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Connectance, Dependence Asymmetries, and Coevolution**

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PATTERNS OF MUTUALISTIC INTERACTIONS IN POLLINATION  
AND SEED DISPERSAL: CONNECTANCE, DEPENDENCE  
ASYMMETRIES, AND COEVOLUTION

PEDRO JORDANO

Unidad de Ecología y Etología, Estación Biológica de Doñana, 41013 Sevilla, Spain

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Animals are the main transfer agents during the two dispersive phases of reproductive cycles in higher plants: pollination of flowers and seed delivery to germination sites. The relationship is mutually beneficial, since animals use the variety of resources provided by plants around the reproductive structures (floral parts, nectar, fragrances, fleshy pulp, etc.). These mutual benefits have been a major factor in the evolution of angiosperms (Mulcahy 1979; Tiffney 1984), insects (Strong et al. 1984), and several groups of vertebrates (Snow 1971, 1981; Stiles 1981; Heithaus 1982; Marshall 1983).

Consideration of the ways plant and animal mutualists interact is fundamental for understanding coevolution as a reciprocal evolutionary change. However, coevolutionary change is basically a diffuse process involving sets of species, and pairwise coevolution (Janzen 1980) is rare in most plant-animal mutualisms (Thompson 1982; several authors in Futuyma and Slatkin 1983; Schemske 1983; Howe 1984). In most instances the interacting taxa lack a common history, such that the established relationship relies on preadaptations evolved in isolation. Second, facultative interactions of low specificity are the rule and generate variable selection regimes. Third, there exists an enormous temporal and spatial variation (e.g., between seasons in flower and fruit production, between localities in the kind of interacting animals), which increases the variance of the mutual selective pressures.

Understanding how the number and the strength of the interactions are distributed among the species pairs is basic for analyzing the evolution of mutualisms in a community context. The mutualistic interactions can be arranged as a matrix of  $m \times n$  dependence values, between the  $m = 1, 2, \dots, i$  species of plants and the  $n = 1, 2, \dots, j$  species of animals, such that  $S = m + n$ , the total number of species in the system. The elements  $a_{ij}$  can take values  $a_{ij} = 1$ , if species  $i$  and  $j$  interact, or  $a_{ij} = 0$ , if no mutual interaction occurs. We may examine which proportion of all the  $mn$  possible interactions,  $C$ , actually takes place. This value ( $C$ ) is defined as the *connectance* of the mutualistic system in a way similar to the well-known connectance of food webs (Yodzis 1980). Furthermore, for every

nonzero element (interacting pair of species), estimates can be made of  $I$ , the relative magnitude of interaction. Examination of both the fraction of mutualistic interactions established and the frequency distributions of mutual dependence values is of great relevance to understanding constraints on plant-animal coevolution.

Here I show that similar patterns exist in the structure of interactions in plant-pollinator and plant-seed-disperser assemblages. Specifically, I wish to examine how these patterns may affect the mode of coevolution between mutualists, rather than dealing with the consequences for the relationship between complexity-stability in these systems. Consideration of the joint behavior of  $S$ ,  $C$ , and  $I$  has generated considerable debate about the stability properties of food webs (May 1972; Lawlor 1978; Rejmánek and Starý 1979; Yodzis 1980; Briand 1983; Auerbach 1984), but discussion of this specific issue with reference to mutualisms is beyond the scope of this paper. Rather, I take this quantitative approach to describe how interactions are distributed between sets of mutualistic plants and animals. First, patterns of occurrence of interactions among plants and their pollinators and dispersers are discussed. Second, I study the frequency distributions of interaction strengths for the particular case of plants with fleshy fruits and their avian seed dispersers. Explicit consideration of multi-species assemblages emphasizes the diffuse nature of these relations and may aid in understanding how diffuse coevolution proceeds.

#### THE DISTRIBUTION OF INTERACTIONS AMONG MUTUALISTS

Levels of mutual dependence between plants and their pollinators and seed dispersers have seldom been quantified for whole sets of interacting species; thus, the analyses below are necessarily restricted to the cases of completely studied subsystems in which interactions have been described for subsets of either the plants or animals. I have assembled a total of 36 pollination studies and 19 seed-dispersal studies (table 1). All the selected papers on seed dispersal focus on frugivorous birds and their food plants; eight of them report interactions for the entire frugivorous avifauna at the specific study sites, and the remaining select particular taxa (usually family-based). The pollination studies are analogous in coverage, focusing on specific families (e.g., Trochilidae, Meliphagidae, Apoidea, Megachilidae) or genera (e.g., *Ficus*, *Bombus*) of either the plants or pollinators. In some sense, these mutualistic systems are analogous to *sink food webs* (Cohen 1978), in which species from either the pollinator, disperser, or host-plant community are selected and records are given of the plants or animals with which they interact. A discussion of the possible biases inherent in comparisons within such a heterogeneous assemblage of field studies is presented in the Appendix.

As expected, the number of interactions increases with the number of species involved in the mutualism (log-transformed data, fig. 1, table 2). This increase is slower for pollination than for dispersal systems, which have a steeper interactions-species line (fig. 1;  $b = 0.9564$  and  $1.2010$ , respectively, table 2). The species richness (i.e., the number of species) of pollination and seed-dispersal systems considered here is similar (table 2, see Appendix), and the average fraction of

TABLE 1

SPECIES RICHNESS AND PROPORTION OF ACTUAL INTERACTIONS IN PLANT-ANIMAL POLLINATION AND SEED-DISPERSAL MUTUALISMS

Organisms, Location	<i>m</i>	<i>n</i>	<i>i</i>	<i>C</i> (%)	Source
PLANT-POLLINATOR SYSTEMS					
Bog plants, British Columbia	14	10	56	40.0	Douglas 1983
Mediterranean shrubland, SW Spain	25	116	295	10.2	J. Herrera 1985
Honeyeater plants, SE Australia	7	7	16	32.6	Pyke 1983
Mistletoes, honeyeaters, dicaeids, Australia	32	27	84	9.7	Reid 1983
Hummingbirds					
Trinidad	43	9	134	34.6	Snow & Snow 1972
Costa Rica	25	5	37	29.6	Wolf et al. 1976
Costa Rica	18	4	46	63.9	Wolf et al. 1976
Arizona	9	4	23	63.9	Brown & Kodric-Brown 1979
SE Brazil	16	7	26	23.2	Snow & Teixeira 1982
Colombia	14	9	46	36.5	Snow & Snow 1980
	23	12	64	23.2	Snow & Snow 1980
	13	6	27	34.6	Snow & Snow 1980
<i>Heliconia</i> spp., hummingbirds, Costa Rica	9	9	53	65.4	Stiles 1975
Bumblebees					
N Sweden	50	9	53	11.8	Ranta & Lundberg 1981
S Finland	59	8	49	10.4	Ranta et al. 1981
Maine	21	6	51	40.5	Heinrich 1976
Rocky Mountains	14	7	39	39.8	Pleasants 1980
	16	8	39	30.5	Pleasants 1980
	11	8	25	28.4	Pleasants 1980
	9	5	21	46.7	Pleasants 1980
Montana	7	11	37	48.1	Bauer 1983
<i>Pedicularis</i> spp., bumblebees, Colorado	7	12	42	50.0	Macior 1970
Bees, bumblebees, Ontario	5	21	54	51.4	Reader 1975
Orchids, euglossine bees					
Panama	21	29	79	13.0	Ackerman 1983
Guyana	9	17	27	17.7	Williams & Dodson 1972
Hymenoptera (not Formicidae), SW Spain	23	67	80	5.2	J. Herrera 1985
<i>Melipona</i> spp., Surinam	56	9	79	15.7	Engel & Dingemans-Bakels 1980
<i>Trigona</i> spp., Surinam	50	17	74	8.7	Engel & Dingemans-Bakels 1980
Megachilidae, Finland	30	5	68	45.3	Kapyla 1978
Bees					
Brazil*	95	33	183	5.8	Roubik 1980
Guyana*	109	38	248	6.0	Roubik 1980
Figs, agaonid wasps					
La Reunión	5	15	15	20.0	Wiebes 1981
Zimbabwe (Rhodesia)	14	86	86	7.1	Bouček et al. 1981
Figs, subsection <i>Varinga</i> , several locations	7	5	7	20.0	Wiebes 1979
<i>Ficus</i> spp., several locations	28	24	38	5.7	Wiebes 1979
Figs, section <i>Conosycea</i> , several locations	10	7	10	14.3	Wiebes 1979

(continued)

TABLE 1 (Continued)

Organisms, Location	<i>m</i>	<i>n</i>	<i>i</i>	<i>C</i> (%)	Source
PLANT-SEED DISPERSER SYSTEMS					
Temperate deciduous forest					
NW Spain	12	7	45	53.6	Gutián 1984
New York	13	15	47	24.1	Sherburne 1972
England	12	6	22	30.6	Sorensen 1981
New Jersey	7	15	26	24.8	Baird 1980
Lowland Mediterranean					
shrubland, SW Spain	14	10	65	46.4	Herrera 1984
Montane Mediterranean shrubland, SE Spain					
<i>Heliconia</i> spp., Costa Rica	9	28	127	50.4	Stiles 1979
Mistletoes, honeyeaters, dicaeids, Australia	32	33	65	6.2	Reid 1983
Frugivorous pigeons, NE Australia	72	7	144	28.6	Crome 1975
Birds of paradise, New Guinea	31	9	119	42.7	Beehler 1983
Tanagers, honeycreepers, Trinidad	65	14	249	27.4	Snow & Snow 1971
Lauraceae, Costa Rica	15	16	94	39.2	Wheelwright et al. 1984
Tropical moist forest, Mexico	57	73	221	5.3	Trejo 1976
Coastal dune forest, South Africa	16	35	143	25.5	Frost 1980
Tropical moist forest, Mexico	5	25	80	64.0	Kantak 1979
Montane rain forest					
Costa Rica†	171	70	709	5.9	Wheelwright et al. 1984
Costa Rica‡	43	55	388	16.4	Wheelwright et al. 1984
Costa Rica§	162	23	550	14.8	Wheelwright et al. 1984

NOTE.—*m*, number of plant species. *n*, number of animal species. *i*, number of interactions recorded. *C*, percentage of interactions with respect to the total possible ( $m \times n$ ).

\* Only interactions between genera of plants and bees.

† Including all records reported by the authors for Monteverde forest.

‡ Including only records for plant species with more than 2 h of observation and 10 or more censuses.

§ Including only records for bird species whose diets are reasonably well documented.

interactions established (average connectance) does not differ significantly between them ( $U = 291$ ,  $t_s = 0.97$ ,  $P > 0.40$ ). When species are added, however, differences already present in the mode of interactions increase. Covariance analysis reveals highly significant differences between the two groups in the number of interactions when the species numbers are kept constant ( $F = 17.08$ ,  $df = 1, 52$ ,  $P < 0.001$ ). The slopes of the two equations also differ ( $F = 4.61$ ,  $df = 1, 51$ ,  $P < 0.05$ ). Thus, an increase of 10 species adds, on the average, 15 new interactions in pollination mutualisms and 29 in seed-dispersal mutualisms, approximately a twofold difference.

In spite of the increase in the number of mutualistic interactions in more-diverse assemblages, the relative value of the interactions with respect to the total possible interactions (the connectance) decreases as species are added (table 1). As shown by an exponential fit (see, e.g., Briand 1983; Auerbach 1984), connectance decreases more rapidly in pollination systems ( $C = 0.4994 \exp[-0.017 S]$ ;  $R^2 = 0.6930$ ,  $P < 0.01$ ) than in dispersal systems ( $C = 0.4745 \exp[-0.009 S]$ ;  $R^2 =$

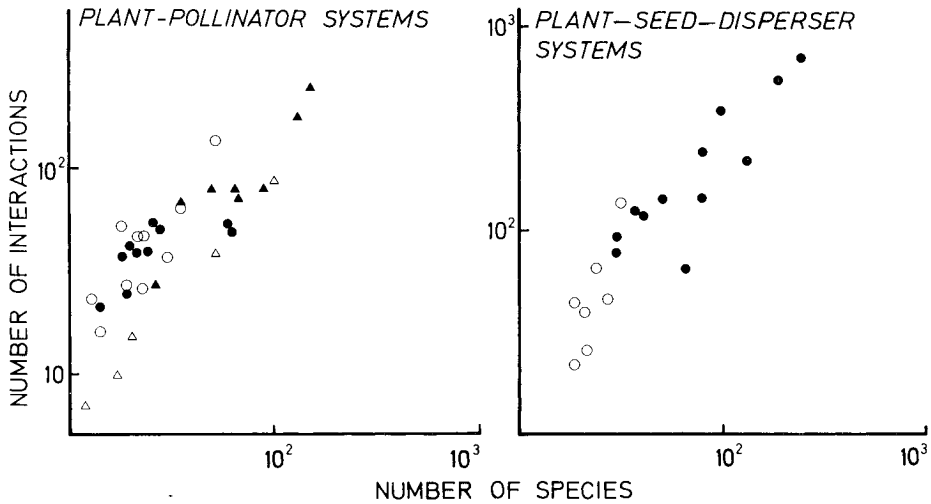


FIG. 1.—The relationship between the total number of plant and animal species involved in pollination and seed-dispersal mutualisms ( $N = 33$  and  $19$ , respectively; see table 1) and the number of pairwise interactions actually observed. Three pollination systems not assignable to a unique pollinator group have been excluded from this figure but included in the calculations. Pollinator systems: *solid circles*, bumblebees; *open circles*, hummingbirds and honey-eaters; *solid triangles*, bees (euglossine, oligolectic, and stingless bees); *open triangles*, fig wasps. Seed-disperser systems: *solid circles*, tropical systems; *open circles*, nontropical systems. For references, see table 1.

$0.5535$ ,  $P < 0.05$ ). The difference between the two regression coefficients is highly significant ( $F = 110.2$ ,  $P \ll 0.001$ ); thus, for a fixed number of species, plant-pollinator assemblages show lower connectances than plant-disperser assemblages. This suggests higher specificity in pollination mutualisms and differences between the two mutualisms in the mode of interaction. Both are consequences of differential rates of interaction increase, as stated above (see the Appendix for further discussion on the effects of sampling biases).

Similar relations between  $C$  and  $S$  have been repeatedly documented in collections of food webs (Cohen 1978; Rejmánek and Starý 1979; Briand 1983; Margalef and Gutiérrez 1983); although the result is consistent with the hypothesis that dynamic constraints exist on food-web design and stability (May 1972; Pimm 1982), there are other explanations for the observed trend. Thus, connectance must decrease with  $S$  if each species in the system has a number of mutualists independent of the total number of species. The actual number of interactions scales in proportion to  $S = m + n$  (the total number of species), but the potential number of interactions scales as  $mn$  (see Pimm 1980, 1982). Interactions therefore become rare as species richness increases because the average fraction of mutualists per species is progressively smaller (see fig. 1). But the average number of interactions per species varies independently of the number of species ( $N = 40$  sets of plant or pollinator species with complete records of mutualists,  $r = 0.176$ ,  $P > 0.20$ ;  $N = 29$  sets of plant or disperser species,  $r = 0.287$ ,  $P > 0.10$ ; table 1).

TABLE 2  
 NUMBER OF INTERACTIONS RECORDED AND NUMBER OF PLANT AND  
 ANIMAL SPECIES INCLUDED IN POLLINATION AND  
 SEED-DISPERSAL SYSTEMS

	MEAN $\pm$ SD	
	Pollination System	Seed-Dispersal System
No. of plant species	25.1 $\pm$ 23.9	40.4 $\pm$ 48.7
No. of animal species	18.7 $\pm$ 24.0	24.3 $\pm$ 20.8
Average no. of interactions per plant species <sup>a</sup>	4.1 $\pm$ 3.2 (11)	6.0 $\pm$ 4.4 (14)
Average no. of interactions per animal species <sup>a</sup>	5.3 $\pm$ 3.5 (29)	9.2 $\pm$ 6.8 (15)
Average connectance	29.4 $\pm$ 18.3	32.4 $\pm$ 17.9
N	36	19
y-intercept <sup>b</sup>	.2124	.0123
Slope <sup>b</sup>	.9564	1.2010
F <sup>b</sup>	89.46***	84.44***

<sup>a</sup> The number of interactions averaged over those studies reporting complete sets of interactions, that is, those focusing on a particular plant or animal taxon and documenting all the species interacting with it. Sample size is in parentheses.

<sup>b</sup> Regressions for the number of species ( $x$ ) versus the number of interactions ( $y$ ). The data are log-transformed.

\*\*\*  $P < 0.001$ .

A significant heterogeneity in connectance values exists between tropical and nontropical plant-disperser assemblages (fig. 1): the nontropical assemblages exhibit higher connectance values ( $U = 10$ ,  $P = 0.036$ ), because they are composed of fewer species. Thus, an analysis of covariance with the number of species as the covariate failed to detect significant heterogeneity in the y-intercepts ( $F = 0.58$ ,  $P > 0.25$ ,  $df = 1, 16$ ); differences in the slopes are only marginally significant ( $F = 4.34$ ,  $0.05 < P < 0.10$ ). Therefore, tropical and nontropical assemblages of plants and avian seed dispersers have similar structure and interaction patterns; the observed differences are attributable to variation in the numbers of species. Since most tropical systems included in table 1 are incomplete (i.e., subsets of either plants or frugivores in particular habitats), connectance values for complete systems in tropical habitats might be even smaller (see, e.g., the values for Monteverde data in table 1; Wheelwright et al. 1984).

Differences in connectance between assemblages involving different types of pollinators are significant (fig. 2): the trend is for average connectance to decrease from plant-hummingbird ( $C = 0.408$ ) through plant-bumblebee ( $C = 0.344$ ), plant-bee ( $C = 0.135$ ), and fig-agaonid ( $C = 0.134$ ) assemblages. Although these differences remain after removing the effects of differences in the number of species ( $F = 9.85$ ,  $df = 3, 28$ ,  $P < 0.001$ ; for the y-intercepts, see fig. 1), the slopes do not differ significantly among the pollinator groups considered here ( $F = 0.95$ ,



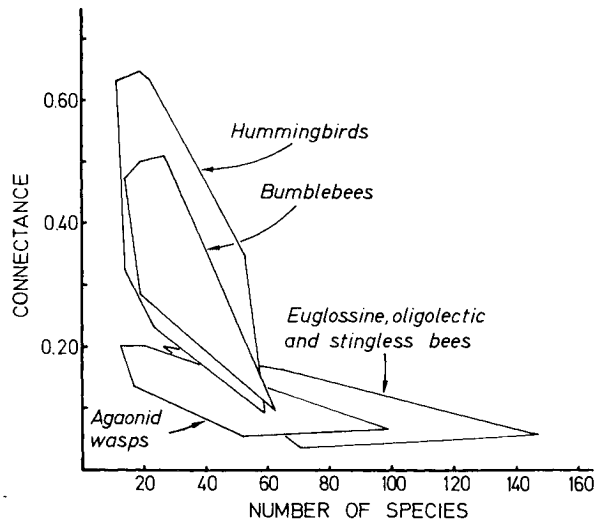


FIG. 2.—Connectance decreases with increasing species richness in plant-pollinator mutualisms. Differences in connectance values for different types of pollinators suggest specific modes of interaction (polygons include the range of values for different groups; see table 1).

$df = 3,25, P > 0.50$ ). This group effect suggests that different kinds of pollinators have particular modes of interaction with plants and that these modes ultimately determine differences in the overall specificity of the mutualism. Thus, the low connectance of fig-agaonid wasp assemblages is probably related to their origin in an extremely specific host-parasite interaction (Ramírez 1970).

#### THE DISTRIBUTION OF DEPENDENCE VALUES: THE CASE OF AVIAN SEED DISPERSAL

For every interacting pair of species ( $a_{ij} = 1$ ), a value for the interaction strength can be obtained to estimate the level of mutual dependence. I define *dependence* as the relative interaction strength between two taxa; that is, the percentage of all interactions occurring between a particular pair of species. The dependence of a plant species on a bird species was estimated from such reported quantities as the percent of seeds ingested, the percent of visits recorded, etc., for the disperser on that particular plant. The relative importance of a given plant to a bird species was derived from the percent of the diet made up by fruits of each plant species, estimated from the number of fruits, calories, etc. These estimates of mutual dependence are probably the best available with the information at hand and provide comparative values of the relative interaction strengths in these mutualisms. Detailed discussions about the quantification of dependence strength in plant-frugivore mutualistic systems have been presented elsewhere (Herrera and Jordano 1981; Herrera 1984; Jordano 1984; see also Primack and Silander 1975; Wheelwright and Orians 1982). Obviously, these values do not indicate any aspect of the “quality” of the interaction, which poses serious interpretational problems (Janzen 1983).

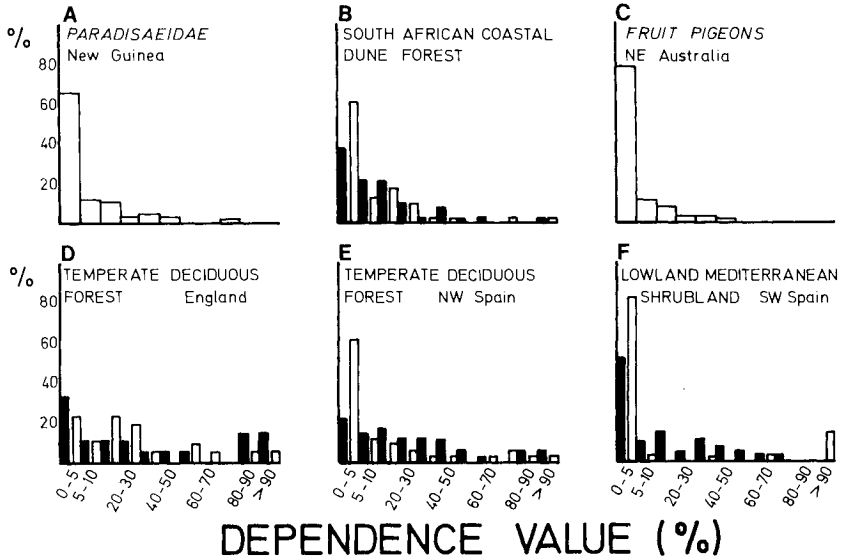


FIG. 3.—Frequency distributions of dependence values in several plant-bird seed-dispersal systems. Different distributions are presented for plant reliance on the bird species in the assemblage (*solid bars*) and bird dependence on the plants (*open bars*). Dependence was quantified by obtaining values of relative importance (0%–100%) from interaction records in the original papers (e.g., number of seeds dispersed, number of visits to plants, etc.); therefore, they represent estimates of quantitative dependence for seed removal (plants) and diet composition (birds). A, Beehler 1983; B, Frost 1980; C, Crome 1975; D, Sorensen 1981; E, Guitián 1984; F, Jordano 1984. See text for further details.

I have assembled the information on plant-disperser systems for which complete sets of species have been studied in detail and for which quantified estimates of the interaction strengths are available (Frost 1980; Sorensen 1981; Guitián 1984; Herrera 1984; Jordano 1984). Obtaining this quantitative information for complete tropical systems is clearly complicated by the large number of species of both the frugivorous avifauna and the food plants (Wheelwright et al. 1984); data are therefore available only for limited subsets of plants and birds (table 1; see the Appendix). I have thus considered the dependence patterns of two groups of tropical frugivorous birds for which detailed information on the plants utilized is available (fruit pigeons, Crome 1975; see also Frith et al. 1976; and birds of paradise, Beehler 1983).

The frequency distributions of the dependence values in the plant-avian disperser mutualisms considered are extremely skewed to the right (fig. 3). Weak interactions greatly exceed in number the rare instances of strong dependence. Skewness values are all positive and significantly greater than zero, ranging from 1.13 to 3.79 ( $t_s \geq 3.06$ ,  $P < 0.05$ ; with the exception of Sorensen 1981,  $g_1 = 0.64$ ). When dependence values are available for both plant and animal species sets, the animals show greater skewness than the plants ( $g_1 = 1.75$  and  $g_1 = 3.26$ ; for the summed frequency distributions of plants and birds, respectively,  $t_s = 119.5$ ,  $P \ll 0.001$ ). This results in significantly different distributions of plants and birds in

all the cases considered ( $D \geq 0.217$ ,  $P < 0.05$ , Kolmogorov-Smirnov test), except for Sorensen's study ( $D = 0.136$ , NS; fig. 3). In addition, the summed distributions of dependence values for tropical and nontropical birds (information is insufficient for comparison of the plant distributions) also differ significantly ( $D = 0.146$ ,  $P < 0.05$ ); bird dependence distributions are much more skewed toward low values in tropical systems ( $g_1 = 3.16$ ) than in temperate assemblages ( $g_1 = 1.88$ ;  $t_s = 65.1$ ,  $P < 0.001$ ).

For every subset of species analyzed (either plant or animal) the average strength of the interaction tends to decrease as the number of species increases ( $N = 10$ ,  $r = -0.829$ ,  $P < 0.01$ ). Thus, systems composed of a large number of species (such as the tropical ones) are characterized by a predominance of weak interactions and an absence of strong ones (see fig. 3), as well as a relatively low number of established interactions (connectance). The simpler temperate assemblages typically show a higher proportion of strong dependence values within a more-interconnected network of relationships. These tendencies in the mode of interaction appear to depend exclusively on the number of species rather than on artifactual patterns caused by the difficulty of documenting interactions in increasingly diverse communities. Thus, the studies included are shown to cover adequately the actual interactions (for further discussion, see the Appendix).

The few observed cases of high dependence in either the plant or bird assemblages (fig. 3) do not necessarily imply strong mutual dependence. A characteristic feature of these mutualistic systems is the high asymmetry of the reciprocal effects within the individual pairs of interacting species (table 3). Thus, the interaction of most (43%) of the species pairs is negligibly significant (the pairs lie in the upper left part of the table). The remaining pairs lie along both the top and left side of the table. The relationships are therefore very asymmetrical (see also Herrera 1984), because either a plant is of great significance to a bird species, which in turn is unimportant for its dispersal (first row of table 3), or a bird species concentrates on the dispersal of a plant species that provides only a small fraction of its diet (values in the first column of table 3). Finally, strong mutual interactions (lower right part of the table) are scarce. The few documented cases of close interdependence in these systems are *Turdus iliacus* with *Ilex aquifolium* (Guitián 1984) and with *Crataegus monogyna* (Sorensen 1981); *Turdus philomelos* with *Vaccinium myrtillus* (Guitián 1984); and *Sylvia atricapilla* with *Rubus ulmifolius* (Guitián 1984; see also Jordano 1982) and with *Pistacia lentiscus* (Herrera 1984; Jordano 1984).

The compartmentalization of the mutualists into different, relatively isolated modules (Paine 1980) or cliques (Yodzis 1980) also increases with increasing diversity ( $N = 7$  frugivore assemblages,  $r_s = 0.732$ ,  $P < 0.05$ ). A *module* is defined here as a set of species (frugivorous birds) with a common major food-plant taxon that is not shared with frugivores in other modules.

I considered a food plant as *major* for a bird species if it accounts for at least 20% of the feeding records. For example, two modules can be distinguished for the temperate deciduous forest studied by Sorensen (1981): one centered on *Sambucus nigra* includes *Sylvia atricapilla*, *Erithacus rubecula*, and *T. philomelos*; three *Turdus* species (*T. merula*, *T. iliacus*, and *T. pilaris*) share *C.*

TABLE 3  
THE DISTRIBUTION OF N = 281 VALUES OF MUTUAL DEPENDENCE BETWEEN PLANTS AND THE FRUGIVOROUS BIRDS THAT DISPERSE THEIR SEEDS

PLANT DEPENDENCE ON BIRD	BIRD DEPENDENCE ON PLANT									
	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
0-10	121 (43.06)	7 (2.49)	6 (2.14)	3 (1.07)	—	1 (.36)	2 (.71)	—	1 (.36)	11 (3.91)
11-20	28 (9.96)	7 (2.49)	4 (1.42)	1 (.36)	—	1 (.36)	1 (.36)	1 (.36)	—	4 (1.42)
21-30	15 (5.34)	1 (.36)	3 (1.07)	—	1 (.36)	—	—	1 (.36)	1 (.36)	—
31-40	14 (4.98)	2 (.71)	1 (.36)	—	—	—	—	—	—	—
41-50	12 (4.27)	5 (1.78)	—	1 (.36)	1 (.36)	—	—	—	—	—
51-60	5 (1.78)	1 (.36)	—	—	—	—	—	—	1 (.36)	2 (.71)
61-70	4 (1.42)	1 (.36)	—	—	—	—	—	—	—	—
71-80	1 (.36)	—	—	—	—	—	—	—	—	—
81-90	1 (.36)	—	—	—	—	—	—	—	—	—
91-100	4 (1.42)	2 (.71)	—	—	—	—	—	—	1 (.36)	1 (.36)

NOTE.—The number and relative frequencies (% in parentheses) of mutualistic pairs of species for certain combinations of interaction strengths (dependence, percentage, see text).

SOURCES.—Frost 1980; Sorensen 1981; Guitián 1984; Jordano 1984; see also Herrera 1984.

*monogyna* as their major food plant and constitute a second module, as defined here. However, module isolation is not complete, provided minor plants are shared with other modules even in the diverse tropical assemblages. Typical major food plants contributing to guild structuring among frugivorous birds are Moraceae (*Ficus* spp.), Lauraceae, and Melastomataceae in the tropics (Crome 1975; Frith et al. 1976; Frost 1980; Beehler 1983; see Wheelwright et al. 1984); Rosaceae (*Crataegus*, *Sorbus*) and Aquifoliaceae (*Ilex*) in temperate assemblages (Sorensen 1981; Guitián 1984); and Anacardiaceae (*Pistacia*) and Oleaceae (*Olea*) in Mediterranean shrubland (Herrera 1984; Jordano 1984).

The qualitative trend of increased division in modules runs parallel to a decrease in the average dependence level in the more diverse systems ( $N = 10$ ,  $r_s = -0.765$ ,  $P < 0.01$ ). Thus, as the system becomes increasingly diverse, each species "dilutes" its interaction strength because it interacts with a smaller fraction of the available partners and because the average dependence decreases as the absolute number of mutualists increases.

#### DISCUSSION

Even if the systems of reciprocal dependence have originated through the progressive addition of species, the resulting web of interactions is not necessarily homogeneous, but most likely anisotropic (Margalef 1980), with several, small nuclei of strong, persistent interactions, a large fraction of weak relationships, and a variable number of null interactions.

The information currently available indicates that the mutualistic relation is extremely skewed toward weak relationships. The few interactive pairs are characterized by a strongly asymmetrical interaction that develops within relatively isolated subsets of mutualists. Several of these issues have been raised previously (see, e.g., Fleming 1979; Janzen 1983; Schemske 1983; Herrera 1984). The quantitative approach followed in this paper provides a rationale for comparative analyses and suggests that all these concepts are not independent but are ultimately related to patterns of interaction that are more general in multispecies assemblages.

#### *The Distribution of Interactions*

The dynamics of species diversity within multispecies collectives generates well-documented cases of structural invariance, but the process is poorly understood (see Sugihara 1980; Briand and Cohen 1984). Global patterns of internal connectance and of distribution of pairwise dependence could be the result of community-level, additive effects of increasing diversity. Whether they are caused by stability constraints or chance effects (May 1972; Pimm 1980; Auerbach 1984), these patterns significantly affect how coadaptations arise within diverse assemblages of mutualists. Since the distribution of interactions for a given species depends on the species' fit within a diverse assemblage, these effects alone might determine the diversity and the intensity of the interactions.

The analogous behavior of connectance in pollination and seed-dispersal mutualisms and the omnipresence of skewed, asymmetrical distributions of de-

pendence values may be the expected result when pairwise interactions develop between two diverse sets of animals and plants with a common underlying distribution of species abundances. Two basic assumptions underlie this hypothesis. First, the frequency distributions of relative abundance of mutualists follow a negative exponential, with many rare species and a few common ones, a characteristic feature of multispecies assemblages (Preston 1980; Sugihara 1980). Second, the fraction of interactions established increases with abundance as a saturation exponential, such that abundant mutualists are likely to interact with almost all the species in the other assemblage. Preston (1981) showed that multiplication of a negative exponential "parent" curve by an exponentially saturating curve, the "multiplier," generates a pseudo-lognormal, combined curve. Frequency distributions such as those presented in figure 3 fit quite well to a lognormal curve when plotted on a scale of "octaves" of dependence (see Preston 1980, 1981).

With increasing diversity, this multiplicative effect has a twofold result: fewer interactions become established, and weak interactions increase in proportion. This result might generate the general patterns observed in the distribution of interactions between sets of mutualists (fig. 1). However, the differences found can be attributed to the effects of differences in the numbers of species and/or in the mode of interaction.

#### *Mode of Interaction*

The pattern of connectance and the distribution of dependence values within mutualistic systems can be envisioned as the results of a process that limits the maximum degree of mutual specificity for any pair of species. Describing how this process works is a first step to understanding how diffuse coevolution works. Why are so many null interactions observed in nature? And once interactions are established, why are they so frequently weak, asymmetrical, and centered on particular subsets of species?

*Null interactions: pairwise noncoincidences within mutualistic assemblages.*— I expect the largest fraction of null interactions in pollination and seed dispersal to be explained by phenological noncoincidences. Conversely, the degree of temporal matching between the flowering and fruiting seasons and the foraging lives of the animals will set limits on the evolution of mutual dependence.

In certain cases of oligolecty among solitary bees with short activity periods (Linsley 1958; Cruden 1972), low connectance is expected (fig. 2) because the staggering of flowering periods prevents a broad sampling of the species sequence by a univoltine pollinator. In contrast, eusocial groups having long-lived colonies (*Apis*, *Trigona*, etc.) or those producing several generations per season (*Bombus*, certain Halictidae) interact with a greater fraction of the available flowers (Heithaus 1979; Roubik 1980) because a greater turnover of flower species during their longer flight periods promotes "sequential specialization" (Heinrich 1979).

Examples of resource tracking by sequential specialization have been documented for tropical frugivores that are year-round residents (Snow 1962; Snow and Snow 1971; Crome 1975; Worthington 1982; Wheelwright 1983; see Marshall 1983). Temporal noncoincidence might therefore account for a greater fraction of null interactions in temperate habitats where nonresident birds are the main seed

dispersers (Thompson and Willson 1979; Herrera 1982*b*). Thus, nearly a quarter of the 121 null interactions between frugivorous birds and fruiting plants at a single locality in southwestern Spain (Jordano 1984) were determined by the temporal uncoupling of the fruit-ripening period and the presence of the birds.

Furthermore, cases of pairwise interactions involving plant and animal species that show partial phenological overlap (but not complete temporal matching) necessarily generate weak interactions. Thus, a substantial fraction of the null and weak pairwise relations that predominate in matrices of community dependence might be explained by differences in the animal and plant phenophases.

*Structural limitations restrict the possibilities of interaction to certain groups of mutualists.*—Nectar and pollen extraction commonly require morphological adjustment between the corolla and the pollinator's mouthparts or body (Dressler 1967; Nilsson 1978); the efficiency of these activities and of the resulting pollinations is closely related to this morphological coupling (Wolf et al. 1972; Harder 1983). In contrast, efficiency thresholds are probably lower for frugivores feeding on particulate foods like fruits, an activity entailing a lower relative energy investment than the foraging of the smaller nectarivorous insects or birds feeding on "diluted" rewards (see Brown et al. 1978). Differences in overall specificity between pollination and seed-dispersal systems (fig. 1; see also Wheelwright and Orians 1982; Janzen 1983) can arise from these structural limitations and ultimately can be related to differences in the heterogeneity of feeding structures and in the mode of interaction between flower visitors and fruit consumers.

From the plant's perspective, phylogenetic and/or developmental constraints on reproductive structures may prevent the evolution of floral arrangements and fruit types that eventually filter out all but one species of mutualist (Herrera 1982*a*; Feinsinger 1983; Schemske 1983). Most likely, broad evolutionary alternatives in fruit and flower design (e.g., length of corolla tube, fruit size, etc.) set up broad limits to the variety of mutualists. A feedback loop accentuates this diffuse adaptation if low-specificity interactions generate variable selection pressures on size-related traits of the flower and the fruit (Howe 1984; Kiestler et al. 1984). The few documented cases of geographic variation in mutualism-related traits (e.g., Chase and Raven 1975; Brink and de Wet 1980; Pudlo et al. 1980; Herrera 1981) illustrate this kind of variability.

Other things being equal, increasing corolla length or fruit cross-width exponentially decreases the fraction of interacting mutualists. Conversely, increasing mouthpart length and gape width exponentially increases the percentage of usable corollas and fruits, respectively (see Wolf et al. 1972; Moermond and Denslow 1985; Wheelwright 1985). The main result for the individual species is an a priori limitation of its possibilities of interaction to certain parts of the mutualistic network. Typical modules of this type, "hummingbird" and "bumblebee" flowers, "lauraceous" and "bat" fruits, etc., have higher internal connectances (see table 1, fig. 2) than the complete systems that include several modules. The documented increase in compartmentalization of seed-dispersal systems with increasing numbers of species may be the result of the accommodation of an increasingly heterogeneous set of feeding structures and fruit types as diversity increases.

Extreme instances of connectance breakdown generate systems of high specificity (as illustrated by the fig–agaonid wasp and orchid–euglossine bee systems; fig. 2), resulting from speciation events' being closely related to the development of pairwise interactions (Dressler 1968; Ramírez 1970). Apparently, structural limitations of the fig ostiole and agaonid morphology have restricted the coevolution of new species pairs within sections of *Ficus* and genera of wasps (Ramírez 1970; Wiebes 1982). Thus, higher taxonomic units (above species) acted as nuclei for mutualism development, ruling out association by descent (parallel cladogenesis; Mitter and Brooks 1983) as the underlying dynamics.

In contrast, the development of specific relations in orchid-bee assemblages depends on the asymmetrical effect of the bees on orchid speciation events (e.g., Dressler 1968; Ackerman 1983). Thus, highly specific orchid-bee interactions are found in areas with a high number of species of closely related orchids (Dressler 1968), suggesting that progressive events of orchid speciation have canalized pairwise relations with individual bee species. This illustrates a mode of "association by descent," with the important difference that, rather than resulting from coevolved speciation, orchid speciation relies on the previous existence of a large pool of potential pollinators (Ackerman 1983). The net consequence in both systems is the maintenance of a striking specificity (i.e., connectance decreases with the addition of new species) by both structural and behavioral constraints that restrict interactions to limited subunits of the system.

Since most of our knowledge of mutualism comes from studies of "mutualistic modules" (see table 1), we can only speculate about the evolutionary dynamics of complete systems. For example, if modules act as attraction domains, on evolutionary time, to canalize coadaptations of new species to module-specific partners, this would explain why connectance decreases as the number of species increases. Note that secondary (weak) relations, which interconnect species from different modules, can act as potential evolutionary bridges to canalize new adaptations.

*Weak interactions and dependence asymmetries: a mode of evolution when coevolution is diffuse.*—There is general agreement that most cases of pollination and seed dispersal by animals illustrate instances of diffuse coevolution, thus ruling out pairwise effects in generating coadaptations (see, e.g., Futuyma and Slatkin 1983). Deciphering the dynamics of this process seems, however, a more intractable problem. When both the pooled community dependence and the distribution for particular species are considered, there emerges a pattern of dependence in mutualisms that is strongly skewed toward low values (fig. 3, table 3). This situation is probably generalizable to most plant-animal interactions, given the diverse array of relationships experienced by individual species (Caughley and Lawton 1981; Schemske and Horvitz 1984; Strong et al. 1984).

Coadaptations are expected between sets of species (e.g., Herrera 1982*b*), involving mutual effects between the species. As stated by Futuyma and Slatkin in their epilogue, "The most prevalent pattern, in fact, seems to be adaptation of a species to a suite of often phylogenetically diverse species, to which it holds a similar ecological relationship, i.e., diffuse coevolution" (1983, p. 460). Even if coevolution is diffuse, conventional gradualistic change need not be absent.



Rather, it would operate at a different level than demographic changes (see Eldredge 1982) and promote both "upward" and "downward" causal patterns (Vrba and Eldredge 1984). I suggest that most coadaptations readily apparent in contemporary multispecies systems (Heithaus 1982; Herrera 1982*b*, 1985; Feinsinger 1983; Wiens et al. 1983) have originated from mutual effects of the interacting species on the demographic features of the populations, without the necessity of genetic, "coevolved" changes. Diffuse coevolution would have produced selective rarefaction predominantly at the species level (Stanley 1975; Fowler and MacMahon 1982; Vrba 1984), thus favoring the establishment of those species combinations exhibiting closer mutual adaptation. The relevant phenomena associated with this process would be that (1) species differ in heritable, mutualism-directed traits; (2) species interact differentially with the set of mutualistic partners because of this variation; (3) as a result, the species experience differences in certain properties, such as birth and death rates, that are related to variation in the mode of interaction; and (4) a pattern of species sorting follows, and changes through time are observed in the mutualistic assemblage (for a discussion of the above phenomena in relation to the process of species selection, see Vrba 1984; Vrba and Eldredge 1984). Such a process may operate either synergistically or antagonistically with microevolutionary change in the mutualism-related traits of individual species. It may operate in response to a variety of selective pressures such as the abiotic environment, pathogens, predators, etc., and to "upward" causation from the genomic and organismal levels (Cracraft 1982; Vrba and Eldredge 1984).

Consideration of the generalized importance of strongly asymmetrical interactions in nature illustrates the improbability of pairwise coevolution (see also Schemske 1983; Howe 1984; Herrera 1985). It is not surprising that most of the recent theoretical models of coevolution (see Boucher et al. 1982) implicitly assume pairwise symmetrical effects between the mutualists: there is a conspicuous neglect of asymmetrical relations (amensalism, commensalism, and related situations) in modern ecological literature (see Lawton and Hassell 1981; Schemske and Horvitz 1984). Weak interactions, especially those involving situations of strong asymmetry, have a central role in mutualistic systems. They provide a number of pathways for rare species to persist and alternative routes for system responses to such perturbations as the deletion of a mutualist.

#### SUMMARY

Patterns of connectance and strength of mutual dependence in mutualisms have been examined by comparing the fraction of possible pairwise interactions established in a series of plant-pollinator and plant-seed disperser systems. As the number of species in the mutualistic system increases, the absolute number of interactions established increases, but connectance decreases exponentially. A given increase in diversity adds twice the number of interactions to dispersal systems as to pollination systems, suggesting a higher global specificity of the latter. Connectance patterns in mutualisms are analogous to some of those observed in complex food webs, suggesting a somewhat invariant structure in the

relations between sets of interacting species. For seed-dispersal systems involving frugivorous birds, mutual dependence values are strongly skewed toward the low end and illustrate generally strong asymmetries in mutualistic interactions. These patterns may be expected by considering simple multiplicative effects within multispecies assemblages as a result of variations in the number of species and in the underlying abundance distributions of the species involved. Coadaptation may originate from a process of species sorting without the necessity of genetic (coevolved) changes. Asymmetrical interactions and the prevalence of weak relations can provide pathways for rare species to persist and alternative routes for system responses to perturbations. These findings emphasize the diffuse nature of coevolution in mutualistic webs and suggest a mode by which diffuse coevolution can proceed.

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#### APPENDIX

##### EVALUATION OF THE DATA SOURCES

For a comparative analysis to proceed it is necessary to consider the possible sampling biases inherent in differences in the numbers of species of the systems being compared and differences in sampling effort, which could influence the accuracy in estimating the number of existing interactions.

The pollination and seed-dispersal systems considered (table 1) span a similar range of species numbers, in either the plant or animal groups ( $U = 131.5$  and  $177.5$ , respectively,  $P > 0.10$ , two-tailed test). If a bias favors reporting a lower number of interactions in the more diverse systems, the reverse was found for comparisons of the pollination and dispersal systems. Pollination systems were slightly less diverse ( $\bar{X} S = 43.8$ ,  $N = 36$ ) yet showed a much lower connectance than the latter ( $\bar{X} S = 64.7$ ,  $N = 19$ ). Thus, differences in connectance patterns between the two types of mutualism are attributable to system-specific ways of interaction.

An additional bias might exist in comparing trends in the number of interactions recorded if the study of increasingly diverse systems is not sufficient to account for a significant fraction of the interactions actually existing. For example, if the number of interactions recorded for a set of frugivorous bird species increases with sampling effort (Wheelwright et al. 1984), to what extent would an increase in effort add new host-plant records as a result of new interactions being sampled? How many interaction records are required for an adequate estimate of the plant species used? To assess this problem, I calculated  $E(s_n)$ ,

the expected number of species in a sample of  $n$  interactions drawn randomly from a collection of  $N$  interactions reported for  $s$  species:

$$E(s_n) = s - \binom{N}{n}^{-1} \sum_{i=1}^s \binom{N - N_i}{n},$$

where  $s$  is the number of mutualist species in a total of  $N$  interactions recorded for a given set of organisms (plant or animal) that are the focus of the study, and  $N_i$  is the number of interactions obtained for the species  $i$ . This procedure is analogous to the rarefaction-diversity measurement (Hurlbert 1971; Heck et al. 1975), in which the number of species is calculated for collections scaled down ("rarefied") to a certain number of individuals ( $n$ ) in order to make the number of species comparable by standardizing samples to equal numbers of individuals. If the proportion of the mutualist species included in the rarefied sample of  $n$  interactions is large for a relatively small  $n$ , I estimate that the values of connectance, interaction strength, etc., are adequate for a certain bias (otherwise unavoidable) resulting from time and effort constraints encountered when dealing with diverse systems.

For a selected sample of 12 plant-avian-seed-disperser systems (Snow and Snow 1971; Sherburne 1972; Crome 1975; Frith et al. 1976; Stiles 1979; Baird 1980; Frost 1980; Sorensen 1981; Beehler 1983; Guitián 1984; Jordano 1984; and Wheelwright et al. 1984), rarefied samples (ranging from 21.4% to 66.6% of the reported  $N$ ) included an average (across studies) of 85.9% of the  $s$  species reported (range: 62.2%–99.1%). This overall high agreement between  $E(s_n)$  and  $s$  for the reduced samples suggests that for most of these studies, additional sampling would add few, if any, new mutualist species. Most likely, these new additions would be rare species with few interactions (see Wheelwright et al. 1984), thus decreasing connectance even more and emphasizing the observed patterns.

An additional effect of this type of bias would emerge if increases in sampling effort also add new interaction records for species already included in the system (i.e., if the interaction of a previously known noninteracting pair of species is recorded). I performed a Monte Carlo simulation of the relationship between  $S$  and  $C$  for 10 iterations of 5000 random values of both variables. Theoretically feasible values for the randomly generated  $C$ , given a value of  $S$ , range between  $2S^{-1}$  and  $2^{-1}(S^2 - S)$  (minimum and maximum possible connectance values, respectively; Briand 1983; Auerbach 1984). An average of 65.1% of the randomly generated  $SC$  combinations in each iteration lie within these limits. For this random subsample,  $C$  decreases with increasing  $S$  but at a rate lower than that observed for real pollination and seed-dispersal systems ( $C_{\text{random}} = 0.1270 \exp[-0.0019 S_{\text{random}}]$ ;  $r = -0.8212$ ,  $P < 0.01$ ). Thus,  $C$  is probably an underestimation for the systems having greater numbers of species. A more intensive sampling of the organisms included in table 1 would most likely increase the observed values of  $C$  for the small fraction of studies with high values of  $S$  (those above  $S = 100$ ), but would not alter the observed relationship between  $C$  and  $S$ . I conclude, therefore, that the sampling of the interactions occurring in the selected systems is reasonably complete and includes, as indicated by the rarefaction analysis, a major portion of the species actually involved in these mutualisms.

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