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The breeding structure of a tropical keystone plant resource

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Despite the recognized importance of maintaining viable populations of keystone plant resources in tropical wildlife parks and forested preserves, the critical question of what constitutes effective breeding units of these species has not been directly addressed. Here we use paternity analysis techniques to reconstruct the genotypes of pollen donor trees and to estimate pollen dispersal distances and breeding population size parameters for Panamanian populations of seven species of monoecious strangler figs (*Ficus*, Moraceae), a particularly widespread and influential group of keystone producers^{1–3}. Despite the minute size (1–2 mm) and short lifespan (2–3 d) of the species-specific wasp pollinators (Agaonidae, Chalcidoidea), pollen dispersal was estimated to occur routinely over distances of 5.8–14.2 km between widely spaced host trees. As a result of such extensive pollen movement, breeding units of figs comprise hundreds of intermating individuals distributed over areas of 106–632 km², an order of magnitude larger than has been documented for any other plant species. Moreover, these results should be generalizable to the 350 or so monoecious fig species that share this pollination system⁴. The large areal extent of breeding units of these keystone plant resources has important implications for our understanding of both the evolution of tropical biodiversity and its maintenance by applied conservation efforts.

Like a keystone supporting an archway, keystone tropical plant resources fruit all year round and so support a broad spectrum of vertebrate frugivores during times of food scarcity. Figs are considered to be the pre-eminent group of keystone plant resources in

southeast Asia and in the Neotropics owing to their heavy fruit production and generally aseasonal patterns of reproduction^{1–3}. Given their disproportionately strong influence on species assemblages at many trophic levels, a failure to maintain viable fig populations in forest preserves is expected to result in a cascade of subsequent extinction events². Information guiding the establishment of reserve areas sufficient for the long-term preservation of fig populations is therefore of vital importance to the management of tropical biodiversity, particularly as large areas of continuous tropical forest become increasingly fragmented by human activity.

We have examined spatial patterns of effective fig wasp and pollen dispersal by using paternity analysis techniques to reconstruct precisely the isozyme genotypes of pollen donors fertilizing the fruit of individual fig trees. The research was conducted on populations of seven monoecious fig species (subgenus *Urostigma* sect. *Americana*) and their wasps (genus *Pegoscapus*) occurring in central Panamá. Adults of the fig species studied, *F. citrifolia*, *F. dugandii*, *F. nymphiifolia*, *F. obtusifolia*, *F. perforata*, *F. pertusa* and *F. popenoei*, occur at average population densities of less than ten individuals per square kilometre on Barro Colorado Island (BCI; C. Handley and E. Kalko, unpublished census data)^{5,6}, a large, 15-km² nature preserve located within the study area. Typical of monoecious figs, these species are obligately outcrossing and produce large fruit crops with reproduction synchronous within individual trees but asynchronous between trees^{6,7}, so that co-flowering individuals are often located substantial distances apart.

The power to reconstruct pollen donor genotypes was facilitated by high levels of assayable genetic variation and access to full-sibling

Table 1 Genetic diversity and probabilities of paternity exclusion

<i>Ficus</i> sp.	Genetic diversity*	Possible isozyme genotypes	Paternity exclusion probability	
			Single offspring	Full-sib progeny array†
<i>F. citrifolia</i>	0.258	15,360	0.769	0.997
<i>F. dugandii</i>	0.235	73,728	0.830	>0.999
<i>F. nymphiifolia</i>	0.169	15,360	0.720	0.995
<i>F. obtusifolia</i>	0.231	13,271,040	0.887	>0.999
<i>F. perforata</i>	0.227	331,776	0.912	>0.999
<i>F. pertusa</i>	0.258	31,104	0.869	>0.999
<i>F. popenoei</i>	0.223	20,736	0.821	>0.999

The precision with which pollen donor genotypes was reconstructed was facilitated by highly variable genetic marker loci and access to single foundress, singly sired fruit. Based on observed genetic diversity and allelic variation, thousands of multilocus allozyme genotypes are possible for each species. As a result, the probability of paternity exclusion, a measure of the power with which the genotype of the actual paternal parent can be distinguished from other putative fathers, is very high (>0.995). This probability is greatly enhanced in the fig species studied because full-sib progeny arrays, as opposed to single offspring, can be used to infer the father's multilocus genotype.

* Calculated as average expected heterozygosity over polymorphic and monomorphic loci.
† Calculated as one minus the probability of genotypic identity.

Table 2 Pollen donor diversity and breeding population size

<i>Ficus</i> species	Trees sampled	No. of fruit per tree	Pollen parents		Breeding unit size	
			d_{\min}	\hat{d}^*	$\hat{N}_{d_{\min}}$	$\hat{N}_{\hat{d}^*}$
<i>F. citrifolia</i>	2	35.0	13.0	20.5 (2.7)	182.5	287.8 (38.3)
<i>F. dugandii</i>	1	15.0	11.0	18.0 (3.7)	154.4	252.7 (51.9)
<i>F. nymphiifolia</i>	2	28.5	10.0	23.0 (5.5)	140.4	322.9 (77.0)
<i>F. obtusifolia</i>	7	26.2	17.3	54.3 (5.6)	242.7	762.1 (79.0)
<i>F. perforata</i>	2	20.5	6.0	11.0 (2.7)	84.2	154.2 (37.2)
<i>F. pertusa</i>	2	16.0	10.0	16.0 (2.5)	140.9	224.6 (34.3)
<i>F. popenoei</i>	3	14.0	10.7	28.0 (5.3)	147.7	393.1 (74.0)

The number of functionally male, staminate phase trees in the breeding population surrounding a given maternal tree is indicated by the total number of different pollen parent genotypes represented in its fruit crop (d) and was estimated in two ways, from the observed number of distinguishable paternal genotypes in a sample of singly sired fruit (d_{\min} , a lower bound), and, more accurately, from the frequency distribution of different paternal genotypes revealed in such a sample (\hat{d} , estimated according to ref. 22). Given the reproductive phenologies of the fig populations studied, the observed patterns of paternity indicate that, despite low population densities, breeding units centred about maternal fig trees consist of hundreds of intermating individuals.

* Standard error in parentheses.

progeny arrays obtained from singly sired fruits (Table 1). Levels of allozyme genetic diversity for the fig species studied (mean 0.229) are significantly higher than population level estimates for other very low-density tropical trees (mean 0.124; ref. 8) and for tropical and temperate woody species in general (mean 0.125 and 0.146, respectively⁸). Given this level of genetic diversity at 7–15 polymorphic loci, analysis of 12–18 full-sibling progeny per fig fruit (syconia) permits very precise reconstruction of the multilocus allozyme genotype of the pollen parent. In the fig species studied, dispersing female fig wasps become trapped in and do not leave the receptive, female-phase syconia post-oviposition and pollination. Thus, full-sibling progeny arrays can be identified before genetic analysis from syconia found to contain the remains of a single wasp foundress⁹.

Paternity analysis revealed that maternal trees of each species were fertilized by numerous, genetically distinguishable pollen donors and that the numbers of pollen donors detected would have continued to rise with additional sampling (Table 2). From information on flowering phenologies, the inferred patterns of paternity indicate that breeding units of the study species consist of 150 to more than 750 individuals (Table 2), a substantially larger number of trees than are known to occur on BCI. For the three species that have been censused extensively on BCI (*F. dugandii*, *F. obtusifolia* and *F. popenoei*), breeding units are estimated to occupy areas of 106–632 km², with fig wasps routinely dispersing pollen over distances of 5.8–14.2 km to receptive flowering trees (Table 3).

The breeding unit areas and intrapopulation pollen dispersal distances described here from monoecious figs are considerably larger than those described for any other animal- or wind-pollinated, tropical or temperate tree species (Table 3). Furthermore, because strangler figs of the section *Americana* are close to Old World *Urostigma* species evolutionarily and in terms of growth form and the highly stereotyped system of pollination by small, species-specific wasps¹⁰, these breeding structures should be generalizable to hundreds of fig species worldwide. Although the mechanism of dispersal over such long distances is poorly understood, one plausible hypothesis is that passive, wind-mediated transport may serve a primary role. Indeed, the direction and velocity of wind currents influence patterns of wasp arrival to and departure from

fruiting fig trees^{11,12} and may account for the occasional long-distance movement of fig wasps over distances of several to tens of kilometres^{13–15}. Although a variety of small insects (including Diptera, Homoptera and Hymenoptera) are known to be wind-dispersed, it has not been demonstrated before that such movement is a natural and routine part of a pollinator's dispersal biology for fig wasps or any other pollinator species.

The capacity for extensive dispersal by fig wasps and the diffuse breeding structure of fig populations has important consequences for the management of diversity in tropical landscapes fragmented by human activity. Because animals are the primary agents of pollen dispersal in tropical trees, the negative reproductive and genetic effects of habitat fragmentation will be most pronounced when vector dispersal is curtailed by fragmentation. Under these conditions fragments become isolated populations of small effective population size, increasingly subject to stochastic demographic and genetic processes, including inbreeding and loss of adaptive genetic variation. The breeding structure of fig populations, as with any plant species, will change when habitat fragmentation results in the loss of reproductive individuals¹⁶. But in contrast to most species, the fig and fig wasp mutualism can apparently form extensive metapopulations in fragmented landscapes, with subpopulations linked both reproductively and genetically by the exceptional dispersal capabilities of the wasp pollinators. Moreover, although frugivore diversity is known to decline as a result of habitat disturbance and disruption of population and community structures¹⁷, isolated fig trees occurring in small forest fragments can contribute to the survival of figs, and vertebrate assemblages, in large forest remnants and reserves. Indeed, on the basis of simulation study estimates of the fig population sizes needed to maintain an uninterrupted temporal sequence of oviposition sites for fig wasps^{18–20}, populations of most of the 12 strangler fig species on BCI consist of too few individuals to keep the species-specific pollinators from local extinction. If isolated from other conspecifics, these populations should exhibit pollinator-limited reproductive failure. Reproductive success is routine on BCI^{6,11}, however, and, as indicated by patterns of paternity (Tables 2 and 3), may be largely sustained by interactions with conspecifics located in surrounding forests.

Table 3 Breeding unit parameters estimated for tropical and temperate tree species

Species	Pollen vector	Density (ha ⁻¹)	Adults	Breeding unit parameters	
				Area (km ²)	Radius (km)
Monoecious figs*					
<i>Ficus dugandii</i>	Fig wasp	0.004	252.7 (51.9)†	631.7 (129.9)†	14.2 (10.9–16.9)‡
<i>Ficus obtusifolia</i>	Fig wasp	0.072	762.1 (79.0)†	105.9 (11.0)†	5.8 (5.2–6.4)‡
<i>Ficus popenoei</i>	Fig wasp	0.013	393.1 (74.0)†	294.8 (55.5)†	9.7 (7.7–11.4)‡
Tropical trees					
<i>Astrocaryum mexicanum</i> ²⁴	Beetle	1364	1542	0.011	0.060
<i>Calophyllum longifolium</i> ²⁵	Small insect	0.28	35	1.241	0.629
<i>Cordia alliodora</i> ²⁴	Small insect	20.9	520	0.249	0.282
<i>Pithecellobium elegans</i> ²⁷	Hawkmoth	0.88	45	0.636	0.450
<i>Platydictyon elegans</i> ²⁸	Small bees	0.78	68	0.866	0.525
<i>Spondias mombin</i> ²⁵	Small insect	0.33	6	0.196	0.250
<i>Turpinia occidentalis</i> ²⁵	Unknown	1.27	5	0.040	0.113
Temperate trees					
<i>Cedrus atlantica</i> ²⁹	Wind	61.7	934	0.151	0.220
<i>Fraxinus americana</i> ²⁹	Wind	24.7	20	0.008	0.050
<i>F. pennsylvanica</i> ²⁹	Wind	61.7	49	0.008	0.050
<i>Pinus cembroides</i> ²⁹	Wind	61.7	49	0.008	0.050
<i>Pinus radiata</i> ³⁰	Wind	2.5	40	0.159	0.225
<i>Populus deltoides</i> ²⁹	Wind	24.7	25,942	10.507	1.829
<i>Pseudotsuga menziesii</i> ³¹	Wind	25	196	0.078	0.158
<i>Pseudotsuga taxifolia</i> ²⁹	Wind	128.4	121	0.010	0.055
<i>Ulmus americana</i> ²⁹	Wind	24.7	31,389	12.714	2.012

The spatial dimensions and numbers of adults characterizing breeding units of three monoecious figs are compared to those of other animal-pollinated tropical and wind-pollinated temperate tree species. For the non-*Ficus* species, the breeding unit corresponds to Levin's²² paternity-pool concept and represents the circular area about a female plant within which 99% of potential mates are expected to occur. Estimates are averages over females and, because breeding units of herbs are much smaller²², are presented for tree species only.

* Breeding unit parameters estimated based on N_g (Table 2).

† Standard errors in parentheses.

‡ 95% confidence limits in parentheses (standard errors are asymmetrical).

In summary, breeding units of the monoecious fig species studied are distributed over a very large area, many times larger than BCI itself (Table 3). As a result, the ability of this reserve to maintain viable populations of these keystone plant resources and, by association, many other plant and animal species, is strongly linked to the management of surrounding forested areas. Moreover, patterns of mating indicate that populations of figs may remain reproductively viable under conditions of insular, and presumably terrestrial, habitat fragmentation, so long as the number of adult trees within the dispersal radius of female wasps does not fall below the minimum critical size needed to support populations of the pollinator. The breeding structure and pollen dispersal dynamics of other keystone plant species will require further investigation before their responses to habitat fragmentation can be accurately predicted. □

Methods

Breeding unit size. Donor number is related to the size of the breeding unit (*N* individuals) as $d = Np$, where *d* is the number of different pollen parent genotypes represented in a maternal tree's fruit crop and *p* is the expected proportion of trees in staminate phase at any given time. Assuming, conservatively, that individual trees reproduce asynchronously twice per year⁶ and that staminate and pistillate flowering phases each last seven days²⁰, *p* is calculated to be 0.0712. Although these estimates could be effected by mosaicism²¹ (the fusion of genetically distinct individuals), its frequency in the species examined here is low.

Breeding unit area and radii. These parameters were calculated from paternity-analysis-based estimates of breeding unit size (\hat{N}_B ; Table 2) and the censused densities of adult, reproductively mature trees over 15 km² BCI. Based on the long-term censuses of C. Handley and E. Kalko, 6, 108 and 20 adults of *F. dugandii*, *F. obtusifolia* and *F. popenoei*, respectively, are known to occur on BCI. Because these species exhibit little spatial aggregation over the area censused, these densities are assumed to be representative of forested areas surrounding BCI, a conservative assumption given that approximately one-third of the area within 10 km of BCI is occupied by Lake Gatun where figs are absent. Breeding unit radii estimate the distances pollen-bearing, female fig wasps routinely disperse in search of receptive host trees. Although actual breeding populations of figs may deviate substantially from the assumed circular distribution, alternative structures (elliptical, for example) increase estimated wasp dispersal distances.

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Female–female cooperation in polygynous oystercatchers

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Waders (Charadrii) provide biologists with an astonishing variety of mating systems to study¹. Male and female birds establish breeding units in which behaviour varies from monogamy, polygyny, polyandry, double clutching, lekking and serial monogamy to sex role reversal, and many mixed mating systems exist¹. This diversity is currently explained by the costs and benefits of males and females either cooperating or defecting during breeding attempts^{2,3}. The oystercatcher (*Haematopus ostralegus*) is a typically monogamous species: removal experiments show that both parents are needed to raise chicks to fledgings^{4–6}. However, occasional polygyny has also been reported⁷. Here we describe polygynous oystercatcher trios and the reproductive consequences of such polygyny. There is a 'classical' form of polygyny (two female territories within the male territory), but oystercatchers also show a remarkable variant, accompanied by female–female cooperation, female–female copulations and joint nesting.

Polygyny was extremely rare in the main study population. Only 1.85 ± 0.52% (mean of 14 years of study ± s.e.m.) of the breeding males and 2.70 ± 0.67% of the breeding females were polygynous. Polygyny usually developed as a result of 'failed' female usurpations⁸ ending in a draw; in other words, females postponed fighting (this occurred in 89% of cases; *n* = 19; usurpations were initiated by 11 non-breeders and 6 neighbouring breeders). More rarely, polygyny was due to a male breeder extending his territory to include the territory of a widowed female (5% of cases) or a male non-breeder joining two female widows which were polygynously mated to a male in the previous year (5% of cases). In 57% of the trios (*n* = 60 females), polygynous females remained highly aggressive towards each other within the male's territory, but defended their half of the