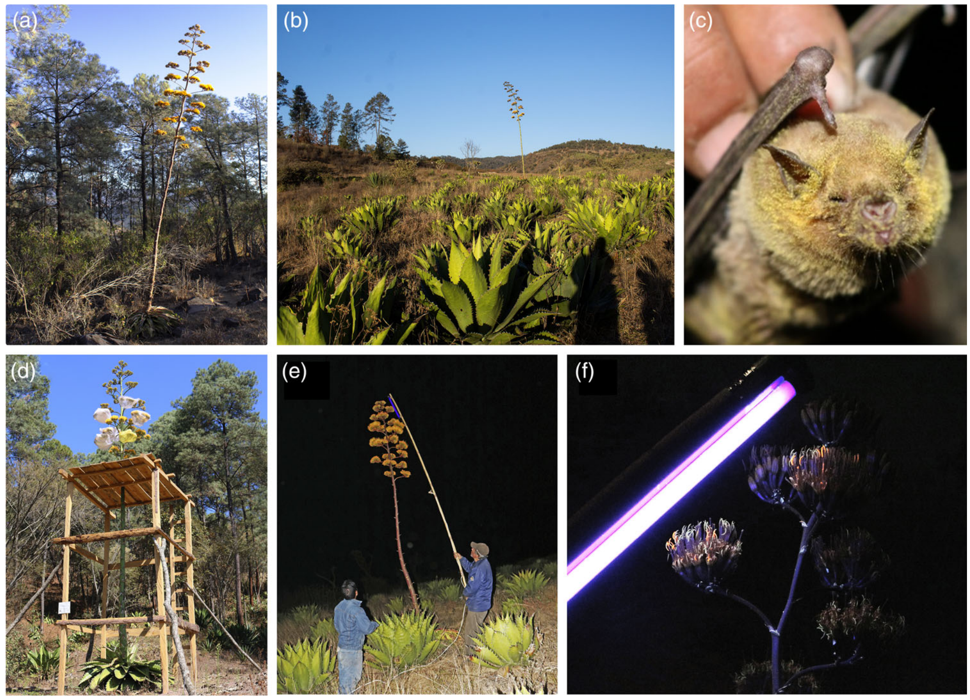

Figure 1. (a) Wild and (b) cultivated *Agave cupreata* plants in Madero, Michoacán, western Mexico; (c) *Leptonycteris nivalis* covered with pollen grains of *A. cupreata*; (d) Wooden platform built to reach the inflorescences of *A. cupreata*; (e) and (f) Nocturnal search for pollen grains of *A. cupreata* marked with fluorescent powder of different colours to differentiate between diurnal and nocturnal movements.

800 and 2,900 m (INEGI, 2009). *A. cupreata* is a species endemic to the Balsas River basin and the Sierra Madre Sur mountains in Guerrero and Michoacán (Martínez Castro *et al.* 2015). It is a semelparous plant with protandrous and multi-ovulate flowers (Illsey Granich *et al.* 2005). This species takes between eight and nine years, approximately, to reach the size to be used to produce mezcal and, in contrast to other agave species, its capacity for vegetative reproduction is null (Illsey Granich *et al.* 2005, Gallardo Valdez *et al.* 2008). This characteristic makes the reproduction of this species highly dependent on animal visitation. The *A. cupreata* has been used in the region to produce mezcal for about 400 years, and it is currently a source of income for an increasing number of families (Martínez Castro *et al.* 2015). In our study area, wild and cultivated agaves coexist. Cultivated agaves are grown in greenhouses for about the first two years. Then, at the onset of the rainy season, they are transplanted to hill slopes, which have been cleared of their natural vegetation, where they reach maturity. Therefore, cultivated agaves are grown in areas with more open vegetation whereas wild agaves are more associated with forested areas (Fig. 1a and 1b). Cultivated agaves tend to be taller than wild agaves (the averages from a sample of eight cultivated agaves and eight wild agaves were 6.67 vs. 5.27 m). This is likely due to greater exposure to sunlight. No other morphology differences are evident between cultivated and wild agaves.

In the February–April 2017 period, we independently evaluated two aspects of the capacity of birds and bats to transport *A. cupreata* pollen: (a) the amount of pollen carried on the animal's body and (b) the distance to which pollen was moved. To quantify the amount of pollen carried by birds and bats visiting *A. cupreata,* we conducted diurnal and nocturnal surveys near cultivated and wild agaves for 22 days (11 days each) using six mist nests (12 m × 2.5 m and 6 m × 2.5 m). These nets were set at an approximate height of three metres and were active from 19:00 to 2:00 to capture bats and from 7:00 to 12:00 and 16:00 to 19:00 to capture birds. The captured bird and bat species were identified using field guides (Howell and Webb, 1995; Medellín *et al.* 1997). Regarding birds, we focused on collecting pollen samples from individuals in the Trochilinae family (hereafter hummingbirds) and the *Icterus* genus (hereafter orioles). For bats, we only collected pollen samples from *Leptonycteris nivalis* and *Choeronycteris mexicana* (Fig. 1c). We focused on these species because a previous study indicated them as the vertebrates that visited the flowers of *A. cupreata* most frequently in our study area (Arreola-Gómez, 2018). To collect samples, we rubbed small cubes of Kisser glycerol gelatine on the plumage or fur of the captured birds and bats' cephalic, dorsal, and ventral areas (Caballero-Martínez *et al.* 2009). These Kisser gelatine cubes were deposited in labelled glass jars. After taking the samples, the animals were safely released, following the corresponding protocols to avoid harming the birds and bats as we handled them (Ralph *et al.* 1996, Suárez-Alvarez and López-Berrizbeitia, 2020).

Once in the lab, we used a syringe to take a 0.05 mL sample from a random spot in the gelatine cube, which was later melted and placed on slides to be observed under the microscope (Model: Trino III). To count all the pollen grains, we selected a point at one end of each slide and visually moved across it horizontally. As a reference for the identification of *A. cupreata* pollen, we used preparations made with pollen grains of this species collected directly from their flowers. We applied an Analysis of Variance and a post hoc Tukey test to assess whether there was a contrast in the amount of moved pollen (Log10 transformed) between the type of agave (cultivated vs. wild) and among animal groups (i.e., hummingbirds, orioles, *L. nivalis,* and *C. mexicana*). We tested for the model's residual normality; analyses were conducted using the R programme (R Core Team, 2021).

A few days after the bird and bat capture, we conducted a separate experiment to estimate the distance that the pollen was moved in which we selected two *A. cupreata* plants (one cultivated and the other wild) with 1,364 m between them. We marked the pollen in these plants with fluorescent powders, which have been widely used to study pollination by animals, mainly insects (Eisikowitch and Galil, 1971, Terry *et al.* 2005). However, its use to

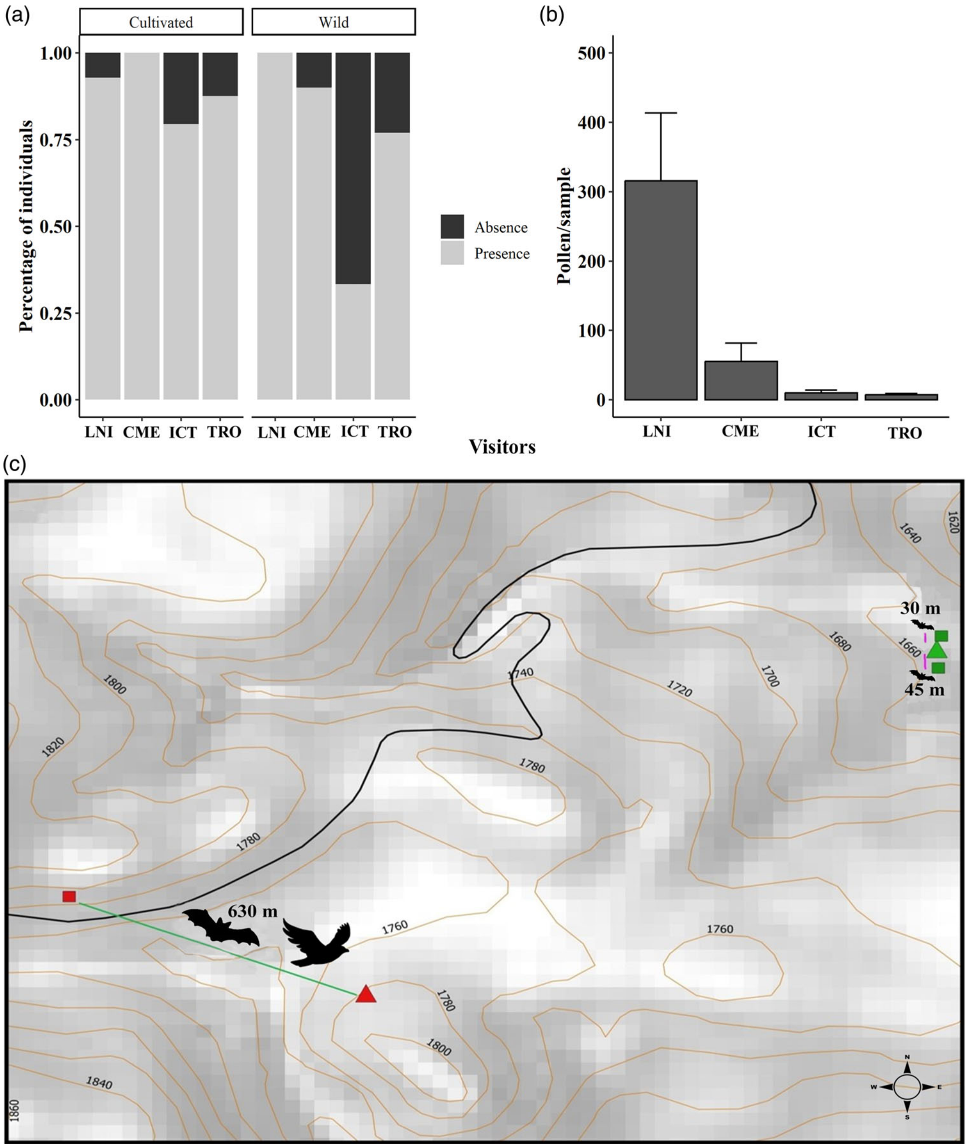

Figure 2. (a) Percentage of captured birds and bats with pollen grains from the endemic *Agave cupreata* in Madero, Michoacan, western Mexico; (b) Differences in the average amount of pollen of *A. cupreata* recorded in samples taken from the body of birds and bats. Species key: CME = *Choeronycteris mexicana,* ICT = *Icterus* spp., LNI = *Leptonycteris nivalis*, TRO = Trochilidae; (c) Map showing pollen movement by birds and bats in Madero, Michoacan, western Mexico. Squares indicate pollen sources and triangles, agaves in which pollen was deposited.

study pollination by bats and birds is more limited. To distinguish between pollen transported by birds or bats, at dusk, we marked the anthers of two umbels of the cultivated agave with green powder and the anthers of two umbels of the wild agave with pink powder. These umbels remained exposed throughout the entire night. At dawn, we covered these umbels with organza bags and then marked two other umbels of the same agaves with orange powder (cultivated agave) and two umbels with blue powder (wild agave). These umbels remained exposed during the day and were covered with organza bags at dusk. We built wooden platforms to allow a person to safely stand on to reach the umbels of the focal agaves. These platforms were finished well in advance of the start of the experiment to minimise any disturbance to plant visitors (Fig. 1d). We repeated both procedures for two consecutive days. After marking the umbels, we searched for fluorescent powder in the inflorescences of eight *A. cupreata* plants, which were distributed along a terrain strip spanning a length of two km. We conducted this search for two nights using an ultraviolet lamp (Model 7020 Hampton Bay) attached to the end of a metallic pole (Fig. 1e and 1f). Once we detected the presence of fluorescent powder, we recorded the coordinates of the agave. We calculated the distance of the movement using the software Qgis ver. 3.22 (QGIS Development Team, 2021).

Results

We completed a nocturnal sampling effort of 8,820 hours, which allowed us to capture 40 bats (17 *L. nivalis* and 23 *C. mexicana*). Moreover, we completed 10,080 hours of diurnal sampling, capturing 58 birds (21 hummingbirds and 37 orioles). Samples from most of the captured bats and birds, in both cultivated and wild agaves, had pollen (Fig. 2a). We did not detect statistical differences in the number of pollen grains from samples of cultivated agave versus wild agave ($F = 0.482$, $df = 1/89$, $P = 0.4892$, Table S1). However, we did find differences among the visitors ($F = 24.295$, $df = 3/89$, $P < 0.001$, Table S1). The Tukey test ($\alpha = 0.05$) indicated that all the animal groups carried different amounts of pollen except for orioles and hummingbirds. Samples from bats had, by far, the greatest amount of pollen, particularly those of *L. nivalis* (Fig. 2b).

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We recorded five events of pollen movement between agaves (Fig. 2c). Three of them were nocturnal, as indicated by the pink, fluorescent powder, and occurred within the forest. One involved the transference of pollen between two umbels of the same wild agave, which were separated by 0.5 m. The other two transferences occurred between wild agaves located at distances of 30 m and 45 m (Fig. 2c). Moreover, we recorded pollen transportation between cultivated agaves located at 630 m (Fig. 2c). This event of pollen transportation involved diurnal and nocturnal fauna, as indicated by the presence of green and orange powder. There was no documented movement between cultivated and wild agaves.

Discussion

We found evidence that bats are highly important pollen vectors for *A. cupreata* in our anthropized landscape. Based on the amount of pollen carried on their bodies and the frequency of pollen movement events between conspecific plants, bats seemed to outperform birds, particularly *L. nivalis*. There were also significant differences in the amount of pollen transported by *L. nivalis* and *C. mexicana*, which are likely related to their different foraging patterns. *L. nivalis* frequently touches the stamens and petals of *A. cupreata* flowers and, in some instances, even hangs on the umbels with its wings opened. In contrast, *C. mexicana* hovers while visiting different flowers in sequence, rarely touching them (Arreola-Gómez, pers. obs.).

Birds transported less pollen on their bodies than bats and seemingly moved it less frequently among agaves as well. However, most of the sampled birds had pollen on their bodies, suggesting they might play an important supporting role in securing a minimum level of pollination success in cases when plants are infrequently visited by bats. This effect can be reinforced by other vertebrates, such as the Grayish mouse opossum (*Tlacuatzin canescens*) and the Virginia opossum (*Didelphis virginiana*), which have also been recorded visiting the flowers of *A. cupreata* and displaying abundant pollen in their fur (Arreola-Gómez and Mendoza, 2020). The existence of a wide number of vertebrate (and likely invertebrate) species moving pollen among *A. cupreata* flowers might provide populations of this plant with a certain level of resilience to the effects of habitat degradation. Furthermore, the wide array of animal species visiting the flowers of *A. cupreata* is indicative of this plant species' great relevance as a local food source (Ornelas *et al.* 2002).

The distance between the wild and cultivated agaves was within the range of movement of the nectarivorous bats (Medellín *et al.* 2018); however, we did not detect pollen transference between them. However, it is necessary to conduct subsequent studies involving a greater sampling effort to establish whether the absence of pollen movement between wild and cultivated agaves is the rule or whether our study design did not capture this type of movement. Moreover, we assumed that diurnal and nocturnal pollen transfer was conducted by the birds and bats we had previously identified as the primary visitors to *A. cupreata* flowers. However, a great variety of animals (including insects) visit *A. cupreata* flowers. The use of selective exclosures would help to gain a more accurate view of the relative importance of different groups of species as pollen vectors for *A. cupreata*.

Our results highlight the need to implement strategies to favour the permanence of bats in the region. For example, it is important to identify sites that are of special importance for bats, such as those that provide them shelter (e.g., caves or hollows in tree trunks), to ensure their protection. Paradoxically, the increased demand for agave plants to produce mezcal can harm the bats (and other animals) that depend on the food resources provided by *A. cupreata* flowers. To increase the size of the agaves and their sugar content, which results in more raw material to produce mezcal, local producers prevent their reproduction because it inevitably leads to the plants' death (i.e., monocarpic reproduction). Moreover, because the only way to have new plants is through seed germination, theft of spikes with mature seeds has surged in our study region. This risk has also motivated people to reduce the number of flowering agaves. If these practices escalate, agave nectar can become a very limited resource for a variety of animal species, including bats, which in turn would have negative repercussions on the pollination service.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0266467424000087.

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Competing interests. The authors declare none.

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