Plant/frugivore interactions in South American temperate forests.

Interacciones planta/frugívoro en bosques templados de Sudamérica

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ABSTRACT

Berry- and nut-bearing plant species comprise more than 70% of the flora in mediterranean shrublands as well as in temperate rain forests in Chile. We examine the role of fruit-eating animals as seed dispersers in South American temperate forests. Among the mammals, foxes (genus *Dusicyon*) are reported to be major dispersers of the seeds of several native plants, especially during summer and fall. A small deer (*Pudu pudu*) and an arboreal marsupial (*Dromiciops australis*) are also fruit eaters, but their role as seed dispersers is unclear. The most important frugivores in South American temperate forests, in terms of species richness, numbers of individuals, and activity, are birds. A total of 17 species of birds consume fleshy fruits. They all have a mixed diet, feeding on fruits and insects, although six species feed primarily on fruit. Several species of avian frugivores are reported to be migratory, but we know little about their seasonal patterns of abundance and their routes of migration.

We discuss a case study of the interaction between fruit-eating birds and plants in the temperate rain forest of Chiloé (42°S, 74°W). Color and size characteristics of fleshy fruits were analyzed in relation to fruit consumption by birds. Black-colored fruits predominated among trees, whereas most shrubs had red fruits. Black hues might be UV-signals to birds in dark forest interiors. Average diameter of fruits (8.93 mm) closely matched the average gape width of frugivorous birds (8.62 mm), but there were several plant species with fruit sizes greater than the widest gape of a forest bird. This differs from the pattern shown for other forests, in the tropics and the north-temperate region, where the distribution of fruit sizes is included within the range of bird gape widths. We suggest that the Quaternary history of disturbances and extinctions in south-temperate forests may have caused some plants to lose their original seed dispersers. Finally, we dicuss the applicability of Herrera's Relative Yield (RY) index for estimating the potential profitability of fruits to birds. An alternative to this index, based on the ratio between pulp dry mass and fruit dry mass, rather than fresh mass as in RY, is proposed as a more suitable estimator of profitability for fruits with a high water content, because it does not cosider water "a priori" as a waste component.

Key words: Fleshy fruits, frugivory, mutualism, temperate forest, seed dispersal.

RESUMEN

Entre las especies de la flora del matorral mediterráneo y del bosque lluvioso templado de Chile más de un 70% posee frutos carnosos o nueces. En este estudio examinamos el rol de los animales frugívoros como dispersantes de semillas en los bosques templados de Sudamérica. Entre los mamíferos, los zorros (género *Dusicyon*) son importantes dispersantes de semillas de varias especies nativas, en especial durante verano y otoño. Un ciervo (*Pudu pudu*) y un marsupial arbóreo (*Dromiciops australis*) también consumen frutos, pero su rol como dispersantes de semillas es desconocido. Los frugívoros más importantes en el bosque templado de Sudamérica, en términos de riqueza de especies, número de individuos y actividad, son las aves. Un total de 17 especies consume frutos carnosos. Todas ellas poseen una dieta mixta, consumiendo frutos e insectos, aunque seis especies se alimentan principalmente de frutos. Varias especies de aves frugívoras son migratorias, pero sabemos muy poco acerca de las variaciones estacionales en su abundancia, o de sus rutas migratorias.

Se discuten los primeros resultados de un estudio de la interacción planta-frugívoro en el bosque lluvioso templado de Chiloé (42°S, 74°W). Características como el color y tamaño de los frutos son analizadas en relación con su consumo por las aves. Los frutos negros son predominantes entre los árboles, mientras que la mayoría de los arbustos tiene frutos rojos. Los frutos negros podrían reflejar en el ultravioleta, siendo visibles para las aves en el interior sombrío del bosque. El diámetro promedio de los frutos (8,93 mm) es similar al promedio de ancho de pico entre comisuras de las aves frugívoras (8,62 mm); sin embargo, hay algunas especies cuyos frutos son de mayor tamaño que el mayor ancho de pico de un ave del bosque. Este resultado difiere del patrón observado en bosques templados del hemisferio norte y tropicales, en donde la distribución de tamaños de frutos está incluida en el rango de valores de anchos de picos de las aves frugívoras. Esta situación podría reflejar la historia Cuaternaria de catástrofes y extinciones en bosques

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templados del hemisferio sur, por las que algunas plantas habrían perdido sus dispersantes originales. Finalmente, discutimos la aplicabilidad del índice de Herrera (RY) para estimar el aprovechamiento potencial de los frutos para las aves. Proponemos un índice alternativo (RY'), basado en la proporción entre los pesos secos de la pulpa y el fruto, en lugar de los pesos frescos como en el índice RY. Este nuevo índice sería un mejor estimador del aprovechamiento potencial de frutos con alto contenido de agua, debido a que no considera "a priori" al agua como un componente desechable.
  Palabras claves: Bosques templados, dispersión de semillas, frugivoría, frutos carnosos, mutualismo.

¡Ah! y mira, Curcunchito; fíjate en que los pájaros gustan del fruto del quintral, y ellos mismos son los que llevan las semillas a otros árboles, y allá prende el quintral, y arruina el árbol del cual vive. Es una planta endemoniada...

"Alsino", Pedro Prado.

INTRODUCTION

Fruits constitute an unusual kind of "prey" for animals. These structures are usually the units of dissemination of a plant's offspring and, consequently, they benefit from being carried away from the parent by a dispersal agent (Howe & Smallwood 1982). A fleshy fruit can be described as a nutritious "package", containing the seeds inside and "designed" to be eaten by animals (Snow 1971). The animals may act as dispersers when they ingest the entire fruit, thus gaining a meal, and transport the seeds undamaged to a different place where germination may occur. Mutualistic interactions between plants and frugivores, most commonly vertebrates, have probably evolved from a relationship that was originally predatory in nature (Thompson 1982). This sequence is suggested by the various cases where either the seeds are harmed by passage through the vertebrate's gut, or animals suffer from the predator-deterrent chemicals present in the fruit flesh. In this review we will concentrate on potentially mutualistic interactions between frugivores and plants, keeping in mind that many situations are hard to classify unequivocally as purely mutualistic (*e.g.* Bonaccorso *et al.* 1980, Murray 1986).
  Much of what we know or conjecture about seed dispersal by vertebrates stems from numerous studies of frugivory in tropical regions, especially the neotropics (Snow 1965, Leck 1969, 1972a, b, Howe & Primack 1975, McKey 1975, Janzen *et al.* 1976, Howe & Estabrook 1977, Howe & De Steven 1979, Howe & Vande Kerckhove 1979, Bonaccorso *et al.* 1980, Howe 1980, 1983; Snow 1981, Greenberg 1981, Janson 1983, Pratt & Stiles 1983, 1985, de Foresta *et al.* 1984, Wheelwright

et al. 1984, Wheelwright 1985). Most species of birds which are primarily frugivorous (Snow 1981), as well as fruit-eating bats, monkeys and other mammals (Heithaus *et al.* 1975, Bonaccorso *et al.* 1980, Janzen *et al.* 1976, de Foresta *et al.* 1984), are almost exclusively tropical. The number of bird species feeding on a single tree in the neotropics (Leck 1972a, Breitwisch 1983) may be higher than the entire frugivorous bird assemblage of a temperate locality. These features of tropical areas, among others, have attracted researchers interested in exploring the relationship between frugivory and seed dispersal. However, by no means should this imply that biotic interactions are less frequent in the dispersal of temperate forest plants, or that frugivory is unimportant within temperate vertebrate assemblages. In recent years, an increasing number of studies has begun to unravel the patterns of interaction between plants and animal dispersers, particularly birds, in temperate and mediterranean regions of North America and Europe (Thompson & Willson 1979; Stiles 1980, Sorensen 1981, Herrera 1981a, 1981b, 1982, 1984, Herrera & Jordano 1981, Willson & Thompson 1982, Stapanian 1982, Piper 1986, Willson 1986). It is now apparent (see Herrera 1985b, Willson 1986) that results from these studies will contribute to improve the theoretical framework generated by early workers (Snow 1971, McKey 1975, Howe & Estabrook 1977), who emphasized tropical areas, and will lead to a better understanding of mutualisms related to seed dispersal.
  At this stage, we know very little about frugivory in nontropical regions of South America (see review by Howe & Smallwood 1982), and regional faunal accounts (Osgood 1943, Johnson 1965) tend to

ignore fruit-eating habits in forest vertebrates. Nevertheless, a quick inspection of published floras for temperate forests of southern South America (Muñoz 1980, Villagrán et al. 1986) reveals that many species have berries or drupes, characteristic of endozoochory (van der Pijl 1982). The purpose of this work is to document the importance of frugivory for the dispersal of temperate forest plants in South America. We will first present quantitative information on the predominance of biotic dispersal in Chilean forests. Subsequently, we will review the data on mammals and birds acting as dispersal agents, and will analyze the preliminary results of a case study on seed dispersal by birds in the Island of Chiloé (Fig. 1). Throughout this analysis, we will put the information in the context of what is known for North-temperate forests.

DISPERSAL SYNDROMES OF TEMPERATE FOREST PLANTS

Dispersal mechanisms can be inferred by examining the morphological traits of plant propagules (see van der Pijl 1982). Although this will not tell us how actual dispersal occurs, it is a valuable approach for determining the relative importance of biotic and abiotic agents in a given plant assemblage (e.g., Howe & Smallwood 1982). Among vertebrate-dispersed propagules, brightly-colored berries and drupes, or seeds surrounded by reddish, fleshy arils, are considered to be dissemi-

nated by avian frugivores, whereas dry, indehiscent nuts usually are dispersed by mammals (van der Pijl 1982).

Hoffmann & Teillier (unpubl. MS) and Armesto (1987) report that a major proportion of the southern South American flora in different forest types, from mediterranean to cold temperate regions, has berries, drupes, arillate seeds, or nuts (Table 1), indicating that frugivorous birds and mammals are important dispersers of seeds. Fleshy fruits are found in 60% to 70% of the species, whereas nuts are less common, suggesting that the most important potential dispersers are birds (Armesto 1987). The frequency of ornithochory (sensu van der Pijl 1962) in South American temperate forests is as high as in some tropical forests, and higher than in some North American temperate forests (cf. Howe & Smallwood 1982, Willson 1986). On the other hand, mammal-dispersed nuts are rare in Chilean forests (Table 1), whereas they are the most frequent fruit type among north-temperate tree species (Armesto 1987). Armesto (1987) speculated that this difference between north- and south- temperate forests is due in part to the paucity of mammals in austral South America. In the next two sections of this paper we will provide evidence of frugivory in temperate-forest mammals and birds, and discuss their relative importance as seed dispers.

Mammalian frugivores

Although Chile has a low diversity of mammals, in comparison to other ver-

TABLE 1

Relative importance of fruit types associated with seed dispersal by frugivorous birds and mammals in temperate forests of Chile.

Importancia relativa de los tipos de frutos relacionados con la dispersión de semillas por aves y mamíferos frugívoros.

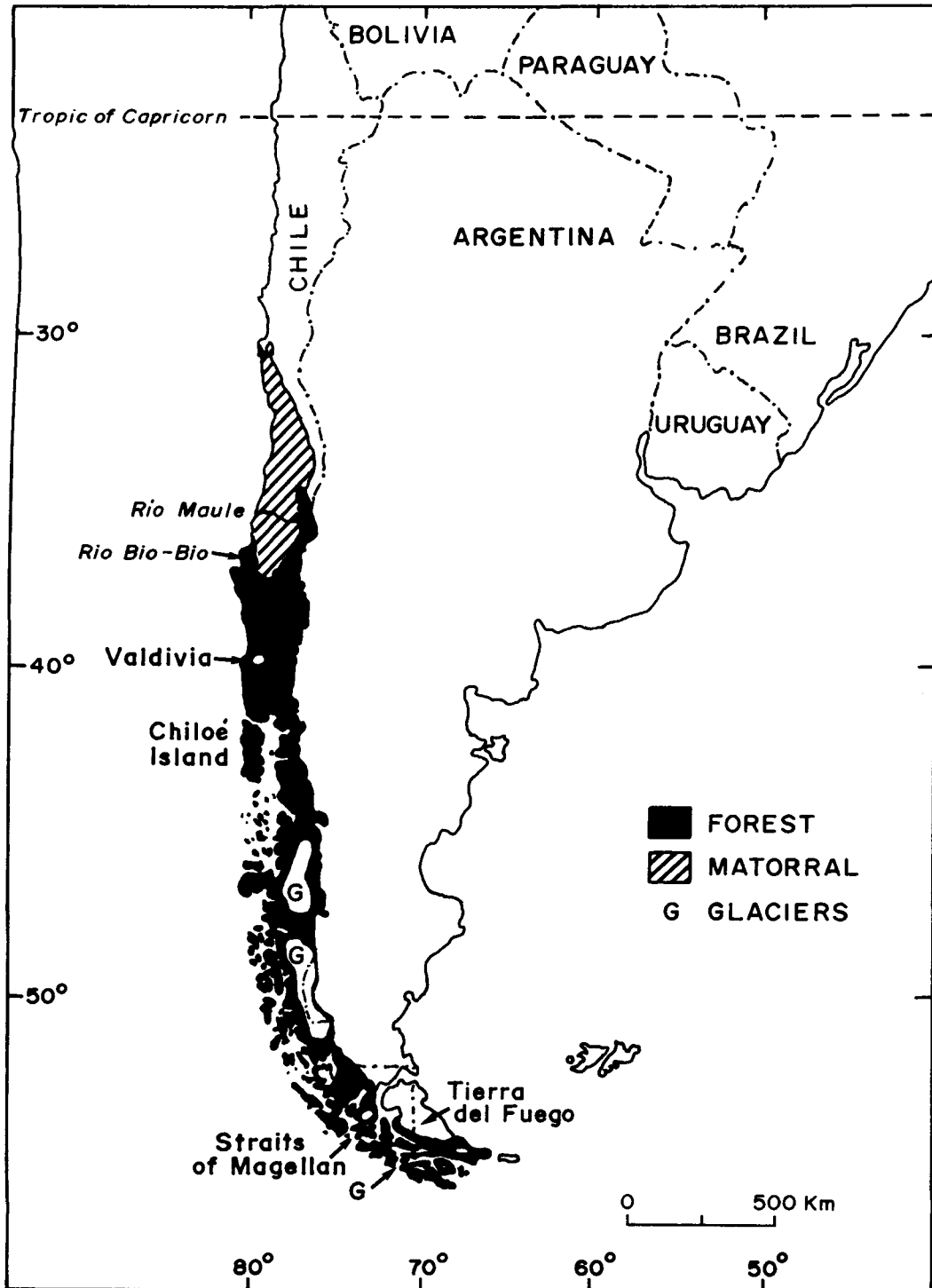| Vegetation type (South lat.)	N° of species	% fleshy fruits	% dry nuts	Source
Sclerophyll forest (35°)	64	64.0	12.0	Hoffmann & Teillier (unpubl. MS)
Mixed-deciduous forest (38 - 39°)	74	66.0	11.0	Hoffmann & Teillier (unpubl. MS)
Evergreen rain forest (42°)	74	68.9	1.4	Armesto (1987)

Fig. 1: Distribution of temperate forests and mediterranean shrublands (matorral) in South America (modified from Vuilleumier 1985).

Distribución de los bosques templados y el matorral mediterráneo en Sudamérica (modificado por Vuilleumier 1985).

tebrate groups such as birds and lizards (Fuentes & Jaksic 1979), some species may be important fruit eaters, possibly contributing to seed dispersal. In central Chile, foxes are reported to consume large quantities of berries, particularly in summer and fall (Table 2), when their mammalian prey populations are less abundant (Jaksic et al. 1980) and fruit availability is greater (Thrower & Bradbury 1977). The smaller fox, Dusicyon griseus, appears to be more frugivorous than the larger Dusicyon culpaeus, although this difference is probably related to the greater abundance of berry-producing shrubs in the foothills of the Coastal Range, where D. griseus occurs (Jaksic et al. 1980); D. culpaeus is mostly restricted to Andean environments in central Chile. The Chiloé fox, Dusicyon fulvipes, is also largely frugivorous during the austral summer (Table 3), when fruits are abundant. A single scat was found to contain up to 174 seeds of Amomyrtus luma, and all scats collected in February 1986 contained seeds of this plant (Armesto & Correa, unpublished data). Other Carnivora found in temperate forests, Galictis cuja and Conepatus chinga, are known to eat fruit in captivity (Housse 1953); however, there are no quantitative data on the frequency of frugivory for these two species in the wild.

Two other species of mammals that inhabit temperate forests, a small deer (Pudu pudu) and an arboreal marsupial (Dromiciops australis), are partly frugivorous (Table 3). In captivity, the marsupial readily eats berries (Greer 1968, Jiménez & Rageot 1979), but we have only anecdotal information on their food in the wild. Although reliable reports on the diet of the austral deer are almost lacking, this species could be an important dispersal agent for plants with dry, indehiscent nuts (e.g. Gevuina avellana; Table 3), a syndrome that is associated with mammalochory (van der Pijl 1982). Hershkovitz (1982) reported that the austral deer feeds on nuts and berries, in addition to other plant parts. Another marsupial inhabitant of southern temperate forests is Ryncholestes raphanurus, which is a rare and endangered species (Miller & Rottman 1976). Its diet is completely unknown, and although it has insectivore-shaped teeth, it may possibly eat some fruit, as do other marsupials. Granivorous rodents could also be occasional dispersers of seeds in temperate forests. Akodon olivaceus, A. longipilis and Oryzomys longicaudatus, all of which occur in the forests near Valdivia, consume primarily fruits of Aextoxicon punctatum and Gevuina avellana Murúa & González) 1985) as well as minor quantities of other berries (Rau et al. 1981). Although these rodents presumably eat and kill most seeds (cf. Janzen 1983), some seeds may escape unharmed and be dispersed to sites where they can germinate.

Mammal-dispersed fruits in the temperate forests of southern Chile clearly depend on the opportunistic behavior of animals that also consume other food items. Nevertheless, the data presented here suggest that foxes could play an important role in the dispersal of seeds of wild plants, given their tendency to eat fruit all year, the numbers of seeds they can carry in their guts, and the long distances they can travel. In North America, it is well

TABLE 2

Incidence of frugivory among central Chilean foxes (data from Jaksic et al. 1980). Number of scats examined in parentheses.

Incidencia de frugivoría en las especies de zorros de Chile central (datos de Jaksic et al. 1980). Número de fecas examinadas entre paréntesis.

| Species | % of scats containing berries | | | |
	Spring	Summer	Fall	Total
Dusicyon culpaeus	5.3 (132)	11.7 (103)	21.7 (83)	11.6 (318)
Dusicyon griseus	17.7 (62)	36.0 (89)	52.0 (127)	39.2 (278)

TABLE 3

Fruit-eating mammals of Chilean temperate forests.

Mamíferos frugívoros de los bosques templados de Chile.

Species	Geographical range*	Species of plant in the diet	References
Carnivora			
Dusicyon culpaeus	18° - 55°	*Aristotelia chilensis* *Cryptocarya alba* *Lithrea caustica* *Muehlenbeckia hastulata* *Schinus latifolius* *Peumus boldus*	1, 2, 3, 4
Dusicyon griseus	20° - 55°	as above	2
Dusicyon fulvipes (All *Canidae*)	42° - 44°	*Amomyrtus luma*	5
Artiodactyla			
Pudu pudu (*Cervidae*)	35° - 48°	*Fuchsia magellanica* *Gevuina avellana* unidentified *Myrtaceae*	6, 7
Marsupialia			
Dromiciops australis (*Didelphidae*)	35° - 45°	*Lapageria rosea* *Pernettya* spp. *Luzuriaga* spp.	5, 8

* After Osgood (1943), Miller & Rottman (1976), Mann (1978).
References: 1 = Yáñez & Jaksic (1978), 2 = Jaksic *et al.* (1980), 3 = Miller & Rottmann (1976), 4 = Housse (1953), 5 = unpublished observations of the authors, 6 = Krieg (1925), 7 = Greer (1968), 8 = Jiménez & Rageot (1979).

known that foxes are important seed dispersers of many wild plants (Martin *et al.* 1951). Unfortunately, most mammal dispersers in temperate South America (Table 3), including foxes, are currently endangered over major parts of their ranges, due to hunting and destruction of their natural habitat by man. This renders it difficult further examination of the nature of the interaction between these frugivores and their food plants in the field.

Avian frugivores

Data on frugivory by birds in South American temperate forests are very scanty. Grigera (1976) provides some information on the food of species of Fringillidae, suggesting that they may be partially frugivorous. In a book directed to amateurs, Solar (1975) indicates that, in central Chile, *Elaenia albiceps, Turdus falklandii, Mimus thenca, Pyrope pyrope,* and *Anair-*

etes parulus eat fruit. According to this author, these birds consume berries of *Aristotelia chilensis* (Eleaeocarpaceae), *Lithrea caustica* (Anacardiaceae), *Luma apiculata* (Myrtaceae), *Muehlenbeckia hastulata* (Polygonaceae), *Maytenus boaria* (Celastraceae), *Tristerix* spp. (Loranthaceae), and *Trichocereus* spp. (Cactaceae), among other native plants. Hoffmann *et al.* (1986) report that *Trudus falklandii, Mimus thenca* and *Curaeus curaeus* feed on the fruits of Chilean mistletoe (*Tristerix tetrandus*). Indirect evidence (Fuentes *et al.* 1984, Armesto & Pickett 1985) suggests that birds are important dispersal agents for the seeds of a large number of tree and shrub species of the Chilean matorral, determining their patterns of invasion during secondary succession.

An ongoing study on seed dispersal in the rainforest of Chiloé (Armesto *et al.*, unpublished), sheds some light on the incidence of frugivory among forest birds (Table 4). Although 17 species

TABLE 4

Frugivorous birds of South American temperature forests. List based on taxa reported by
Vuilleumier (1985) and the authors' unpublished data.

Aves frugívoras de los bosques templados de Sudamérica. La lista se basa en los taxa citados por
Vuilleumier (1985) y en datos no publicados de los autores.

Species*	Common name	Northern limit of distrib.	Status	Species of plant in the diet**
Passeriformes				
Anairetes parulus	cachudito	30°S	locally migrat.	?
Carduelis barbatus	jilguero	23°S	largely migrat.	?
Cinclodes fuscus	churrete acanelado	23°S	migratory	?
Cinclodes patagonicus	churrete	33°S	migratory?	?
Curaeus curaeus	tordo	23°S	resident?	?
Diuca diuca	diuca	30°S	resident	?
Elaenia albiceps+	fío-fío	23°S	migratory	*Drimys winteri, Amomyrtus luma, Ovidia pillo-pillo*
Phrygilus patagonicus+	cometocino	33°S	migratory	?
Phytotoma rara	rara	23°S	migratory	?
Pteroptochos tarnii	hued-hued	36°S	resident	*Amomyrtus luma*
Pyrope pyrope	diucón	30°S	migratory	*Drimys winteri*
Scelorchilus rubecula	chucao	35°S	resident	*Amomyrtus luma*
Sicalis luteola	chirihue	23°S	resident	*Drimys winteri*
Turdus falklandii+	zorzal	23°S	resident	*Amomyrtus luma, Aristotelia chilensis, Drimys winteri, Ovidia pillo-pillo*
Zonotrichia capensis+	chincol	widespread in South America	locally migrat.	*Nertera granadensis, Relbunium hypocarpium*
Piciformes				
Colaptes pitius	pitío	29°S	resident?	*Drimys winteri*
Columbiformes				
Columba araucana+	torcaza	30°	resident?	*Amomyrtus luma, Drimys winteri*

* Nomenclature follows Araya (1985).
** Preliminary data based on stomach contents (Armesto et al. unpublished).
? Indicates unidentified seed.
+ Feeds largely on fruit during austral summer.

consume fleshy fruits, our present data do not allow assessment of what proportions of their diets are made up by berries. A few species, however, appear to rely mainly on fleshy fruits as their food source during the season of greatest fruit abandance (Table 4), and the individuals of these species constitute 82% of the total number of passerines active during summer (Armesto 1987, and unpublished data). Nevertheless, all species, with the sole exception of *Phytotoma rara* (Johnson 1965), have a mixed diet, feeding on insects and vegetable matter, just as most birds do in north-temperate and tropical areas (Thompson & Willson 1979, Snow 1981, Herrera 1984). Some species,

such as the Rhinocryptids *Sclerochilus rubecula* and *Pteroptochos tarnii*, are considered insectivorous by Johnson (1965); we have found, however, that their stomachs contain intact seeds of *Amomyrtus luma*, whose berries are frequently found on the forest floor (Armesto, unpublished data), the typical habitat of these birds. We also report on fruit consumption by a species of flicker (*Colaptes pitius*), a specialized insectivore according to Johnson (1965). These observations suggest that frugivory might be an opportunistic response to high fruit availability during summer (Armesto 1987).

Chilean fruit-eating birds have widespread ranges (Table 4), which most

often transcend the limits of the temperate forest (Fig. 1). Hence, most frugivorous birds may interact with a different plant species assemblage in other parts of their geographical range. This supports the view that there is not a close relationship between temperate rainforest plants and their dispersal agents, in line with the reasoning of Herrera (1986), who argues that phenotypically matching, tightly co-adapted plant-seed disperser systems are unlikely to occur (see also Wheelright & Orians 1982, Feinsinger 1983, Janzen 1983, Howe 1984). The degree of interdependence between plants and their seed dispersal agents can only be evaluated on the basis of detailed knowledge of the food habits of bird species throughout their range, complete accounts of the birds feeding on the fruit crop of a given plant species, and information on the ultimate fate of the dispersed seeds.

Although a disperser species as a whole could hardly develop strong links with particular fruiting species, local populations might depend, at least temporarily, on a given kind (or kinds) of fleshy fruits. To test this hypothesis, we need more reliable information on the mobility of local populations of forest birds. It is known that several species migrate locally (Solar 1975, Vuilleumier 1985), presumably following spatial, altitudinal, or latitudinal variations in food supply. This could have important consequences in extending the ranges of their food plants, and in reinforcing the patchy distributions of fruiting species (see Herrera 1985a). Migratory routes of non-resident species are almost completely unknown. The only report is that of Johnson (1965), who claims that *Elaenia albiceps* populations move to tropical areas of southern Brazil between April and September. Data on the other potential migrants (Table 4) are urgently required to understand the dynamics of avian populations in the temperate forest.

PLANT/FRUGIVORE INTERACTIONS IN THE FOREST OF CHILOE: A CASE STUDY

We examined the characteristics of fleshy fruits from the forest of Chiloé Island (Fig. 1) in order to determine possible traits (Table 5) that influence fruit consumption by birds. The study area, described by

Villagrán *et al.* (1986), includes old-growth forest as well as successional fields. Low and mid elevation (100-400 m) forests are dominated by broad-leaved evergreen species. The most frequent species are Myrtaceous trees (genera *Amomyrtus* and *Luma*), along with *Eucryphia cordifolia, Laurelia philippiana,* and *Aextoxicon punctatum.* At higher altitudes, *Nothofagus* spp. and some Conifers (*Podocarpus, Saxegothacea)* dominate the landscape. The most abundant species in successional fields are Ericaceous shrubs (*Pernettya* and *Gaultheria*), and several species of *Berberis.* In second-growth forests, *Drimys winteri, Raphithamnus spinosus,* and *Luma apiculata* are generally the most common species.

Fruit colors

The colors of ripe fruits are a "signal" for attracting dispersal agents (Willson & Thompson 1982). Birds have well-developed color vision (Varela *et al.* 1983) that allows them to find and recognize conspicuously-colored fruit displays. In the temperate rainforest of Chiloé, the great majority of bird-dispersed species have black (including dark blue and purple colors, as in Wheelright & Janson 1985) or red berries (28 and 26%, respectively; Fig. 2). These are also the most frequent colors of ripe fruits eaten by birds in North American (Willson & Thompson 1982), European (Turcek 1963), and neotropical forests (Wheelright & Janson 1985). There is some variation, however, in the proportions of red and black fruits in each area. Blacks are more important than reds in neotropical localities, whereas red is the most common hue among European plant species (Wheelright & Janson 1985). In Chiloé, the proportions of red and black colors are different among shrubs and trees (Fig. 2). Red is the dominant hue of ripe fruits produced by shrubs, whereas fruits of forest trees are usually black. Shrubs are seldom found in the forest understory, but they are common in open, successional areas. Most tree species, in turn, are found in the forest interior, at or below the main canopy. It is clear that, in open areas, red is a conspicuous color to birds (Raven 1972, Varela *et al.* 1983), but black berries would seem to be inconspicuous, especially among forest species that usually occur

TABLE 5

Characteristics of fruits of bird-dispersed plants in the forest of Chiloé.

Características de los frutos dispersados por aves en el bosque de Chiloé.

Species*	Family	Fruit color	X̄ cross diameter (mm)	Mean Fresh weight (g)	N⁰ seeds per fruit (range)
Trees					
Aextoxicon punctatum	Aextoxicaceae	black	7.5	0.43	1
Amomyrtus luma	Myrtaceae	red/black**	7.8	0.36	1 (1 - 3)
Amomyrtus meli	Myrtaceae	black	9.0	−	?
Aristotelia chilensis	Elaeocarpaceae	red/black**	6.0	0.12	3 (2 - 5)
Drimys winteri	Winteraceae	green/black	6.0	0.18	2 (1 - 5)
Luma apiculata	Myrtaceae	black	10.0	−	4 (3 - 6)
Maytenus boaria	Celastraceae	red***	5.0	−	2
Maytenus magellanica	Celastraceae	yellow***	6.5	−	2
Myrceugenia chrysocarpa	Myrtaceae	orange	10.0	−	?
Myrceugenia exsucca	Myrtaceae	black	9.0	−	2 (1 - 5)
Myrceugenia ovata	Myrtaceae	orange	11.0	0.25	2
Myrceugenia parvifolia	Myrtaceae	red	7.0	−	−
Myrceugenia planipes	Myrtaceae	black/red**	15.0	1.59	2 (1 - 4)
Ovidia pillo-pillo	Thymeliaceae	red	9.4	0.33	1
Podocarpus nubigena	Podocarpaceae	red***	9.0	−	1
Pseudopanax laetevirens	Araliaceae	blue	5.5	−	4 (4 - 5)
Raphithamnus spinosus	Verbenaceae	blue	12.1	0.14	2 (1 - 4)
Saxe-gothaea conspicua	Podocarpaceae	red	12.0	0.47	2
Shrubs					
Azara lanceolata	Flacourtiaceae	orange	6.5	−	10
Berberis buxifolia	Berberidaceae	red/blue**	9.0	0.50	8 (5 - 11)
Berberis darwini	Berberidaceae	red/black**	9.9	0.74	9 (5 - 12)
Berberis serrato-dentata	Berberidaceae	black	7.0	−	3
Desfonatinea spinosa	Desfontaineaceae	yellow	14.0	−	?
Empetrum rubrum	Empetraceae	red	6.1	0.14	7 (6 - 8)
Fuchsia magellanica	Onagraceae	red	6.7	0.62	50
Gaultheria antarctica	Ericaceae	red	−	−	−
Gaultheria phyllyreaefolia	Ericaceae	red/black**	9.2	0.30	50
Myoschilos oblonga	Santalaceae	blue	7.0	−	?
Pernettya furiens	Ericaceae	red	10.0	0.11	33 (31-37)
Pernettya mucronata	Ericaceae	red	7.0	−	10
Pernettya poeppigii	Ericaceae	red	8.0	−	10
Ribes magellanicum	Saxifragaceae	black	6.5		
Ugni molinae	Myrtaceae	blue	7.0	0.14	9 (3 - 18)
Vines and epiphytes					
Asteranthera ovata	Gesneriaceae	brown	11.5	0.63	10
Boquila trifoliolata	Lardizabalaceae	blue	7.0	−	(1 - 4)
Cissus striata	Vitaceae	black	5.0	0.31	(2 - 3)
Ercilla syncarpelata	Phytolaccaceae	green	4.5	−	1 (1 - 2)
Greigia landbeckii	Bromeliaceae	red	18.0	−	10
Griselinia racemosa	Cornaceae	black	5.0	0.20	1
Griselinia ruscifolia	Cornaceae	black	4.5	−	1
Luzuriaga marginata	Philesiaceae	orange	?	−	?
Luzuriaga polyphylla	Philesiaceae	green	11.3	0.64	1 (1 - 2)
Luzuriaga radicans	Philesiaceae	orange	16.4	0.69	4
Mitraria coccinea	Gesneriaceae	green/red**	15.0	0.69	50
Philesia magellanica	Philesiaceae	yellow	14.0	−	10

*   Nomenclature follows Villagrán *et al.* (1986)
**   Bicolored displays (see text)
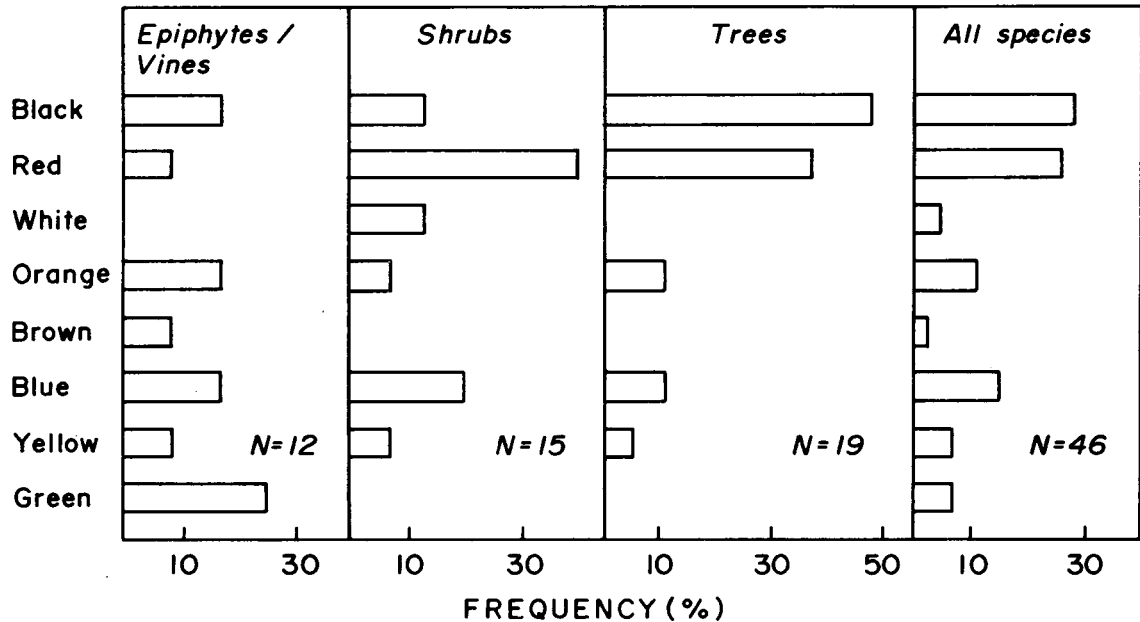*** Color refers to aril

Fig. 2: Frequencies of color hues of fleshy fruits in species from the forest of Chiloé.

Frecuencias de colores de los frutos carnosos en las especies del bosque de Chiloé.

in the shade. Perhaps black berries reflect ultraviolet (Burkhardt 1982), a color to which some birds are sensitive (Varela *et al.* 1983). This hypothesis would lead to the prediction that black (UV-reflecting) colors are more common in evergreen rainforests, such as some neotropical forests and the temperate forest in Chiloé, than in open woodlands or deciduous forests where light penetration is greater. Further research on the visual perception of frugivorous birds is needed to determine how their behavior can be modified in response to the colors of their food.

In Chiloé, several species (Table 5) exhibit bicolored fruit displays (Willson & Thompson 1982), where berries turn from red to black during ripening, or where black or green berries are associated with conspicuously red structures (*e.g.* pedicels, bracts), presumably serving as "signals". Willson & Thompson (1982) hypothesize that these unusually conspicuous displays are more frequent in species that produce fruit at times when frugivore abundance is low. We do not have, at present, data to test this hypothesis.

Fruit sizes versus bird-gape widths

In neotropical (Wheelright 1985) and mediterranean forests (Herrera 1984), the

sizes of fleshy fruits and the gape widths of frugivorous birds have similar frequency distributions, and the average gape widths are about 2 mm larger than the average diameters of fruits (Herrera 1985a). The frequency distribution of fruit diameters (or widths) of bird-dispersed species in the temperate forest of Chiloé (Table 5) was analyzed by Armesto (1987). Overall, there is a close coincidence (difference nonsignificant according to the Mann-Whitney U-test; $P > 0.90$) between the average cross diameter of berries ($\bar{x} = 8.93$ mm, range $4.5 - 18.0$, $n = 43$) and the mean gape width (or mouth width) of fruit-eating birds ($\bar{x} = 8.62$ mm, range $6.2 - 12.0$, $n = 12$; Table 6). Several species have fruits greater than 12 mm (Table 5), which is the upper limit of gape widths of local avian frugivores (Table 6). If, as asserted by Herrera (1985a) and Wheelright (1985), gape width imposes an upper limit to the size of fruits that can be swallowed by a bird, there would be a number of plant species in Table 5 whose dispersal is impaired.

Thus, South American temperate forests differ from the trend described by Herrera (1985a), where North American and European plant assemblages have no fleshy fruit larger than the widest gape of a frugivorous bird. It does not seem likely

TABLE 6

Beak dimensions of frugivorous and non-frugivorous (insectivorous) birds in the temperate forest of Chiloé. Data from Museum specimens (Armesto & Sabag, unpublished).

Dimensiones de los picos de aves frugívoras y no-frugívoras (insectívoras) del bosque templado de Chiloé. Datos de especímenes de Museo.

Species	N	X̄ Gape Width (mm)	SD	X̄ Beak Length (mm)	SD
Frugivorous					
Cinclodes fuscus	8	7.8	0.4	21.7	0.7
Cinclodes patagonicus	11	8.2	0.6	25.1	2.5
Curaeus curaeus	20	9.7	0.7	29.3	1.6
Diuca diuca	1	7.7	–	14.3	–
Elaenia albiceps	20	8.3	0.4	16.1	0.9
Phrygilus patagonicus	20	7.6	0.4	13.2	1.0
Phytotoma rara	18	12.0	0.7	15.8	0.8
Pyrope pyrope	11	10.5	0.7	21.9	1.2
Sicalis luteola	10	6.2	0.5	9.4	0.6
Carduelis barbatus	14	6.4	0.3	10.9	0.4
Turdus falklandii	22	12.0	0.7	27.1	2.4
Zonotrichia capensis	48	7.0	0.3	12.1	0.9
Group mean		8.6	2.0	18.1	6.4
Non-frugivorous					
Anthus correndera	7	6.9	0.4	16.2	0.7
Aphrastura spinicauda	7	5.7	0.5	15.1	0.5
Cinclodes oustaleti	8	6.9	0.6	21.5	1.5
Colorhamphus parvirostris	1	7.3	–	14.0	–
Leptasthenura aegithaloides	9	5.3	0.3	11.1	1.3
Lessonia rufa	9	6.5	0.5	14.0	1.0
Muscisaxicola macloviana	13	7.5	0.7	17.0	1.1
Muscisaxicola maculirostris	4	6.8	0.5	18.0	1.1
Phrygilus unicolor	23	5.8	0.3	11.1	0.5
Pygochelidon cyanoleuca	5	8.0	0.4	10.7	0.7
Tachuris rubrigastra	5	4.4	0.4	12.7	1.4
Tachycineta leucopyga	3	8.7	1.1	11.4	0.7
Troglodytes aedon	20	6.2	0.5	15.7	1.2
Group mean		6.6	1.2	14.5	3.2

that these large-sized berries are dispersed by forest mammals in southern Chile, as they are in tropical forests where arboreal mammals are major dispersers (see Janson 1983). The presence of fruits larger than the gapes of frugivorous birds in Chiloé might result from the history of disturbance of southern South America during the Cenozoic (Armesto 1987). During the early Tertiary, tropical humid forests covered most of what is now the Patagonian steppe and extended as far south as the present limit of temperate forests (Menéndez 1971, Romero 1978). Climatic and geological events, such as the Pleistocene glaciation and the rising of the Andean chain (Hollin & Schilling 1981, Simpson 1979), severely shrunk the area of forests in southern South America, turning them into relicts. As a consequence, the forest avifauna that survived these events in temperate South America is considered depauperate (Vuilleumier 1985). It is conceivable that some plant taxa have outlived their mutualistic dispersers (cf. Janzen & Martin 1982, Herrera 1985b), which may be now extinct. Another possibility is that birds may eat large-sized berries bite by bite (Moermond & Denslow 1983), but in that case dispersal is not as effective as when birds swallow and carry the entire fruit with its seeds.

Another interesting point is the fact that gape widths of frugivorous passerines are larger (U-test; $P < 0.01$), on the average, than those of non-frugivorous species

($\bar{x}$ = 6.64 mm, range 4.4 – 8.7, n = 15; Table 6). This observation raises interesting questions concerning the phenotypical traits that enable a bird to become a fruit eater. For instance, do birds with large gapes become frugivorous more often than birds with smaller gapes?, and if this is so, are large gapes a characteristic of birds before they become frugivorous or is this trait selected for during the interaction with fruiting plants? Therefore, is the observed coupling between gape widths of frugivores and fruit diameters the result of coevolution between birds and plants?

Estimating fruit profitabilities

The fleshy tissues surrounding the seeds constitute the nutritional "reward" offered by the plant to the seed dispersal agent. Dispersal quality could be related to the "attractiveness" of fruits to frugivores, in terms of the quality and quantity of this nutritional reward (McKey 1975, Stiles 1980, Herrera 1981a, b, Johnson *et al.* 1985). One way of estimating the profitability of fruits to frugivores is to determine the proportion represented by the dry weight of nutritive structures, relative to the fresh weight of the fruit (Herrera 1981b). This proportion is termed relative yield (RY) by Herrera and it is expressed as a percentage. In support of the operational value of this index in comparative studies, Herrera (1981a) showed that the fruits of *Smilax aspera* had a greater fraction of pulp dry mass in areas where frugivore abundance was low, relative to fruit availability.

To estimate potential profitabilities of fruits to frugivorous birds, and to compare these profitabilities with those obtained for fruits in other temperate and tropical forests, we calculated RY values for the fleshy fruits of species in the forest of Chiloé (Table 7). RY values ranged from 2.7% to 29.6%, with a mean value ($\bar{x}$ = 11.3%, SD = 7.9; n = 19) close to the averages for tropical and north-temperate forests but lower than the average for the mediterranean vegetation of Spain (Armesto 1987). The low values for fruits of Chiloé are due to their high and fairly uniform water contents ($\bar{x}$ = 77.6%, SD = 8,2; Table 7), in comparison to fleshy fruits of mediterranean woodlands (cf. Herrera

1981a). Herrera's RY assumes that water in the pulp decreases the profitability and "attractiveness" of a fruit and, along with the seeds, contributes to the "waste load" of a fruit. This is an unwarranted assumption because fruits may be a source of water to birds (Snow 1971). In addition, RY shows a low sensitivity to changes in the proportions of pulp with respect to seed dry weights, when water contents of fruits are high. This is shown by the lack of correlation between RY and the pericarp/seed dry weight ratio for the fleshy fruits of Chiloé (Table 7).

As an alternative to Herrera's RY, we introduce an alternative profitability index (RY'), defined as the percent dry weight of pulp, relative to the dry weight of the whole fruit, an index that is positively correlated with the pericarp/seed dry weight ratio (Table 7). We prefer to use RY' because it is independent of the fruit water content and, like RY, provides a relative figure allowing one to compare on the same scale values for fruits of different species. Values of RY' for the fruits of Chiloé ranged between 19.9% and 84.6% ($\bar{x}$ = 51.8%; SD = 17.0; n = 19), thus encompassing a greater span of the percentage scale than RY (Table 7). The convenience of using RY' to estimate overall profitability is encouraged by preliminary data for the species of Chiloé showing that RY' values are better related than RY values to the percent of these fruits in the diet of frugivorous birds, estimated from the percent of seeds present in bird feces (Fig. 3).

CONCLUSIONS

Given the abundance of species with fleshy fruits, a great potential exists for the development of mutualistic interactions between plants and frugivores in South American temperate forests. However, few field studies have dealt with seed dispersal by animals in this environment. We have documented the importance of vertebrates as seed vectors in southern South America and have proposed several lines of promising research to pursue in the future. As a part of an ongoing research project, we have assessed the importance of fruit colors, sizes, and profitability indices in relation to fruit consumption by birds in the forest of Chiloé. As long as the importance of

TABLE 7

Percent water content and profitability indices for fleshy fruits of the forest of Chiloé.

Porcentajes de agua e índices de aprovechamiento potencial de los frutos carnosos del bosque de Chiloé.

Species	% water	RY	RY'	P/S
Aextoxicon punctatum	60.6	29.6	65.3	1.8
Amomyrtus luma	77.8	4.8	45.3	0.6
Aristotelia chilensis	67.4	6.4	19.9	0.3
Berberis buxifolia	81.1	7.6	40.8	0.7
Berberis darwini	71.6	7.6	45.6	0.9
Cissus striata	76.7	12.4	53.5	1.0
Drimys winteri	73.3	14.9	66.6	2.1
Empetrum rubrum	79.7	5.3	55.0	1.2
Fuchsia magellanica	85.6	2.7	25.7	0.4
Gaultheria phyllireaefolia	82.7	6.1	63.6	1.8
Griselinia racemosa	78.5	20.9	84.6	5.5
Luzuriaga radicans	74.3	4.6	31.6	0.4
Mitraria coccinea	90.3	5.9	61.0	1.6
Myrceugenia ovata	72.2	20.1	72.9	2.5
Myrceugenia planipes	84.8	*	*	*
Nertera granadensis	94.4	2.2	39.1	0.7
Ovidia pillo-pillo	75.6	5.1	43.8	0.8
Pernettya furiens	60.5	28.2	70.1	2.3
Pseudopanax laetevirens	79.3	14.2	69.9	2.0
Raphithamnus spinosus	78.0	6.3	30.9	0.5
Ugni molinae	84.0	*	*	*

% water = (fresh weight of fruit − dry weight of fruit / fresh weight of fruit) x 100
RY = (dry weight of pulp/fresh weight of fruit) x 100
RY' = (dry weight of pulp/dry weight of fruit) x 100
P/S = dry weight of pericarp/dry weight of seeds
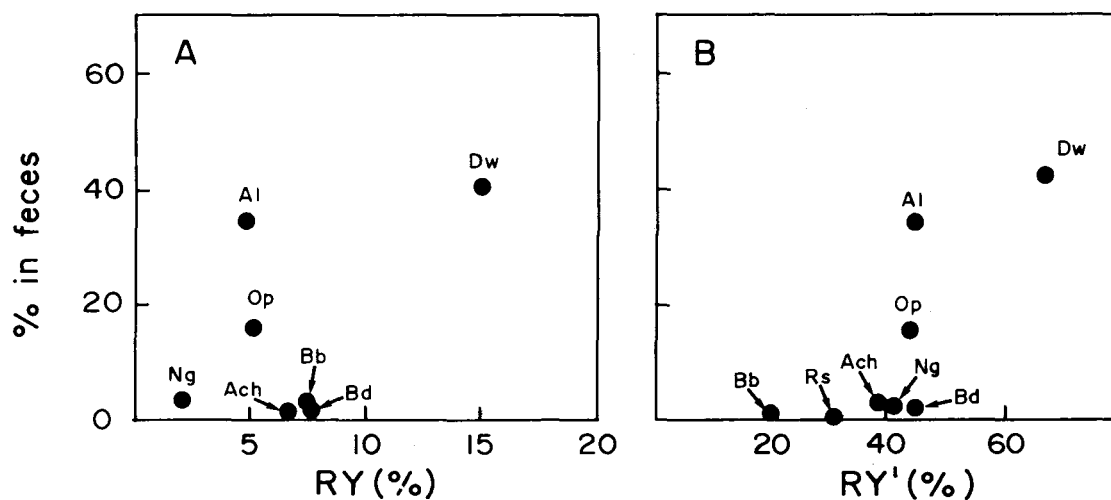* Data unavailable owing to insect destruction of seeds

Fig. 3: Relationship between the estimates of profitability of fleshy fruits (RY and RY', see text for definitions) and the presence of berries in bird droppings in the forest of Chiloé (Armesto & Sabag, unpublished data). RY explains 25% of the variance of the percent number of berries in feces (A), whereas RY' explains 50% of the variance (B). Plant species included in the plot are designated by the initials of their scientific names as listed in Table 7.

Relación entre los índices de aprovechamiento potencial de frutos carnosos (RY y RY', ver el texto para su definición) y la presencia de frutos en las fecas de aves del bosque de Chiloé (Armesto & Sabag, datos no publicados). RY da cuenta del 25% de la varianza en los porcentajes de frutos en fecas (A), mientras que RY' explica un 50% de dicha variación (B). Las especies de plantas incluidas en este gráfico están designadas por las iniciales de sus nombres científicos, tal como se listan en la Tabla 7.

water in the diet of frugivorous birds remains uncertain, we propose that RY' is an appropriate estimator of the potential profitability of fleshy fruits to frugivorous birds, especially when comparing fruits with a high water content. Studies of the characteristics of fleshy fruits and fruit-eating vertebrates in South American temperate forests may help elucidate current problems concerning the ecology and evolution of mutualistic interactions. The study system appears particularly suited to investigate the constraints imposed upon patterns of interaction by recent geological and climatic changes, which have greatly altered the composition of the flora and fauna in southern South American forests.

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