

Bird-mediated effect of deforestation on potential seed dispersal does not increase the seed recruitment of *Fuchsia magellanica*

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Abstract

Key message This work contributes to clarify the effects of small-scaled deforestation and key traits of plants and animals on frugivory, seed dispersal and seedling recruitment of a shade-intolerant plant.

Abstract Habitat destruction usually reduces the frugivory and seed dispersal by animals. This negative effect could be counterbalanced by seedling recruitment in shade-intolerant plants. We tested this assumption using the shrub *Fuchsia magellanica* as a model. We estimated the deforestation as the percentage of ground surface devoid of native forest at small and large scales around 20 plants per population and 12 populations. This procedure was performed to evaluate the effects of deforestation, at both spatial scales, on fruit traits, frugivory, seed dispersal, and seedling recruitment. Fruit traits (size, shape, color, sugar concentration, and number of seeds) were measured in each plant. Frugivory by lizards and birds were recorded as the percentage of fruit consumed, using ten artificial play dough fruits per plant. Putative seed dispersal was estimated as the product of the number of play dough fruits attacked and mean number of seeds per fruit. Seedling recruitment was evaluated as the density of seedlings growing around adult plants. The fruit

traits of *F. magellanica* varied among populations in size, shape, color, sugar concentration and number of seeds. Only color correlated with deforestation at a large scale, the fruits being more reddish-brown in deforested populations. This variation, however, did not affect frugivory. The number of play dough fruits attacked by birds exhibited a tendency to be positively affected by deforestation at a large scale, which could be translated into a positive effect of deforestation on potential seed dispersal. Nevertheless, there was not an increase in seedlings recruitment. Consequently, the deforestation did not increase the seedling recruitment of this pioneer species.

Keywords Frugivory · Ornithocory · Saurocory · Recruitment niche · Scale dependency

Introduction

Seed dispersal by animals increases the reproductive success of plants, distancing the progeny from parental individuals and increasing the probabilities of seedling recruitment (Herrera and Pellmyr 2002; Schaefer and; Ruxton 2006). This type of plant–animal interaction is widely represented in tropical and some temperate forests (Hanya and Aiba 2010; Fleming and Kress 2013). Unfortunately, one of the human disturbances that mostly affects the forests and, as a result, modifies these mutualistic systems, is the fragmentation and destruction of habitats (Markl et al. 2012; Rey and Alcántara 2014). These disturbances modify the richness and abundance of disperser animals in the remaining patches of forests (Markl et al. 2012; Rey and Alcántara 2014). Consequently, the visitation rates and seed removal are usually, but not always, negatively affected, putatively triggering functional extinctions (Markl et al. 2012; Rey

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and Alcántara 2014; Valiente-Banuet et al. 2015). Dispersal capacity, niche breadth and reproductive potential are three traits hypothesized to be key determinants of species persistence in these human-modified habitats (Öckinger et al. 2010; Marini et al. 2012).

In terms of dispersal capacity, animal abundances along a deforestation gradient can be determined by traits such as locomotion forms (Öckinger et al. 2010). Animals with a restricted capacity of dispersal, mostly using terrestrial methods of locomotion, are usually strongly and negatively affected by deforestation and fragmentation (Öckinger et al. 2010). On the contrary, animals with a high capacity of dispersal, usually using aerial forms of locomotion, are less prone to face the negative effects of these disturbances (Öckinger et al. 2010). This situation, however, may vary according to the spatial scale of deforestation and also to the identity of the taxon (García and Chacoff 2007; Fontúrbel et al. 2015). Animals with a restricted capacity of movement will respond more tightly to deforestation occurring at a small spatial scale, than those using aerial forms of locomotion, which may respond more tightly to deforestation occurring at a large scale (García and Chacoff 2007; Fontúrbel et al. 2015). Nevertheless, deforestation and forest fragmentation affect habitat use by organisms across multiple scales, which may provoke complex responses, from negatives to positives (García and Chacoff 2007; Vergara and Armesto 2009; Vergara et al. 2010; Fontúrbel et al. 2015).

The consequences of the modifications of the distance of seed dispersal, across multiple scales on plant fitness, will ultimately depend on the regeneration niche of plants, in terms of their shade tolerance, among other causes (Horvitz et al. 2002; Côrtes and Uriarte 2013). Shade-intolerant plants have evolved in “light islands” (i.e., gaps) in a “sea of shadows” (i.e., forest), therefore, facing two types of selection pressures (Horvitz et al. 2002). First, shade-intolerant plants are favored when they exhibit fruit traits highly attractive to frugivores which usually move in a wide space, because these traits allow fruits to increase their probabilities to be found by these animals and, therefore, to be eaten and dispersed (Horvitz et al. 2002). The traits that can trigger changes in the visitation rates and seed removal, because they modify the attractiveness of plants, are the size, shape and color of fruits (Schaefer and Ruxton 2006; Schaefer and Schaefer 2007). The sugar concentration or number of seeds can trigger responses in the animals such as to continue foraging on a given individual or to move away in search of another plant (Schaeffer and Ruxton 2006). Second, shade-intolerant plants from forests are favored when they are dispersed far away from maternal plants, because it allows to increase their probabilities of arriving to safe sites for recruitment (i.e., forest gaps). Certainly, animals capable of traveling long distances are able to do this more properly (Horvitz et al. 2002).

Even though deforestation may simultaneously affect seed dispersal and seedling recruitment, the assessments of these ecological processes have traditionally been performed independently, and without considering the traits of animals and plants involved in such processes (Markl et al. 2012; but see; Fontúrbel et al. 2015). This approach, albeit convenient, may lead to a misunderstanding of the isolated and combined effects on plant performance, thereby hindering our understanding of complex ecological scenarios.

We hypothesized that, if shade-intolerant plants from forests are mostly dispersed by flying animals capable of traveling long distances, a negative and smooth effect of deforestation on fruit attractiveness, and on the rates of frugivory and seed dispersal, could occur although mainly at a large scale of deforestation (but see Fontúrbel et al. 2015). Nevertheless, a positive effect for seedling recruitment is expected whether these logged habitats resemble the naturally occurring forest gaps, therefore the putative negative effects of deforestation on the seed dispersal could be counterbalanced by the positive effects upon seedling recruitment (Horvitz et al. 2002; Markl et al. 2012). The aim of this study is to evaluate the effects of deforestation, at a small and large scale, on the fruit attractiveness, visitation rates, seed removal by frugivores, and seedling recruitment of the shade-intolerant shrub *Fuchsia magellanica* but taking into account the locomotion of animals, such as lizards (terrestrial) and birds (flying).

Materials and methods

Sites and species studied

Field work was undertaken in two provinces of the district “Región de Los Lagos”, Chile (Chiloé island and Palena in the continent) between February and April, 2014. The climate is temperate rainy with precipitations fluctuating between 1600 and 2500 mm/year, falling throughout most of the year (Luebert and Plischoff 2006). Specifically, 12 populations of *F. magellanica* were studied, six located in Chiloé and six in Palena (Fig. 1). The landscape around each population was composed largely of native forest and anthropogenic pastures, the main tree species being *Nothofagus nitida*, *Podocarpus nubigena* and *Pilgerodendron uviferum*, among others (Luebert and Plischoff 2006).

Fuchsia magellanica (Onagraceae) is a deciduous shrub that reaches 2–4 m in height (Hoffmann 1997). In Chile, it is distributed from Coquimbo to Tierra del Fuego, and is frequent in damp areas, usually close to waterways (Hoffmann 1997). The red, bell-shaped, hanging flowers are mostly pollinated by hummingbirds and bumblebees, although they are also robbed by some birds (Traveset et al. 1998). Fruit and seed production are highly, but not totally,

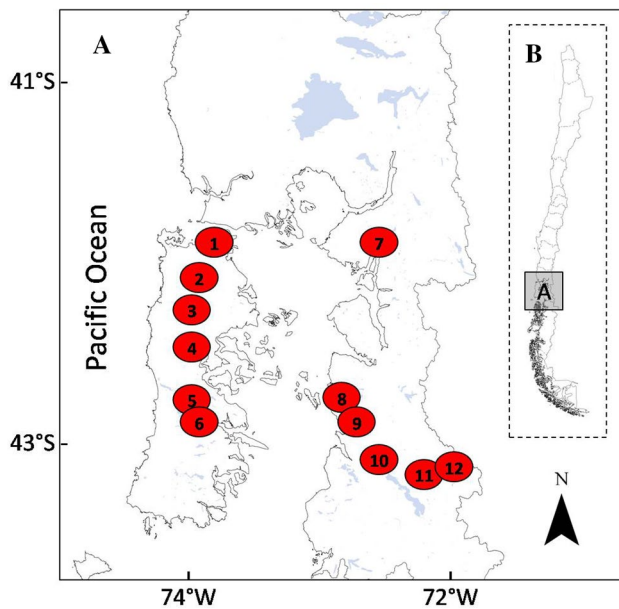


Fig. 1 Study sites for the assessment of frugivory and seed dispersal, by birds and lizards, of *F. magellanica* in the temperate rainforests of Chile. Sites from the island (Province of Chiloé): Chacao (1), Puntra (2), Nercón (3), Yerba Loza (4), Quellón 1 (5), Quellón 2 (6). Sites from the continent (Province of Palena): Hornopirén (7), Santa Bárbara (8), Chaitén (9), Puerto Cárdenas (10), Puente Dumontt (11), and Futaleufú (12)

dependent on pollinators (Riveros et al. 1996). The fruit is an elongated berry, with numerous small seeds, varying in color from green to reddish-brown or brown, and a fresh weight of 0.62 g with a water content of 85.6%, approximately (Armesto et al. 1987; Fig. 2a). Fructification occurs between November and May (Hoffmann 1997). There are no previous reports about frugivores as seed dispersers; nevertheless, numerous species of birds and some mammals and reptiles have been described as generalist frugivores of these forests and, as such, they could be acting as potential seed dispersers for *F. magellanica* (Armesto et al. 1987; Aizen et al. 2002; Fig. 2b, c). In terms of regeneration niche, *F. magellanica* is a shade-intolerant shrub inhabiting more frequently the forest gaps and also deforested habitats (Lusk et al. 2006).

Deforestation

To determine the magnitude of deforestation faced by *F. magellanica*, a sample of 20 plants was selected in each population ($n = 12$ populations, 240 plants in total). Each studied plant was located close to waterways to avoid putative biases in recruitment due to this variable. Each plant was georeferenced in the field with a portable GPS, to a precision error of ca. 7 m. Then, using aerial photographs



Fig. 2 Fruits of *F. magellanica* (a), the lizard *Liolaemus pictus*, the single terrestrial frugivore of *F. magellanica* (b), and the thrush *Turdus falcklandii*, one of the main flying frugivores (c) from the temperate rainforests of Chile

available in Google Earth, two circular lines of 10 and 100 m radius (r) were established centered around each plant, to evaluate the small- and large-scale deforestation in the neighborhood of plants (see García and Chalcoff 2007; Fontúrbel et al. 2015). The first line allowed to define a circular-shaped plot, running between 0 and 10 m of distance from the focal plant, which corresponded to a surface area of 314 m² per plant. The second ring-shaped plot, running from 10 up to 100 m from the focal plant, corresponded to a surface area of 31,086 m² per plant. Within these non-overlapped plots the ground surface devoid of native forest was estimated, and the percentage of deforestation was determined, at a small and large scale, using the ARCVIEW v. 3.0 cartographic software package. We chose the non-overlapping ring approach to avoid multicollinearity among scales (García and Chacoff 2007). The small scale depicts the immediate vicinity of the plant, and the large scale depicts the plant neighborhood and hence the approximate foraging area for the frugivores (see Fontúrbel et al. 2015). The aforementioned procedure was performed following previous works that found that the magnitude of deforestation here assessed, at both scales, lies in the range in which frugivores significantly perceive the landscape and respond to its modifications (Fontúrbel et al. 2015). This occurs even though the birds, such as those recorded foraging on the studied plant, can forage at longer distances than 100 m (Vergara et al. 2014).

Fruit traits

To evaluate the effects of deforestation on fruit traits of *F. magellanica* that act as visual signals, five mature fruits were collected from each experimental plant ($n = 1200$ natural fruits in total). The size of each fruit was estimated first by measuring the longest ($2a$) and widest ($2b$) section using a digital vernier caliper (0.01 accuracy). Subsequently, the equation for the volume of an ellipsoid:

$$V = 4/3\pi abc,$$

was assessed, where c was considered to be equal to b . This was applied to estimate the size of fruits (mm^3). The shape of each fruit was estimated by obtaining a symmetry index using the quotient of flattening of an ellipsoid:

$$f = (a - b)/a.$$

Thus, negative values indicate an asymmetrical form (i.e., an elongated ellipsoid), values near zero indicate symmetrical forms (i.e., a spherical form), and positive values also indicate an asymmetrical form (i.e., a flattened ellipsoid). Color was estimated by photographing each fruit under standardized conditions; that is, in complete darkness, using a flash, with a distance of 60 cm between the camera and the fruit. Subsequently, the RGB color pattern was obtained at five random points in each fruit, by recording the values for the red (R), green (G) and blue (B) signal, using the Adobe Photoshop® software v. 13.0. Finally, a principal component analysis was undertaken on the average values recorded for each fruit, to obtain a single color measurement; from this analysis, the score factor 1 was obtained as a single color measurement. In the present case, negative values indicate greenish fruits and positive values indicate reddish-brown fruits. It is worthwhile highlighting that all fruits (greenish and reddish-brown fruits) corresponded to mature fruits.

To assess fruit traits selected mainly for taste, each fruit, already evaluated for size, shape and color, was dissected and the sugar content (% weight/volume) of the pulp extracted was determined using a portable digital refractometer. Number of seeds lodged in the fruit was determined by isolating all the seeds in the pulp and counting them under a stereoscopic microscope. Finally, the average value for each trait studied was determined in each individual plant, in every population, based on averages obtained from each one of the five fruits evaluated per plant.

Frugivory and seed dispersal

To determine the identity of frugivorous animals consuming fruits of *F. magellanica*, six randomly chosen plants from each population were observed. These observations were performed during the morning (07:00 a.m. and 10:00 a.m.)

in two different days, per each population, around the peak of the activity of frugivores (Deslauriers and Francis 1991; Trnka et al. 2006). In these plants, we only registered the identity of animals eating fruits in a qualitative assessment. Thereafter, to quantitatively evaluate the rates of frugivory, the fruit removal rate by frugivorous animals in *F. magellanica* plants was estimated by arranging artificial play dough fruits on the reproductive branches of the plants. Artificial fruits were made in advance; however, they were re-designed when they were attached to plants, to enhance the similarity of them with the naturally occurring fruits from every single individual. Using this technique, the frugivorous species can be identified through imprints of mouth parts, and frequency of consumption by the animals can be determined (Valdivia and Simonetti 2007). Thus, ten artificial fruits were randomly attached to each plant under study ($n = 2400$ artificial fruits in total) using adhesive tape, 1–2 m in height. This procedure allows frugivores (i.e., flying birds and the terrestrial but also scansorial lizards) to reach the fruits. The fruits were arranged in such a way as to ensure that they remain separate from, but surrounded by, real mature fruits, to confuse the frugivores and avoid biases. The play dough fruits were exposed to frugivores during the season of maximum fructification (i.e., February to March 2014), over a period of approximately 45 days, sufficient time for the different visiting species to leave their imprints (Valdivia and Simonetti 2007). Consumption frequency on each individual plant was estimated by counting, only once, the number of fruits bitten per plant, after elapsing 45 days. We are not aware that fruits attacked once remain equally attractive to animals, but the results indicate that fruits are attacked more than once, suggesting that fruits remain attractive to animals for a long period of time. Thereafter, at each plant from each population, the percentage of fruits attacked was determined, identifying whether the frugivore corresponded to an animal with terrestrial or aerial locomotion, that is, if the fruits presented imprints of avian beaks or lizard/mammal teeth. Finally, to estimate the effects of deforestation on the number of seeds potentially dispersed by frugivores, the probability of attacks by frugivores per each plant was multiplied by the mean number of seeds per fruit of that specific individual plant.

Seedling recruitment

To evaluate the effects of deforestation on seedling recruitment of *F. magellanica*, around each experimental plant previously assessed, two plots of 1 m^2 ($n = 240$ pairs of plots) were established. One plot was set up beneath the canopy of each shrub to evaluate a putative facilitation or allelopathic effect of adult plants on seedling recruitment, and a second plot was established immediately outside the canopy, and exposed to the sun. All seedlings

of *F. magellanica* growing in each plot were registered once at the end of the dispersal period. A seedling was operationally defined as an individual of less than 50 cm in height, even though different sizes of plants, between 1 and 50 cm in height, can indicate different cohorts. This means that some of these plants could not necessarily have been dispersed by the animals at the same time of the experiment (Valdivia and Simonetti 2007).

Statistical analyses

One-way ANCOVA tests were performed to evaluate putative dissimilarities among populations (i.e., categorical predictor) on fruit traits per plant (i.e., plant attributes as dependent variables), in which the effects of deforestation (at a small and at a large scale) were incorporated as independent continuous co-variables. Similar models were used to test for effects on frugivory and seed dispersal (i.e., animal attributes), except that fruits traits (if significant in the previous models) were also included as covariates to account for the trait effects in the frugivory and seed dispersal. Thereafter, dissimilarities among populations on seedling recruitment were assessed using ANCOVA tests, in which the effects of deforestation were incorporated as independent continuous co-variables. Because some shrubs were lost during fieldwork, all the analyses were performed with the surviving plants ($n = 216$ individuals), using the software package STATISTICA v. 10.0 (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Deforestation

Deforestation significantly varied across populations, at a small and large scale (ANOVA, small-scale deforestation: $F_{1,11} = 67.88$, $P < 0.001$; large-scale deforestation: $F_{1,11} = 458.00$, $P < 0.001$). In fact, at the small scale of deforestation, Chacao, Hornopirén y Quellón 1 corresponded to the more deforested populations, with 100% of their surface areas devoid of forest (Table 1). By contrast, Futaleufú, Nercón, Puerto Cárdenas, Puntra, and Yerba Loza were not deforested (Table 1). At the large scale of deforestation, Chacao was the most deforested population, with 100% of deforestation, whereas Futaleufú and Yerba Loza did not exhibit signs of deforestation (Table 1). Both scales of deforestation exhibited a significant and positive correlation ($r = 0.714$; $P < 0.05$).

Fruit traits

Fruit size was highly variable among populations; however, it was not affected by deforestation at smaller or larger scales (ANCOVA, small-scale deforestation: $F_{1,11} = 0.57$, $P = 0.451$, large-scale deforestation: $F_{1,11} = 0.84$, $P = 0.361$, population effect: $F_{1,11} = 10.99$, $P < 0.001$). In fact, fruits from Chaitén were 2.3 times bigger than those from Yerba Loza (Table 2). Similarly, fruit shape was highly variable among populations, although it was not affected by deforestation at smaller or larger scales (ANCOVA, small-scale deforestation: $F_{1,11} = 0.91$, $P = 0.341$, large-scale

Table 1 Populations of *F. magellanica* in the temperate rainforests of Chile

Population	Forest strata	Localization			Deforestation (%)	
		Latitude	Longitude	Altitude	Small scaled	Large scaled
Chacao	a	41°49'03"S	73°31'39"W	24	100.0 ± 0.0 ^a	98.0 ± 0.5 ^a
Chaitén	a	42°57'16"S	72°38'28"W	320	52.6 ± 12.1 ^b	69.9 ± 2.7 ^b
Futaleufú	b	43°11'21"S	71°50'05"W	647	0.0 ± 0.0 ^c	0.0 ± 0.0 ^c
Hornopirén	a	41°56'54"S	72°27'09"W	369	100.0 ± 0.0 ^a	83.1 ± 1.5 ^d
Nercón	a	42°31'28"S	73°47'53"W	57	0.0 ± 0.0 ^c	64.1 ± 0.9 ^b
Pte. Dumontt	b	43°18'47"S	71°59'21"W	426	54.1 ± 10.3 ^b	25.0 ± 2.7 ^e
Pto. Cárdenas	a	43°12'29"S	72°27'10"W	174	0.0 ± 0.0 ^c	16.0 ± 3.2 ^e
Puntra	a	42°06'59"S	73°51'05"W	12	0.0 ± 0.0 ^c	0.6 ± 0.6 ^c
Quellón 1	a	43°07'37"S	73°39'13"W	98	100.0 ± 0.0 ^a	90.3 ± 1.3 ^f
Quellón 2	a	43°02'49"S	73°38'29"W	156	22.1 ± 7.9 ^b	42.2 ± 2.4 ^g
Sta. Bárbara	a	42°51'55"S	72°46'43"W	181	25.3 ± 5.5 ^b	7.6 ± 1.5 ^e
Yerba Loza	c	42°50'27"S	73°45'44"W	77	0.0 ± 0.0 ^c	0.0 ± 0.0 ^c

Forest strata (sensu Luebert and Pliscoff 2006): (a) evergreen inland temperate forests of *Nothofagus nitida* and *Podocarpus nubigena*, (b) evergreen inland temperate forest of *Nothofagus betuloides* and *Desfontainea spinosa*, (c) Resinous coastal temperate forests of *Pilgerodendron uviferum* and *Tepualia stipularis*. Deforestation at a small scale (2140 m²) and at a large scale (19,260 m²) around each plant. Mean ± 1SE are depicted. Dissimilar superscript letters represent significant differences ($P < 0.05$) after performing Tukey HSD tests for pairwise comparisons between populations

Table 2 Fruit traits (size, shape, color, sugar concentration, and seed crop) of *F. magellanica* from plants growing in temperate rainforests of Chile and frugivory and potential seed dispersal by terrestrial (i.e., lizards) and flying animals (i.e., birds), on the fleshy fruited shrub *F. magellanica* in the temperate rainforest of Chile

Population	Fruit traits				Frugivory (% of fruits attacked/ plant/45 days)				Potential seed dispersal (No. of seeds dispersed/fruit/plant/45 days)			
	Size (mm ³)	Shape (flattening index)	Color (PC 1)	Sugar concentration (%)	Seed crop (No. of seeds/fruit)	Terrestrial	Flying	Both	Terrestrial	Flying	Both	
Chacao	228.4 ± 16.6 ^a	-2.02 ± 0.28 ^a	-0.02 ± 0.09 ^a	9.4 ± 0.3 ^a	135.4 ± 7.2 ^a	1.9 ± 1.4 ^a	4.6 ± 2.0 ^a	6.5 ± 2.2 ^a	2.3 ± 1.6 ^a	5.7 ± 2.7 ^a	8.0 ± 2.9 ^a	
Chaitén	305.3 ± 12.3 ^b	-0.77 ± 0.04 ^b	0.02 ± 0.13 ^a	9.3 ± 0.3 ^a	170.3 ± 6.7 ^b	6.6 ± 2.6 ^a	26.8 ± 7.4 ^a	32.4 ± 8.0 ^a	10.5 ± 4.0 ^a	47.7 ± 14.6 ^a	56.0 ± 14.9 ^a	
Futaleufú	242.5 ± 13.4 ^b	-1.41 ± 0.08 ^c	-2.50 ± 0.20 ^b	10.3 ± 0.2 ^a	160.8 ± 8.1 ^b	11.5 ± 2.5 ^a	12.6 ± 2.5 ^a	24.1 ± 4.1 ^a	17.7 ± 3.9 ^a	20.5 ± 4.7 ^a	38.2 ± 7.4 ^a	
Hornopirén	291.7 ± 13.8 ^a	-2.17 ± 0.12 ^a	0.88 ± 0.10 ^c	7.8 ± 0.3 ^c	167.3 ± 7.9 ^b	3.8 ± 1.9 ^a	31.9 ± 15.9 ^a	35.7 ± 15.9 ^a	6.4 ± 3.4 ^a	54.8 ± 29.9 ^a	61.2 ± 29.9 ^a	
Nercón	172.6 ± 17.0 ^b	-2.46 ± 0.13 ^a	-0.86 ± 0.12 ^a	4.8 ± 0.7 ^b	150.0 ± 6.7 ^b	5.3 ± 5.3 ^a	11.2 ± 8.7 ^a	16.5 ± 9.8 ^a	8.6 ± 8.8 ^a	15.6 ± 12.2 ^a	24.2 ± 14.6 ^a	
Pte. Dumontt	230.9 ± 16.4 ^b	-1.87 ± 0.15 ^a	0.74 ± 0.10 ^c	10.0 ± 0.1 ^a	146.1 ± 10.4 ^b	7.0 ± 3.3 ^a	4.2 ± 2.5 ^a	11.2 ± 3.6 ^a	9.2 ± 4.5 ^a	5.8 ± 3.4 ^a	14.9 ± 4.9 ^a	
Pto. Cárdenas	273.3 ± 24.1 ^a	-1.41 ± 0.09 ^c	0.98 ± 0.09 ^c	8.7 ± 0.5 ^a	175.6 ± 10.8 ^b	4.2 ± 1.3 ^a	11.7 ± 3.3 ^a	15.9 ± 3.5 ^a	7.3 ± 2.3 ^a	18.7 ± 4.9 ^a	25.9 ± 5.3 ^a	
Puntra	165.3 ± 13.1 ^a	-2.41 ± 0.08 ^a	-0.20 ± 0.09 ^a	7.8 ± 0.2 ^c	144.6 ± 10.0 ^b	3.9 ± 1.5 ^a	24.3 ± 4.3 ^a	28.2 ± 4.2 ^a	4.7 ± 1.8 ^a	33.9 ± 6.3 ^a	38.7 ± 6.3 ^a	
Quellón 1	179.8 ± 11.6 ^b	-2.33 ± 0.13 ^a	-0.19 ± 0.11 ^a	10.5 ± 0.5 ^a	143.2 ± 9.7 ^b	7.2 ± 2.4 ^a	4.9 ± 1.7 ^a	12.1 ± 2.4 ^a	10.8 ± 3.4 ^a	7.3 ± 3.0 ^a	18.1 ± 3.9 ^a	
Quellón 2	211.3 ± 20.7 ^b	-2.17 ± 0.11 ^a	0.22 ± 0.09 ^a	10.0 ± 0.3 ^a	158.6 ± 7.4 ^b	7.2 ± 2.8 ^a	15.6 ± 3.7 ^a	22.8 ± 4.6 ^a	13.4 ± 5.7 ^a	24.3 ± 5.6 ^a	37.7 ± 8.6 ^a	
Sta. Bárbara	257.9 ± 16.3 ^c	-3.06 ± 0.15 ^d	-0.20 ± 0.13 ^a	8.6 ± 0.4 ^a	197.4 ± 17.6 ^b	9.2 ± 2.9 ^a	4.2 ± 2.0 ^a	13.3 ± 3.1 ^a	18.2 ± 6.6 ^a	8.0 ± 4.2 ^a	26.3 ± 6.8 ^a	
Yerba Loza	134.2 ± 7.8 ^b	-2.16 ± 0.09 ^a	0.62 ± 0.08 ^d	12.3 ± 0.5 ^a	123.5 ± 4.7 ^a	1.0 ± 1.1 ^a	18.8 ± 5.3 ^a	19.8 ± 5.2 ^a	1.5 ± 1.6 ^a	24.2 ± 7.3 ^a	25.7 ± 7.1 ^a	

Mean ± 1SE are depicted. Dissimilar superscript letters represent significant differences ($P < 0.05$) after performing Tukey HSD tests for pairwise comparisons between populations

deforestation: $F_{1,11} = 1.80$, $P = 0.181$, population effect: $F_{1,11} = 24.76$, $P < 0.001$). Fruits from Santa Bárbara population were 4.0 times more asymmetric (i.e., elongated) than those from Chaitén, which showed a more spherical shape (Table 2). By contrast, the color of fruits significantly varied with deforestation at a larger scale, and among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 1.90$, $P = 0.170$, large-scale deforestation: $F_{1,11} = 5.63$, $P = 0.019$, population effect: $F_{1,11} = 62.75$, $P < 0.001$). In fact, populations varied from Futaleufú, exhibiting the most greenish fruits, to Puerto Cárdenas with the most reddish-brown fruits (Table 2).

Sugar concentration of fruits was highly variable among populations, although it was not affected by deforestation at smaller or larger scales (ANCOVA, small-scale deforestation: $F_{1,11} = 0.58$, $P = 0.447$, large-scale deforestation: $F_{1,11} = 0.16$, $P = 0.691$, population effect: $F_{1,11} = 18.75$, $P < 0.001$). Fruits from Yerba Loza were 2.6 times more concentrated in sugar than those from Nercón (Table 2). Finally, the number of seeds per fruit was not significantly affected by deforestation at smaller or larger scales, although it also varied significantly among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 0.26$, $P = 0.609$, large-scale deforestation: $F_{1,11} = 0.03$, $P = 0.873$, population effect: $F_{1,11} = 4.51$, $P < 0.001$). In fact, the mean number of seeds per fruit was 1.6 times higher for fruits from Santa Bárbara than those from Yerba Loza (Table 2).

Frugivory and seed dispersal

In the study area, only a total of five species of frugivorous were recorded for *F. magellanica*, probably due to the small sampling effort. The lizard *Liolaemus pictus* (Tropiduridae) was the only terrestrial animal, while the flying animals corresponded to the birds *Curaeus curaeus* (Icteridae), *Elaenia albiceps* (Tyrannidae), *Phrygilus patagonicus* (Thraupidae) and *Turdus falcklandii* (Turdidae).

Frugivory by lizards was not significantly affected by deforestation, at smaller or larger scales, it did not vary among populations, and it was not modulated by the color of fruits, in spite of the fact that this was the only trait significantly affected by deforestation (ANCOVA, small-scale deforestation: $F_{1,11} = 1.96$, $P = 0.163$, large-scale deforestation: $F_{1,11} = 0.08$, $P = 0.771$, population effect: $F_{1,11} = 0.92$, $P = 0.524$, color effect: $F_{1,11} = 0.05$, $P = 0.822$) (Table 2). Moreover, frugivory by birds was not significantly affected by the deforestation at a small scale, but exhibited a tendency ($0.05 > P < 0.1$) to be positively affected by deforestation at a large scale; also, it significantly varied among populations, but not with the color of fruits (ANCOVA, small-scale deforestation: $F_{1,11} = 1.46$, $P = 0.229$, large-scale deforestation: $F_{1,11} = 3.26$, $P = 0.072$, population effect: $F_{1,11} = 2.69$, $P = 0.003$, color effect: $F_{1,11} = 0.62$, $P = 0.432$).

In fact, plants from Hornopirén exhibited a rate of frugivory 7.6 times higher than that from Puente Dumontt and Sta. Bárbara (Table 2). As a whole, frugivory by both groups of animals exhibited a tendency to be positively affected by deforestation, at smaller and larger scales, and it significantly varied among populations, although these differences were not given by the color of fruits (ANCOVA, small-scale deforestation: $F_{1,11} = 3.27$, $P = 0.072$, large-scale deforestation: $F_{1,11} = 3.38$, $P = 0.068$, population effect: $F_{1,11} = 2.51$, $P = 0.005$, color effect: $F_{1,11} = 0.70$, $P = 0.403$). Thus, frugivory upon plants from Hornopirén was 5.5 times higher than that from Chacao (Table 2).

The potential seed dispersal by terrestrial animals was not significantly affected by neither, deforestation at smaller or larger scales, nor by the color of fruits; also, it did not significantly vary among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 1.21$, $P = 0.272$, large-scale deforestation: $F_{1,11} = 0.39$, $P = 0.534$, population effect: $F_{1,11} = 1.19$, $P = 0.296$, color effect: $F_{1,11} = 0.16$, $P = 0.690$) (Table 2). The potential seed dispersal by flying animals was significantly affected by deforestation at a large scale, and it also varied among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 1.45$, $P = 0.229$, Large-scale deforestation: $F_{1,11} = 4.27$, $P = 0.040$, population effect: $F_{1,11} = 2.59$, $P = 0.004$, color effect: $F_{1,11} = 0.33$, $P = 0.562$). In fact, seed dispersal was 9.6 times higher in plants from Hornopirén than that from Chacao (Table 2). Similarly, seed dispersal by both groups of animals was significantly affected by the deforestation at a large scale, varying significantly among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 2.89$, $P = 0.091$, large-scale deforestation: $F_{1,11} = 4.90$, $P = 0.027$, population effect: $F_{1,11} = 2.59$, $P = 0.004$, color effect: $F_{1,11} = 0.50$, $P = 0.479$). Thus, potential seed dispersal was 7.7 times higher in plants from Hornopirén with respect to Chacao (Table 2).

Seedling recruitment

Seedling recruitment beneath the canopy was not significantly affected by deforestation, neither at smaller nor larger scales, and it did not vary among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 0.37$, $P = 0.545$, large-scale deforestation: $F_{1,11} = 0.95$, $P = 0.332$, population effect: $F_{1,11} = 1.30$, $P = 0.224$) (Table 3). Similarly, seedling recruitment outside the canopy was not significantly affected by deforestation, neither at smaller nor larger scales, and it did not vary among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 0.07$, $P = 0.788$, large-scale deforestation: $F_{1,11} = 0.77$, $P = 0.381$, population effect: $F_{1,11} = 1.14$, $P = 0.333$) (Table 3). The whole seedling recruitment both, beneath and outside the canopy, was not significantly affected by deforestation, although it varied among populations (ANCOVA, small-scale deforestation: $F_{1,11} = 0.11$,

Table 3 Seedling recruitment beneath and outside the canopy of the shrub *F. magellanica* in temperate rainforests of Chile

Population	Recruitment		
	Beneath (no. of seedlings/m ²)	Outside (no. of seedlings/m ²)	Both plots pooled (no. of seedlings/2 m ²)
Chacao	0.24 ± 0.11 ^a	0.76 ± 0.45 ^a	1.00 ± 0.45 ^a
Chaitén	0.42 ± 0.18 ^a	0.37 ± 0.18 ^a	0.79 ± 0.28 ^a
Futaleufú	0.05 ± 0.05 ^a	0.00 ± 0.00 ^a	0.05 ± 0.05 ^a
Hornopirén	0.00 ± 0.00 ^a	0.00 ± 0.00 ^a	0.00 ± 0.00 ^a
Nercón	0.20 ± 0.12 ^a	0.05 ± 0.05 ^a	0.25 ± 0.13 ^a
Pte. Dumont	0.13 ± 0.13 ^a	0.13 ± 0.13 ^a	0.25 ± 0.18 ^a
Pto. Cárdenas	0.83 ± 0.41 ^a	0.00 ± 0.00 ^a	0.83 ± 0.41 ^a
Puntra	0.83 ± 0.45 ^a	0.33 ± 0.34 ^a	1.17 ± 0.67 ^a
Quellón 1	1.22 ± 1.14 ^a	1.11 ± 0.77 ^a	2.33 ± 1.31 ^b
Quellón 2	0.12 ± 0.08 ^a	0.00 ± 0.00 ^a	0.12 ± 0.08 ^a
Sta. Bárbara	0.00 ± 0.00 ^a	0.11 ± 0.07 ^a	0.11 ± 0.07 ^a
Yerba Loza	0.00 ± 0.00 ^a	0.00 ± 0.00 ^a	0.00 ± 0.00 ^a

Mean ± 1 SE are depicted. Dissimilar superscript letters represent significant differences ($P < 0.05$) after performing Tukey HSD tests for pairwise comparisons between populations

$P = 0.741$, large-scale deforestation: $F_{1,11} = 1.73$, $P = 0.190$, population effect: $F_{1,11} = 2.16$, $P = 0.017$). In fact, the seedling recruitment was significantly higher at Quellón 1 than at Hornopirén or Yerba Loza (Table 3).

Discussion

In the temperate rainforests of Chile, and at the large spatial scale here analyzed, there was a tendency for a bird-mediated positive effect of deforestation on the number of fruits attacked of the shade-intolerant shrub *F. magellanica*, but not an increase in its seedling recruitment. Consequently, there was not a counterbalanced effect of deforestation upon frugivore-mediated seed dispersal and seedling recruitment, as expected.

The large-scale deforestation triggered significant changes only in the color of fruits, among other traits. The reddish-brown fruits from plants growing in more deforested habitats are usually thought to be more attractive than greenish fruits (Schaefer and Schaefer 2007). This is in agreement with the initial prediction indicating an increase of attractiveness of fruits in deforested habitats (Horvitz et al. 2002). In the present case, however, the color of fruits seems to be the result of phenotypic plasticity rather than due to animal-mediated selection. This is stated because color did not play a significant role in the rates of frugivory exerted by both, lizards and birds, and because fruits exposed to the sun are usually more colorful than those ripening under

shade conditions, regardless their genetic load (Schaefer and Schaefer 2007).

In the temperate rainforests of Chile, frugivory on *F. magellanica* fruit was relatively low, but in accordance with the initial expectations; that is, with a lower frequency of consumption (ca. 25%) by terrestrial (i.e., lizards) than by flying animals (i.e., birds), as revealed by their imprints on fruits. In these forests, lizard populations show diets richer in fruits, which is in agreement with the present results (Vidal and Sabat 2010). Although *L. pictus* has suffered a historical reduction in its distribution range due to deforestation (Vera-Escalona et al. 2010), no significant effect of this disturbance on frugivory rates was observed. This situation allows us to hypothesize that, at a regional scale, *L. pictus* is negatively affected by deforestation, but at much smaller scales as those here assessed, there is no negative effects of deforestation on fruit consumption (i.e., a scale-dependent process).

At the large scale of deforestation here assessed and contrary to the initial expectations, there was a tendency to positive effect of deforestation on frugivory and seed dispersal mediated by birds upon *F. magellanica*. This finding, however, is in agreement with the effects of deforestation and human-mediated habitat transformation of the same temperate rainforests (Fontúrbel et al. 2015). In fact, the pollination by hummingbirds (*Sepphanoides sepphanoides*), and frugivory and seed dispersal by mammals (*Dromiciops gliroides*), of the mistletoe *Tristerix corymbosus*, is roughly enhanced with increments of deforestation in the neighborhood of plants (≥ 100 m away from focal plants; Fontúrbel et al. 2015). For this reason, the present study and also the work of Fontúrbel et al. (2015) lead us to consider that the normal effect of recruitment of a pioneer plant species is a putative increase coupled to deforestation. This finding, however, must be interpreted with caution because of the numerous evidence of the negative effects of deforestation on plant–animal interactions and, consequently, on plant reproduction, which seem to depend on the scale of analysis (Markl et al. 2012).

At larger scales than those assessed in the present study, plant–animal interactions could change drastically in magnitude and sign. In fact, the deforestation and fragmentation of the temperate rainforests of Chile have usually negative consequences on bird abundances (e.g., Sieving et al. 1996, 2000; De Santo et al. 2002; Vergara and Simonetti 2003). These changes are not only given by the loss of forests and connectivity among them, but also by the loss of structural complexity and the loss of key species of the understory (Reid et al. 2004; Castellón and Sieving 2005; Díaz et al. 2005, 2006; Vergara and Armesto 2009). In fact, human-mediated disturbances significantly change the reproductive success and survival of birds (e.g., Willson et al. 2001; De Santo et al. 2002; Vergara and Simonetti 2003; Díaz et al. 2006; Vergara and Armesto

2009). Dispersal capacity and niche breadth in terms of feeding behavior are important traits accounting for bird fitness (e.g., Díaz et al. 2006; Vergara et al. 2010; Orellana et al. 2014). For instance, birds with a high dispersal capacity, as those eating fruits of *F. magellanica*, which also exhibit a wide niche breadth (i.e., a generalist feeding behavior), show little, but a negative effect of habitat fragmentation, because frugivory exhibits enhanced responses to plant attributes only in the more connected fragments (Vergara et al. 2010). Taken together, the present study plus the numerous previous works highlight that the effects of deforestation are widespread and variable in fragmented forests, resulting from the link between the spatial scales over which frugivores forage and the life history traits of the interacting species.

Deforestation is the creation of a more continuous habitat in terms of light, but probably with a high incidence of winds and, therefore, with a low atmospheric and soil moisture (Matlack 1993). Because *F. magellanica* also depends on a high water supply (Hoffmann 1997), seedling recruitment may be limited by this resource (Dalling and Hubbell 2002). This situation may contribute to explain the absence of an increased seedling recruitment in more deforested populations, in spite of the positive effects of deforestation on bird-mediated frugivory and seed dispersal.

The temperate rainforests of South America harbor a great diversity of fleshy fruited plants dispersed by numerous frugivorous animals (Armesto et al. 1987; Aizen et al. 2002). These mutualistic relationships, however, are currently facing complex ecological scenarios because of the long-standing exploitation (Armesto et al. 2010). Disentangling the effects of these disturbances at multiple scales, but enlightened by the life history traits of the interacting species, is a key aspect to properly protect the functional diversity of these forests. Therefore, the retention of native forest patches in deforested landscapes is of paramount importance for the establishment of adequate conservation strategies.

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Compliance with ethical standards

Conflict of interest All authors have no conflict of interest.

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