



Effects of habitat fragmentation on pollen flow and genetic diversity of the endangered tropical tree *Swietenia humilis* (Meliaceae)

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ABSTRACT

Fragmentation of tropical forest represents a major threat to some tree populations by reducing local population size and gene flow from other populations. Both processes can decrease outcrossing rates and genetic variation in remnant stands. Despite these risks, some tree species have pollen vectors that mitigate these negative consequences for fragmented populations. In this paper, we assess both pollen flow and diversity of pollen sources in continuous forest and isolated stands of *Swietenia humilis*, a tropical tree species pollinated by small insects. Using seven nuclear microsatellite markers, we test the hypothesis that genetic diversity and the number of pollen donors are lower in remnant populations. Results show that allelic richness of seeds is lower in isolated populations (6.1 vs. 8.3 alleles per locus), even though adult populations do not show this difference.

Pollen pool structure is greater in isolated patches ($\Phi_{iso} = 0.26$) than in continuous forest ($\Phi_{for} = 0.14$), which yields estimates of the average effective number of pollen donors (N_{ep}) of 1.9 and 3.6 respectively. In addition, estimates of number of sires per mother indicate that isolated trees have half the number of pollen sources (4.98) than trees in the forest (9.8). Although extensive pollen movement (>2000 m) was recorded on both habitat conditions, indicating that fragmented patches are not isolated from pollen-mediated gene flow, this extensive pollen flow among trees in fragmented landscapes may not serve to counteract deleterious reproductive and genetic consequences of habitat fragmentation.

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1. Introduction

Tropical forests have experienced considerable habitat loss and fragmentation over the last century, representing serious threats for conservation of viable natural populations of trees (Saunders et al., 1991; Fahrig, 2003). Forest destruction and fragmentation directly reduces the size and increases the spatial isolation of populations, often with negative consequences on reproduction, gene flow and genetic diversity (Templeton et al., 1990; Ledig, 1992; Lowe et al., 2005; Aguilar et al., 2006, 2008). It is expected that reduction in population size restricts the number of local mating partners, increases the probability of inbreeding in self compatible species, limits pollen availability in outcrossing species or reduces the quantity and/or quality of sires involved in seed production (Charlesworth and Charlesworth, 1987; Ellstrand and Elam, 1993). Likewise, the spatial isolation of populations may restrict connectivity, leading to low levels of gene flow between fragments, with subsequently higher genetic structure and lower genetic

diversity in remnant populations (Young et al., 1996; Sork et al., 1999; Sork and Smouse, 2006).

It has been suggested that tree populations may be less vulnerable and more resilient to fragmentation impacts than other plants because of their longevity, high standing genetic diversity, and extensive pollen movement (Hamrick, 2004). For example, some studies of animal pollinated tropical tree species have reported widespread pollen flow in fragmented landscapes and among isolated remnant trees (Nason et al., 1998; Dick et al., 2003). These studies illustrate the possibility that this high level of pollen flow may counteract the negative impacts related to fragmentation (White et al., 2002). In contrast, other studies have shown negative effects of habitat disruption by a reduction in pollen flow among trees left in pastures (Lowe et al., 2003), reduction in the reproductive output, number of sires, and/or genetic diversity found in the progeny of isolated trees or fragmented patches (Cascante et al., 2002; Fuchs et al., 2003; Fernández-M and Sork, 2007). Moreover, a recent meta-analysis found that in most cases, trees in remnant fragments have altered mating patterns, increased inbreeding and decreased genetic diversity (Aguilar et al., 2008). In accordance with the available information, it appears that even when pollen

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movement among trees is extensive, and persists at fragmented landscapes, remnant forest patches may be at risk of loss of genetic diversity because of the reduction of local and immigrant pollen sources (Sork and Smouse, 2006). Hence, to better understand whether fragmentation has harmful genetic and reproductive impacts on plant populations, it is critical to assess not only the degree of pollen inflow or the distance that pollen has traveled but also the genetic diversity of the pollen pool (Sork and Smouse, 2006), and when possible, other measures of fitness (e.g. Nason and Hamrick, 1997). Ideally, these studies would compare patterns of genetic connectivity in continuous forest against those in patches of isolated trees that characterize contemporary fragmented landscapes.

In this study, we compare patterns of contemporary pollen flow in the endangered, insect-pollinated tropical tree *Swietenia humilis* in a continuous forest control area of 13,200 ha and in the surrounding remnant stands of highly deforested and fragmented mosaic landscape. Populations of *S. humilis* have been severely reduced and fragmented throughout its distributional range from Costa Rica to Mexico. Populations of this species are found in the highly conserved tropical dry forest of the Chamela-Cuixmala biosphere reserve in Mexico, surrounded by fragmented populations and isolated trees of *S. humilis* in the adjacent area. By comparing mating patterns and pollen movement between conserved populations and fragmented patches, our overall objective will be to assess whether fragmentation reduces pollen flow, number of pollen donors and genetic diversity in this species. Specifically we will test four hypotheses: (1) that progeny of trees in remnant patches have lower genetic diversity than those in continuous forest, (2) that pollen pools of isolated stands have greater genetic structure, (3) that progeny of isolated trees have less pollen sources and higher degree of genetic relatedness, and (4) that distance of gene flow is less for trees in isolated stands than those in continuous forest. Our assessment of pollen movement between fragments will provide insights into the role that remnant forest patches and isolated trees play in providing genetic connectivity, which may reflect their potential value for conservation of viable tree populations.

2. Methods

2.1. Study species

S. humilis (Meliaceae) is a deciduous tropical tree distributed on the Pacific Coast from Central-America to Mexico. *S. humilis* is a monoecious, self-incompatible species (Boshier, unpublished data, cited in White et al. (1999)) with unisexual flowers that are visited mainly by small bees (*Trigona* spp., Apidae), butterflies and other insects including feral honeybees (Pers. observation). The fruits are ovoid capsules containing seeds that are wind dispersed. Adult trees grow up 20 m tall and in the tropical dry forest natural populations occur mainly along riparian areas. The species is economically important and appreciated because of its hardwood. Populations of this tree have been reduced and fragmented over the majority of its distribution. *S. humilis* is listed on the Appendix II of the Convention on International Trade in Endangered Species (CITES since 1973), and along with the other two species of *Swietenia* has been the focus for studies and conservation concern (Newton et al., 1996).

2.2. Study site

Tree populations evaluated in this study are located within and surrounding the Chamela-Cuixmala biosphere reserve (ca. 19°30'N, 105°03'W), which encompasses 13,200 ha of land and is located on

the Pacific Coast in the state of Jalisco, Mexico. The site is characterized by a marked dry season from November to May, with 80% of the precipitation falling from July to October (707 mm year). The vegetation type is dense tropical deciduous forest, composed of two main habitats: dry forest and riparian vegetation found along large rivers and seasonal arroyos (Bullock, 1986; Lott et al., 1987; Lott, 1993). Tropical dry forests constitute one of the most endangered ecosystems in the world. Studies indicate that dry forests have been the preferred zones for agriculture and human settlement in the neotropics (Murphy and Lugo, 1986) and are among the most heavily utilized, perturbed, and least conserved of the large tropical ecosystems (Quesada and Stoner, 2004). A recent evaluation of land cover and fragmentation patterns in the study area (Sánchez-Azofeifa et al., 2009) indicates that land cover within the reserve includes: 92.1% of dry forest, 2% of riparian forest, and 3.7% of area transformed to agricultural fields or pastures. In contrast, the same categories of land cover were respectively 79.85%, 1.65% and 16.55% within an area of 10 km radius surrounding the reserve, where isolated stands of *Swietenia* trees were located in patches of average size ranging from 0.1 to 4 ha.

2.3. Field sampling

We located trees in two habitat conditions: (a) isolated stands in agricultural fields, pastures, or remaining patches of riparian vegetation, and (b) patches of trees along arroyos in the continuous forest. Isolated trees ($n = 29$) were sampled from four sites [EBCh (seven focal trees), JGP (three trees), SM (four trees) and PP (15 trees)] at distances of 1.7–11 km from the Chamela-Cuixmala Biosphere Reserve. Trees in continuous forest ($n = 86$) were localized along two arroyos separated by a mean distance of 7.21 km from one another [S (67 trees) and AC (19 trees)] surrounded by undisturbed mature forest within the Chamela-Cuixmala Biosphere Reserve. We recorded the coordinates of all trees using a GPS unit (Garmin 300) and constructed a map to illustrate the spatial distribution of sampled stands (Fig. 1).

On February of 2007, we sampled open pollinated fruits from 13 and 17 seed sources, for isolated and continuous forest respectively, attempting to collect at least five fruits per tree and five seeds per fruit. Also, we collected fresh leaf tissue from the 115 adult trees to extract DNA and obtain the genotypes of the maternal trees and the candidate male parents of progeny. DNA extraction (Doyle and Doyle, 1987) and genotyping of samples were performed using seven microsatellite loci previously reported in the literature (White and Powell, 1997; Lemes et al., 2002). Procedures and details are described in the Supporting Information.

2.4. Data analysis

2.4.1. Genetic diversity

To test the hypothesis that fragmentation has negative effects on genetic diversity, we compare the allelic richness of adult trees and progeny on isolated and forest populations. For adult trees, the average number of alleles per locus (A), observed heterozygosity (H_o), expected heterozygosity (H_e), fixation index (F) and the paternity exclusion probability (Excl1) were estimated across sites within habitat using Cervus 3.0. Allelic richness is a useful measure of genetic diversity for variable genetic markers, however this measure is highly dependent on sample size. Hence, because the uneven sample sizes in our field design, we evaluated the number of alleles in both the adult and progeny arrays by using rarefaction with the program HP-RARE 1.0 (Kalinowski, 2005). This statistical procedure accounts for variation in sample sizes, yielding unbiased estimates of allelic richness and private allelic richness for hierarchical designs. The sample sizes for rarefaction were set as the

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