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Reproductive Dominance of Pasture Trees in a Fragmented Tropical Forest Mosaic

Preston R. Aldrich*† and J. L. Hamrick

Tropical forest fragmentation threatens biodiversity, yet basic information on population responses for major groups such as plants is lacking. Hypervariable genetic markers were used to reconstruct a population-level pedigree in fragmented tropical forest for the tree *Symphonia globulifera*. Though seedlings occurred only in remnant forest, the pedigree showed that most seedlings had been produced by sequentially fewer adults in pasture, creating a genetic bottleneck. The pedigree also implicated shifts in the foraging of animals that disperse pollen and seed in a secondary constriction of the bottleneck. These results suggest that tropical conservation strategies should anticipate complex, cryptic responses to fragmentation.

Most tropical plants use animals to disperse their pollen and seed (*1*). Plants in highly specialized obligate associations are considered susceptible to forest fragmentation through loss of their dispersal agent, which could result in isolation and reproductive failure. However, obligate associations are less common than those involving a guild or group of several dispersers (*1*). Moreover, many fragmentation responses appear subtle and involve shifts in foraging behavior and guild composition that influence pollination and seed set (*2*). Genetic research also reveals that tropical tree pollen can travel far even in fragmented terrain (*3*), suggesting that spatially isolated trees might form vital links among populations (*4*). Here we demonstrate that spatially isolated trees in pasture can dominate reproduction in remnant forest.

The reproductive response to forest fragmentation was evaluated for *Symphonia globulifera* L., a late-successional, shade-tolerant canopy tree (*5*). In the Neotropics its red, bisexual flowers are pollinated primarily by hummingbirds (*6*), though perching birds also may play a role (*7*). Bats disperse the green, single-seeded fruits at our site (*8*). We conducted research (1993 to 1996) in recently fragmented (10 to 30 years) mid-elevation (1000 m) rain forest in southern Costa Rica (*8, 9*). We established a 38.5-ha circular plot encompassing remnant forest (three 1-ha patches and riparian corridors) and pasture with occasional primary forest trees. Our control plot (3.2 ha) was located in the adjacent continuous forest of the Las Cruces Reserve (235 ha), Organization for Tropical Studies.

All adults, saplings, and most seedlings of *S. globulifera* were mapped in these plots (*8*, *10*). Seedlings and saplings were absent from pasture, suggesting that the habitat was of poor quality for *S. globulifera* recruitment. The optimal environment (determined on the basis of seedling densities) appeared to be remnant forest, where the abundance of *S. globulifera* seedlings (152.3 ha^{-1}) was more than five times that of continuous forest (27.5 ha^{-1}). This was surprising because *S. globulifera* is a late-successional species (*5*) and not expected to thrive in habitat that is mostly forest edge.

We then determined origins of reproduction by evaluating genetic signatures of parentage in the seedling and sapling pools. Tissue samples were genotyped (*10*) with three microsatellite markers that we developed for *S. globulifera* (*8*). With slight modifications of established protocols (*11*), seedlings and saplings were assigned to pairs of parents in the study area on the basis of multilocus segregation probabilities, yielding a population-level pedigree (*12*). The loci had a total of 55 alleles, which is sufficient information to detect that any given pair of parents were not the true parents 99.6% of the time. By allocating half of each seedling or sapling to each parent of a compatible pair, we estimated adult fecundity (the number of progeny produced by an adult). These estimates retain information on the composite effects of pollen and seed dispersal as well as on survivorship to the time of sampling.

Pedigree reconstruction showed that fragmentation had not isolated individuals in remnant forest, nor was remnant forest necessarily optimal for recruitment (Fig. 1, A and B). Adults in pasture produced most (68.0%) of the *S. globulifera* seedlings in remnant forest. Remnant forest adults, in contrast, produced few (4.6%) of the seedlings residing in their own patch. This pattern of recruitment resembles a source-sink (*13*) in that seedling densities are sustained by overflow from an external source. It differs primarily by the low apparent survivorship in the source habitat (that is, pasture). Removal of the source, by reforestation or adult mortality, could yield demographic failure (remnant forest is a sink) or restore recruitment to continuous forest levels (remnant forest is a pseudo sink) (*13*). Judging from current matings, the removal of pasture adults would reduce *S. globulifera* seedling densities in remnant forest by nearly a factor of 7 (to 21.8 ha^{-1}), slightly below continuous forest levels.

Pedigree reconstruction also revealed changes in the mating system. Self-fertilization was consistently low in seedlings produced in continuous ($s = 0.098$; Fig. 1C) and remnant ($s = 0.114$; Fig. 1D) forest. Selfing

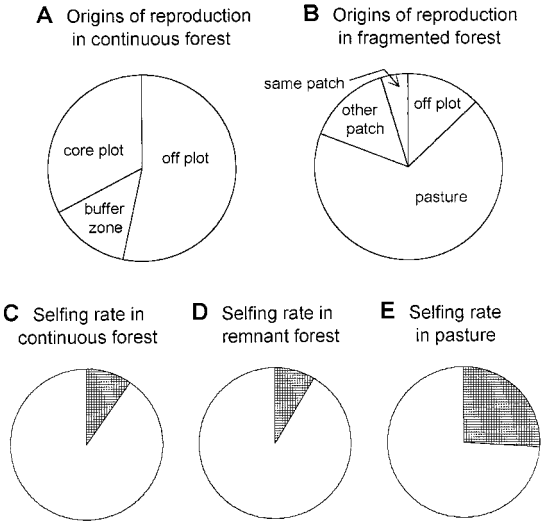

Fig. 1. Landscape-level sources of seedling production. Proportion of seedlings in (**A**) 1 ha of continuous forest and (**B**) 3.2 ha of remnant forest produced by adults in different habitats. Proportion of seedlings produced by self-fertilization of adults in (**C**) continuous forest, (**D**) remnant forest, and (**E**) pasture.

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rates were significantly greater (*14*) (*G* test; $P < 0.001$) in the remainder of remnant forest seedlings, wherein more than one in four ($s = 0.261$) derived from a mating pair involving one pasture adult acting as both pollen and ovule donor (Fig. 1E).

The pasture dominance and higher selfing rate reflects the emergence of a small but influential subset of adults in the population that have dominated seedling production after fragmentation. These "superadults" were relatively obscure donors to the sapling pool, presumably because pasture was not present at the time. After fragmentation, half of the 22 adults in pasture at that time experienced an increase in fecundity beyond levels characteristic of remnant forest (Fig. 2B). These 11 superadults produced 57.1% of the old seedlings, compared with 17.2% from the 21 adults in remnant forest. Dominance continued into the new seedling pool for only two superadults (Fig. 2C), which produced 52.5% of new seedlings. The other superadults may have incurred damage from wind and desiccation (*15*). Dominance of the largest individual [plant diameter at breast height (dbh), 49.5 cm] may antedate fragmentation because it consistently displayed high fecundity (Fig. 2, B and C).

To eliminate outlier bias, we tested the significance of a pasturewide effect by analyzing fecundity ranks. The rank fecundity of pasture adults was significantly greater than that of adults in remnant forest (all seedlings, Mann-Whitney *U* test, $P = 0.009$) (Fig. 2F). The rank of donors contributing to the sapling pool did not explain variation in their rank within the old seedling pool (coefficient of determination $R^2 = 0.026$, $P = 0.304$) because of the dominance shift coincident with fragmentation. In continuous forest, these associations were greater and marginally significant (Fig. 2E) ($R^2 = 0.164$, $P = 0.056$), consistent with seasonal variation in rank (*16*). The strongest correlations in fragmented forest were among the sapling and new seedling pools (Fig. 2H) ($R^2 = 0.399$, $P < 0.001$), presumably because nine superadults had reverted closer to their ranks before fragmentation.

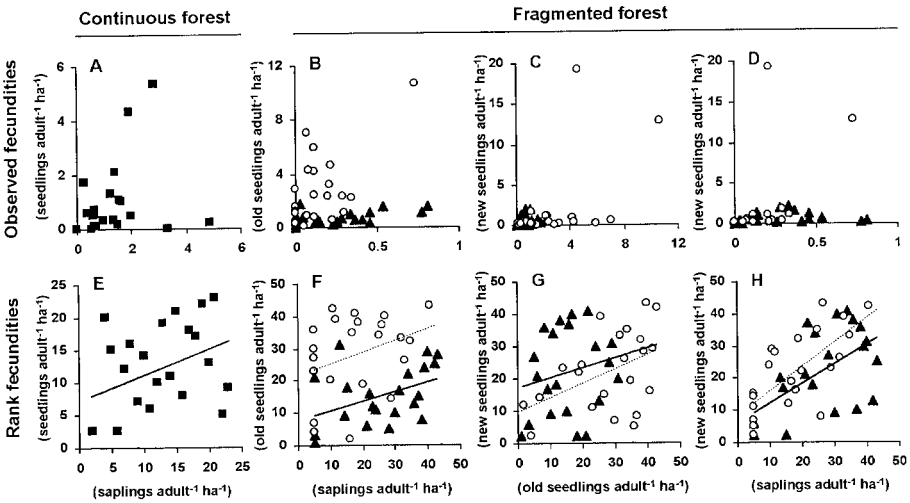

Fig. 2. Changes in reproductive dominance. (**A** to **D**) Observed fecundities were standardized by forest area and (**E** to **H**) ranked. Symbols: adults in pasture (open circles), remnant forest (closed triangles), continuous forest (closed squares), and regression lines for adults in forest (solid) and pasture (dashed).

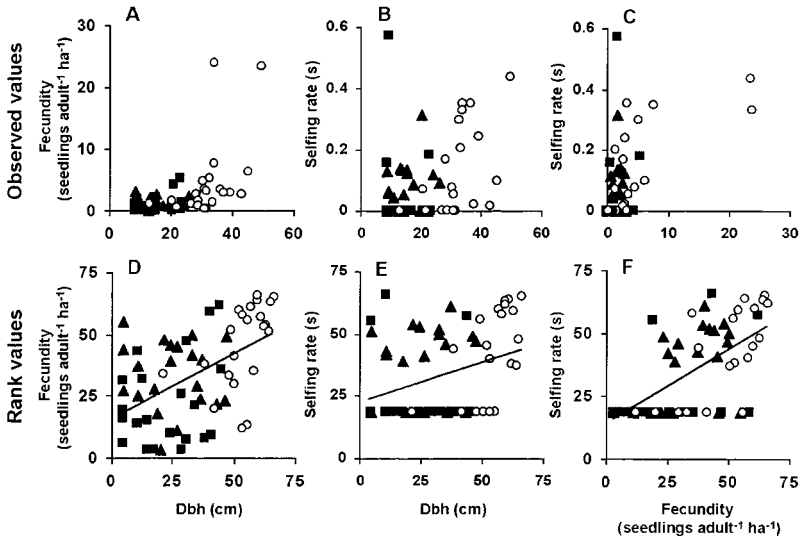

Fig. 3. Relation between dominance, size, and selfing rate. Fecundities and symbols follow Fig. 2. Selfing rate (*s*) is the proportion of seedlings attributed to an adult that resulted from self-fertilization. Regression lines are from data for all habitats.

These sequential reductions in donorship have created a genetic bottleneck (few genotypes producing most offspring). The variance effective population size (*17*) for fragmented forest ($N_{ev} = 17.3$) was only slightly greater than for continuous forest ($N_{ev} = 16.7$). Accounting for gene flow (*m*, the proportion of migrants) (*12*), fragmented forest experienced one-third the migrants per generation ($N_{ev}m = 2.8$ compared with 9.4, respectively). Therefore, this gene pool in 38.5 ha of fragmented forest has experienced more random genetic drift than a gene pool in 1 ha of continuous forest, despite substantial increases in seedling production. This was unexpected because random processes typically prevail in spatially and demographically constrained populations.

One potential constraint on reproduction involved a difference in plant size that likely represents a growth or sampling response to fragmentation. Pasture adults were significantly larger than adults in forest (Mann-Whitney *U* test, $P < 0.001$); in fact, size distributions were mostly nonoverlapping (Fig. 3). Generally, the larger individuals produced more offspring (Fig. 3D) ($R^2 = 0.264$, $P < 0.001$), a relation observed in many natural plant populations (*18*). Pasture adults may have grown faster as a physiological release from competition for light because the sides of a tree crown can be shaded in forest (*19*). It is also likely that small adults in pasture had lower survivorship and that 1-ha patches failed to capture the high end of the size distribution.

The effective foraging pattern of the pollinators tracked these habitat-specific differences in the plant population. Rank of the selfing rate was a positive correlate of rank in plant size (Fig. 3E) ($R^2 = 0.124$, $P = 0.004$) and rank in fecundity (Fig. 3F) ($R^2 = 0.415$, $P < 0.001$). High pasture floral or nectar density could have shifted foraging of the pollinator species or guild from forest-based traplining (moving among widely spaced plants) to pasture-based territoriality (remaining at a single plant) (*2*). The three most common matings involved selfing (12.3%), but also outcrossing (9.0%) among two superadults. This pattern is unlikely without

pollinator service and resembles a hummingbird territory. These results are consistent with mist-net data from the same site (*20*) that show higher capture rates for territorial hummingbirds in the fragmented forest.

Subsequently, not all pasture seeds passively dropped beneath parent trees and died; many were actively transported, often hundreds of meters, to remnant forest (3.2 ha) that contained as many seedling genotypes as expected for the entire plot (38.5 ha) (*8*). Bats rarely eat in the fruiting trees where they forage. Instead they carry fruits to roosts or feeding sites in dense foliage where seeds are dropped in clusters (*21*). We frequently observed putative roosts in remnant forest as thick foliage with distinct clusters of several *S. globulifera* seedlings below, often far from any potential parent. These patterns indicate that bats loaded remnant forest with pasture seeds, fueling the preexisting reproductive imbalance.

Our findings show that the composition and performance of tropical tree subpopulations can differ among fragmented habitats. These differences can skew donorship to the gene pool. Donorship patterns also indicate shifts in the effective foraging of dispersal agents. These shifts appear to track the redistribution of food (flowers and fruits) and shelter (remnant forest) in the landscape, which further constricts the bottleneck. Notably, this feedback loop can yield abnormally high seedling densities in suboptimal habitat. These results deserve further research because mechanisms favoring some species immediately after fragmentation could determine the pool of species available for long-term forest recovery. Failure to detect such dynamics, however, could lead to mismanagement of landscapes.

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$$\Psi_{ijk} = \frac{\prod_{l=1}^{L} P(\delta_{kl} \mid \alpha_{il}, \alpha_{jl})}{\sum_{i=1}^{a+1}\sum_{j=1}^{a+1}\prod_{l=1}^{L} P(\delta_{kl} \mid \alpha_{il}, \alpha_{jl})} \quad (1)$$

where i and j denote a possible parents and k progeny, with α_{il}, α_{jl}, and δ_{kl} the respective genotypes (L loci). This resolves ties by fractional assignment. Gene flow from off-plot was estimated by inclusion of an $a+1$'th possible parent, g, where α_{gl} is the allele frequency. Progeny of adults that die before sampling are attributed to the pool of adults off-plot, producing an inflated gene flow estimate (a conservative bias in fragmented forest).
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Interaction of Human Arp2/3 Complex and the *Listeria monocytogenes* ActA Protein in Actin Filament Nucleation

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Actin filament assembly at the cell surface of the pathogenic bacterium *Listeria monocytogenes* requires the bacterial ActA surface protein and the host cell Arp2/3 complex. Purified Arp2/3 complex accelerated the nucleation of actin polymerization in vitro, but pure ActA had no effect. However, when combined, the Arp2/3 complex and ActA synergistically stimulated the nucleation of actin filaments. This mechanism of activating the host Arp2/3 complex at the *L. monocytogenes* surface may be similar to the strategy used by cells to control Arp2/3 complex activity and hence the spatial and temporal distribution of actin polymerization.

The pathogenic bacterium *Listeria monocytogenes* initiates actin filament polymerization at its cell surface after it gains access to the cytosol of infected host cells (*1*). Actin polymerization is tightly coupled to intracellular bacterial motility (*2*) and may provide the motile force (*3*). Thus the *L. monocytogenes* cell surface is functionally similar to the leading edge of lamellipodia in locomoting cells, where actin polymerization is linked with membrane protrusion (*4*). Understanding the mechanism by which polymerization is instigated by *L. monocytogenes* should shed light both on an essential aspect of bacterial pathogenesis and on the general mechanisms by which actin filament assembly is modulated in cells.

Actin polymerization at the *L. monocytogenes* surface is mediated by bacterial and

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