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FOREST FRAGMENTATION, POLLINATION, AND PLANT REPRODUCTION IN A CHACO DRY FOREST, ARGENTINA[1]

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Abstract. In a fragmented, dry subtropical forest in northwestern Argentina, we compared pollination levels, fruit set, and seed set among small (<1 ha) forest fragments, large (>2 ha) fragments, and continuous forest in 16 plant species representing a wide range of pollination systems, breeding systems, and growth forms. For three species, *Prosopis nigra* (Mimosoideae), *Cercidium australe* (Caesalpinoideae), and *Atamisquea emarginata* (Capparaceae), the three treatments were replicated across four sites; we achieved less replication for other species. Because comparisons between forest and fragment populations for different species took place in different sites, however, by treating all 16 species as a unit we lessened the potential bias of confounding site effects and could evaluate the overall impact of fragmentation.

Significant or marginal ($P < .10$) fragmentation-related declines in number of pollen tubes per style, fruit set, and seed set occurred in 9 of 16, 5 of 15, and 3 of 14 species, respectively. Overall, significant or nonsignificant declines occurred in 81% (pollen tubes), 73% (fruit set), and 79% (seed set) of the species. In all cases these proportions were greater ($P \leq .06$) than the null binomial expectation of a 1:1 ratio of increases to decreases. Breeding system did not explain sensitivity to fragmentation: the magnitudes of declines in pollen tubes, fruit set, and seed set were virtually indistinguishable between self-compatible and self-incompatible species. At least 4 of the 10 self-incompatible species, however, were heavily visited in small fragments by Africanized honey bees, which may have compensated for a decline in visits by native pollinators.

The exact nature of responses varied among plant species. In some, the absolute quantity of pollen grains transferred to stigmas decreased with fragmentation, and sometimes this was reflected in reduced fruit or seed set. In *Cercidium*, *Prosopis*, and *Atamisquea*, the quality of the grains transferred apparently changed: number of pollen tubes produced per pollen grain on the stigma declined with increasing fragmentation, and at least in the latter two species seed production declined as well.

Overall, levels of pollination and seed production undoubtedly integrated many idiosyncratic effects of fragmentation on particular plant and animal populations, and indicated that "community health" of fragments suffered in comparison with that of continuous forest. Median decreases in pollination levels and seed output from forest to fragments approached 20%. The impact of these declines on plant recruitment is less clear, however, because cattle grazing and trampling of seedlings and saplings in fragments may constitute a much more serious short-term conservation problem.

Key words: Argentina; Chaco Serrano; conservation; edge effects; forest fragmentation; habitat fragmentation; isolates; neotropical forests; plant breeding systems; plant reproduction; pollination; seed output.

INTRODUCTION

Animals impinge on the life cycle of vascular plants at many stages: pollination, seed production (predispersal, dispersal, and postdispersal stages), seedling growth, and maturation. How might anthropogenic habitat changes affect the nature of these plant–animal interactions? One of the most widespread changes is the fragmentation and degradation of formerly continuous vegetation (Saunders et al. 1991). Such drastic changes in landscape geometry are likely to affect plant–animal interactions at critical life history stages, consequently affecting plant demography and recruitment (e.g., Janzen 1974, 1983, Kevan 1975, Howe 1984, Dirzo and Miranda 1991). Thus, subtle impacts of habitat change on plant–animal interactions may be amplified into long-term effects on the integrity of reserves or other managed landscapes (Dirzo and Miranda 1991,

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Redford 1992). Disruption of mutualisms at pollination and seed dispersal stages has been advanced as one of the most threatening consequences of fragmentation to neotropical forests (Gilbert 1980, Bawa et al. 1985, Terborgh 1986, Feinsinger 1987, Bawa 1990), although few published studies address this possibility. We examined pollination and seed ouput of 16 plant species residing in fragments and continuous expanses of dry subtropical forest. Our objectives were to explore (1) whether pollination and seed output declined overall with increasing fragmentation, and (2) whether any obvious reproductive or life history traits could explain differential responses among plant species to fragmentation.

Habitat fragmentation introduces two fundamental changes. In contrast to original vegetation, fragments are discontinuous and much reduced in area. Furthermore, fragmentation introduces "edge" into a landscape: a patch of vegetation whose neighborhood once consisted of similar vegetation now experiences a different, usually more simplified, matrix as neighbor. The restricted size, discontinuity, and increased edge of fragments may impose many ecological and genetic effects on plants, both directly and indirectly (via animals).

First, plant reproductive output may be affected directly by microclimatic changes induced by fragmentation, such as increased exposure to wind, insolation, and desiccation (Lovejoy et al. 1986, Saunders et al. 1991). Plant reproductive output overall may also reflect changes in population genetic structure (cf. Levin 1984, Ledig 1986, Sobrevila 1988, Waser and Price 1989, 1991*a*, Menges 1991): as continuous spatial distributions become discontinuous, the upper limits to genetic neighborhood sizes (Wright 1943, Levin and Kerster 1974, Handel 1983, Loveless and Hamrick 1984) are set by the physical boundaries of each fragment. Second, plant reproductive ouput may reflect changes among animal interactors. Fragmentation can affect animal population densities and the amplitude of population fluctuations, activity patterns of individual animals, and foraging ranges (MacArthur and Wilson 1967, Levins 1970, Shaffer 1981, Gilpin and Soulé 1986, Pulliam 1988). Particular animal pollinators may disappear, decline or, in the case of species that thrive in the surrounding anthropogenic matrix, increase in abundance (Powell and Powell 1987, Sowig 1989, Aizen and Feinsinger 1994), thus potentially affecting pollination and seed output levels in plants (Thomson 1983, Jennersten 1988, Menges 1991). Fragmentation may also affect predispersal seed predators, herbivores, and flower parasites. Therefore, at the scale of the entire plant assemblage, the overall level of pollination and seed output represents a direct, quantifiable measure that integrates numerous interacting factors, both biological and physical, providing an index of community integrity or "health."

The degree to which fragmentation may affect pollination and reproductive success is expected to vary among plant species. Fragmentation-related effects are apt to differ among taxa of animal flower visitors (Lovejoy et al. 1986, Kwak 1987, Powell and Powell 1987, Sowig 1989) and, as a consequence, among plant species interacting with different pollinators. Also, plants vary widely in their degree of polyphily, or "interchangeability" of effective pollinators (Faegri and van der Pijl 1979, Feinsinger 1983), such that pollen transfer may be sensitive or insensitive to the population dynamics and behavior of a particular animal species. Plant species may be differentially sensitive to animal-mediated pollen transfer itself: plant breeding systems range from obligate outcrossing or dioecy to facultative selfing, in which quantitative reproductive output may be largely uncoupled from animal-mediated pollen transfer (Feinsinger et al. 1991). The extent to which seed output reflects pollination at all also varies: in many species, availability of maternal resources limits seed production, such that much pollination is extraneous (Stephenson 1981, Willson and Burley 1983, Snow 1986, Lee 1988). Finally, the proximate importance of pollination to plant demography varies with the growth form and life history. All else equal, recruitment and population dynamics of short-lived, semelparous plant species will reflect a single season's pollination much more closely than will dynamics of long-lived, iteroparous species (cf. Andersen 1989). Thus, differential sensitivity at the pollination stage to all possible correlates of habitat disruption could favor some plant species and disfavor others, erecting a "selective filter" on contributions to the seed bank and potentially affecting vegetation dynamics and composition (Streng et al. 1989) both inside the fragment and outside, in regenerating matrix.

The dry tropical and subtropical forests of South America are presently experiencing rapid habitat degradation, including widespread fragmentation (Bucher 1987, Adamoli et al. 1990, Lerdau et al. 1991). Although these forests have received much less attention than their Central American counterparts or wetter South American sites, they are species rich and of special conservation interest (Redford et al. 1990, Mares 1992). For this study, we selected dry "Chaco Serrano" forests in Argentina for three reasons: their fragmentary nature, their floristic diversity, and the accessibility of most plants due to the low canopy.

Materials and Methods

Study region

The study took place between July 1989 and December 1990 in the Chaco Serrano vegetation province (Cabrera 1976, Cabrera and Willink 1973), Tucumán Province, Argentina. We established study sites in the Tapia–Trancas watershed (26°50′ S, 65°20′ W), which is flanked by the Sierra de Medina (2400 m elevation) to the east and the Cumbres Calchaquies (4200 m) to

TABLE 1. Characteristics of the study sites. "Minimum distance" is shortest line from edge of fragment to nearest continuous forest. Sites are listed from south to north. The corresponding site numerals (1–5) denote the different sites throughout the text and in Appendix I.

Site	Small fragments		Large fragments		Year of deforestation	Matrix
	Area (ha)	Minimum distance (m)	Area (ha)	Minimum distance (m)		
1. India Muerta	0.8	80	3.8	160	1985	Cattle pasture
2. Comedor Sur	0.5	720	2.2	480	1960	Bean field
3. Comedor Norte	0.6	400	3.2	40	1982	Corn field + cattle
4. Mujer Loca	0.2	60	6.4	150	1978	Corn field + cattle
5. Vipos	0.7	50	20.5*	100	1968	Cattle pasture

* Area greatly exceeded area of other large fragments, but plant populations of the study species were restricted to an approximately 3-ha area in the northern part of the fragment.

the west. The orographic rain shadow limits annual rainfall to 400–500 mm (Vervoorst et al. 1981), falling almost entirely during the austral summer. Natural vegetation includes many species of small trees, spiny shrubs, and cacti as well as some herbs, xerophytic epiphytes, and vines (Meyer and Weyrauch 1966, Vervoorst et al. 1981). The region has experienced fire, grazing pressure, and other forms of habitat degradation for centuries (Bucher 1987, Adamoli et al. 1990, Lerdau et al. 1991). Only during the past 30 yr, however, have large areas of forest been cleared, along National Route 9. The result is a fragmented landscape of forest isolates and peninsulas amidst a matrix of cattle pastures and corn, sorghum, or legume fields, but on a larger scale the agricultural zone is still surrounded by nearly continuous Chaco Serrano forest.

Study sites

Along a 25 km N–S transect between Choromoro and Tapia, we selected five sites each containing three habitat units: a small (<1 ha) forest fragment, a large (>2 ha) fragment, and continuous forest (Table 1; see Fig. 1 in Aizen and Feinsinger 1994). Fragments were isolated from the nearest continuous forest by 50–750 m. Vegetation in each pair of fragments was comparable to that of nearby continuous forest.

Plant species

From among the many plants in the flora we selected 16 species that occurred in sufficiently high densities to provide adequate sample sizes (Table 2). Each species occurred minimally in one fragment and its comparable continuous forest (see "Study sites" in Appendix I). Because fragmentation has occurred recently (Table 1), except for annuals many of the individual plants now existing in fragments and sampled by us undoubtedly existed in the prefragmentation forest as well. Concentration on such long-lived, relatively common "survivors" of the fragmentation process lends a conservative bias to any conclusions reached here.

Phenology and floral biology of the 16 species are summarized in Appendix II. These attracted diverse flower visitors (Table 2); many were visited primarily by bees, but the list also included plants attracting primarily hawk moths, hummingbirds, or butterflies. In a related study (M. A. Aizen and P. Feinsinger, 1994 and *personal observations*), we found that the diverse visitor faunas associated with four species (*Prosopis, Cercidium, Atamisquea,* and *Acacia praecox*) were dominated by Africanized honey bees (*Apis mellifera*). To evaluate the possibility that honey bees, by compensating for a decline with fragmentation in the frequency of visits by native insects (Aizen and Feinsinger 1994), might ameliorate impacts of fragmentation on pollination levels and seed set, we subdivided the 16 plant species into three "pollination guilds" (Table 2): (1) two species attracting primarily hummingbirds; (2) the four species attracting numerous honey bees; and (3) 10 species primarily attracting native insects.

Breeding systems

To determine breeding systems of shrub, tree, and hemiparasitic plant species (Table 2), we enclosed flowering branches in pollination bags made of nylon mesh. As buds opened, we assigned individual flowers, inflorescences, or entire branches (depending on species) to one of three treatments: (1) no pollination; (2) hand-pollination with self pollen; or (3) hand-pollination with pollen from one to five other individuals. To determine breeding systems of other plant species, we transferred potted individuals of the two herbs, and branches bearing individuals of the two epiphytes, to a common garden and covered each with nylon mesh. In both epiphytes and herbs, we applied the three standard treatments listed above and (4) in a different subset of flowers, emasculated flowers and excised stigmas before anthesis. Treatment 4 was also applied to the hemiparasite *Ligaria* in the field. We recorded fruits set per flower (per inflorescence, in the Mimosoideae) from each treatment. Following Bawa (1974) and Bullock (1985), we classified as self-incompatible (SI) those species in which fruit set resulting from self-pollination was <25% of that resulting from cross-pollination.

To compare pollen tube growth in self- and cross-pollinated flowers of *Prosopis* and *Cercidium,* we collected virgin, receptive flowers from bagged branches

TABLE 2. Plant species, growth forms (H = herb, S = shrub, T = tree, E = epiphyte, Hp = hemiparasite), principal visitor categories observed, and results of controlled pollinations. Other sources on compatibility are cited when available. SI = self-incompatible, SC = self-compatible. A question mark indicates an "educated guess," i.e., the absence of conclusive evidence on breeding system. Hand-pollinations in three of the four *Acacia* species were unsuccessful.

Species	Growth form	Visitor type	Fruit set* (*n*)†				Compatibility
			(*n*)‡	Emasculated	Control	Self-pollinated	Cross-pollinated	
Acanthaceae								
Justicia squarrosa Griseb.	H	Butterflies	10	0 (20)	0 (30)	0.25 (40)	0.35 (34)	SC
Bromeliaceae								
Tillandsia ixioides Griseb.	E	Hummingbirds	16	0 (20)	0 (25)	0 (25)	0.85 (26)	SI
Cactaceae								
Opuntia quimilo R. Schum.	T	Medium-sized to large bees	3	···	0 (5)	0 (5)	0.50 (6)	SI ?
Rhipsalis lumbricoides Lem.	E	Butterflies, bees, wasps	6	0 (55)	0.05 (60)	0.10 (60)	0.78 (60)	SI
Capparaceae								
Atamisquea emarginata Miers	S	Bees‖, wasps, moths	3	···	0 (180)	0.02 (130)	0.47 (130)	SI
Leguminosae: Caesalpinoideae								
Caesalpinia gilliesi Wall. ex Hook.	S	Hawk moths	6	···	0.03 (226)	0.23 (47)	0.35 (40)	SC
Cassia aphylla Cav.	S	Large bees	3	···	0 (35)	0.45 (29)	0.28 (32)	SC§
Cercidium australe Johnst.	T	Bees‖, wasps	5	···	0 (500)	0.01 (166)	0.32 (177)	SI§
Leguminosae: Mimosoideae								
Acacia aroma Gill.	S, T	Medium-sized to large bees	3	···	···(94)	···(46)	···(45)	SI§
A. atramentaria Benth.	T	Bees, beetles	4	···	···(40)	···(24)	···(25)	SI ?
A. furcatispina Burkart	S	Butterflies, bees, wasps	4	···	···(264)	···(107)	···(152)	SI§
A. praecox Griseb.	S, T	Bees‖, wasps	6	···	0 (250)	0.05 (83)	0.21 (99)	SI
Mimosa detinens Benth.	S	Moths, wasps	5	···	0.05 (150)	0.45 (162)	0.81 (164)	SC
Prosopis nigra (Griseb.) Hieron.	T	Bees‖, flies, wasps	5	···	0 (24)	0 (19)	0.85 (19)	SI§
Loranthaceae								
Ligaria cuneifolia (R. et P.) Tieghem	Hp	Hummingbirds	6	0 (97)	0.10 (107)	0.26 (79)	0.34 (67)	SC
Portulacaceae								
Portulaca umbraticola H.B.K.	H	Small bees, butterflies	18	0.10 (10)	0.61 (23)	1.00 (26)	1.00 (32)	SC

* Number of fruits/flower (or per inflorescence in the Mimosoideae).
† Number of flowers (or inflorescences in the Mimosoideae).
‡ Number of plants.
§ Information on incompatibility also reported in Neff et al. (1977).
‖ Including a large proportion of visits by honey bees (*Apis mellifera*).

on five plants per species and pollinated these with either self pollen or a mixture of pollen from all five trees, for a total of 20 flowers per treatment in *Prosopis*, 12 in *Cercidium*.

Sampling procedure

For shrubs, trees, hemiparasites, and the epiphyte *Rhipsalis* we typically tagged 10 individuals per species per habitat unit (Appendix I). In small fragments these were often nearly the entire population. Most plants sampled in continuous forest were <50 m from the forest edge. Except as noted below, all data on pollen tubes, fruit set, and seed set came from the same sample of individuals. For the two herbaceous species, rather than tagging individuals we sampled flowers, infructescences, and fruits randomly from an area of ≈2500 m^2 within each habitat unit. For the epiphyte *Tillandsia ixioides*, from continuous forest at site 1 (cf. Table 1) we collected numerous ramets each bearing 1–2 immature inflorescences, and attached ramets having a total of 4 inflorescences to long wires, with at least 25 cm between ramets. In each habitat unit of sites 1, 2, and 5 we introduced five inflorescence quartets by affixing wires to branches 2–3 m high on trees separated by at least 10 m. Most inflorescences introduced into sites 2 and 5 were consumed by cattle or destroyed by ants, also after a second attempt, such that here we present data from site 1 only.

Most species were sampled during the 1989 flowering season (i.e., austral spring 1989–summer 1990). We sampled *Prosopis* and *Cercidium* twice, in the springs of both 1989 and 1990. The same individuals were sampled both years, except that in 1990 we expanded the *Prosopis* sample to include a fourth site

(site 1), and in continuous forest at site 2 the leaf and inflorescence buds of those trees studied in 1989 were killed by a late spring frost in 1990, so that we substituted new individuals that grew in nearby stands.

Pollen loads and pollen tubes

We collected flower styles or complete pistils at the end of flower life, fixed them in FAA, then stained and counted pollen tubes using the aniline blue technique (Martin 1959) and epifluorescence microscopy (see Feinsinger et al. 1991). In *Atamisquea,* which lacks a well-differentiated style, we counted tubes in the upper one-third of the ovary. In *Prosopis, Cercidium,* and *Atamisquea,* we also counted the number of pollen grains still adhering to undamaged stigmas (≈80% of all styles inspected).

Pollen tubes failed to stain consistently in the two herbaceous species, *Portulaca* and *Justicia.* Because both herbaceous species are self-compatible (cf. Table 2), numbers of pollen tubes should roughly reflect numbers of pollen grains, which we counted. Therefore, we used these counts as surrogates for counts of tubes when making among-species comparisons.

Sample sizes varied among species according to morphology and the typical number of flowers per plant. In the Mimosoideae, we sampled 50–60 pistils spread among 10 inflorescences per plant. We collected styles from ≈50 flowers per individual *Cercidium*; ≈20 per *Cassia, Rhipsalis,* and *Ligaria*; and 10 per *Caesalpinia* and *Opuntia.* In virtually style-less *Atamisquea,* we collected 50 pistils per shrub. For statistical purposes, because the sampling unit was the individual plant, each observation consisted of the mean number of pollen tubes or pollen grains among the 10–60 subsamples. For the two herbaceous species, we counted pollen grains on one flower from each of 100 plants per habitat unit. For *Tillandsia,* we collected styles from flowers of two inflorescences (5–10 flowers per inflorescence) in each experimental group and treated the average number of pollen tubes per experimental group as the individual observation. Overall, we examined ≈45 000 flowers.

When possible, we sampled a given plant species in all the habitat units of a given site during a single day at peak flowering and sampled from different sites on consecutive days. For *Caesalpinia, Opuntia, Rhipsalis,* and *Tillandsia,* asynchronous maturation of the few flowers per plant necessitated sampling on 2–4 different days over the flowering peak.

Fruit set

To determine fruit set per flower (per inflorescence in the Mimosoideae), we counted flower or inflorescence buds just before anthesis and later counted fruits just prior to seed dispersal. In each individual *Acacia* (all species) or *Prosopis,* we tagged five branches bearing a total of 250 inflorescence buds. For *Mimosa* and *Cassia,* we counted the total number of inflorescence or flower buds, respectively, on each individual. We tagged five branches each with 100 buds (total 500 flowers) per individual *Cercidium,* 5 × 50 per *Atamisquea,* and 4 × 25 per *Ligaria.* A total of 20 flower buds was tagged per *Rhipsalis* clone, and 10 per individual *Opuntia.* In *Caesalpinia,* where aborted flowers leave distinctive scars, we counted maturing fruits and scars (the total of which equalled the number of flowers originally produced) on 10 randomly chosen infructescences per shrub. In *Tillandsia,* we determined fruit set per flower per experimental group by counting flowers and fruits from all four inflorescences used, as no significant differences in numbers of set fruits were found between the two inflorescences from which we had removed styles and the two unmanipulated inflorescences. In *Justicia,* both viable fruits and aborted ovaries or calyces persisted after flowering. Here, we determined fruit set for each of 100 randomly collected inflorescences per habitat unit. We did not determine fruit set for *Portulaca,* which usually retains fruits even when they contain few or no seeds (M. A. Aizen and P. Feinsinger, *personal observation*).

In the Mimosoideae, although we report fruit set per inflorescence we also estimated fruit set per flower by multiplying fruit set per inflorescence by the mean number of flowers per inflorescence. Combining estimated numbers of flowers sampled in the Mimosoideae with known numbers sampled in the other species, fruit set frequencies were obtained from a total sample size of ≈3×10^6 flowers.

Seed set

We determined seed set in the six Mimosoideae and *Cercidium* by counting fully developed seeds from ≈50 randomly selected fruits per individual, from ≈25 fruits per shrub of *Cassia,* 20 per clone of *Rhipsalis,* 15 per *Caesalpinia* shrub, and 10 per *Opuntia.* For these species, the average number of seeds per fruit per individual was used in statistical analyses below. In *Justicia,* we counted seeds from ≈100 randomly collected fruits per habitat unit, and in *Portulaca* from 100 or 60 fruits per habitat unit of Sites 5 and 2, respectively. For both herbaceous species, we used each seed count as an independent observation. In *Tillandsia,* we counted seeds from two fruits per inflorescence, and treated the average over the eight fruits per experimental group as the individual observation. We did not measure seed set in *Ligaria* or *Atamisquea,* because the former possesses ovaries that mature into a one-seeded fruit, and in the latter only 1 of 15–20 ovules per ovary typically develops (M. A. Aizen, *personal observation*). Overall, we counted ≈1×10^6 seeds from a total of 35 000 fruits.

Data analysis

Plant–pollinator interactions are characterized by a high degree of spatial and temporal heterogeneity, regardless of changes in habitat characteristics (Feinsinger et al. 1986, Herrera 1988, Horvitz and Schemske

1990, Roubik 1992). In order to ascribe changes to a single factor such as habitat fragmentation, adequate replication of treatments is crucial (cf. Hurlbert 1984, Mead 1988). Here, due to vagaries of plant distribution we could replicate the comparisons for some species but not all (Appendix I). Results for any one species in a single site only must be interpreted with caution. On the other hand, power may be obtained by considering results across species in assemblage-wide comparisons.

To compare variables among habitat units, we used ANOVA, treating "site" as a second factor in those species sampled in more than one. Both factors were fixed. For those species (nearly all) that occurred in both small and large fragments as well as continuous forest, we further analyzed differences among categories of habitat with orthogonal comparisons: that between continuous forest and both sizes of fragments taken together, and that between large and small fragments. Because most data sets were unbalanced, we based significance tests on Type III sums of squares (Freund and Littel 1982). Where transformations were applied to increase normality and homoscedasticity, we report the back-transformed means (Mead 1988). In *Justicia,* seed set took four discrete values (1–4), and fruit set in *Opuntia* had a modal value of zero. No transformation could normalize these data. Nevertheless, we report results from ANOVAs, as these were qualitatively similar to results of nonparametric Kruskal–Wallis and Friedman tests.

Hand-pollinations of *Prosopis* and *Cercidium* were analyzed with a mixed-model ANOVA (Sokal and Rohlf 1981) with treatment (self or cross) and individual (tree) as fixed and random factors, respectively.

To compare pollination quality among habitat units in *Prosopis, Cercidium,* and *Atamisquea,* we applied nonlinear regressions of the form $y = K[1 - \exp(-bx)]$ where x is stigmatic pollen load, y is pollen tube number at the base of the style, and K and b are fitted constants, then analyzed residuals by means of a two-way ANOVA, with site and habitat unit as main factors (cf. Waser and Price 1991*a*). In *Rhipsalis* and *Acacia aroma,* where mean seed output per flower on a plant was strongly correlated with mean pollen tube counts, we applied a similar nonlinear ANCOVA to test for differences among habitat units after controlling for variations in pollination.

To assess the overall effect of fragmentation on this set of 16 species, for each reproductive variable in each species we calculated the percent change from continuous forest to fragments. This was defined as the difference between the average between the mean values for the large and small fragments, and the continuous forest mean, divided by the latter term and expressed as a percentage. A negative percent change represents a decrease in the value of the variable from the continuous forest to the average fragment. For a given reproductive variable, in the absence of an overall effect of fragmentation equal numbers of species should show negative and positive changes. In multispecies comparisons that involved *Prosopis* and *Cercidium,* we used data only from the 1989 season, the reproductive period when all other species were investigated.

Results

Breeding systems

Of the 12 species for which we obtained conclusive results from hand-pollinations, half were self-incompatible (SI) and half self-compatible (SC) (Table 2). The limited sample from *Opuntia* suggests self-incompatibility, as in many other *Opuntia* species (Bullock 1985, McMullen 1987, Osborn et al. 1988, McFarland et al. 1989). Except in *A. praecox,* hand-pollinations of *Acacia* inflorescences failed to set fruits. Neff et al. (1977) reported *A. aroma* and *A. furcatispina* to be SI, and we assumed the same for *A. atramentaria,* given the prevalence of SI in the genus (Kenrick and Knox 1989). Exclusion of the three *Acacia* and *Opuntia* from comparisons of SC and SI species below does not change qualitative results.

No species demonstrated high levels of autogamy. The autogamous fruits of *Portulaca* (Table 2) each contained <10 seeds whereas fruits from hand-pollinations, either self or cross, typically held >100 seeds. Thus, even in SC species pollination was primarily animal mediated.

Pollen tubes and pollen loads

The mean number of pollen tubes at the base of the style varied significantly among habitat units in 7 of 14 species (Table 3), with *Cassia* marginally significant ($P < .10$) as well. In both herbaceous species, *Justicia* and *Portulaca,* mean number of grains on the stigma varied significantly among habitat units (Table 3). As 10% of the species would show a significant or marginally significant fragmentation effect by chance alone, the existence of 10 out of 16 species showing such a significance level indicates that the possibility of committing an overall Type I error is extremely remote (binomial test, $P = 5 \times 10^{-7}$) and that a true difference exists among habitat units, at least for some species. In 9 of the 10 species showing a significant or marginally significant fragmentation effect, change was in the direction of a decrease from continuous forest to fragments (Table 3, Fig. 1), an unlikely outcome under the null hypothesis of a 1:1 ratio of increases to decreases (binomial test, $P = .01$). Likewise, when species having nonsignificant responses to fragmentation were included, 13 of 16 exhibited a decline in pollination levels from forest to fragments (Fig. 2a; binomial test, $P = .01$). The only species in which pollination levels increased significantly from continuous forest to fragments was the hummingbird-pollinated hemiparasite *Ligaria,* where plants in the small fragment of site 1 had almost three times as many pollen tubes per style

TABLE 3. Results of two- and one-way ANOVAs on number of pollen tubes (PT) or pollen grains (PG). Habitat unit means that share the same superscript letter do not differ significantly (GT2 Method, Sokal and Rohlf 1981). A significant ($P <$

Species		Effect of site (A)		Effect of habitat unit (B)	
		df	F	df	F
Acacia aroma‡	PT	1	0.25	2	14.89****
A. atramentaria	PT	...	...	1	2.94
A. furcatispina	PT	...	...	2	0.02
A. praecox	PT	1	21.48****	1	2.53
Atamisquea emarginata	PG	3	29.65****	2	0.73
	PT	3	19.18****	2	4.78*
Caesalpinia gilliesi‡	PT	...	...	2	3.74*
Cassia aphylla	PT	...	...	1	3.40†
Cercidium australe (1989)	PG	3	31.36****	2	4.69*
	PT	3	10.19****	2	38.39****
C. australe (1990)	PG	3	17.30***	2	2.64†
	PT	3	18.44****	2	4.15*
Justicia squarrosa‡	PG	...	...	2	5.82**
Ligaria cuneifolia§	PT	...	...	1	25.64****
Mimosa detinens	PT	...	...	2	0.66
Opuntia quimilo§	PT	1	20.56****	2	0.66
Portulaca umbraticola‡	PG	1	0.34	2	5.32**
Prosopis nigra (1989)	PG	2	1.63	2	0.79
	PT	2	4.65*	2	3.72*
P. nigra (1990)	PG	3	1.10	2	3.12*
	PT	3	0.87	2	0.52
Rhipsalis lumbricoides‡	PT	...	...	2	3.44*
Tillandsia ixioides‡	PT	...	...	2	1.14

† $.05 < P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$, **** $P < .0001$.
‡ ANOVA performed on square-root transformed data.
§ ANOVA performed on ln-transformed data.

as those in continuous forest there (Figs. 1 and 2a). Significant decreases in average numbers of pollen tubes per style were as common in SC species (4 of 6) as in SI species (5 of 10) (Tables 2 and 3).

Among species, percent change in mean number of pollen tubes per style (pollen grains per stigma, in the two herbaceous species) from continuous forest to fragments ranged from −42.7% (*Rhipsalis*) to +185.6% (*Ligaria*), with a grand median of −22.1%. Medians across SC and SI species were −21.9 and −18.0%, respectively (Kruskal–Wallis $H = 0$, $P > .95$). There were, however, marginal significant differences among "pollination guilds" (Kruskal–Wallis $H = 5.17$, $P = .07$). Medians for the hummingbird, honey bee, and native-insect visitor categories were +94.2, −12.3, and −25.5%, respectively.

Of 12 species sampled in all three habitat units (including the two herbaceous species), 9 displayed monotonic decreases in numbers of pollen tubes or grains from continuous forest through small fragments (Table 3, Fig. 1), a highly significant deviation ($P = .0005$) from the binomial expectation that one-quarter of the species would exhibit such a pattern (i.e., one of four equi-probable order relationships). Accordingly, the percent decline in pollination levels comparing small fragments with forest was, on average, significantly greater than the decline from forest to large fragments (medians = −33.1 vs. −12.1%, respectively; Wilcoxon paired-sample signed-ranks $T = 11$, $P < .05$).

In three species yielding counts of pollen tubes we also counted stigmatic pollen loads. Loads in *Atamisquea* did not vary significantly among habitat units (Table 3). In *Cercidium*, loads decreased from forest to fragments in 1989 but not in 1990 (Table 3, Fig. 1). In both years, a strong site × habitat interaction existed (Table 3, Appendix I). In 1990, *Prosopis* received significantly larger pollen loads in fragments (Table 3). Nevertheless, in all three species the number of pollen tubes decreased significantly from forest to fragments (Table 3).

For the same three species, nonlinear regressions of pollen tubes on pollen grains explained between 47 and 78% of the variation among individuals in numbers of pollen tubes (Fig. 3). In all three species examined in 1989, residuals were greatest for continuous forest and least for small fragments (Table 4), and this was repeated in 1990 for the two species (*Prosopis* and *Cercidium*) examined both years. Thus, on average, the chances that a pollen grain landing on a floral stigma would germinate and send a pollen tube down the style decreased monotonically from plants in continuous forest to plants in small fragments. Among-habitat differences in residuals may relate to frequency of self and outcross pollinations. The hand-pollination experiments showed that self-pollen tubes of *Cercidium* and *Prosopis* were, respectively, 2.5 and 3.5 times less likely to reach the base of the style by 36 h than were outcross pollen tubes (Table 5).

Relative rankings among individual trees in pollination success, as measured by number of pollen tubes

.05) comparison between continuous forest and the two fragment units combined is indicated by italicizing the continuous forest category mean, a significant "large vs. small" comparison by italicizing the small fragment unit mean.

Interaction (A × B)		Error		Habitat unit		
df	*F*	df	ss	Continuous	Large fragment	Small fragment
2	3.97†	44	6.426	*5.08*[a]	3.56[b]	*2.30*[c]
...	...	18	38.882	5.51[a]	4.39[a]	...
...	...	27	85.557	3.63[a]	3.61[a]	3.49[a]
1	0.34	46	60.618	4.02[a]	4.86[a]	...
6	1.30	101	5710.9	24.4[a]	24.8[a]	27.0[a]
6	0.60	101	1175.2	*12.4*[a]	11.2[ab]	10.0[b]
...	...	25	6.655	1.93[a]	1.86[a]	*0.65*[a]
...	...	18	462.73	17.0[a]	...	12.8[a]
6	4.66***	104	2471.8	*21.0*[a]	19.2[ab]	17.3[b]
6	4.06***	108	353.60	*8.64*[a]	6.75[b]	*5.10*[c]
6	3.49**	109	1978.7	16.4[a]	18.6[a]	17.3[a]
6	1.39	109	342.96	6.56[a]	6.40[ab]	*5.55*[b]
...	...	303	765.26	*8.59*[a]	4.87[b]	5.62[b]
...	...	18	3.874	3.60[a]	...	10.28[b]
...	...	28	51.764	3.53[a]	3.48[a]	2.93[a]
2	0.11	49	28.424	218[a]	186[a]	146[a]
2	2.76†	612	10,022	*163*[a]	142[ab]	131[b]
4	3.24*	67	2412.3	16.2[a]	17.3[a]	15.3[a]
4	2.64*	72	392.03	*6.86*[a]	6.05[ab]	4.35[b]
6	1.33	101	3469.0	*11.3*[a]	14.3[a]	12.9[a]
6	1.73	101	919.40	6.39[a]	6.12[a]	5.01[a]
...	...	27	230,025	*228*[a]	109[a]	153[a]
...	...	12	34.359	96.2[a]	115.0[a]	83.0[a]

per style, remained consistent from year to year. In *Cercidium* and *Prosopis,* mean number of pollen tubes was significantly correlated among trees between 1989 and 1990 (respectively, Spearman $r_s = 0.292$, $n = 122$, $P < .005$; $r = 0.389$, $n = 81$, $P < .0001$). Rankings in terms of pollen loads on stigmas also stayed consistent for *Cercidium* ($r_s = 0.392$, $n = 118$, $P < .0001$) but not for *Prosopis* ($r_s = 0.192$, $n = 76$, $P = .10$).

Fruit set

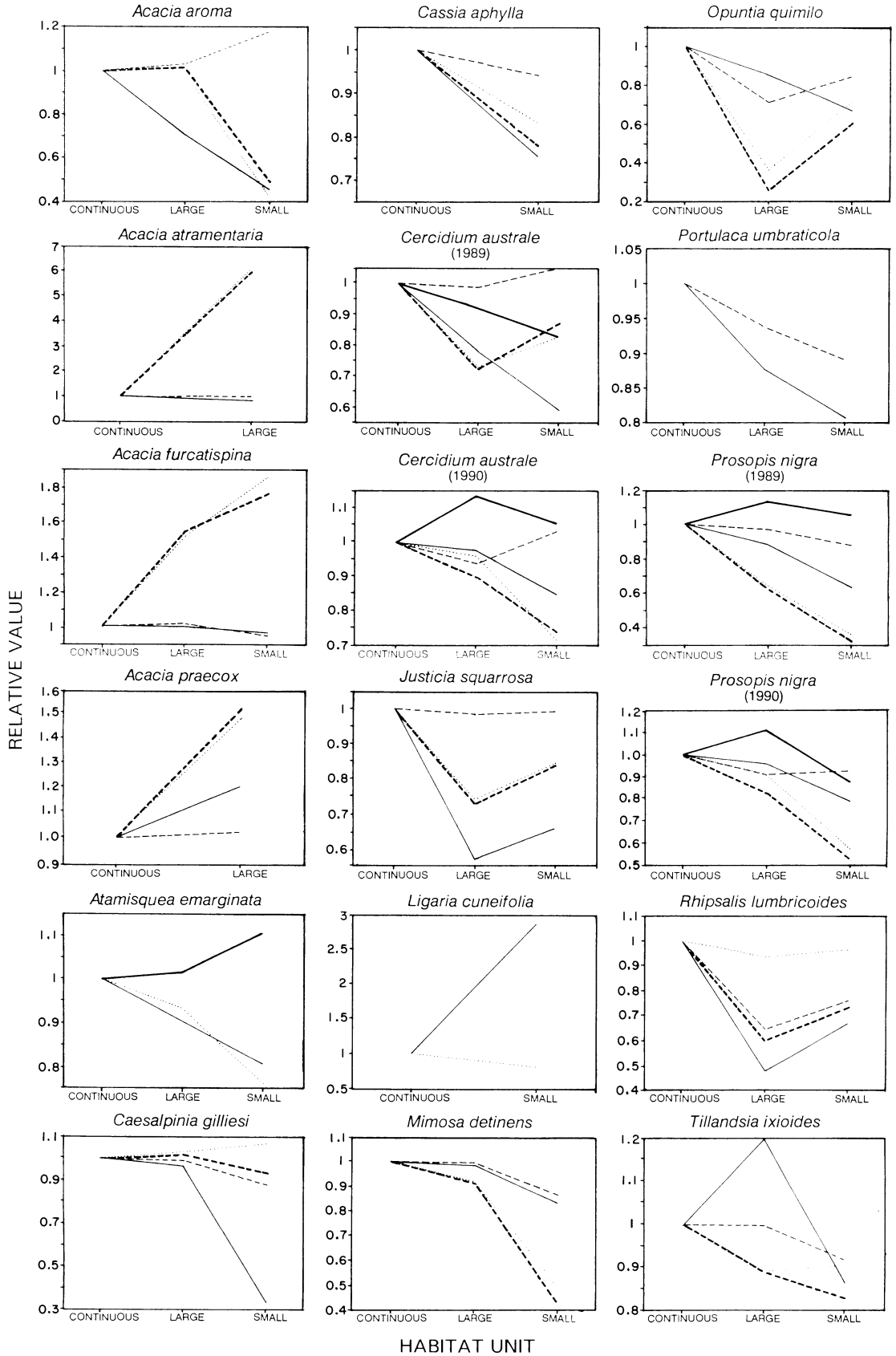
In 7 of 15 species, variation of fruit set with fragmentation was significant or marginally significant (Table 6), a number far greater than the expected 1.5 species showing such result by chance alone (binomial test, $P = .0003$). In 2 of the 7 (*Acacia praecox* and *A. atramentaria*), fruit set increased with increasing fragmentation, whereas in the other 5 it decreased with fragmentation (Table 6, Fig. 1). This 5:2 ratio did not differ significantly from the 1:1 random expectation (binomial test, $P = .23$).

Percent change in fruit set between continuous forest and fragments varied from −59.2% (*Ligaria*) to +502% (*Acacia atramentaria*) (Fig. 2b), with a median of −17.0%. Considering the direction of change in all 15 species (Fig. 2b), fruit set decreased with fragmentation in 11 and increased in 4 (binomial test, $P = .06$). Percent change did not differ significantly between SC and SI species (medians = −21.0 vs. −12.8%, respectively; Kruskal–Wallis $H = 0.74$, $P > .40$) or visitor categories (medians = −34.1, −18.8, and −17.0% for the hummingbird, honey bee, and native-insect visitor groups, respectively; Kruskal–Wallis $H = 0.94$, $P > .60$). Of the 11 species examined in all three habitat units, fruit set decreased monotonically with decreasing fragment size in four, not significantly different from the binomial mean expectation of 2.75 ($P = .29$). Among these 11 species, percent change from continuous forest to large fragment did not differ significantly from percent change from forest to small fragment (medians = −7.8 and −17.5%, respectively; Wilcoxon paired-sample signed-rank $T = 32$, $P > .10$).

In *Cercidium,* individuals with high fruit set frequencies in 1989 tended to repeat in 1990 ($r_s = 0.243$, $n = 122$, $P < .01$), although in neither year did fruit set vary significantly with fragmentation (Table 6). In contrast, fruit set in *Prosopis* declined significantly from forest through small fragments in both 1989 and 1990, but there was no consistency across years among individual rankings in fruit production ($r_s = 0.013$, $n = 80$, $P = .90$).

Seed set

In 5 of the 14 species with multiseeded fruits, relationships between the number of seeds per fruit and habitat unit was significant or marginally so (Table 7), a number far greater than that expected by chance alone (binomial test, $P = .009$). In *Portulaca* and *Rhipsalis,* seed set decreased strongly from continuous forest to fragments (Table 7, Fig. 1). Seed set also decreased with fragmentation in *Prosopis* in 1990 (Table 7, Fig. 1). In *Acacia aroma,* fruits on plants in small fragments held the most seeds (Table 7, Fig. 1), but this varied among sites (Appendix I), as denoted by a significant site × habitat unit interaction (Table 7).



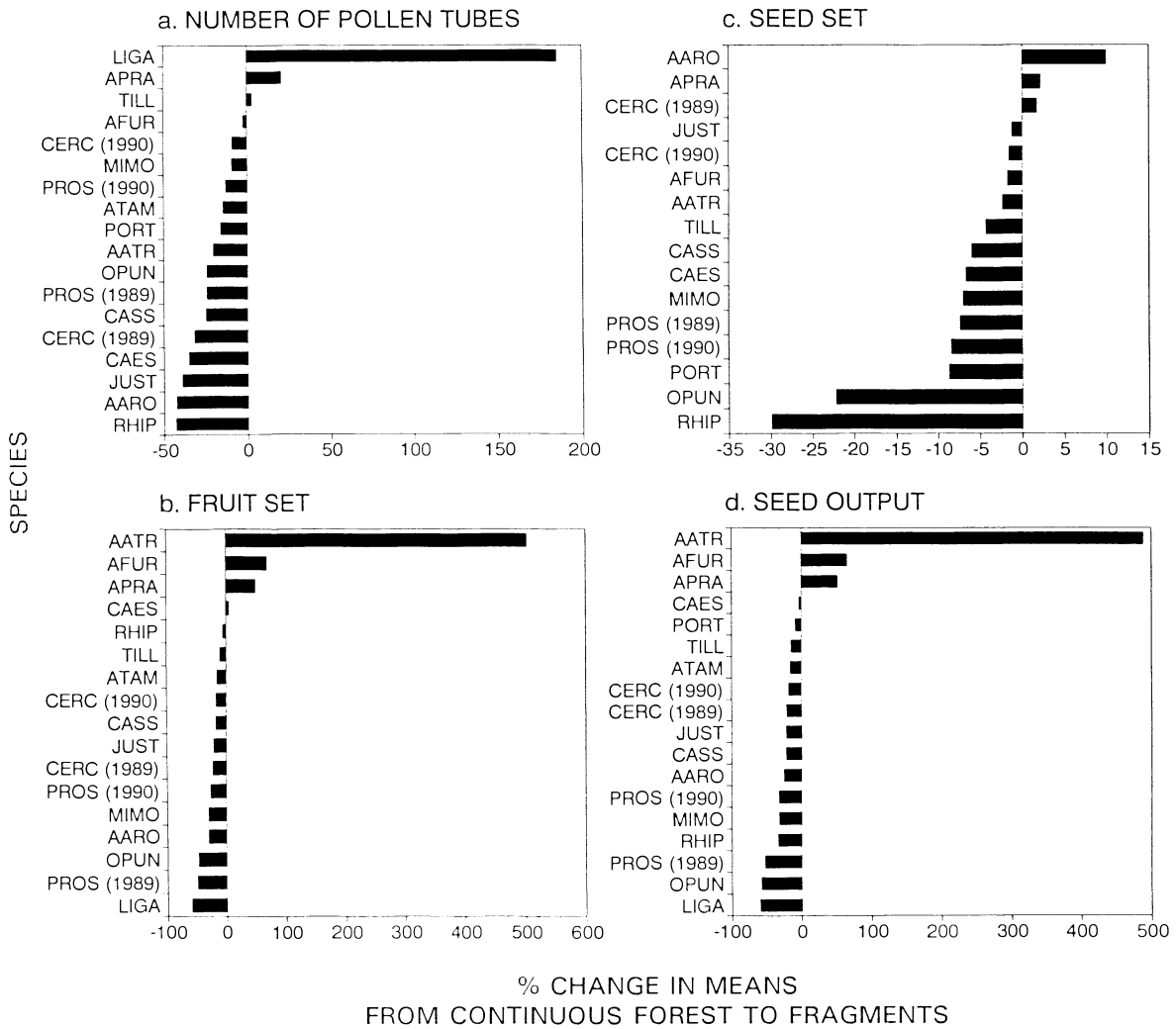


FIG. 2. Percent change from values in continuous forest to values in fragment habitat units (combined), ranked in descending order, for (a) mean number of pollen tubes (in *Portulaca* and *Justicia*, number of pollen grains), (b) fruit set, (c) seed set, and (d) seed output. Species codes are: AARO = *Acacia aroma*, AATR = *A. atramentaria*, AFUR = *A. furcatispina*, APRA = *A. praecox*, ATAM = *Atamisquea emarginata*, CAES = *Caesalpinia gilliesi*, CASS = *Cassia aphylla*, CERC = *Cercidium australe*, JUST = *Justicia squarrosa*, LIGA = *Ligaria cuneifolia*, MIMO = *Mimosa detinens*, OPUN = *Opuntia quimilo*, PORT = *Portulaca umbraticola*, PROS = *Prosopis nigra*, RHIP = *Rhipsalis lumbricoides*, TILL = *Tillandsia ixioides*.

Percent change in seed set from forest to fragments varied from −29.9% for *Rhipsalis* to +10.0% for *A. aroma*, with a median of −5.2%. Considering all 14 species (Fig. 2c), seed set decreased with fragmentation in 11 and increased in 3 (binomial test, $P = .03$). Breeding system did not significantly affect the amount of change (medians = −6.7 and −2.3% for SC and SI species, respectively; Kruskal–Wallis $H = 0.54$, $P = .46$). Percent change did not differ among visitor categories (medians = −4.3, +1.7, and −6.3% for the hummingbird, honey bee, and native-insect visitor groups, respectively; Kruskal–Wallis $H = 1.09$, $P > .50$).

Of the 11 species for which we collected seed set data in all three habitat units, 5 showed monotonic decreases in seed set from forest through small fragments, not

←

FIG. 1. Habitat unit means for the different reproductive variables measured (see Tables 3, 6, and 7), expressed relative to means for continuous forest (1.0). Lines join values for pollen grains/stigma (——); pollen tubes/style (——); fruit set per flower or, in Mimosoideae, per inflorescence (· · · · ·); seed set per fruit matured (– – –); and seed output per flower or inflorescence (– – –). Seed output was computed as the product of mean seed set and mean fruit set. For some species, certain variables were not measured, or data were collected from two of the three habitat unit categories only (see Appendix I).

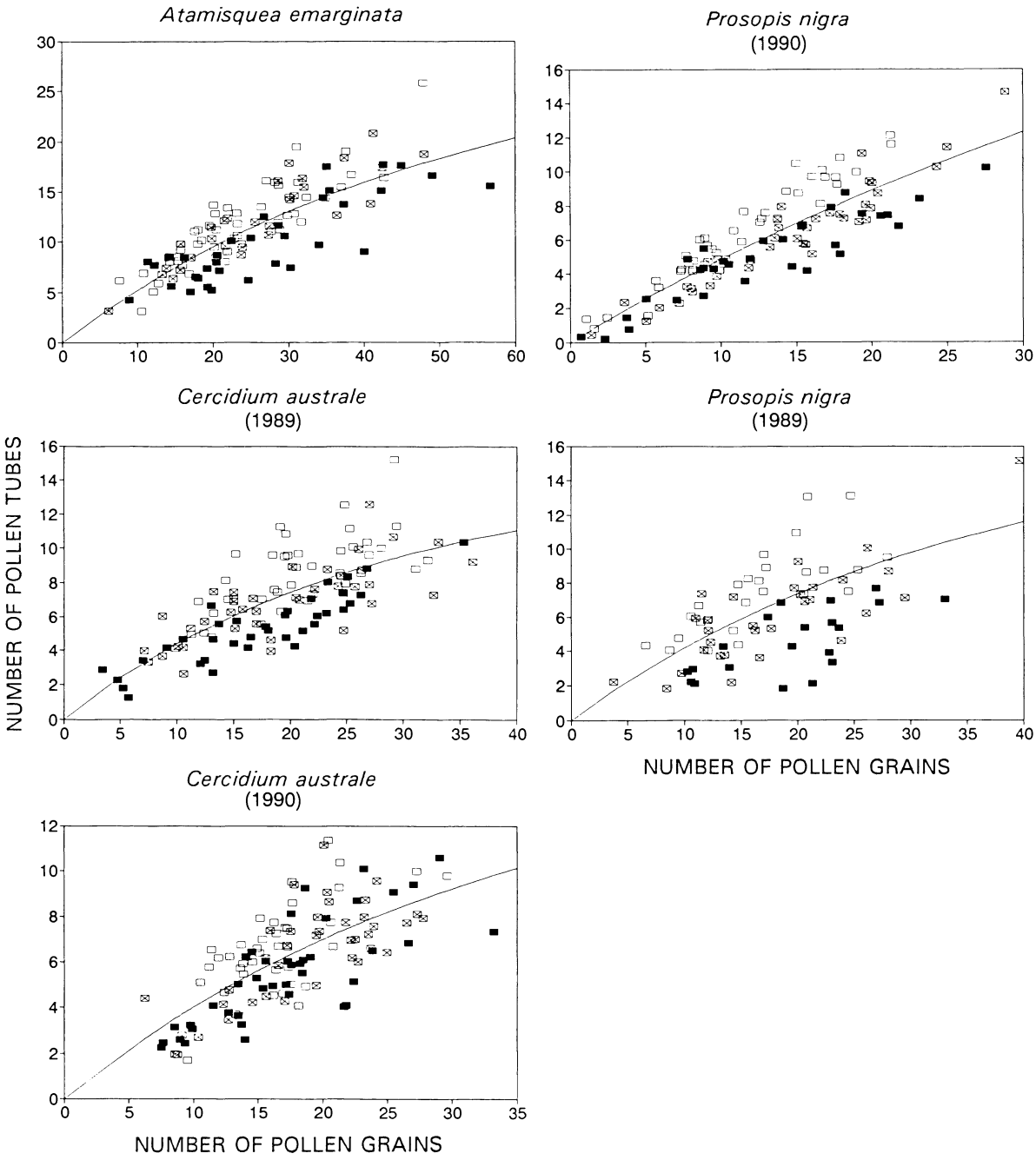


FIG. 3. Relationships between mean number of pollen tubes in styles and mean number of pollen grains on stigmas, across individual plants within *Cercidium, Prosopis,* and *Atamisquea.* Regression equations are: $y = 14.5\ [1 - \exp(-0.036x)]$, $r^2 = 0.56$, $n = 116$ (*Cercidium* 1989); $y = 15.9\ [1 - \exp(-0.029x)]$, $r^2 = 0.52$, $n = 121$ (*Cercidium* 1990); $y = 17.5\ [1 - \exp(-0.028x)]$, $r^2 = 0.46$, $n = 76$ (*Prosopis* 1989); $y = 30.2\ [1 - \exp(-0.017x)]$, $r^2 = 0.78$, $n = 113$ (*Prosopis* 1990); $y = 29.9\ [1 - \exp(-0.019x)]$, $r^2 = 0.67$, $n = 113$ (*Atamisquea*). Each point represents an individual plant from small fragments (■), large fragments (⊠), or continuous forest (□). Analyses of residuals relative to habitat unit are reported in Table 4.

significantly different from the null mean expectation of 2.75 (binomial test, $P = .11$). The magnitude of change from forest to large fragments did not differ significantly from that from forest to small fragments (medians = −1.4 vs. −11.0%, Wilcoxon paired-sample signed-rank $T = 33$, $P > .10$).

Trees producing many seeds per fruit in 1989 tended to repeat in 1990 for *Cercidium* ($r_s = 0.428$, $n = 122$,

TABLE 4. Results of two-way ANOVAs on the residuals of number of pollen tubes after adjusting for differences in number of pollen grains (Fig. 3). Notation as in Table 3.

Species	Effect of site (A) df	Effect of site (A) F	Effect of habitat unit (B) df	Effect of habitat unit (B) F	Interaction (A × B) df	Interaction (A × B) F	Error df	Error ss	Habitat unit: Continuous	Habitat unit: Large fragment	Habitat unit: Small fragment
Atamisquea emarginata	3	6.81***	2	21.95****	6	0.30	100	389.75	*1.39*[a]	0.11[b]	*−1.76*[c]
Cercidium australe (1989)	3	4.39**	2	26.51****	6	0.38	103	194.67	*1.16*[a]	−0.16[b]	*−1.09*[c]
C. australe (1990)	3	6.76***	2	7.89***	6	0.38	108	204.47	*0.61*[a]	−0.09[ab]	−0.58[b]
Prosopis nigra (1989)	2	2.65	2	10.27****	4	0.78	66	178.80	*1.40*[a]	−0.33[b]	−1.27[b]
P. nigra (1990)	3	0.90	2	33.50****	6	1.54	100	105.11	*1.10*[a]	−0.41[b]	−0.92[b]

† $.05 < P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$, **** $P < .0001$.

$P < .0001$) but not *Prosopis* ($r_s = 0.117$, $n = 70$, $P = .34$).

Seed output and relationships among reproductive stages

To obtain an index to total seed output per flower (per inflorescence in the Mimosoideae), we multiplied fruit and seed set. In *Atamisquea* and *Ligaria* this variable equalled fruit set alone, whereas in *Portulaca* it equalled seed set as measured. As expected from the separate results on seed set and fruit set reported above, for most species total seed output decreased from forest to fragments (Fig. 2d). Percent change ranged from −59.2 to +489%, with a median of −21.3% (Fig. 2d). This figure did not differ significantly between SC and SI species (medians = −21.9 and −18.0%, respectively; Kruskal–Wallis $H = 0.29$, $P > .50$) or visitor categories (medians = −36.7, +8.0, and −21.9% for the hummingbird, honey bee, and native-insect visitor groups, respectively; Kruskal–Wallis $H = 0.64$, $P > .70$).

Across species, no significant correlation existed between percent change in number of pollen tubes from forest to fragments and percent change in seed output ($r_s = 0.202$, $n = 16$, $P = .45$). Among plants within individual species, seed output usually showed positive but weak correlations with number of pollen tubes (r_s's < 0.300; Fig. 4a). In *Rhipsalis* and *Acacia aroma,* correlations were stronger (r_s's > 0.300; Fig. 4a). Although seed output of *Rhipsalis* varied significantly among habitat units (ANOVA, $F_{2,27} = 6.31$, $P < .01$), paralleling the results for seed set alone (Table 7), the

TABLE 5. Two-way mixed-model ANOVAs of the effects of hand-pollination treatment (self vs. cross) and tree individual on the number of pollen grains deposited on stigmas (PG) and number of pollen tubes (PT) reaching the base of the style after 36 h, for *Prosopis* and *Cercidium.*‡

Source	df	ss	F	Self n	Self Mean	Self SD	Cross n	Cross Mean	Cross SD
Prosopis nigra (PG)									
Treatment	1	0.805	0.49	95	12.95	1.948	94	13.97	1.735
Tree	4	47.263	7.29****						
Interaction	4	6.595	1.02						
Error	179	290.161							
P. nigra (PT)									
Treatment	1	28.825	64.52***	97	1.10	1.168	94	3.32	1.128
Tree	4	5.457	1.18						
Interaction	4	1.787	0.39						
Error	181	209.816							
Cercidium australe (PG)									
Treatment	1	4.858	6.72†	64	13.54	2.016	57	11.22	1.874
Tree	4	9.372	0.32						
Interaction	4	2.890	0.83						
Error	111	220.580							
C. australe (PT)									
Treatment	1	6.893	9.98*	65	0.73	1.041	62	1.68	0.949
Tree	4	6.347	1.61						
Interaction	4	2.762	0.70						
Error	115	113.215							

† $.05 < P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$, **** $P < .0001$.

‡ Data were square-root transformed. To compute the F value associated with the treatment effect the treatment mean square was divided by the interaction mean square. Treatment means and standard deviations were back-transformed.

TABLE 6. Results of two- and one-way ANOVAs on fruit set (fruit/flower ratio, or number of fruits/inflorescence in the Mimosoideae). Notation as in Table 3.

Species	Effect of site (A)		Effect of habitat unit (B)		Interaction (A × B)		Error		Habitat unit		
	df	*F*	df	*F*	df	*F*	df	ss	Continuous	Large fragment	Small fragment
Acacia aroma‡	1	0.67	2	2.72(*)	2	7.73**	52	0.887	0.063[a]	0.062[a]	*0.027*[a]
A. atramentaria‡	...	...	1	8.73**	...	...	18	0.155	0.007[a]	0.043[b]	...
A. furcatispina	...	...	2	4.72*	...	...	27	0.175	*0.129*[a]	0.195[ab]	0.238[b]
A. praecox	1	0.19	1	2.62	1	1.59	46	0.911	0.164[a]	0.243[a]	...
Atamisquea emarginata‡	3	7.33***	2	5.04**	6	2.51*	101	1.092	*0.391*[a]	0.364[ab]	*0.298*[b]
Caesalpinia gilliesi	...	...	2	0.03	...	...	24	0.032	0.063[a]	0.065[a]	0.067[a]
Cassia aphylla‡	...	...	1	0.62	...	...	18	0.297	0.259[a]	...	0.215[a]
Cercidium australe‡ (1989)	3	3.20*	2	2.01	6	0.51	108	1.410	0.107[a]	0.078[a]	0.088[a]
C. australe‡ (1990)	3	1.72	2	1.90	6	1.44	112	1.349	0.074[a]	0.071[a]	0.053[a]
Justicia squarrosa	...	...	2	7.93***	...	...	309	15.873	*0.475*[a]	0.350[b]	0.401[ab]
Ligaria cuneifolia‡	...	...	1	1.07	...	...	18	0.353	0.451[a]	...	0.368[a]
Mimosa detinens‡	...	...	2	5.05*	...	...	28	1.159	0.488[a]	0.450[a]	*0.240*[b]
Opuntia quimilo	1	2.95(*)	2	1.53	2	0.52	49	5.703	0.290[a]	0.105[a]	0.206[a]
Prosopis nigra‡ (1989)	2	4.98**	2	2.52(*)	4	0.73	72	4.944	*0.165*[a]	0.106[a]	0.060[a]
P. nigra‡ (1990)	3	2.26(*)	2	5.89**	6	1.93	99	18.122	*1.404*[a]	1.272[ab]	*0.799*[b]
Rhipsalis lumbricoides§	...	...	2	0.60	...	...	27	0.667	0.867[a]	0.810[a]	0.837[a]
Tillandsia ixioides	...	...	2	0.54	...	...	12	0.295	0.822[a]	0.732[a]	0.742[a]

† $.05 < P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$, **** $P < .0001$.
‡ ANOVA performed on square-root transformed data.
§ ANOVA performed on data transformed according to $\arcsin(\times^{0.5})$.

significant relationship vanished when seed output residuals were analyzed following a nonlinear regression (ANOVA $F_{2, 25} = 0.74$, $P > .40$), suggesting that differences in seed output among habitat units may be fully accounted by differences in pollination levels. Likewise, the marginally significant among-habitat variation in seed output for *A. aroma* ($F_{2, 43} = 2.70$, $P = .07$), paralleling the results of fruit set alone (Table 6), disappeared when residuals were analyzed (ANOVA $F_{2, 41} = 0.11$, $P = .74$). On the other hand, in *Atamisquea* seed output per plant tended to reflect numbers of pollen tubes (Fig. 4a), but differences in fruit set (= seed output) among habitat units (Table 6) remained significant (ANOVA $F_{2, 100} = 3.38$, $P < .05$) following analysis of residuals, showing that differences in seed output among habitat units cannot be fully accounted for by differences in pollination levels.

In most species, fruit and seed set were correlated

TABLE 7. Results of two- and one-way ANOVAs on seed set (number of seeds/fruit matured). Notation as in Table 3.

Species	Effect of site (A)		Effect of habitat unit (B)		Interaction (A × B)		Error		Habitat unit		
	df	*F*	df	*F*	df	*F*	df	ss	Continuous	Large fragment	Small fragment
Acacia aroma	1	0.04	2	3.45*	2	4.49*	49	93.180	6.08[a]	6.25[a]	*7.12*[a]
A. atramentaria	...	...	1	0.03	...	...	16	47.901	6.12[a]	5.98[a]	...
A. furcatispina	...	...	2	0.31	...	...	27	25.956	4.77[a]	4.85[a]	4.52[a]
A. praecox	1	0.21	1	0.37	1	1.99	46	21.064	6.65[a]	6.80[a]	...
Caesalpinia gilliesi	...	...	2	0.64	...	...	21	11.599	3.14[a]	3.10[a]	2.76[a]
Cassia aphylla	...	...	1	1.04	...	...	18	103.73	18.3[a]	...	17.2[a]
Cercidium australe (1989)	3	6.87***	2	1.43	6	2.27*	108	5.007	1.43[a]	1.41[a]	1.50[a]
C. australe (1990)	3	2.86*	2	2.50(*)	6	0.91	112	10.813	1.59[a]	1.49[a]	*1.64*[a]
Justicia squarrosa	...	...	2	0.29	...	...	313	93.759	3.75[a]	3.69[a]	3.72[a]
Mimosa detinens	...	...	2	1.92	...	...	28	16.714	4.36[a]	4.33[a]	3.78[a]
Opuntia quimilo	1	1.01	2	0.37	2	0.54	22	193.441	125.0[a]	88.9[a]	105.7[a]
Portulaca umbraticola‡	1	113.41****	2	4.89**	2	0.23	474	1734.2	*121.5*[a]	113.8[ab]	108.2[b]
Prosopis nigra (1989)	2	7.26***	2	2.68(*)	3	1.46	64	223.26	8.44[a]	8.18[a]	7.45[a]
P. nigra (1990)	3	5.85***	2	5.71**	6	3.34**	97	243.63	*7.96*[a]	7.24[b]	7.34[b]
Rhipsalis lumbricoides[1]	...	...	2	9.35***	...	...	27	16.166	*55.4*[a]	35.6[b]	42.0[b]
Tillandsia ixioides	...	...	2	0.28	...	...	12	12.377	160.7[a]	160.3[a]	147.3[a]

† $.05 < P < .10$, * $P < .05$, ** $P < .01$, *** $P < .001$, **** $P < .0001$.
[1] ANOVA performed on square-root transformed data.

among individuals, with r_s's > 0.300 for five species (Fig. 4b). In *A. aroma*, however, these two variables were highly negatively correlated.

Discussion

"Community-level health" as reflected in pollination

Treating the assemblage of plants in the Chaco Serrano as a whole, pollination and, to a lesser extent, seed production declined with increasing fragmentation. The subset of the flora we studied represented a diversity of breeding systems, growth forms, phylogenetic lineages, and pollination guilds. We conclude that subtle multispecific functions and interrelationships within ecological communities are affected, in general negatively, through habitat fragmentation. This is not unexpected (cf. Lovejoy et al. 1986, Dirzo and Miranda 1991, Saunders et al. 1991, Redford 1992). To our knowledge, however, ours is the first such result from a comprehensive, multispecies study on a particular mode of plant–animal interaction. Our results parallel those of studies on individual plant species by Spears (1987), Jennersten (1988), and Menges (1991), all of whom found that plant reproductive success in habitat isolates suffered relative to that in larger populations. The relative ease with which pollination levels can be assessed suggests that monitoring pollination and seed output over a reasonable fraction of a site's flora may provide a useful, integrated measure of "community-level health" in basic and applied contexts even when, as in our study, the specific mechanisms are unknown.

The pollination stage as a "selective filter" on plant recruitment

Effects of fragmentation on fruit and seed production varied widely among species (Fig. 2b–d), suggesting that events at pollination might alter species' relative contributions to the seed bank. Results provide some evidence that plants belonging to different pollination guilds might indeed differ in their sensitivity to fragmentation. Species with potentially "interchangeable" pollinators, such as those heavily exploited by honey bees, exhibited a slightly smaller decline in mean tube numbers with fragmentation than did plant species primarily attracting native insects; in a related work, native insects were found to decrease in abundance and diversity in these forest fragments (Aizen and Feinsinger 1994). Except for *Cercidium* in 1989, no plant species in the "honey bee visitor group" experienced a decline with fragmentation in the absolute number of pollen grains received on stigmas, which suggests that honey bees may compensate quantitatively for the decrease in natives. In the four species showing the largest fragmentation-related decline in pollination levels (Fig. 2a), flower visits were infrequent regardless of habitat unit (M. A. Aizen and P. Feinsinger, *personal observation*), indicating that plant species associated with

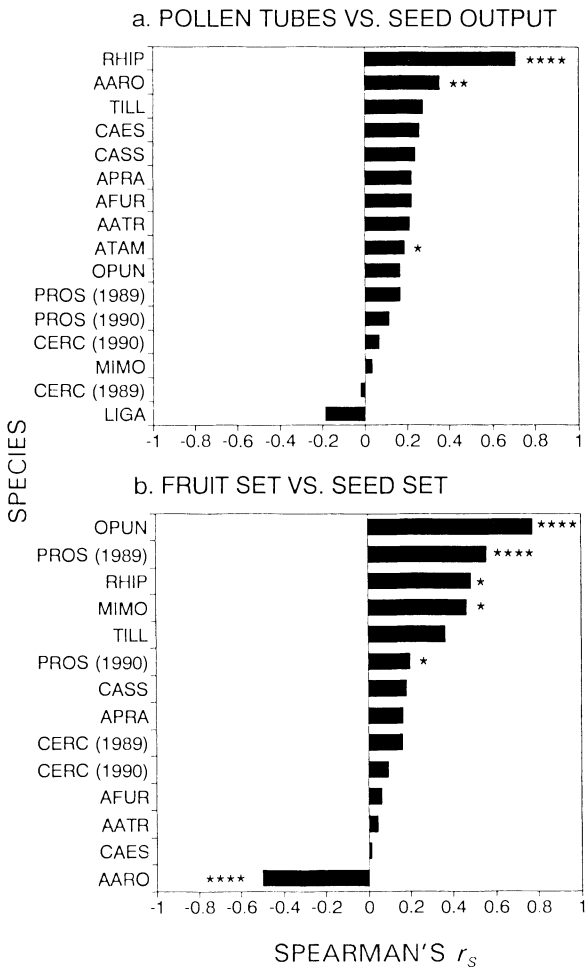


FIG. 4. Relationships between (a) mean number of pollen tubes and seed output, and (b) fruit set vs. seed set, as measured by Spearman rank correlations among plants within each species. * $P < .05$, ** $P < .01$, *** $P < .001$, and **** $P < .0001$. Species codes as in Fig. 2.

relatively scarce pollinators might be the most sensitive to fragmentation. In contrast, pollination levels of the two hummingbird-pollinated species, *Tillandsia* and *Ligaria*, failed to decline with fragmentation (Fig. 2a). This result may be a consequence of the particular foraging behavior of the two hummingbirds involved rather than a characteristic of hummingbird pollination in general: both *Chlorostilbon aureoventris* and *Sappho sparganura* are opportunistic species that frequent open, disturbed habitat, and shrubby edges but rarely enter forest interior (P. Feinsinger, *personal observation*).

At the stage of seed output, intensity and even direction of the fragmentation effect bore little relation to visitor taxa or degree of pollinator "interchangeability" (Table 2, Fig. 2d). Neither did sensitivity to fragmentation reflect the extent of internal constraints on fruit production. Seed output by plants such as the legumes, which matured fruits from only a small pro-

portion of flowers and presumably experienced maternal resource limitation, was as likely to change with fragmentation as was seed output by other plants that apparently matured most fertilized ovaries (Figs. 1 and 2). Our results did not support the prediction that fragmentation would affect SI species more severely than SC. The limited sample of species, 16, prevents us from controlling for associations between breeding system and growth form, phylogeny, or pollination guild (see Mazer 1989). For instance, all four species observed to be heavily exploited by honey bees (Table 2) were both SI and woody, whereas SC species tended to have specialized pollination systems (Table 2; M. A. Aizen and P. Feinsinger, *personal observations*). All told, the present study provides rather little support for putting the concept of the selective filter on a firm predictive footing.

The three major species: Prosopis, Cercidium, *and* Atamisquea

Some of the lack of consistent pattern in species-specific results (Figs. 1 and 2) may be an artifact of inadequate replication. Of the 16 species, 7 were sampled only in the three habitat units of a single site, and 3 only in two habitat units of a single site, increasing the likelihood that some results in Fig. 2 are site rather than treatment effects (see Hurlbert 1984). The three species with the strongest sampling designs (*Prosopis, Cercidium,* and *Atamisquea*) all displayed significant negative effects of fragmentation on one stage or another of reproduction. These effects were not identical among species or even among years within species, however (Figs. 1 and 2, Tables 3, 6, and 7). In the following sections we detail the pollination and post-pollination mechanisms presumably involved in the species-specific effects of fragmentation, emphasizing the three principal species where appropriate but referring to the remaining species as well.

Changes in pollen quantity and quality

Both the quantity and quality of pollen received by stigmas can affect seed output (Galen and Newport 1988, Waser and Price 1983, 1991*a*). In animal-pollinated plants studied elsewhere, reductions in pollinator activity and spatial restrictions on their foraging result in decreased numbers of ovules fertilized and seeds matured, either because the total numbers of pollen grains deposited decline (Bierzychudek 1981, Snow 1982, 1986, Hainsworth et al. 1985, Whelan and Goldingay 1989, Feinsinger et al. 1991, Johnston 1991) or because the transfer of incompatible or low-quality pollen increases (Levin 1989, Waser and Price 1991*a*).

In the two herbaceous species we studied, *Justicia* and *Portulaca,* differences in seed production among habitat units (Tables 6 and 7) may have resulted directly from differences in pollen quantity (Table 3). Experimental pollinations showed *Portulaca* to be fully self-compatible and suggested the same for *Justicia* (M. A. Aizen, *unpublished data*), such that changes in seed production were unlikely to result from among-habitat differences in pollen quality. Even in small fragments, populations of either species included hundreds of individuals, a size unlikely to lead to severe inbreeding depression (Crow and Kimura 1970) over the few generations since fragmentation occurred. We made no direct observations on visitor frequency to either species, but results imply that bee and butterfly visitors simply deposited fewer pollen grains on stigmas in fragments than in continuous forest. Seed output also appeared to reflect pollen limitation in *Rhipsalis,* where significant correlations occurred across plants between mean number of pollen tubes and seed output (Fig. 4a) or between seed and fruit set (Fig. 4b). *Rhipsalis* flowered early in springtime, when native bees were particularly scarce (Aizen and Feinsinger 1994).

Results for *Acacia aroma* also suggest pollination limitation of some plants (Fig. 4a), but at the level of the inflorescence rather than the flower. Among individuals, a trade-off existed between numbers of fruit set per inflorescence and numbers of seeds per pod (Fig. 4b). In the genus *Acacia* the pollination unit is a polyad usually composed of 16 grains, sufficient to fertilize all ovules in the ovary (Kenrick and Knox 1982). Thoroughly pollinated inflorescences may lead to intense competition for resources among developing fruits and increased seed abortion in consequence, whereas inflorescences receiving few compatible polyads may channel adequate resources into each fertilized ovary. Of course, the trade-off may not be sufficient to compensate for especially low pollination rates, as may have happened in the small fragments (Fig. 1, Table 3). Overall effects of fragmentation on fruit set (Table 6) would have been much stronger but for the unexpectedly low fruit production in the continuous forest unit of site 2 (Appendix I), despite relatively high pollination levels there (Appendix I). The trade-off between fruit set per inflorescence and seeds per fruit was not observed in the other three *Acacia* species, perhaps because fruit output was not apparently pollen limited.

In the three principal species, pollen quality apparently varied with fragmentation along with, or independently of, pollen quantity. Populations of *Cercidium, Prosopis,* and *Atamisquea* existing in fragments experienced lower ratios of pollen tubes to pollen grains received than did plants in continuous forest (Tables 3 and 4, Fig. 3). In hand-pollinations of *Cercidium* and *Prosopis,* many tubes from self pollen grains eventually reached the ovary and the ovules' micropyles (M. A. Aizen, *personal observation*; see also Seavey and Bawa 1986, Waser and Price 1991*b*), but overall these tubes experienced much higher attrition rates than tubes from outcross grains (Table 5). Thus, the reduced tube : grain ratios most likely reflect increased animal transfer of self pollen in fragment plants.

Three factors, not mutually exclusive, may have contributed to fragmentation-related declines in pollen quality. First, near neighbors are expected to be more closely related than are plants distant from one another (Wright 1943, Levin and Kerster 1974, Handel 1983, Loveless and Hamrick 1984). Closely related individuals may share incompatibility alleles (Levin 1989). The boundary of a fragment necessarily restricts most pollen flow to the few close neighbors inside, possibly increasing the proportion of incompatible or less fully compatible grains within the pollen loads transferred to stigmas. Second, if pollinators restrict most flights to plants within a fragment, the frequency of revisits to the same individual may increase, resulting directly in greater frequencies of self-pollinations (Menges 1991). Third, the nature of pollinators themselves may change with fragmentation. Elsewhere (Aizen and Feinsinger 1994) we show that frequencies of Africanized honey bees (*Apis mellifera*) visiting flowers of *Prosopis* and *Cercidium* tend to increase, those of native bees, wasps, and flies to decrease, from continuous forest to small fragments. Honey bees can dominate the entire flowering canopy of a tree, passively excluding other flower visitors that might effect more outcrossing (Roubik 1991). Here (M. A. Aizen, *personal observation*), honey bee workers tended to remain foraging within a tree canopy longer, and to move among trees more rarely, than did individuals of native species (see also Gary et al. 1972, Visscher and Seeley 1982). Honey bees also visited *Atamisquea* frequently, but we did not quantify visit frequencies in different habitat units. Other species may also have experienced fragmentation-related changes in pollen quality, but we lack data for additional direct analyses such as those reported in Fig. 3.

Pollination and seed output

Effects of fragmentation on pollination did not usually translate into effects on fruit and seed production. Although numbers of pollen tubes in *Cercidium* flowers decreased with increasing fragmentation, neither seed nor fruit set declined significantly (Tables 6 and 7). *Caesalpinia* in the small fragment experienced a pronounced decline in pollen tubes (Table 3), but not in fruits or seeds per fruit, relative to plants in continuous forest (Tables 6 and 7). The dramatic increase in *Ligaria*'s pollination from forest to small fragment (Fig. 2, Table 3) was not reflected in fruit set (Table 6). In *Prosopis,* both fruit and seed set declined significantly with fragmentation (Tables 6 and 7), but among-individual variation in seed output was not explained by variation in pollination levels (Fig. 4a). Absence of strong pollen limitation in *Prosopis* is also suggested by its fruit production in 1990, nearly 10 times as great as in 1989 (Table 6) despite little change in pollination levels (Table 3).

Perhaps the scarcity of clear relationships between pollination levels and seed output was an artifact of the different time frames sampled by the two techniques we employed. Counts of pollen grains and tubes usually involved flowers produced during a single day per site, whereas counts of fruits and seeds resulted from flowers produced over a span of several days at least. Should the pollination environment per plant vary greatly over time, and vary independently among plants, then the two measures might be poorly correlated even when seed ouput is highly pollen limited. Nevertheless, for both species that we investigated twice (*Prosopis* and *Cercidium*), plants experiencing high pollination levels one year were apt to experience high levels the next. These correlations held even within habitat unit categories (M. A. Aizen and P. Feinsinger, *unpublished data*). At least for those species, then, it seems unlikely that lack of correspondence between pollination and seed output is an artifact of sampling design.

Fragmentation and inbreeding depression

Several species experiencing pronounced decreases in seed output (Fig. 2d) with fragmentation had not experienced equally strong declines in pollination (Fig. 2a). This result suggests that fragmentation may have induced changes in the nature of postpollination events, for example, in the frequency of inbreeding.

Changes in the normal pattern of gene flow may disrupt the genetic structure of plant populations and affect plant reproductive output through altered genetic and physiological processes during zygote formation and seed development. In natural populations of many outbreeding plant species, controlled crosses between near neighbors result in reduced seed production (Coles and Fowler 1976, Park and Fowler 1982, Levin 1984, Sobrevila 1988, Waser and Price 1989, 1991*a*). When a continuous natural population of outbreeding plants is fragmented, pollen flow will be restructured accordingly, such that dispersal distances are likely to be less than previously (see *Changes in pollen quantity and quality* above) and the stage for inbreeding depression is set. Fragmentation-related inbreeding depression might be particularly severe in woody species whose prefragmentation genetic neighborhoods might have involved plants scattered over tens of hectares (Ledig 1986, Bawa 1990). Woody, long-lived species also tend to accumulate large genetic loads, which may lead to high rates of seed and fruit abortion when inbreeding occurs (Wiens 1984, Ledig 1986, Klekowski 1988).

In contrast to the herbaceous and epiphytic species we studied, population sizes in fragments of *Atamisquea, Cercidium,* and *Prosopis,* for example, were small ($\approx$10 individuals in small and 20–40 in large fragments). Some results we obtained here, such as depressed fruit and seed set for fragment populations of *Prosopis* in both years (Tables 6 and 7), may have partially resulted from inbreeding depression. Furthermore, the existence of inbreeding depression may

explain the positive correlations between seed and fruit set across plants (Fig. 4b) independent of pollination levels (Fig. 4a), as the likelihood of fruit abortion in many plants tends to increase with the number of aborted seeds (Lee 1988).

Alternative explanations

In the Chaco Serrano forest, pollination and seed production of plants might have been influenced by aspects of fragmentation other than its direct effect on pollinator behavior or plant population structure. For example, physiological stress on plants near edges could affect flower output, flower viability, viability of the developing fruit, and fruit abortion rates. We could not conduct experiments to examine this possibility. Nevertheless, it seems unlikely that such stress would have major impacts on the xerophytic species we examined, all of which also prosper under drier, hotter conditions (e.g., in "Chaco Occidental" of Salta and other regions of north–central and northwestern Argentina). Also, edge formation might expose plants to higher rates of herbivory and seed predation (cf. Saunders et al. 1991). All leafy plant species in the Chaco Serrano undergo intense herbivory by leaf-cutter ants (*Atta, Acromyrmex*) (M. A. Aizen and P. Feinsinger, *personal observation*; see Meyer and Weyrauch 1966), and we noted high rates of predispersal beetle attack (Bruchidae) in leguminous fruits (e.g., *Acacia aroma,* Aizen 1991). Nevertheless, neither damage by leaf-cutter ants nor predispersal seed predation varied conspicuously with extent of fragmentation (M. A. Aizen and P. Feinsinger, *personal observation*), and in any event we include fruits with bruchid exit holes in fruit set data. Thus, we cannot easily attribute the results of our study to effects either of microclimate change or change in the impact of other animal groups.

Fragmentation and plant reproduction in perspective

Aside from obvious effects of fragmentation such as the extinction of larger vertebrates (e.g., Harris 1984, Kinnaird and O'Brien 1991), of particular concern are possible long-term, directional changes in vegetation, perhaps brought about by the changed nature of plant–animal interactions in fragments (Janzen 1983, Howe 1984). A shift in the floristic composition of species in habitat fragments might generate a "downward spiral" of extinction of animals dependent on plants and plants dependent on the animals (Janzen 1983, Dirzo and Miranda 1991). Examining fragments isolated from continuous forest by only a few tens or hundreds of metres, we have documented overall declines in pollination and seed production of $\approx 20\%$, with a great deal of variation in response among species. Undoubtedly these overall effects, many or most of which probably resulted directly from fragmentation-related changes, are biologically meaningful. All else equal, then, fragmentation-related changes in pollination events alone could have profound impacts on the fate of habitat isolates and their component species.

Is pollination the key life history stage explaining plant recruitment in the Chaco Serrano, though? Habitat fragmentation may alter events at other stages in the plant life cycle as well. The fragments we studied, immersed in an agricultural matrix, served as sources of fuelwood for local people and of fodder and shade for cattle. Adults of most plant species we studied were sturdy, well provided with mechanical (and chemical?) defenses, and little grazed by cattle (Bucher 1987). We rarely encountered seedlings or saplings, however, particularly in small fragments (M. A. Aizen and P. Feinsinger, *personal observations*). Perhaps episodes of regeneration are naturally rare in the Chaco Serrano, but we now suspect that trampling and overgrazing are far more important factors in plant demography than are changes in seed output due to pollination. In other studies (M. A. Aizen and P. Feinsinger, *unpublished data*), we also noted that forest fragments in wetter subtropical cloud forests ("yungas") of Tucumán Province exhibited highly altered understories with almost no regeneration of old-growth species. Such incidental observations imply that while effects of forest fragmentation on pollination and seed production, as detailed here, provide conceptual insights into the nature of plant–pollinator interactions and the potential for community-level change, other stages in plant life histories may play far more important roles in the short-term conservation problems inherited by fragmented landscapes.

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Literature Cited

Adamoli, J., E. Sennhauser, J. M. Acero, and A. Rescia. 1990. Stress and disturbance: vegetation dynamics in the dry Chaco region of Argentina. Journal of Biogeography **17**:491–500.

Aizen, M. A. 1991. Predación de semillas de *Acacia aroma* por el brúchido *Pseudopachymerina grata* en función de la posición de las semillas y el número de semillas por vaina. Ecología Austral **1**:17–23.

Aizen, M. A., and P. Feinsinger. 1994. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "chaco serrano." Ecological Applications **4**, *in press.*

Andersen, A. N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? Oecologia (Berlin) **81**:310–315.

Bawa, K. S. 1974. Breeding systems of tree species of a lowland tropical community. Evolution **28**:85–92.

———. 1990. Plant–pollinator interactions in tropical rain forests. Annual Review of Ecology and Systematics **21**:399–422.

Bawa, K. S., S. H. Bullock, D. P. Perry, R. E. Colville, and M. H. Grayum. 1985. Reproductive biology of tropical trees. II. Pollination systems. American Journal of Botany **69**:122–134.

Bierzychudek, P. 1981. Pollinator limitation of plant reproductive effort. American Naturalist **117**:838–840.

Bucher, E. H. 1987. Herbivory in arid and semi-arid regions of Argentina. Revista Chilena de Historia Natural **60**:265–273.

Bullock, S. H. 1985. Breeding systems in the flora of a deciduous forest in Mexico. Biotropica **17**:287–301.

Cabrera, A. L. 1976. Regiones fitogeográficas argentinas. ACME, Buenos Aires, Argentina.

Cabrera, A. L., and A. Willink. 1973. Biogeografía de America Latina. Organización de Estados Americanos, Washington, D.C., USA.

Coles, J. F., and D. P. Fowler. 1976. Inbreeding in neighboring trees in two white spruce populations. Silvae Genetica **25**:29–34.

Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Harper & Row, New York, New York, USA.

Dirzo, R., and A. Miranda. 1991. Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. Pages 273–287 *in* P. W. Price, T. W. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. Plant–animal interactions: evolutionary ecology in tropical and temperate regions. Wiley, New York, New York, USA.

Faegri, K., and L. van der Pijl. 1979. The principles of pollination ecology. Third edition, revised. Pergamon, New York, New York, USA.

Feinsinger, P. 1983. Coevolution and pollination. Pages 282–310 *in* D. J. Futuyma and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Massachusetts, USA.

———. 1987. Approaches to nectarivores–plant interactions in the New World. Revista Chilena de Historia Natural **60**:285–319.

Feinsinger, P., K. G. Murray, S. Kinsman, and W. H. Busby. 1986. Floral neighborhood and pollination success in four hummingbird-pollinated Costa Rican plant species. Ecology **67**:449–464.

Feinsinger, P., H. M. Tiebout III, and B. E. Young. 1991. Do tropical bird-pollinated plants exhibit density-dependent interactions? Field experiments. Ecology **72**:1953–1963.

Freund, R. J., and R. C. Littel. 1982. SAS for linear models. SAS Institute, Raleigh, North Carolina, USA.

Galen, C., and M. E. A. Newport. 1988. Pollination quality, seed set, and flower traits in *Polemonium viscosum*: complementary effects of variation in flower scent and size. American Journal of Botany **75**:900–905.

Gary, N. E., P. C. Whitherell, and J. Marston. 1972. Foraging range and distribution of honey bees used for carrot and onion pollination. Environmental Entomology **6**:637–640.

Gilbert, L. E. 1980. Food web organization and conservation of neotropical diversity: an evolutionary–ecological perspective. Pages 19–34 *in* M. E. Soulé and B. A. Wilcox, editors. Conservation biology: an evolutionary–ecological perspective. Sinauer, Sunderland, Massachusetts, USA.

Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinctions. Pages 11–34 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Hainsworth, F. R., L. L. Wolf, and T. Mercier. 1985. Pollen limitation in a monocarpic species, *Ipomopsis aggregata*. Journal of Ecology **73**:263–270.

Handel, S. N. 1983. Pollination ecology, plant population structure, and gene flow. Pages 163–211 *in* L. Real, editor. Pollination biology. Academic Press, New York, New York, USA.

Harris, L. D. 1984. The fragmented forest. University of Chicago Press, Chicago, Illinois, USA.

Herrera, C. M. 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. Biological Journal of the Linnean Society **35**:95–125.

Horvitz, C. C., and D. W. Schemske. 1990. Spatio-temporal variation in insect mutualists of a neotropical herb. Ecology **71**:1085–1097.

Howe, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. Biological Conservation **30**:261–281.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological experiments. Ecological Monographs **54**:187–211.

Janzen, D. H. 1974. The deflowering of Central America. Natural History **83**:48–53.

———. 1983. No park is an island: increase in interference from outside as park size decreases. Oikos **41**:402–410.

Jennersten, O. 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. Conservation Biology **2**:359–366.

Johnston, M. O. 1991. Pollen limitation of female reproduction in *Lobelia cardinalis* and *L. siphilitica*. Ecology **72**:1500–1503.

Kenrick, J., and R. B. Knox. 1982. Function of the polyad in the reproduction of *Acacia*. Annals of Botany **50**:721–727.

Kenrick, J., and R. B. Knox. 1989. Quantitative analysis of self-incompatibility in trees of seven species of *Acacia*. Journal of Heredity **80**:240–245.

Kevan, P. G. 1975. Pollination and environmental conservation. Environmental Conservation **2**:293–298.

Kinnaird, M. F., and T. G. O'Brien. 1991. Viable populations for an endangered forest primate, the Tana River Crested Mangabey (*Cercocebus galeritus galeritus*). Conservation Biology **5**:203–213.

Klekowski, E. J. 1988. Mutation, developmental selection, and plant evolution. Columbia University Press, New York, New York, USA.

Kwak, M. M. 1987. Pollination and pollen flow disturbed by honeybees in bumblebee-pollinated *Rhinanthus* populations? Pages 273–283 *in* J. van Andel, editor. Disturbance in grasslands. Dr. W. Junk, Dordrecht, The Netherlands.

Ledig, F. T. 1986. Heterozygosity, heterosis, and fitness in outbreeding plants. Pages 77–104 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Lee, T. D. 1988. Patterns of fruit and seed production. Pages 177–202 *in* J. Lovett Doust and L. Lovett Doust, editors. Plant reproductive strategies. Oxford University Press, New York, New York, USA.

Lerdau, M., J. Whitbeck, and N. M. Holbrook. 1991. Tropical deciduous forest: death of a biome. Trends in Ecology and Evolution **6**:201–202.

Levin, D. A. 1984. Inbreeding depression and proximity-dependent crossing success in *Phlox drummondii*. Evolution **36**:116–127.

———. 1989. Proximity-dependent cross-compatibility in *Phlox*. Evolution **43**:1114–1116.

Levin, D. A., and H. W. Kerster. 1974. Gene flow in seed plants. Evolutionary Biology **7**:139–220.

Levins, R. 1970. Extinction. Pages 75–108 *in* M. Gerstenhaber, editor. Some mathematical questions in biology.

Volume II. American Mathematical Society, Providence, Rhode Island, USA.

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcom, C. E. Quintela, L. H. Harper, K. S. Brown, A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Loveless, M. D., and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. Annual Review of Ecology and Systematics **15**:65–95.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Mares, M. 1992. Neotropical mammals and the myth of Amazonian biodiversity. Science **255**:976–979.

Martin, F. M. 1959. Staining and observing pollen tubes by means of fluorescence. Stain Technology **34**:436–437.

Mazer, S. J. 1989. Ecological, taxonomic, and life history correlates of seed mass among Indiana dune angiosperms. Ecological Monographs **59**:153–175.

McFarland, J. D., P. G. Kevan, and M. A. Lane. 1989. Pollination biology of *Opuntia imbricata* (Cactaceae) in southern Colorado. Canadian Journal of Botany **67**:24–28.

McMullen, C. K. 1987. Breeding systems of selected Galapagos islands angiosperms. American Journal of Botany **74**:1694–1705.

Mead, R. 1988. The design of experiments. Cambridge University Press, Cambridge, England.

Menges, E. S. 1991. Seed germination percentage increases with population size in a fragmented prairie species. Conservation Biology **5**:158–164.

Meyer, T., and W. K. Weyrauch. 1966. Guía para dos excursiones biológicas en la provincia de Tucumán. Instituto Miguel Lillo, Universidad Nacional de Tucumán, S.M. de Tucumán, Tucumán, Argentina.

Neff, J., B. B. Simpson, and A. R. Moldenke. 1977. Flowers–flower visitor system. Pages 204–224 *in* G. H. Orians and O. T. Solbrig, editors. Convergent evolution in warm deserts. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.

Osborn, M. M., P. G. Kevan, and M. A. Lane. 1988. Pollination biology of *Opuntia polyacantha* and *Opuntia phaecanta* (Cactaceae) in southern Colorado. Plant Systematics and Evolution **159**:85–94.

Park, Y. S., and D. P. Fowler. 1982. Effects of inbreeding and genetic variances in a natural population of tamarack (*Larix laricina* (Du Roi) K. Koch) in eastern Canada. Silvae Genetica **31**:21–26.

Powell, A. H., and G. V. N. Powell. 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. Biotropica **19**:176–179.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652–661.

Redford, K. H. 1992. The empty forest. BioScience **42**:412–422.

Redford, K. H., A. Taber, and J. A. Simonetti. 1990. There is more to biodiversity than the tropical rain forests. Conservation Biology **4**:328–330.

Roubik, D. W. 1991. Aspects of Africanized honey bee ecology in tropical America. Pages 259–281 *in* M. Spivak, D. J. C. Fletcher, and M. C. Breed, editors. The "African" honey bee. Westview, Boulder, Colorado, USA.

———. 1992. Loose niches in tropical communities: why are there so few bees and so many trees? Pages 327–353 *in* M. D. Hunter, T. Ohgushi, and P. W. Price, editors. Effects of resource distribution on animal–plant interactions. Academic Press, New York, New York, USA.

Saunders, D. A., Jr., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology **5**:18–32.

Seavey, S. R., and K. S. Bawa. 1986. Late-acting self-incompatibility in angiosperms. Botanical Review **52**:195–219.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. BioScience **31**:131–134.

Snow, A. A. 1982. Pollination intensity and potential seed set in *Passiflora vitifolia*. Oecologia (Berlin) **55**:231–237.

———. 1986. Pollination dynamics in *Epilobium canum* Onagraceae: consequences for gametophytic selection. American Journal of Botany **73**:139–151.

Sobrevila, C. 1988. Effects of distance between pollen donor and pollen recipient on fitness components in *Espeletia schultzii*. American Journal of Botany **75**:701–724.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W.H. Freeman, New York, New York, USA.

Sowig, P. 1989. Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia (Berlin) **78**:550–558.

Spears, E. E. 1987. Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta*. Journal of Ecology **75**:351–362.

Streng, D. R., J. S. Glitzenstein, and P. A. Harcombe. 1989. Woody seedling dynamics of an East Texas floodplain forest. Ecological Monographs **59**:177–204.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Annual Review of Ecology and Systematics **12**:253–279.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pages 330–344 *in* M.E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer, Sunderland, Massachusetts, USA.

Thomson, J. D. 1983. Component analysis of community-level interactions in pollination systems. Pages 451–460 *in* C. E. Jones and R. J. Little, editors. Handbook of experimental pollination ecology. Scientific & Academic Editors, New York, New York, USA.

Vervoorst, F., P. R. Legname, and A. Grau. 1981. Excursión botánica a Hualinchay, Tacanas, y Gonzalo. XVIII Jornadas Argentinas de Botánica, proceedings. S.M. de Tucumán, Tucumán, Argentina.

Visscher, P. K., and T. D. Seeley. 1982. Foraging strategies of honeybee colonies in a temperate deciduous forest. Ecology **63**:1790–1801.

Waser, N. M., and M. V. Price. 1983. Optimal and actual outcrossing in plants, and the nature of plant-pollinator interaction. Pages 341–359 *in* C. E. Jones and J. E. Little, editors. Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, New York, USA.

Waser, N. M., and M. V. Price. 1989. Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. Evolution **43**:1097–1109.

Waser, N. M., and M. V. Price. 1991*a*. Outcrossing distance effects in *Delphinium nelsonii*: pollen loads, pollen tubes, and seed set. Ecology **72**:171–179.

Waser, N. M., and M. V. Price. 1991*b*. Reproductive costs of self-pollination in *Ipomopsis aggregata* (Polemoniaceae): are ovules usurped? American Journal of Botany **73**:1036–1043.

Whelan, R. J., and R. L. Goldingay. 1989. Factors affecting fruit-set in *Telopea speciosissima* (Proteaceae): the importance of pollen limitation. Journal of Ecology **77**:1123–1134.

Wiens, D. 1984. Ovule survivorship, brood size, life history, and reproductive success in plants. Oecologia (Berlin) **64**: 47–53.

Willson, M. F., and N. Burley. 1983. Mate choice in plants: tactics, mechanisms, and consequences. Princeton University Press, Princeton, New Jersey, USA.

Wright, S. 1943. Isolation by distance. Genetics **28**:114–138.

APPENDIX I

TABLE A1. Among-plant means and standard deviations of per-plant mean number of pollen grains per flower (PG); mean number of pollen tubes per flower (PT); number of fruits per flower, or per inflorescence in the Mimosoideae (FS); and mean number of seeds per fruit (SS) for each sampled habitat unit and species. See Table 1 for characteristics of the study sites.

	Study sites	Continuous forest			Large fragment			Small fragment		
		n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
Acacia aroma										
PT	2	8	4.4	1.1	8	3.7	0.9	8	3.0	0.5
	4	10	6.0	2.4	9	3.6	1.6	7	1.9	1.8
FS	2	9	0.05	0.08	10	0.13	0.09	9	0.03	0.02
	4	10	0.12	0.08	10	0.04	0.06	10	0.05	0.05
SS	2	8	5.9	1.6	10	5.7	1.9	8	7.9	1.5
	4	10	6.3	1.3	9	6.9	1.6	10	6.5	1.2
*A. atramentaria**										
PT	1	10	5.5	1.4	10	4.4	1.5	...	...	...
FS	1	10	0.01	0.02	10	0.05	0.04	...	...	...
SS	1	8	6.1	2.1	10	6.0	1.4	...	...	...
A. furcatispina										
PT	5	10	3.6	1.5	10	3.6	2.6	10	3.5	1.0
FS	5	10	0.13	0.08	10	0.20	0.07	10	0.24	0.09
SS	5	10	4.8	1.2	10	4.9	0.9	10	4.5	0.8
*A. praecox**										
PT	4	20	3.4	1.4	10	4.2	1.1	...	...	...
	5	10	5.2	0.8	10	5.4	1.0	...	...	...
FS	4	20	0.14	0.11	10	0.26	0.18	...	...	...
	5	10	0.21	0.14	10	0.23	0.16	...	...	...
SS	4	20	6.6	0.8	10	7.0	0.4	...	...	...
	5	10	6.8	0.7	10	6.6	0.5	...	...	...
Atamisquea emarginata										
PG	1	10	21.6	5.9	10	23.9	9.3	6	24.8	8.6
	2	10	17.8	5.7	9	21.3	9.7	9	15.8	4.3
	3	10	22.8	6.3	10	21.0	7.8	9	25.5	5.7
	5	10	35.5	6.4	10	32.8	8.3	10	39.7	10.2
PT	1	10	11.8	3.1	10	10.7	3.8	6	10.5	4.6
	2	10	10.4	2.7	9	10.3	5.0	9	7.0	1.3
	3	10	10.8	2.6	10	8.6	3.3	9	8.2	2.7
	5	10	16.7	4.1	10	14.3	3.5	10	14.1	3.3
FS	1	10	0.50	0.15	10	0.50	0.09	6	0.34	0.14
	2	10	0.30	0.11	9	0.41	0.13	9	0.26	0.11
	3	10	0.46	0.14	10	0.32	0.14	9	0.39	0.16
	5	10	0.36	0.07	10	0.28	0.10	10	0.27	0.09
Caesalpinia gilliesi										
PT	3	9	2.0	1.0	10	2.2	2.1	9	0.9	0.8
FS	3	9	0.06	0.04	9	0.07	0.03	9	0.07	0.04
SS	3	8	3.1	0.8	8	3.1	0.5	8	2.8	0.8
Cassia aphylla†										
PT	5	10	17.0	3.9	...	...	...	10	12.8	6.0
FS	5	10	0.28	0.14	...	...	...	10	0.23	0.11
SS	5	10	18.3	2.1	...	...	...	10	17.2	2.7
Cercidium australe (1989)										
PG	1	10	22.7	3.7	10	22.4	6.4	6	19.1	5.2
	2	10	17.4	5.6	10	11.5	5.1	10	18.3	3.6
	3	10	17.7	3.4	10	17.4	3.5	10	8.6	3.9
	5	10	26.2	4.2	10	25.5	4.6	10	24.1	5.1
PT	1	10	8.6	1.7	10	7.6	1.9	10	4.6	2.0
	2	10	7.3	1.9	10	4.5	1.6	10	5.5	0.9
	3	10	8.9	2.4	10	7.0	1.4	10	3.3	1.3
	5	10	9.8	2.1	10	7.9	2.2	10	7.1	1.7
FS	1	10	0.14	0.09	10	0.08	0.05	10	0.08	0.06
	2	10	0.12	0.06	10	0.10	0.07	10	0.10	0.09
	3	10	0.10	0.06	10	0.05	0.04	10	0.09	0.08
	5	10	0.12	0.04	10	0.12	0.04	10	0.12	0.04
SS	1	10	1.6	0.2	10	1.4	0.1	10	1.6	0.3
	2	10	1.4	0.2	10	1.6	0.3	10	1.6	0.3
	3	10	1.5	0.2	10	1.3	0.1	10	1.5	0.3
	5	10	1.3	0.1	10	1.4	0.1	10	1.3	0.1

APPENDIX I. Continued.

	Study sites	Continuous forest			Large fragment			Small fragment		
		n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
C. australe (1990)										
PG	1	10	14.9	2.9	10	14.0	5.2	10	12.2	3.5
	2	10	15.2	3.1	10	17.4	4.8	11	20.1	3.7
	3	10	15.8	2.7	10	20.6	4.5	10	13.7	4.2
	5	10	19.6	5.5	10	20.2	4.1	10	22.9	5.6
PT	1	10	4.9	1.3	10	4.3	1.4	10	3.6	1.1
	2	10	7.0	1.8	10	6.7	2.7	11	7.0	2.1
	3	10	6.8	2.0	10	7.1	1.7	10	4.5	1.7
	5	10	7.6	1.9	10	7.6	1.0	10	6.9	1.7
FS	1	11	0.10	0.07	10	0.05	0.03	10	0.04	0.05
	2	10	0.07	0.06	10	0.07	0.04	11	0.07	0.04
	3	11	0.09	0.07	11	0.08	0.05	10	0.08	0.04
	5	10	0.08	0.04	10	0.13	0.08	10	0.07	0.07
SS	1	11	1.7	0.3	10	1.5	0.1	10	1.7	0.3
	2	10	1.6	0.2	10	1.5	0.4	11	1.7	0.5
	3	11	1.6	0.3	11	1.5	0.3	10	1.8	0.4
	5	10	1.4	0.1	10	1.5	0.3	10	1.4	0.2
Justicia squarrosa										
PG	5	101	11.4	10.7	104	7.2	8.1	101	8.0	7.9
FS	5	102	0.48	0.23	105	0.35	0.22	105	0.40	0.24
SS	5	103	3.8	0.5	103	3.7	0.6	110	3.7	0.5
*Ligaria cuneifolia**										
PT	1	10	3.9	1.5	...	...	...	10	11.3	4.8
FS	1	10	0.48	0.21	...	...	...	10	0.38	0.15
Mimosa detinens										
PT	5	10	3.5	1.4	10	3.5	1.3	11	2.9	1.4
FS	5	10	0.52	0.25	10	0.49	0.31	11	0.24	0.19
SS	5	10	4.4	0.7	10	4.3	0.7	11	3.8	0.8
Opuntia quimilo										
PT	2	10	429.4	256.5	9	410.5	246.2	6	364.3	353.1
	5	10	158.7	88.7	10	143.9	90.1	10	125.7	72.5
FS	2	10	0.43	0.47	9	0.14	0.31	6	0.28	0.44
	5	10	0.15	0.28	10	0.07	0.22	10	0.16	0.29
SS	2	6	147.0	91.0	2	78.5	33.2	3	167.3	123.7
	5	6	103.0	73.7	3	95.8	117.6	8	82.5	74.3
Portulaca umbraticola										
PG	3	104	162.1	95.4	101	170.1	117.0	105	149.6	100.6
	5	106	195.8	114.0	109	151.0	98.6	93	141.8	81.9
SS	3	100	139.4	40.4	100	131.6	41.3	100	123.7	36.6
	5	60	101.5	32.5	60	92.7	29.4	60	90.7	26.3
Prosopis nigra (1989)										
PG	2	6	14.9	6.3	10	15.1	6.2	1	12.7	...
	3	10	17.6	4.8	10	23.1	6.6	9	13.1	5.4
	5	10	15.6	5.7	10	13.8	5.1	10	17.5	7.2
PT	2	10	5.1	2.7	10	4.8	1.8	1	4.3	...
	3	10	9.0	2.8	10	8.3	2.9	10	3.8	2.0
	5	10	6.5	2.0	10	5.1	2.1	10	4.9	2.1
FS	2	10	0.23	0.30	10	0.21	0.30	1	0.00	...
	3	10	0.33	0.40	10	0.36	0.43	10	0.15	0.15
	5	10	0.15	0.18	10	0.04	0.06	10	0.06	0.07
SS	2	9	8.0	1.5	8	7.2	1.8	...	...	...
	3	10	9.1	1.7	9	10.1	2.1	10	8.0	2.3
	5	10	8.3	2.2	7	6.9	1.3	9	6.9	1.8
Prosopis nigra (1990)										
PG	1	10	10.5	3.4	10	12.1	4.8	10	12.5	6.7
	2	10	10.0	5.8	10	14.7	7.2	2	19.4	1.7
	3	10	13.8	5.8	10	13.2	6.2	10	11.3	7.3
	5	11	10.9	4.9	10	17.1	5.7	10	13.5	6.0
PT	1	10	5.9	2.5	10	5.4	2.0	10	5.5	2.2
	2	10	6.0	3.4	10	5.9	3.2	2	8.1	1.0
	3	10	7.5	3.2	10	5.3	2.9	10	3.9	2.8
	5	11	6.2	2.9	10	7.9	3.3	10	5.1	2.1

APPENDIX I. Continued.

	Study sites	Continuous forest			Large fragment			Small fragment		
		n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
FS	1	10	1.81	1.19	10	1.29	0.80	10	1.64	1.71
	2	10	1.36	1.00	10	1.06	0.84	2	0.29	0.40
	3	10	1.98	1.00	10	1.65	0.67	10	0.54	0.42
	5	9	1.10	0.74	10	1.76	1.27	10	1.10	0.60
SS	1	10	7.7	1.5	10	7.6	1.6	10	6.6	1.0
	2	10	8.3	0.9	9	5.8	1.0	1	4.4	···
	3	10	8.0	1.2	10	7.0	0.9	10	7.6	1.7
	5	9	8.0	1.1	10	8.6	1.6	10	8.1	1.4
Rhipsalis lumbricoides										
PT	5	10	232.5	68.2	10	125.2	105.4	10	166.1	99.1
FS	5	10	0.85	0.12	10	0.80	0.13	10	0.83	0.09
SS	5	10	56.0	12.3	10	36.3	10.6	10	42.4	8.5
Tillandsia lumbricoides										
PT	1	5	97.0	19.0	5	115.6	20.3	5	88.5	47.1
FS	1	5	0.82	0.06	5	0.73	0.17	5	0.74	0.12
SS	1	5	160.7	17.0	5	160.3	33.9	5	147.3	40.7

* Adequate sample sizes existed only for plants occurring in the large fragment and nearby continuous forest units.
† Adequate sample sizes existed only for plants occurring in the small fragment and nearby continuous forest units.

APPENDIX II

TABLE A2. Phenology and floral characteristics of the 16 study species.

Species	Flowering phenology	Flower life-span (d)*	Flower biology
Acacia aroma	Mid Oct–end Nov	1+	Compound yellow flower heads (diameter ≈ 1.5 cm) containing 50–110 florets
A. atramentaria	End Aug–end Sep	1+	Compound yellow flower heads (diameter ≈ 1.5 cm) containing 40–80 florets
A. furcatispina	End Nov–end Dec	1+	Compound creamy-white flower heads (diameter ≈ 1.5 cm) containing 20–30 florets
A. praecox	Mid Aug–end Sep	1+	Compound cream-colored flower heads (diameter ≈ 2 cm) containing 25–35 florets
Atamisquea emarginata	End Sep–end Dec	2–3	Zygomorphic, protandrous cream-colored flowers (≈ 1.5 cm)
Caesalpinia gilliesi	End Sep–mid Dec	1	Zygomorphic, yellow flowers (≈ 10 cm)
Cassia aphylla	Mid Oct–end Nov	1	Asymmetric, yellow flowers (≈ 2 cm)
Cercidium australe	Mid Oct–end Nov	1	Zygomorphic, yellow flowers (≈ 1.5 cm)
Justicia squarrosa	End Jan–mid Feb	2	Zygomorphic, protandrous, light blue flowers (≈ 2.5 cm)
Ligaria cuneifolia	Mid Mar–end Apr	2–4	Actinomorphic, tubular, protandrous, red flowers (≈ 4 cm)
Mimosa detinens	Mid Oct–end Nov	1+	Compound white flower heads (≈ 2 cm) containing 20–40 florets
Opuntia quimilo	End Sep–mid Dec	1	Actinomorphic, bowl-shaped orange flowers with numerous stamens (≈ 7 cm)
Portulaca umbraticola	Mid Dec–mid Jan	1	Actinomorphic, purple flowers with numerous stamens (≈ 5 cm)
Prosopis nigra	Mid Sep–mid Oct	3–7	Compound cream-colored flower brushes containing 150–350 florets (4–8 cm)
Rhipsalis lumbricoides	Mid Aug–mid Sep	1	Actinomorphic, white flowers (≈ 2 cm)
Tillandsia ixioides	Mid Jul–mid Aug	7–14	Actinomorphic, tubular, yellow flowers (≈ 2 cm)

* Inflorescence life-span in the Mimosoideae.