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Dispersal of seeds by frugivorous animals in temperate forests

Dispersión de semillas por animales frugívoros en bosques templados

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ABSTRACT

Wet temperate forests in Chile have many more fleshy-fruited species (especially trees) than North American temperate forests. Chilean forests harbor a lower diversity of frugivores than North America, and their density in the main season of dispersal may be lower also. The composition of the frugivore fauna in both regions is similar at the level of taxonomic class and general foraging guild, and both regions differ sharply from temperate forests in New Zealand. Birds and mammals in tropical forests and in Spain (and perhaps Chile) often favor fruits with different suites of characters, but in North America, there is extensive overlap in the fruit genera consumed by these two kinds of frugivores. These basic patterns are used to generate some elementary predictions that may provide a focus for comparative studies.

Key words: Seed dispersal, frugivory, fleshy fruits, Chile, temperate forests.

RESUMEN

Los bosques húmedos templados de Chile tienen más especies con frutos carnosos (especialmente árboles) que los bosques templados de Norteamérica. Los bosques de Chile tienen una diversidad menor de frugívoros que los bosques de Norteamérica y su densidad durante la estación de dispersión de semillas puede también ser más baja. La composición de la fauna de frugívoros en ambas regiones es similar al nivel de Clase taxonómica y también en cuanto a la estructura de gremios tróficos. Sin embargo, ambas regiones difieren marcadamente de los bosques de Nueva Zelandia. En bosques tropicales, en España, y posiblemente en Chile, aves y mamíferos están asociados a diferentes síndromes de caracteres del fruto, pero en Norteamérica existe una gran sobreposición en los géneros de frutos consumidos por estos dos grupos de frugívoros. Estos patrones básicos son usados para generar algunas predicciones simples que podrían guiar futuros estudios comparativos.

Palabras claves: Chile, dispersión de semillas, frugivoria, frutos carnosos, bosques templados.

INTRODUCTION

The strongholds of temperate rainforest lie along the northern Pacific coast of North America and the southern Pacific coast of South America, with important outposts in New Zealand and southeastern Australia and small enclaves in a few other places. Temperate rainforests are defined chiefly in terms of climatic and structural features; biological patterns and processes may –or may not– be similar in different regions. The aim of this essay is to compare some biological characteristics of different temperate rainforests, with particular reference to a widespread and common plant-animal mutualism in which plants provide fleshy fruits to animals that consume the fruits and disperse the plant's offspring. For purposes of perspective, I will also provide comparative information from other kinds of forests. Throughout, my emphasis is, of necessity, on comparisons of patterns; questions about ecological processes and consequences will need to be addressed before we can fully understand the implications of the mutualism.

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THE FREQUENCY OF FLESHY-FRUITED PLANT SPECIES

Mutualism between vertebrate frugivores and fleshy-fruited plants received their first serious attention in tropical studies. Vertebrate-dispersed plants are extremely common in many wet tropical forests, constituting over 70 percent of the flora, with lower frequencies reported for southeast Asia and for most tropical dry forests (Table 1).

However, temperate forests also contain respectable frequencies of fleshy-fruited plant species (Table 1). For a variety of North American forests the modal frequency is about 30-40 percent (see also Willson 1986), and several Alaskan forest stands fall in a comparable range. Most New Zealand forests also have 30-50% fleshy-fruited species (see Willson *et al.* 1990). Chilean forests stand apart from most other temperate forests in their relatively high frequency of fleshy-fruited species (Table 1).

Although a correlation between the frequency of fleshy-fruited species and precipitation has been noted for the tropics (Gentry 1982, Willson *et al.* 1989; and for Chilean matorral vegetation, Hoffman *et al.* 1989), it is plain that many of the differences seen in Table 1 are not easily related to climate alone. There are clear regional differences –in the lower diversity of fleshy-fruited plants in southeast Asian floras, and in the rather high diversity in a spectrum of Chilean forests of differing physiognomy and climate.

There are regional differences in the representation of fleshy fruits in trees, shrubs and vines, and herbs (Table 2). Shrubs and vines are often vertebrate-dispersed; in most of the available data sets the frequency is well over 50 percent. The few existing data for forest herbs show that the frequency of herbaceous fleshy-fruited species varies considerably, both

TABLE 1

Frequency (percent of flora) of fleshy-fruited species in selected forests around the world. In general, the numbers of fleshy-fruited species are higher in tropical than temperate regions, higher in Chile than in North America (intermediate in New Zealand), but the numbers cannot be compared directly because of differences in sampling methods

Frecuencia (% de la flora) de especies con frutos carnosos en bosques seleccionados de todo el mundo. En general, el número de especies con frutos carnosos es más alto en las regiones tropicales que en las templadas, más alto en Chile que en Norteamérica (intermedio en Nueva Zelandia), aunque los números no pueden ser comparados directamente debido a las diferentes metodologías

	Frequency (%)
A. Tropical forests	
Wet-Australia	85
neotropics (woody plants)	~70-86
Nigeria (woody plants)	~80
Borneo	35-40
Malaya	26-41
Dry-Australia	~21-70
neotropics	~57-70
B. Temperate forests	
North America	
eastern coniferous	3-53
eastern deciduous	8-52
western hemlock	28-39
western fir-hemlock	29-37
interior Alaska	24-44
coastal Alaska	47
Chile	
Chiloé rainforest	69
sclerophyll, deciduous	65
New Zealand	
podocarp	28-58
broadleaf	27-60
Australia	
Victoria rainforest	33-44
wet sclerophyll	8-31

Sources of data: Armesto *et al.* (1987), Armesto and Rozzi (1989), Bkady and Hanley (1984), Alaback and Hermann (1988), Franklin *et al.* (1988), Topik *et al.* (1986), Willson *et al.* (1989), Willson *et al.* ms., Wong (1986).

TABLE 2

Frequency (percent of flora) of fleshy-fruited species for three growth forms in selected forests.
Frecuencia (% de la flora) de especies con frutos carnosos de tres formas de crecimiento en algunos bosques seleccionados

	Trees	Shrubs & vines	Herbs
North America			
eastern coniferous & deciduous	9-30%	48-90%	2-25%
western coniferous	0-12	47-89	0-27
Alaska coastal coniferous	0	86	32
Chile			
Chiloé rainforest	70	64	22
New Zealand			
mixed	79	67	?
Tropical rainforest			
Australia	80-100	85	44-60
neotropics	52-58	36	?

Sources of data: Armesto and Rozzi (1989); Willson (1986 and unpubl.), and references for Table 1.

within and among vegetation types. Trees are often fleshy-fruited in tropical wet forests, comprising as much as 100 percent of tree species in some Australian stands (Willson *et al.* 1989). Wet forests in both New Zealand and Chile have high frequencies of fleshy-fruited trees –as high or higher than some tropical areas. In contrast, the frequency of fleshy-fruited tree species in North American forests is relatively low and reaches 0 percent in a variety of western coniferous forests (including Alaskan temperate rainforest).[a]

In sum, there is little correspondence in temperate forests in the distribution of fleshy-fruited species across growth forms. Regional differences are pronounced and both Chile and New Zealand have many more fleshy-fruited trees than North America.

THE DIVERSITY OF ANIMAL DISPERSERS OF SEEDS

Animal consumers of four vertebrate classes and one group of insects (Hymenoptera: Formicidae) are important seed dispersers for plants, although their importance varies regionally (Table 3A; see Willson *et al.* 1990). Fishes are notable seed dispersers only in the tropics, apparently, and reptiles decrease in importance at higher latitudes. New Zealand lacks native frugivorous mammals, except for one partly frugivorous bat. Although ants do not commonly transport the seeds of typical fleshy fruits, they are common dispersers of seeds that bear elaisomes (attractive, nutritious appendages, usually white and lipid-rich), which they consume, while discarding the seed. Ground-foraging ants are very important dispersal agents in certain communities in some regions (Willson *et al.* 1990), but I have no information on their dispersal activity in temperate rainforests in Chile or Alaska, hence their omission from the rest of this paper. However, plants with elaiosome-bearing seeds do occur in some areas of Chile (Villagrán *et al.* 1986, though possibly not

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[a] [Vertebrates are also responsible for scatter-hoarding and dispersal of many North American species with dry, hard diaspores (e.g., *Quercus*, *Carya*, *Juglans*, and some *Pinus* in the southwest). Addition of such species to the tallies for the forests in which they occur raises the total frequency for vertebrate-dispersed trees to 21-45% for eastern deciduous forest. However, the low figures for western coniferous forests do not change.]

the rainforests; Juan Armesto, pers. comm.) and in boreal forests in interior Alaska. In addition, ants eat the fruits of certain Chilean cacti, often dropping the seeds, but sometimes carrying off bits of pulp (Adriana Hoffman, pers. comm.), perhaps with enclosed seeds.

At the ordinal level (Table 3B), there emerge some salient differences between tropical and temperate regions and some similarities among temperate regions. Tropical forests are distinguished by the presence of important vertebrate dispersers of several orders that do not generally have this ecological role in temperate forests: Perissodactyla are absent from modern temperate forests; fruit-eating Chiroptera are well represented in the tropics but temperate bats are apparently almost exclusively insectivorous, for reasons not entirely clear; primates are a principally tropical group, although there are a few temperate-zone outliers (such as the Japanese macaque). Tropical rodents that serve as seed-dispersal agents include large, terrestrial scatter-hoarders (i.e., agoutis, pacas) that do not occur in temperate regions. However, smaller rodents (squirrels, mice) that harvest and store seeds occur in many regions.

Carnivora includes numerous fruit-eating species that are known to be important dispersers of seed in many regions. This group may be the most ubiquitous type of mammal that regularly act as dispersal agents, but their ecological role in relation to dispersal has been relatively little studied (e.g., Jaksić *et al.* 1980, Herrera 1989, Bustamante *et al.*, 1992). Artiodactyla also eat fruits (i.e., bovids in Africa, Jarman 1974; cervids in America, Armesto *et al.* 1987) but the ecology of dispersal by these fruit-eating herbivores seems to be quite unstudied. Marsupialia contributes fruit-eaters in many areas, although their importance dwindles in the northern hemisphere and in southern South America.

Among the birds, there are seed-dispersal agents in many tropical orders (Snow 1981 gives some of the principal families of specialized frugivores) and the Columbiformes are probably more important in the tropics than elsewhere. The Piciformes include fruit-eaters of importance to seed dispersal in regions where this order is found. The order Passeriformes provides many dispersal agents all over the world. The extinct moas (Dinornithiformes) of New Zealand were probably important seed dispersers until recently.

Land tortoises (Order Chelonia) constitute significant agents of seed dispersal in many regions, but are largely unstudied (except for gut passage rates, refs. in Willson 1989, Bjorndal 1989). They are absent, however, from temperate forests in southern South America. Lizards (part of the Order Squamata) are sometimes frugivorous and potentially important (but relatively unstudied) dispersers in New Zealand, Australia, the neotropics, Chile (Armesto *et al.* 1987, Armesto and Rozzi 1989, Carolina Villagrán and Carlos Sabag, pers. comm.), and perhaps other regions.

The spectrum of vertebrate fruit consumers/seed dispersers can also be compared in terms of ecological rather than taxonomic categories (Table 4). A simple subdivision can be made on the basis of locomotor habits and the strata of forest structure that is used for foraging. Some regions have relatively well–developed frugivorous faunas that search for fallen fruits on the ground and/or for fruits on low-growing plants. In tropical forests, this guild of fruiteater includes large rodents that scatter-hoard seeds, tapirs and elephants, some primates and ungulates, a number of Carnivora, birds such as cassowaries in Australia and New Guinea and trumpeters in South America, and tortoises (e.g., Smythe 1986). In North America, the Carnivora probably comprise the major element of the terrestrial frugivores, although deer and tortoises and occasionally birds also fall in this category. In Chile, rhinocryptid birds are probably the major members of this guild; foxes and some small mammals consume fruit (Meserve *et al.* 1988, Bustamante *et al.* 1992; and probably also the pudu) and may disperse some seeds.

A second category is composed of animals that sometime climb to harvest fruit but also forage on the ground. Exam-

TABLE 3

Taxonomic distribution of animal dispersers of seeds in selected forests. The number of + 's indicates the estimated comparative importance of each taxon; minus signs indicate that the taxon is not known to disperse seeds in a given region

Distribución taxonómica de animales dispersantes de semillas en algunos bosques seleccionados. El número de "+" indica la importancia comparativa estimada de cada taxon. Los signos '–' indican que el taxon no es conocido como dispersante de semillas en la región

A. By Class

	Mammals	Birds	Reptiles	Fishes	Insects
North America					
Mexico to S. Canada	+++	++++	+	–[a]	++
Alaska	+++	++++	–	–	+
Chile	++	++++	+?	–?	?
New Zealand	+[b]	++++	+	–	+
Tropical forests	+++	++++	+	+	+

[a] There are a few reports of North American fishes eating fruits, however.

[b] The only native mammalian frugivore is a bat that includes fruit in its varied diet.

B. By Order. For three regions of immediate concern, the approximate number of species is indicated. Names in parentheses indicate taxon in which seed predation may be at least as prevalent as seed dispersal.

	Mammals	Birds	Reptiles
North America[a].			
Mexico to Canada	~15+ Carnivora Artiodactyla Marsupialia (Rodentia)	~30+ Passeriformes Piciformes (Columbiformes) (Galliformes)	~3+ Chelonia Squamata
Alaska	~7 (~3)[e] Carnivora Artiodactyla (Rodentia)	~27 Passeriformes Piciformes (Columbiformes) (Galliformes)	–
Chile[a]	~7 Carnivora Artiodactyla Marsupialia (Rodentia)	~17 Passeriformes Piciformes (Columbiformes)	Squamata?
New Zealand	Chiroptera[b]	Passeriformes Columbiformes [Dinornithiformes][d]	Squamata[c]
Tropics[a]	Carnivora Chiroptera Primates Perissodactyla Artiodactyla Proboscidea Marsupialia Rodentia	Passeriformes many others	Chelonia Squamata

[a] Data from many sources, including Martin *et al.* (1951), Armesto *et al.* (1987), and others.

[b] Daniel (1976).

[c] Whitaker (1987).

[d] Burrows (1980); these large birds are now extinct.

[e] The value in parentheses is for southeastern Alaska rainforests.

TABLE 4

Ecological distribution of animal seed-dispersers
Distribución ecológica de animales dispersantes de semillas

Region	Foraging Category			
	Terrestrial	Terrestrial /Scansorial	Arboreal, nonvolant	Volant
North America				
Coterminous US.	++ (M)	++ (M; S)	–	++++ (B)
Alaska	++ (M)	+? (M; S)	–	++++ (B)
Chile	+ (M)?	+? (R?)	–?	++++ (B)
New Zealand	(+) (B)	+? (R?)	+? (R)	++++ (B)
Australia (temp)	+?	+? (M)	+? (M)	++++ (B)
Tropics	+++ (M+B; S)	++ (M; S)	+++ (M)	++++ (B, M)

ples would include raccoons (*Procyon*) and some marsupials, some rodents (including some scatter-hoarders) and primates, and probably some lizards (in New Zealand these may be the principal members of this category).

Arboreal but nonvolant fruit-eaters include animals that seldom descend to the ground to forage, and include some primates and Carnivora in the tropics, and perhaps some lizards there and in New Zealand. They are not represented, to my knowledge, in either North America or Chile, despite the presence of a variety of trees that bear fruit (especially in Chile). Volant frugivores are found among both mammals (bats) and birds in the tropics, but almost exclusively among birds in the temperate regions.

Thus, the major regional differences seem to be found in the well-developed terrestrial and arboreal/nonvolant fruit-foraging guild in at least some tropical forests. In addition, the taxonomic composition of certain guilds changes (e.g., bats in the tropics, lizards in New Zealand).

The diversity of frugivore species is high in much of the tropics, and probably low in New Zealand (especially in the past century when many native bird populations have been decimated). In the remainder of this section, I will focus particularly on North America and southern South America.

In most of North America, the chief season of seed dispersal for fleshy fruits is late summer and fall, during the autumnal migration of many bird species. Many birds that are highly or exclusively insectivorous during the breeding season shift their diets to include large quantities of fruit during this time of year. Several authors (e.g., Karr 1975) have noted that the high diversity of tropical birds (compared to the temperate zone) may be maintained partly by the additional fruit resources in the tropics. These studies have been concerned mostly with breeding or resident bird species. Use of fleshy fruit during the breeding season is not common among North American birds, being known chefly in mimids, turdids, and bombycillids (Willson 1986). However, if one considers the season of fall migration, the importance of fruit resources to birds even in the temperate zone becomes quickly apparent (Thompson and Willson 1979; Table 5). It will be interesting to add Alaska and Chile to this comparison.

TABLE 5

Relative importance (percent of avifauna, total avian population, and avian biomass) of avian frugivores in the understory of selected forests. Although definitions of "frugivore" may differ in these studies, the table nevertheless documents the relative importance of avian frugivores in fall in North America.

Importancia relativa (% de la avifauna, población total de aves o biomasa de aves) de los frugívoros en el sotobosque de bosques seleccionados. Aunque la definición de "frugívoro" puede diferir en estos estudios, la Tabla documenta la importancia relativa de las aves frugívoras en otoño en Norteamérica

	Species	Abundance	Biomass
Central U.S., fall	35-44%	26-52%	40-54%
Northeastern U.S., fall	23-50	15-47	21-71
Panama, Costa Rica	21-33	11-57	–
Africa (tropical)	13-15	–	–
Malaya	4-20	+/–13	+/–17

Sources of data: Blake and hoppes (1986), Martin and Karr (1986), Karr (1980), Wong (1986), Levey (1988), Willson *et al.* (1982), Holmes and Sturges (1975).

In the north-central part of North America, there may be 30 or more species of seasonally frugivorous birds and up to 15 or so species of fruit-eating Carnivora, one marsupial, 1-2 deer, and an assortment of small rodents (e.g., *Scirius, Tamias, Eutamias, Peromyscus,* etc.). The number of frugivorous bird species may be considerably smaller in some eastern subboreal forests (Holmes and Sturges 1975). In central Alaska, there may be about 25 fruit-eating bird species, about 7 Carnivora, 1-2 deer, and a few rodents. In southeastern Alaska's rainforests, there are about 4 fruit-eating Carnivora (2 bears, marten, and coyote; occasionally wolves), one deer, and a few rodents (e.g., *Tamiasciurus* harvests many fruits and may be chiefly a seed predator; nevertheless, if some fruits are cached and not retrieved, this squirrel may also be a disperser). Also the southeastern rainforests of Alaska seasonally harbor about 25 avian frugivores.

In southern South America, on the other hand, up to ≈ 17 species of avian frugivores have been reported, as well as up to ≈ 7 Carnivora (mostly rare), a deer, and a few marsupials and some rodents that may contribute to dispersal (Armesto *et al.* 1987, Jaksic *et al.* 1980, Jaksic and Feinsinger 1991, Meserve *et al.* 1988). In terms of mammalian frugivore species richness, Chile thus seems to be intermediate between northcentral North America and central Alaska, on the one hand, and southeastern Alaska on the other. Species richness of southern South American avian frugivores seems to be considerably less than that of North American temperate forests.

Thus, southern South America may have a lower diversity of frugivorous vertebrates than much of north temperate North America. However, it has a much higher diversity of fleshy-fruited plants, especially trees.

FRUITS EATEN BY DIFFERENT TYPES OF VERTEBRATES

The overlap between the fruits eaten by various mammalian and avian dispersers in tropical forests is often substantial but by no means complete. For example, bats often favor a rather distinct subset of all available fleshy fruits (Fleming 1988). Primates and birds also tend to use rather different sets of fruit species in Peru, although the primates forage on some of the species used by birds (Janson 1983). In Gabon, a distinction can be made between fruits eaten by birds and monkeys and those eaten by ground-foraging vertebrates (Gautier-Hion *et al.* 1985). Recently, Herrera (1989) has shown that Carnivora eat only some of the fleshy-fruited species in Spain, although birds eat them all (Table 6). Recasting Herrera's data by genus, we find that 37 genera of fleshy fruits are eaten by birds, but that carnivores consume only 16 of these. Two of those sixteen genera contain some species that are eaten by carnivores and some that are not. Of 21 plant genera whose fruit is not eaten by Spanish carnivores in Herrera's sample, 9 also occur in North America where carnivores eat the fruits of at least 6 congeneric species.

I have attempted a similar analysis for North America, using data extracted from Martin *et al.* (1951) (see Appendix 1 for species and system of scoring). My preliminary analysis is, of necessity (because of the form of the data in Martin *et al.*), based on genera rather than species. North American genera with few available data have been excluded, leaving 34 genera with usable information (Table 6, Appendix 1). I emphasize that more up-to-date information may alter the details of the analysis, but Martin *et al.* (1951) offer a good standardized basis for a beginning.

Of the North American genera with adequate sample sizes, all are eaten by birds (Table 6, Appendix 1), although I will guess that *Diospyros* is not dispersed well by avian foragers because both fruit and seeds are relatively large. *Asimina* was not adequately represented in the data set, but the large, green fruit, enclosing large seeds, is also not eaten by birds. Carnivora eat fruits of at least 31 of the 34 genera. Only *Sambucus, Lindera,* and *Rhus* are not recorded (by Martin *et al.* 1951) as being eaten by carnivores, and I expect that all of these are, in fact, consumed by carnivores to some extent. The genus *Prunus* has one species (*P. americana*) that is probably eaten more by mammalian dispersers than by birds, but such distinctions are not obvious in other North American genera. Thus, North America appears to differ from Spain (and tropical forests) in the very extensive overlap (at the generic level) in the fruit diets of mammals (Carnivora) and birds.

Avian dispersers are collectively more important consumers than mammals for 27 of the 31 genera eaten by both. Mammalian dispersers are collectively more important than birds for only two plant genera (*Diospyros, Arctostaphylos*), and the two groups of animals are similar in

TABLE 6

Partitioning of fruits between mammals (mainly Carnivora) and birds.
Repartición del consumo de frutos entre mamíferos (principalmente carnívoros) y aves.

		Mammals		Birds	
Region	Nº of species or genera	Eaten	Not eaten	Eaten	Not eaten
Spain	68 spp	27	41	68	0
	37 gen	16	21	37	0
North America	34 gen	31	3?	34	0+
Chile	50 spp	11+	39–	45	6
	37 gen	12	25	31	6

Sources of data: Herrera (1989), Armesto *et al.* (1987), Martin *et al.* (1951). The data for Chile are very preliminary estimates; see text.

importance (scores differ by < 2*, see Appendix 1) for two genera (*Crataegus, Opuntia*). The greater apparent importance of birds as dispersers in North America might result simply from the greater number of frugivorous seed-dispersing birds than mammals (about 6 times as many in Martin *et al.* 1951). If we assume, for the sake of argument, that the average frugivore scores per species are similar for mammals and birds, we would expect the total score for birds to be about 6 times that for mammals. For 16 of the species in Appendix 1, the score for avian dispersers was greater than 6 times the mammalian-disperser score, so for these species at least, birds are disproportionately (with respect to the number of species available) more important dispersers than mammals.

A very preliminary comparison can be made for Chilean fruits (Table 6), using the data presently available (Armesto *et al.* 1987). Birds are known to eat most of the species and genera of fruits, but mammals (foxes) are recorded to eat only a rather small subset of fruits (Jaksic *et al.* 1980). Thus, fruit partitioning in Chile may be less like that in North America than elsewhere (at this level of analysis), but additional information for more habitats and sites will no doubt increase the list of fruits eaten by foxes.

Partitioning of fruits between mammals and birds is related to differing fruit morphology and fruiting displays (Table 7), although the relationship is not a tight one (see also Fleming 1988, Howe 1986, Janson 1983, Debussche and Isenmann 1989, Willson *et al.* 1989 and references therein). For tropical fruits, some differences between mammal-fruits and bird-fruits emerge, particularly in terms of aroma. Differences in fruit size that are

TABLE 7

Tropical fruit characters, relative to type of dispersal agent.
Plus signs indicate a trait that is generally present or well-developed;
minus signs indicate traits that are generally absent or poorly developed.
Caracteres de frutos tropicales en relación al tipo de agente dispersante. Signos '+' indican que el carácter está presente o bien desarrollado; signo '–' indica carácter ausente o poco desarrollado.

	Mammals			Birds	
	Terrestrial	Arboreal	Aerial	Terrestrial	Arboreal
Average fruit size	variable	variable	variable	variable	variable
Maximum fruit size	large	large	large	large	small-medium
Average seed size	variable	variable	variable	variable	variable
Maximum seed size	large	large	large	medium	small-medium
Color[a]	gr, or, br?	gr, or, br	gr, wh, yel	variable	red, blk
Aroma	+	+	variable	–	–
Presentation	fallen	variable?	exposed	fallen	exposed
Protection (physical)	+	+	–	–	–[b]
Nutrient content	variable	variable	variable	variable	variable

[a] Abbreviations for colors: gr=green, or=orange, br=brown, wh=white, yel=yellow, blk=black, bl=blue.

[b] But compare Pratt and Stiles (1985) for New Guinea.

Sources of data: Howe (1986), Janson (1983), Fleming (1988), Willson *et al.* (1989), Gautier-Hion *et al.* (1985).

apparent in neotropical surveys (Janson 1983) become less evident when one considers the large fruits ingested by cassowaries in Australia and New Guinea; this observation may indicate merely that partioning patterns vary among regions. As a rule, mammals can probably handle larger seeds than most birds (the ratites being notable exceptions). And, as trees and large herbaceous plants often have relatively large seeds (Thompson and Rabinowitz 1989, Mazer 1989 and references therein), there may be a tendency (to the extent that seed size exceeds the handling capacity of birds) for such plants to be dispersed disproportionately often by mammals (and ratites). Nutrient content of tropical fruits eaten by birds and by mammals is not known, but differences may be small (e.g., Fleming 1988).

Herrera (1989) contrasted Spanish fruits that are eaten by carnivores with those that are recorded to be eaten only by birds (Table 8). Bird-fruits are more often small and black, with little aroma, less fiber and more protein (but compare Debussche and Isenmann 1989) and minerals, and have persistent fruiting displays. In North America, with less apparent partitioning of fruit resources, differences between types of fruit are few (Table 8). Fruits eaten chiefly or exclusively by mammals are few, and variable in color (red, orange, green), fruit size (< 1 cm to > 5 cm), seed size (< 1 mm to > 1 cm), aroma (little to strong), and persistence on the plant. (A statistical comparison between mammal- and bird-fruits in North America is not possible, because of the small number of known mammal-fruits.)

A survey of New Zealand fruits would be expected to conform largely to the bird-fruit syndrome, although the extinct moas might have been able to use a subset of fruits not readily available to smaller birds (as cassowaries do in Australia, references in Willson *et al.* 1989). Identification of any such species in the New Zealand flora would be of interest, as they might now have poor dispersal capacities. Comparable analyses are not yet possible for Chile.

TABLE 8

Fruit characters, relative to type of dispersal agent, in temperate forests.
Caracteres de los frutos en relación al tipo de agente dispersante en bosques templados.

	Mammal (Carnivora)	Bird (arboreal)
A. Spain (Herrera 1989)		
Fruit size ($\bar{x}$)	larger	smaller
Seed size ($\bar{x}$)	small-medium	small-medium
Color[a] (common)	gr, br, wh, bl	blk
Aroma	+	–
Presentation	fallen	on plant
Protection	––	––
Nutrient content	more fiber, less protein and minerals	less fiber, more protein, minerals
B. North America		
Fruit size	variable	variable
Fruit size (max)	larger	smaller
Seed size ($\bar{x}$)	variable	variable
Seed size (max)	larger	smaller
Colors (common)	red/blk	red, blk
Aroma	––	––
Presentation	fallen or exposed	exposed
Protection	––	––
Nutrient content	variable	variable

[a] See footnote for Table 7.

FLESHY-FRUITS IN SUCCESSION

In the eastern deciduous forest of North America, reproductively mature fleshy-fruited species occur at all stages of succession, although the majority are found in middle and late seral stages (Table 9). A few species occur only in early successional stages, and later stages tend to have more habitat specialists (Table 9). As a simple descriptive exercise, I was curious to see if this pattern prevailed in temperate forests in western North America. From the preliminary survey presented in Table 9, it is clear that fleshy-fruited plants commonly mature and reproduce at all stages of succesion (the notable exception derives from post-glacial succession at Glacier Bay), and are seldom restricted to a single seral stage. However, when seral specialists do occur in the west, they usually occupy middle or late seral stages, although these are exceptions. A paucity of early-seral specialists may not be surprissing, given the very transient nature of that habitat, but the apparent absence of specialists from other stages in certain seres is more challenging to explain. A comparable survey for Chilean forests is not yet available (but could be constructed by reanalysis of the original data of Villagrán *et al.* 1986).

DISCUSSION

The austral forests of South America and the northern coastal forests of western North America share a number of topographic and climatic features that allow them both to be labelled "temperate rainforest". This term also includes forests in southern New Zealand and southeastern Australia. The shared epithet should not imply climatic equality, however, as differences can be observed among the temperate rainforest areas in different geo-

TABLE 9

Percent of all fleshy-fruited plant species that occurs in each seral stage or that is found only in a particular seral stage (habitat specialist), for selected temperate forests. (from Willson and Alaback, unpubl.).

Porcentaje de todas las especies con frutos carnosos que se encuentran en distintas etapas serales, o en una sola etapa seral particular (especialista de hábitat), en bosques templados seleccionados (Willson & Alaback, datos no publicados).

		Occurrence			Habitat specialist		
Location	Seral Type	Early	Middle	Late	Early	Middle	Late
Illinois	oldfield	7%	66%	73%	7%	20%	27%
Alaska, southeast	upland, hemlock, clearcut	32	76	38	0	38	6
	riparian, spruce, flood-stripped	32	68	80	8	12	12
	post-glacial	0	0	100	0	0	100
Alaska, central	glacial outwash	63	83	50	0	13	13
	black spruce, post-fire	67	100	89	0	11	0
	white spruce, post-fire	83	100	83	0	0	0
British Columbia	conifer, clearcut	82	91	64	9	0	0
	conifer, floodplain	36	45	82	18	0	36

graphic regions (Young 1972, Du Rietz 1960, Alaback 1991). Furthermore, the regions differ substantially in their biogeographic/evolutionary history, and the southern hemisphere forests are more similar taxonomically to each other than to northern hemisphere forests (e.g., Barlow 1981, Godley 1960, Raven 1963, Raven and Axelrod 1974, 1975 Axelrod *et al.*, this volume). Although much has been made of reported ecological similarities between regions of similar climates in the Americas (e.g., Mooney 1977, Moldenke 1979, Parsons and Moldenke 1975, Cody 1973, Sage 1973), it is equally easy to point to evident ecological differences (e.g., Sage 1973, this survey, see also Ricklefs 1987). For example, in Chilean and Californian areas of mediterranean climate, aspects of plant morphology and physiology (and possibly animal form and function?), whose relationship to climate is fairly direct, appear to show greater correspondence than community and population traits such as species diversity patterns, niche breadths, populations densities (Mooney 1977). The same may be true of temperate rainforests in North and South America, but the issue is not to argue about whether the differences are greater than the similarities, for that may be chiefly a matter of perspective. Two other approaches are useful, however: 1) Determination of what kinds of ecological features exhibit similarity (and to what degree) and what kinds exhibit differences (and to what degree). Our knowledge of temperate rainforests is still too preliminary to permit an assessment. 2) Exploration of the possible ecological consequences of the differences. On this we can perhaps make a small beginning. I will focus principally on comparisons between Chile and North America, in keeping with the interests of the symposium of which this paper is a part, but comparisons with other forests are equally useful and timely.

Diversity of fleshy fruits and frugivores

Chilean rainforests harbor many more species of fleshy-fruited plants but fewer species of avian frugivores than North American rainforests. Assuming that the total density of fruit-bearing plants is not less in Chile, there may be several possible ecological consequences: 1) Population density of Chilean frugivores might be higher. Cody (1973) reported a slightly higher density for Chilean birds in matorral habitats than for their "ecological equivalents" in California chaparral. However, for "beech" forest, Cody's (1973) overall density estimates were similar for central North America and sclerophyllous Chilean forests (New Zealand densities were somewhat lower). Chilean omnivore (including fruiteaters) in sclerophyll forest had a somewhat higher density than the North American site (Cody 1973). On the other hand, the evergreen forests of southern South America are reported to support much higher total densities of breeding birds than forests in western North America (Jaksic and Feinsinger 1991). Frugivores in six forests in southern Argentina accounted for < 4% of avian density in the breeding season (Jaksic and Feisinger 1991), but the frugivore component of the summer avifauna may be relatively high in Chilean temperate forests (Armesto *et al.* 1987, Armesto 1987). In North America, breeding-season densities of frugivores are often low also (Jaksic and Feisinger 1991, Thompson and Willson 1979), contrasting dramatically with high densities of fruit-eaters in fall (Table 5; Thompson and Willson 1979), when most plants mature their fruits. Similar patterns may obtain in Chile (Juan Armesto 1987 and pers. comm.), despite the lower level of migratoriness (see below). Assessment of frugivore densities should focus on seasons when fruits are present, and existing data do not permit the appropriate quantitative comparisons. Year-round censuses of frugivores in southern South America are needed to determine regional and seasonal differences in densities.

2) Given equal consumption rates (which needs to be determined), the region with the higher density of frugivores (relative to fruit abundance) should have better seed dispersal than the region with lower frugivore density (referring here only to frugi-

vores that are not seed predators). This prediction could be examined by comparing fruit removal rates and seed shadows for vertebrate-dispersed seeds in both places. The fruits of some Chilean forest plants appear to be too large (> 2.5 cm) for the existing avian frugivores and maybe poorly dispersed for this reason (Armesto *et al.* 1987, Hoffman *et al.* 1989, Carolina Villagrán, pers. comm.). Therefore the proposed regional comparison should be made without these species.

It is important to note that there is no comparative information on the density of fruits. If the many fleshy-fruited species in Chile are rare, on average, or bear fruit crops only sporadically and sparsely, the predictions about avian density and its consequences for dispersal obviously must be revised. For both regions, we need data on fruit abundances (mean and variance in both space and time).

3) The proportion and abundance of migratory bird species in Chile appears to be less than in North America (Cody *et al.* 1977 for matorral vs. chaparral; Jaksic and Feinsinger 1991, for temperate forests). During fall migration in at least parts of central North America, a series of migration peaks occur, with a succession of different avian frugivore species (Thompson and Willson 1979, and M.F. Willson unpublished). Because the mutualism between frugivores and fleshy-fruited plants is a very generalized one (Malmborg and Willson 1988 and references therein), successive waves of migrants can (and do) utilize the same fruit species. If a fruit crop is missed by one wave of migrants, there are usually several subsequent opportunities for dispersal (e.g. Skeate 1987), often by vectors with differing fruit-handling and post-foraging behaviors (Malmborg and Willson 1988). However, other parts of North America apparently do not exhibit the conspicuous peaks of abundance of fall migrants (Holmes and Sturges 1975 data for mid elevation in New Hampshire; in lowland riparian areas, abundances are probably higher; C.J. Whelan, pers. comm.). Nevertheless, a seasonal succession of frugivore species can still be expected, and the proportion of frugivores in the avifauna is similar to that in central North America. In Chile, however, more of the frugivores appear to be year-round residents. A fruit crop that is missed by frugivores early in the season may be dispersed later by the same species. Thus, the seed shadows for Chilean plants may be less varied, seasonally, than in North America (assuming that seasonal changes in foraging behavior within a species are less than the differences among species). A year-round population of frugivorous birds might also increase the advantage of winter fruiting phenology, and winter fruiting is moderately common in southern North America (Skeate 1987) and Chile (Cecilia Smith, pers. comm.). In addition, reduced seasonality of disperser populations could also favor very persistent fruits that are retained on the parent plant for many months.

Growth form and fruiting strategy

The prevalence of fleshy-fruited trees is much greater in Chile than in northern North America, and in both areas numerous shrubs and vines produce fleshy fruits. There may be several ecological consequences: In the eastern deciduous forest of northern North America, plants bearing fruit crops are prevalent in and around treefall gaps in the forest, along forest edges, and in intermediate seral stages of oldfield succession. Fruit-eating birds also congregate in such areas (Blake and Hoppes 1986, Martin and Karr 1986, Wilsson *et al.* 1982, Malmborg and Willson 1988). (The same is true for some tropical forests, Levey 1988, but see also Murray 1988, Schemske and Brokaw 1981, Willson *et al.* 1982). Within the deciduous forest, one result is that seedfall is often concentrated in and near gaps (Hoppes 1987, 1988; compare Schupp *et al.* 1989 for the neotropics). These patterns of spatial distribution are likely to be less well developed in Chilean temperate forests, in which a high proportion of fruiting plants are trees.

Arrival of a seed in a pre-existing gap may or may not be beneficial, depending on the age of the gap, local effects of natural enemies, and the plant's ability to exploit that microenvironment. Many species in eastern North America have a seed bank and wait for a gap to form (dispersal in time). In Alaskan rainforest, seed banks are less common and a number of plant species instead wait as seedlings for a gap to open up (P.B. Alaback, pers. comm.). Perpetually wet conditions at ground level in temperate rainforest may make dormant seed strategies less successful than in eastern deciduous forests. If so, plants of the Chilean rainforest also may be expected to make relatively little use of seed banks. Seedling banks, on the other hand, may be better developed in Alaskan than in Chilean wet forest. The cooler temperatures of Alaska reduce the metabolic costs of maintenance and perhaps the threat from pathogenic fungi, thus enhancing the potential probability of survival and/or the longevity of the seedlings.

Seed shadows

Animal dispersers are believed to extend the tails of seed shadows and to influence patterns of forest succession (e.g., Howe 1986, Janzen 1988). Volant dispersers create quite different patterns of seed deposition than nonvolant dispersers (e.g., Hatton 1989, Herrera 1989, Fuentes *et al.* 1986). Both birds and bats commonly deposit large numbers of seeds under convenient and/or habitual perches and these deposits serve as foci of recruitment (e.g., Fleming and Heithaus, 1981, Fuentes *et al.* 1984, Janzen 1988, Willson and Crome 1989). Where birds and bats are relatively abundant, such foci may be more numerous (if not erased by density- or distance-responsive seed/seedling predators; references in Fleming and Heithaus 1981), such that patterns of succession differ both in spatial aspects and in rates of change of species composition, compared to regions where volant dispersers are fewer. The population biology (including genetic structure) of species with differing disperser assemblages will also be altered (Herrera 1989).

Morphological differentiation of fruits relative to class of disperser

Although it has proved possible to identify some fruit traits associated with consumption by particular kinds of mammals or birds, the distinctiveness of fruits dispersed by reptiles (or fishes) has apparently not been assessed. As reptiles were the earliest (Paleozoic) fruit-eating terrestrial vertebrates that regularly dispersed seeds, a close look at fruits dispersed chiefly by present-day reptiles might be interesting. However, given the close phylogenetic relationship between birds and reptiles, the overlap in fruit diets and in traits of those fruits may be extensive (except that most modern fruit-eating reptiles probably forage on or near the ground). The distinctiveness of morphological "syndromes" for animal dispersal in different regions may reflect phylogenetic and biogeographic origins as much or more than present-day disperser faunas (Herrera 1986) (but see E, below).

Fruit patchiness and resource partitioning

Fleming *et al.* (1987) suggested that high patchiness of fruit resources in space and time should favor dietary generalization and more dietary overlap among frugivores, whereas low patchiness should favor dietary specialization and less dietary overlap. Even within the tropics, patchiness may vary from region to region and may be related to both foraging and ranging behavior of frugivores. If this argument is valid, we could predict (from the observed levels of dietary overlap) that, despite the lower species richness, the patchiness of fruit resources in North America should be substantially greater than in the tropics, Spain, and perhaps Chile. Although fruit-crop production for some North American species is highly variable in time and space (e.g., *Celtis, Vitis, Parthenocissus, Celastrus, Prunus americana, Asimina* in central Illinois; unpubl. obs.), there are at present no quantitative data to test this prediction. A potentially serious complication is that important segments of the frugivore fauna in many regions is now extinct or nearly so (references in Herrera 1989), so that present-day dietary overlap may be different than in the recent past.

To sum up: The diversity of fleshy-fruited plants (especially trees) is higher but the diversity of frugivorous vertebrates is lower in Chile than in North America. The composition of the frugivore fauna is broadly similar at higher taxonomic levels and in general foraging ecology. Information on density of both frugivores and fruiting plants is scarce, and seasonal patterns of fruiting and fruit consumption need documentation.

Fruits consumed by birds and by mammals often differ morphologically and chemically, but in North America the fruit diets of these two taxonomic classes overlap almost completely. However, birds appear to be more important dispersers

APPENDIX 1

Frugivory scores for North American plant genera for data from Martin *et al.* (1951)[a].

Indices de frugivoría para géneros de plantas de Norte América según datos de Martin *et al.* (1951).

Plant genus	Mammals		Birds
	Carnivora	Others	
Amelanchier	2.0	–	23.0
Arctostaphylos	4.5	–	2.0
Callicarpa	0.5	0.5	6.0
Celtis	3.5	1.5	34.5
Cornus	1.5	–	37.5
Crataegus	4.5	–	5.5
Diospyros	17.0	1.5	(4.5)
Fragaria	0.5	4.0	4.0
Ilex	2.5	0.5	24.5
Juniperus	3.5	1.0	17.5
Lindera	–	–	6.5
Morus	4.0	2.0	22.0
Myrica	0.5	–	20.5
Nyssa	3.0	0.5	17,5
Opuntia	4.0	1.0	5.5
Parthenocissus	1.0	–	22.0
Phoradendron	1.0	–	9.0
Phytolacca	2.0	0.5	14.5
Prunus	9.5	0.5	34.5
Rhamnus	2.0	–	15.5
Rhus	–	–	23.5
Ribes	2.5	–	9.0
Rubus	4.5	1.0	49.0
Sabal	3.0	–	6.0
Sambucus	–	–	42.5
Sassafras	0.5	–	9.5
Smilax	3.0	1.5	14.0
Solanum	4.0	–	6.5
Sorbus	1.0	2.5	2.5
Symphoricarpos	0.5	–	6.5
Toxicodendron	0.5	–	41.0
Vaccinium	10.5	0.5	20.5
Viburnum	1.5	–	5.0
Vitis	11.5	1.5	50.0

[a] Martin *et al.*, ranked the amount of fruit eaten by animal consumers, using a number of symbols to indicate the percentage of the diet composed of particular plants; + = 0.5 – 2% of diet, * = 2 – 5%, ** = 10 – 25%, **** = 25 – 50%, ***** = > 50%. From their tallies, I calculated a total score for the various categories in the table (using 2 + = 1 *). Ungulates were omitted from the "others" column because the data in Martin *et al.*, did not permit discrimination of fruit-eating from foliage-eating, and this problem was most acute for ungulates. Rodents were also excluded here because of their usually high rates of seed predation.

Plant genera were included in this table when their total scores > 6 * for mammal-plus-bird-dispersers.

than mammals for many of the North American fleshy-fruited species.

A set of simple predictions is generated from the available information. This exercise serves, simultaneously, to emphasize the need for more information and to focus attention on comparative questions of importance to both population biology and community structure. The principal predictions are briefly summarized here:

A) High frugivore density may lead to better overall dispersal, but high frugivore diversity and/or seasonal variation in abundance may lead to higher variance in the shapes of seed shadows. B) A prevalence of fleshy-fruited trees may lead to a lesser concentration of bird activity in treefall gaps. Seed banks tend to be uncommon in wet forests and seedling banks may be less common in cold-wet than in warm-wet forests. C) The relative abundances of volant and nonvolant seed dispersers may alter the patterns of succession in space and time. D) The distinctiveness of fruits consumed by different classes of dispersal agents varies regionally and may reflect phylogeny and biogeography as much as contemporary ecology.

These suggestions cover but a few of the ecological consequences of regional differences in the structure and function of the diffuse mutualism between fruit-eating animals and fleshy-fruited plants. Nevertheless, perhaps they serve as a jumping-off place for comparative studies.

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