

Frugivory on *Persea lingue* in temperate Chilean forests: interactions between fruit availability and habitat fragmentation across multiple spatial scales

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Abstract Habitat degradation and fragmentation are expected to reduce seed dispersal rates by reducing fruit availability as well as the movement and abundance of frugivores. These deleterious impacts may also interact with each other at different spatial scales, leading to nonlinear effects of fruit abundance on seed dispersal. In this study

we assessed whether the degradation and fragmentation of southern Chilean forests had the potential to restrict seed dispersal the lingue (*Persea lingue*) tree, a fleshy-fruited tree species. Of five frugivore bird species, the austral thrush (*Turdus falcklandii*) and the fire-eyed diucon (*Xolmis pyrope*) were the only legitimate seed dispersers as well as being the most abundant species visiting lingue trees. The results showed little or no direct effect of habitat fragmentation on seed dispersal estimates, possibly because the assemblage of frugivore birds was comprised habitat-generalist species. Instead, the number of fruits removed per focal tree exhibited an enhanced response to crop size, but only in the more connected fragments. In the fruit-richer fragment networks, there was an increased fragment-size effect on the proportion of fruits removed in comparison to fruit-poor networks in which the fragment size effect was spurious. We suggest that such nonlinear effects are widespread in fragmented forest regions, resulting from the link between the spatial scales over which frugivores sample resources and the spatial heterogeneity in fruiting resources caused by habitat fragmentation and degradation.

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Introduction

Habitat fragmentation and degradation are among the most important causes of biodiversity loss in temperate and tropical forest regions (Geist and Lambin 2002; Smith and Hellmann 2002). Although both processes differ in their intrinsic spatial scales and causal mechanisms, they both have the potential to reduce habitat quantity, quality and connectivity for several organisms, resulting in population

decline, genetic erosion and, consequently, an elevated risk of extinction (Lens et al. 2002; Smith and Hellmann 2002). In the particular case of fleshy-fruited plants, these deleterious effects may reduce population persistence, both directly through reducing habitat suitability and indirectly through reducing seed dispersal by frugivore animals (Jordano and Godoy 2002; Cordeiro and Howe 2003).

The conservation of plant species in fragmented or degraded habitats involves determining the ecological mechanisms responsible for a reduction of seed dispersal. Seed dispersal is expected to increase when frugivores are able to track fruit resources at multiple spatial and temporal scales (Ortiz-Pulido and Rico-Gray 2000; Saracco et al. 2004). In an ideal scenario, frugivore species should increase their resource intake by selecting individual plants, micro-sites, fragments and landscapes on the basis of their fruit quantity and quality, thereby influencing the dynamic and spatial/genetic structure of plant populations (Jordano and Godoy 2000; García and Ortiz-Pulido 2004; García et al. 2009). Fruit tracking by frugivores across the landscape should result in a spatio-temporal overlap between the distribution of fruiting plants and their dispersers (i.e., the “fruit abundance effects hypothesis”; Table 1).

A number of studies have provided evidence of a reduction in seed removal rates and the diversity or abundance of frugivore animals in degraded habitats (Kirika et al. 2008a, b; Lehouck et al. 2009a), in isolated forest fragments relative to continuous forests (Cordeiro and Howe 2003; Vergara and Simonetti 2004; Valdivia and Simonetti 2007; see also Kirika et al. 2008a) and in small fragments compared to large fragments (Santos and Tellería 1994). Such findings suggest that habitat degradation and fragmentation directly decrease the amounts of seeds dispersed by reducing the dispersal ability and abundance of frugivores at different spatial scales (e.g., Lens et al. 2002; Table 1).

Although the negative effects of habitat degradation–fragmentation can be widespread in forested landscapes, these processes can also have the opposite (positive) effect on frugivory due to the replacement of habitat-specialist frugivore species by habitat-generalist frugivore species, thereby compensating the decrease in the overall seed dispersal rates (e.g., Graham et al. 2002; Moore and Swihart 2007; Farwig et al. 2006; Table 1).

In fragmented landscapes, suitable sites, such as dense patches of fruiting plants, can be under-utilized or remain unused if frugivore animals can neither disperse to these fragments nor gather information about their spatial location (Gilroy and Sutherland 2007; Vergara and Armesto 2009). The association between frugivores and fruit density might also be weaker in fragmented landscapes due to the availability of alternative resources for frugivores in the matrix habitat (Lehouck et al. 2009a, b). These detrimental effects on animal-dispersed plants can be further increased if, for environmental reasons, the plant’s investment in reproduction (i.e., the crop size) is higher in sites with a low abundance of frugivores. Nonlinear effects of fruit abundance (i.e., statistical interactions between fragmentation and fruit abundance) imply that the expected positive relationship between fruit availability and seed dispersal rate occurs only below some critical levels of habitat degradation or fragmentation (hereafter referred to as the “nonlinear fruit abundance effects hypothesis”; Table 1). Although the assessment of such nonlinear effects may be of paramount importance for understanding to what extent changes of landscape and habitat characteristics will lead to “quantitatively restricted seed dispersal” (sensu Schupp et al. 2002), they have rarely been assessed (but see Farwig et al. 2006; Kirika et al. 2008a).

In the study reported here, we assessed whether the degradation and fragmentation of temperate forests in southern

Table 1 Three hypotheses and their predictions accounting for frugivory on *Persea lingue* trees by frugivore birds in a fragmented forest landscape of southern Chile

Hypothesis	Predictions	Effects of habitat degradation–fragmentation	Example references
Fruit abundance effects	NFT and PFT should increase with an increase in fruit abundance	No	Ortiz-Pulido et al. (2007); Blendinger et al. (2008)
Habitat degradation–fragmentation effects	NFT and PFT should decrease (or increase) with an increase in habitat degradation or habitat fragmentation levels	–/+	Farwig et al. (2006); Valdivia and Simonetti (2007); Lehouck et al. (2009a)
Nonlinear fruit abundance effects	NFT and PFT should be positively (or negatively) associated with fruit abundance only at low levels of habitat degradation or habitat fragmentation	–/+	Farwig et al. (2006); Kirika et al. (2008a)

Predictions are concerned with changes in the number of fruits removed per focal tree (NFT) and the proportion of fruits removed per focal tree (PFT). Positive effects of habitat degradation-fragmentation are predicted if generalist-species overcompensate the reduction in frugivory of specialist species

–, Negative effect; +, positive effect; no, no effect

Chile and their interactions with fruit abundance have the potential to restrict seed dispersal of the lingue (*Persea lingue*) tree, a fleshy-fruited tree species whose fruits are mostly consumed by birds (Veblen et al. 1979). Lingue is one of the few plant species bearing fleshy fruits during the mid and late austral autumn. As such, it is a good model for testing for fragmentation effects during this season, when no fruits are available from other species. We tested the predictions of the hypotheses stated in Table 1, considering three increasing spatial scales through which frugivory on lingue trees could respond to different ecological variables: within-fragment, fragment and landscape.

Materials and methods

Study area and study species

We studied a human-fragmented forest landscape located west of Lake Panguipulli (39.4°S, 72.3°W), at 300 m.a.s.l. in the central valley of the River-District of south-central Chile (Fig. 1). The central valley was once mostly covered by continuous lowland forests of mixed deciduous *Nothofagus obliqua*–evergreen tree species (Donoso 1993). The average annual temperature in this region is about 12°C, with a rainy season from June to September (average annual precipitation 1,800 mm). Lowland forests have been largely cleared by humans for agriculture and livestock grazing by fire and logging, resulting in landscapes with small forest remnants surrounded by pastures and, in some

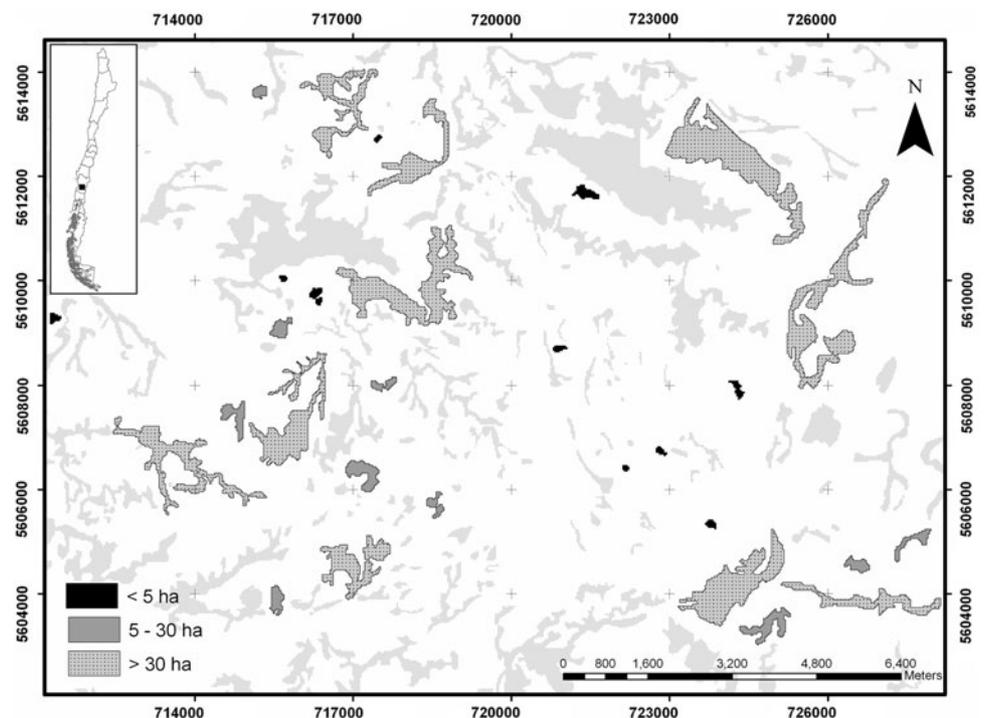
cases, connected by riparian corridors (Echeverría et al. 2006). The study landscape was selected using a GIS vegetation database (CONAF–CONAMA–BIRF 1999) which allowed us to identify forest fragments with the presence of lingue trees (Fig. 1).

Persea lingue (Lauraceae) is a fleshy-fruited tree that is endemic to the temperate forests of Chile; it is up to 18 m tall and 80 cm in diameter. Lingue blooms in the austral summer, and the fruit ripens during mid to late autumn, 13–14 months after flowering. The fruit is a shiny black drupe resembling the fruits of avocado (*Persea americana*), but smaller. Lingue fruits are 14.0–17.0 mm in length and 11.0–14.0 mm in diameter, and they contain only one seed that is, on average, 10.2 mm wide and 13.0 mm long and weighs 0.81 g. Lingue is a semi-shade-tolerant and co-dominant tree species. In the study area, Lingue is a frequent tree species in forest fragments and is the only tree species with fleshy fruits during the study period (late autumn), with the exception of *Aextoxicon punctatum* trees and *Rhaphithamnus spinosus* shrubs, which were occasionally recorded in some fragments ($n = 5$ fragments). We did not detect the presence of other species bearing fleshy fruits in the study fragments (see below), such as native *Myrtaceae* shrub species (e.g., *Luma apiculata*) and introduced plant species (e.g., *Crataegus monogyna*).

Sampling design

Within our study area, we established a 20 × 15-km plot in which 30 focal forest fragments were selected according to

Fig. 1 Map (inset) showing the study landscape. Bright-grey polygons Forest fragments composed of *Nothofagus*–evergreen tree species, white areas represent open pasture matrix. The location of the 30 focal forest fragments of different sizes selected for this study is also shown



a stratified random sampling design which involved first classifying forest fragments in three different categories (small 1–5 ha; medium >5–30 ha; large >30 ha) and then randomly selecting ten forest fragments from each size category (Fig. 1). Focal fragments were not connected to each other through riparian strips (Fig. 1). Once focal fragments had been selected, we used high-resolution satellite imaging data (ALOS/AVNIR-2, 2007) and a group of eight observers to intensively look for adult lingues [>20 cm diameter at breast height (dbh)] within fragments. Since fruit–frugivore interactions can be influenced by fragment edges (e.g., Restrepo et al. 1999), in each focal fragment we selected two focal trees for later analysis (see below), one tree at the edge (i.e., with a fraction $>30\%$ of its crown surface directly exposed to the matrix) and another one in a fragment core section (>100 m distant from the edge). Within fragments, focal trees were >200 m apart, and all had been tagged and georeferenced using GPS. Since only one focal tree could be selected in small-sized fragments (8 fragments had edge focal trees, and 2 fragments had core focal trees; Table 2), we covered a total of 50 focal trees.

Habitat variables

Habitat and landscape structures were characterized at three increasing spatial levels: within-fragment (i.e., habitat), fragment, and landscape. First, in 10-m radius plots centered on each focal tree we measured eight different habitat variables (Table 2) that can be considered as indicators of

habitat degradation, with the exception of proximity to the edge, which is associated with habitat fragmentation (e.g., Vergara and Simonetti 2004). The cover of *Chusquea valdiviana* (Bambusaceae) increases after selective logging or fire (Donoso 1993; Gonzalez et al. 2002). Furthermore, degraded sites usually support a large understory cover, low canopy cover, low tree density and diversity, as well as small-sized trees (i.e., low dbh and height). Second, fragments were characterized according to their size and perimeter:area ratio (Table 2). Third, at the landscape scale we estimated the connectivity of each focal fragment to its neighboring fragments using a fragment connectivity index [Hanski 1994; Electronic Supplementary Material (ESM) 1].

Fruit abundance

Fruit abundance was characterized at four different spatial levels: focal tree, within-fragment, fragment and landscape (Table 2). The crop size of each focal tree was measured during the peak fruiting period of lingue trees at the study site (mid-austral autumn) by taking five photographs (1-m^2 section) of its crown (between 3 and 9 m above ground level) using a digital camera with an object of known scale present in each photograph. In the crown of lingue trees, fruits are located in terminal branches that are not regularly distributed. For this reason, we counted all fruiting branches present in each photographed section. We then pruned five randomly selected fruiting branches per photo-

Table 2 Habitat and fruit abundance variables measured at three increasing spatial scales (within-fragment, fragment and landscape) in the fragmented area of the study

Scale	Habitat variables		Fruit abundance variables	
	Name	Description	Name	Description
Within-fragment	Height	Mean tree (>10 cm DBH) height per plot (m)	F-focal	Crop size of focal lingue trees (fruits tree ⁻¹)
	DBH	Mean tree diameter at breast height (>10 cm DBH) per plot (cm)	FD-plot	Lingue fruit density per plot (fruits ha ⁻¹)
	Canopy	Canopy cover per plot (%)	L-plot	Lingue tree density per plot (trees ha ⁻¹)
	Density	Tree (>10 cm DBH) density (trees ha ⁻¹) per plot		
	Understory	Understory cover per plot (%)		
	Chusquea	<i>Chusquea valdiviana</i> cover per plot (%)		
	Edge	Focal tree location in relation to the fragment edge (fragment edge or core)		
	Diversity	Tree and shrub diversity per plot (species number)		
Fragment	Size	Fragment size (ha)	LD-frag	Lingue tree density per fragment (trees ha ⁻¹)
	P:A	Perimeter:area ratio		
Landscape	Connectivity	Connectivity index (see S1)	L-network	Total lingue trees per network component (trees)

For simplicity crop size is included in the within-fragment scale. For parameter specifications see “Materials and methods”

graphed section and counted all fruits per pruned branch. The number of fruits per square meter of photographed section was calculated by multiplying the number of fruits per fruiting branch by the number of fruiting branches in that area. We then estimated the fruit crop size by scaling the average number of fruits per photographed section to the total crown surface area, previously estimated using the crown height and its mean diameter.

In order to control for the fruit abscission effect on crop size, we monitored weekly the fall of ripe fruits using 2×2 -m seed traps set under nine different trees during 4 consecutive weeks since mid autumn. Seed traps were placed about 1 m above the ground surface (hung from adjacent trees) in order to prevent seed predation by rodents. Although not verified, we expect seed predation by rodents from seed traps to be limited. From these seed traps, we determined that the percentage of fruits that naturally fell off the tree per day was only $0.40 \pm 0.11\%$ [mean \pm standard error (SE)] of the crop size. Accordingly, and considering that frugivory observations were taken no more than 2 weeks after crop size was measured, the effect of fruit abscission on our estimates of fruit crop size could be considered to be negligible.

Fruit abundance within-fragments was estimated as: (1) lingue tree density (trees ha^{-1}) and (2) total number of fruits of lingue trees located up to 20 m around the focal tree, as estimated from a power law regression of crop size against dbh (ESM 2). At the fragment scale, we quantified the density of lingue trees as an estimate of fruiting resource per unit area (Table 2). Lingue trees were sampled in focal fragments using 100- to 150-m long and 20-m-wide transects whose starting positions were selected randomly along edges. Two to three different 150-m-long transects (separated by >150 m) were established in the largest focal fragments (>30 ha) while one 100-m-long transect was placed in the smallest focal fragment (<2 ha). Lingue density varied widely between fragments (1.1–318.4 trees ha^{-1}), with pairwise differences averaging 64.7%. In contrast, there was only a small variation in density within large fragments (average pairwise differences between transects: 15.2%).

Fruit abundance at the landscape scale was estimated as the total number of lingue trees in the landscape. For this analysis we used a graph approach in an attempt to define the spatial dimension at which frugivore birds use the landscape. First, using Conefor Sensinode ver. 2.2 software (Saura and Torné 2009), we determined “network components”, i.e., clusters of connected fragments representing forest fragments located within the bird home range (e.g., Minor and Urban 2007). For this analysis, we used a probabilistic connection model implemented with an estimated kernel function for establishing graph edges (ESM 1, ESM Table S1; Saura and Pascual-Hortal 2007). Second, for

each component, we summed the total number of lingue trees per fragment using the density of lingue trees per fragment predicted from a regression of tree density against fragment size ($R^2 = 0.66$, $p < 0.001$).

Fruit removal

We quantified the number of fruits removed by frugivore bird species using combined information from focal and scan sampling data between 15 May and 31 May 2009 (e.g., Farwig et al. 2006). This approach implied the following steps:

1. We conducted scan sampling observations in which all frugivore individuals and species visiting each focal tree were recorded systematically for 1-min periods at 4-min intervals. Observations were taken about 10 m away from the focal tree using binoculars and a stopwatch on clear days with little or no wind. The effective sampling duration (i.e., the total time during which observations were made) had been determined previously using accumulation functions fitted to scan sampling observations (Fig. 2). Using an accumulation function, we determined that a 60-min session was a reasonable time period to detect most ($>97.5\%$) bird individuals as well as species of frugivore birds arriving at fruiting lingue trees (Fig. 2, S3). Frugivore birds were monitored twice in each of the 50 focal trees (60 min each time), for a total of 100 observation hours. On separate days, two 60-min sessions were made per

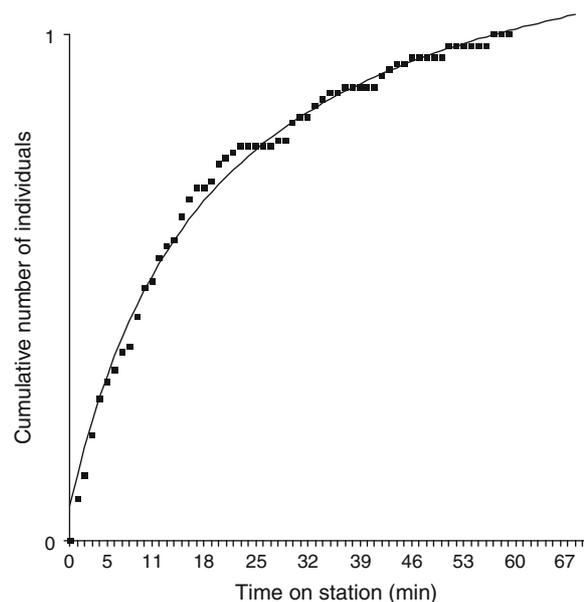


Fig. 2 Accumulation function (solid lines) fitted to scan sampling data (ESM 3). Filled squares correspond to the averaged observed data. The time required to register 97.5% of the expected number of individuals is about 58 min (ESM 3)

focal tree: the first during the morning (0600–1200 hours) and the second during the evening (1400–1700 hours) because bird activity peaked during these two time periods (R.P. Schlatter, personal communication). For each 60-min session, we calculated for each bird species the summed number of visits to a focal tree during the 12 consecutive 1-min scans. The latter variable is not sensitive to double counting of the same bird because it represents the accumulated rate of visitation to a focal tree during a 12-min period.

2. We recorded the feeding behavior of the frugivorous birds by means of focal sampling observations on lingue trees located either at the focal fragments, or at other fragments of similar size, covering a total of 36 trees and 85 observation hours. For this sampling, an observer selected an individual bird and followed it from its arrival at a lingue tree until it left the tree. The variables recorded were: (1) time spent on the tree; (2) number of fruits swallowed during the observation period; (3) fruit-handling behavior; (4) regurgitation rate, recorded only when there was high visibility to detect regurgitation events; this estimation was possible because regurgitated seeds were large enough to be identified in focal samplings and because regurgitation frequently occurred in the same trees where birds were observed to be feeding on fruits; (5) frugivory type, distinguishing legitimate seed dispersers from pulp consumers (species that perform infrequent dispersal of seeds) and seed predators. Data from germination experiments indicated that regurgitation does not affect germination success and, hence, species that regurgitated seeds may be considered as legitimate seed dispersers (Gho 2010). Using variables 1 and 2, we calculated the average per capita fruit consumption rate, averaging all focal observations of the respective species over all the sampled trees.
3. We quantified the number of fruits removed per focal tree by multiplying for each species the summed number of visits (step 1) and the average per capita fruit consumption rate (step 2). We had previously determined that fruit consumption rates of the two most abundant bird species were not correlated with patch size, edge distance or crop size ($r = 0.05$, $p = 0.81$; $r = 0.04$, $p = 0.85$; $r = -0.06$, $p = 0.77$, respectively). Therefore, consumption rates of each species could be averaged over all trees and used as an unbiased estimate of seed dispersal.

Data analysis

We used the linear mixed-effects models (LMM; Pinheiro and Bates 2000; Venables and Ripley 2002) to test fragmentation effects on: (1) the number of fruits removed per

focal tree; (2) the proportion of fruits removed per focal tree. We specified a nested random-effect structure, including focal fragments, observers and time of day as nested random factors (Table S4). At the individual (focal tree) level, we included a spherical spatial autocorrelation structure with nugget effect to controlling for spatial dependence in the data (Pinheiro and Bates 2000). Unlike the fixed-effect “time” (see below), the random effect “time” represents temporal heterogeneity in seed dispersal emerging from differences in the observer’s skill and fragment characteristics. Such complex random-effect structure allows us to take into account correlation within random levels (Table S4; e.g., Bolker et al. 2009). We used the log-transformed (log +1) number of fruits removed and the arcsine-transformed proportion of fruits removed as dependent variables.

An information-theoretical approach [Akaike’s information criterion modified for small sample sizes (AIC_c)] was used to evaluate the support for competing models, with each of the latter representing a hypothesis of the ecological processes influencing frugivory on lingue trees (Burnham and Anderson 2002; Table 1). We developed four model subsets, with the best candidate models for each effect: (1) fruit abundance; (2) habitat degradation–fragmentation; (3) nonlinear fruit abundance; (4) “mixed”, i.e., the combined effects of variables incorporated in the other three model subsets and hence supporting several hypotheses at once. From the above four model subsets, we then selected the best models again based on AIC_c values. Since the number of fruits removed was dependent on the time of day, we included this variable in a “base model” over which we added fixed-effect variables. Models were ranked from the most to least supported given the data on the basis of ΔAIC_c (the difference in AIC_c between the model with the smallest AIC_c value and the current model). The relative importance of individual models was examined using Akaike weights (w), which represent the weight of evidence (i.e., relative likelihood) in favor of a model (Burnham and Anderson 2002). Only models with $\Delta AIC_c \leq 2$ were considered as evidence for supporting hypotheses. Correlated variables ($r > 0.5$) were not included as predictors in the same model in order to avoid multi-collinearity problems and achieve balanced data to test for interactions between fruit abundance and fragmentation (Table S5). Analyses were made using R 2.8.1 software (R Development Core Team 2008).

Results

Frugivore assemblage

We recorded a total of 857 visits to focal trees, belonging to four frugivore species and averaging 0.71 individuals per

1-min scan (Table 3). The most abundant and frequent frugivore species was the austral thrush (recorded in >50% of fragments), followed by fire-eyed diucons and Chilean pigeons (both present in >20% of fragments; Table 3). In contrast, the austral blackbird was recorded only in four fragments (Table 3). Frugivore species also differ in their fruit-handling behavior, frequency of regurgitation and type of frugivory. Of the bird species that swallowed lingue fruits, the austral thrush and the fire-eyed diucon were the only ones that acted as legitimate dispersers (by regurgitating seeds), while Chilean pigeons were observed neither defecating nor regurgitating intact seeds. Consequently, we classified pigeons as seed predators (Table 3). Another possible disperser of lingue seeds was the austral blackbird through its fruit pecking and fruit carrying behavior (Table 3).

Fruit removal rates

The number and proportion of fruits removed per focal tree were estimated only for the austral thrush and the fire-eyed diucon because they were the only species regurgitating viable seeds and, hence, the only species acting as legitimate dispersers (Table 3).

The number of fruits removed per focal tree was dependent on the interactions between crop size and both functional connectivity and cover of the understory bamboo *Chusquea valdiviana*, thereby supporting the nonlinear fruit abundance effects (Tables 4, 5). Akaike weights indicated that the nonlinear effects model was about 5.5-fold more likely than the second best model, the mixed-effects model, which also included the positive effect of lingue density per fragment (Table 4). In all selected models, the time of day had a significant effect on the number of fruits removed per focal tree ($\beta = 0.80$; $p < 0.001$ for the base model), with more frugivory during the evening than in the morning. The interaction between crop size and functional connectivity implied that the positive effect of crop size on the quantity of fruit removed was amplified in the most connected fragments (Table 5; Fig. 3). The interaction between crop size and *C. valdiviana* cover implied that the positive effect of crop size on the quantity of fruit removed was less pronounced in sites with abundant *C. valdiviana* cover (Table 5).

The proportion of fruits removed per focal tree was affected negatively by the *C. valdiviana* cover and positively by the interaction between the number of lingue trees per network component and patch size, thereby supporting the fruit abundance effects as well as the nonlinear fruit abundance effects (Tables 4, 5). Akaike weights indicated that the mixed-effects model was about 2.8-fold as likely as the second-best model, the fruit abundance effects model, which included the positive effects of lingue density per

Table 3 Frugivore species visiting *P. lingue* trees with the total number of visits (i.e., accumulated number of individuals seen during 100 observation hours over all focal trees), the percentage of trees and fragments at which each species was recorded, the fruit-handling behavior (estimated as a rate), the seed regurgitation rate, the frugivory type and the habitat specificity of the bird species

Common and scientific name	Family	Visiting birds		Fruit-handling behavior (mean of fruits/min \pm SE)				Regurgitation rate ^b	Frugivory type	Habitat specificity ^c		
		Total number of visits	Trees (%)	Fragments (%)	n	Pecking	Dropping				Swallowing ^a	Carrying
Austral thrush (<i>Turdus falcklandii</i>)	Turdidae	627	42	53.3	58	0.02 \pm 0.01	0.01 \pm 0.01	0.47 \pm 0.15	0	0.10 \pm 0.05	SD, PC	G
Fire-eyed diucon (<i>Xolmis pyrope</i>)	Tyrannidae	125	28	36.7	10	0.30 \pm 0.23	0	0.22 \pm 0.09	0	0.03 \pm 0.03	SD, PC	G
Chilean pigeon (<i>Patagioenas araucana</i>)	Columbidae	90	16	23.3	5	0	0	0.28 \pm 0.05	0	0	SP	G
Austral Blackbird (<i>Curaeus curaeus</i>)	Icteridae	15	12	13.3	5	0.18 \pm 0.04	0	0	0.13 \pm 0.07	0	PC	G

SD seed dispersers; PC pulp consumers; SP seed predators; G habitat-generalist species; S forest-specialist species; SE standard error

^a Per capita fruit consumption rate

^b Mean of seeds/min \pm SE

^c Habitat specificity during the breeding period (spring)

Table 4 Regression models accounting for the number and proportion of fruits removed per focal tree

Effect	Model variables	<i>K</i>	AIC _c	ΔAIC _c	<i>w</i>
Number of fruits removed per focal tree					
Landscape–habitat	Time, Chusquea (–), height (–), connectivity (+)	6	238.43	7.72	0.02
Fruit abundance	Time, F-focal (+), LD-frag (+)	4	239.72	9.01	0.01
Nonlinear fruit abundance	Time, F-focal × connectivity (+), F-focal × Chusquea (–)	4	230.71	0.00	0.82
Mixed	Time, F-focal × connectivity (+), F-focal × Chusquea (–), LD-frag	5	234.06	3.34	0.15
Proportion of fruits removed per focal tree					
Landscape-habitat	Size (+), density (–), Chusquea (–)	4	108.95	5.41	0.04
Fruit abundance	LD-frag (+), L-network (+)	2	105.59	2.05	0.23
Nonlinear fruit abundance	L-network × size (+)	3	107.66	4.13	0.08
Mixed	L-network × size (+), Chusquea (–)	3	103.54	0.00	0.64

AIC_c Akaike's information criterion modified for small sample sizes

The number of fixed-effect parameters (*K*), differences in AIC_c (ΔAIC_c) and Akaike weights (*w*) are shown. Models supported by the data (ΔAIC ≤ 2) are denoted in bold, and the effect of each variable is represented by (+) for a positive effect or (–) for a negative effect

See Table 2 for model variable definitions

Table 5 Estimates of regression coefficients (β), SE, and *p* values of the best supported models accounting for the avian frugivore richness per focal tree (Table 3), the number of fruits removed per focal tree and the proportion of fruits removed per focal tree (Table 4)

Response variable/independent variables	β^a	SE	<i>p</i>
Number of fruits removed			
Time	0.517	0.286	0.047
F-focal × connectivity	0.025	0.009	0.011
F-focal × Chusquea	–0.008	0.004	0.040
Proportion of fruits removed ^a			
Chusquea	–8.285	3.541	0.019
L-network × size	2.776	0.466	0.002

See Table 2 for model variable definitions

^a For this model, β values were multiplied by 10⁴

fragment and the number of lingue trees per network component (Table 4). The significant interaction between the number of lingue trees per network component and fragment size implied that the positive effect of the number of lingue trees per network on the proportion of fruits removed was amplified in the large-sized fragments (Fig. 3).

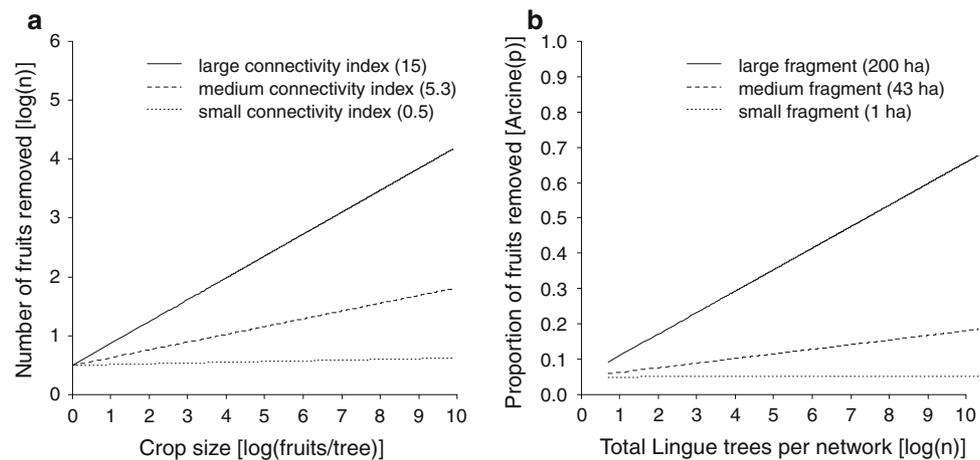
Discussion

As shown by the results, fruit removal from lingue trees by frugivore species was directly affected by fruit abundance and its interaction with habitat–landscape variables, whereas habitat–fragmentation variables had little or no direct effect. However, testing for fragmentation effects

implies understanding how the population and behavioral processes of frugivore animals, such as dispersal and habitat selection, have contributed to shape the distribution of plant populations in their natural (undisturbed) landscapes (e.g., García et al. 2009). Fruit abundance, however, is a critical factor influencing seed dispersal and the abundance of frugivore birds in temperate forests of South America (García et al. 2010). Accordingly, the fruit abundance hypothesis tested in this study can be considered as a suitable null hypothesis for testing for fragmentation effects, since it proposes that frugivores have the natural ability to track fruits across the landscape and select the more suitable fruiting patches among those available. However, in undisturbed habitats, the fruit abundance hypothesis could not be fully supported if frugivory is spatially localized (e.g., Saracco et al. 2004), frugivore species are not more abundant in fruit-rich patches (Restrepo et al. 1999; Saracco et al. 2005), competition levels among plants for dispersers are high (Saracco et al. 2005) and frugivore activity is reduced as a result of frugivore satiation (Hampe 2008). Although the latter mechanisms could influence plant–frugivore interactions in Chilean lowland forests, our results provide enough evidence to suggest that the abundance of fruits has scale-dependent effects on avian generalist frugivores.

The austral thrush and the fire-eyed diucon were the only legitimate dispersers of lingue seeds and the most abundant frugivore bird species. In fact, the austral thrush is one of the most important seed disperser birds in temperate forests of South America (Armesto et al. 1987; Aizen et al. 2002; Amico and Aizen 2005). Both species are usually classified by the literature as habitat-generalist species as they use multiple habitat types, such as native forest, exotic plantations, shrub formations, urban areas and open pasture (e.g.

Fig. 3 Graphical representation of nonlinear fruit abundance effects on frugivory of lingue trees in a fragmented forest landscape of southern Chile. Estimated values from best regression models (Tables 4, 5) of the number of fruits removed (a) and proportion of fruits removed [b, $p = \log(\text{fruits removed}/\text{crop size})$] are plotted against three different levels of connectivity and fragment size, which were drawn from the observed distribution of the focal fragments



Estades and Temple 1999; Vergara and Simonetti 2004; Vergara and Armesto 2009). However, most studies of habitat selection of Chilean forest birds have been carried out during the breeding season (spring), and not during the autumn (the post-breeding season). Thus, habitat specificity of thrushes and diucons could respond to seasonal changes in life-history traits and resources (e.g., Vergara and Marquet 2007). For example, Erazo (1984) and García (1982) showed an important decrease in the abundance of thrushes and diucons in mature lowland forest from autumn to winter, possibly due to the reduction in the number of fruits of olivillo and lingue trees as well as of *Rhaphithamus* and *Luma* shrubs. These omnivore bird species could respond seasonally to available resources, switching their diet from fleshy fruits during the autumn to invertebrates during the winter and early spring. Although further studies should address whether thrushes and diucons select for available fruits (instead of insects) during the autumn, it would be more important in terms of conservation purposes to establish if fragmented and perturbed forests provide these species with alternative resources (e.g., worms in the pasture matrix), thereby resulting in “habitat supplementation”. Furthermore, the open habitat matrix could function as an alternative feeding habitat not only for habitat-generalist species, as shown by our study, but also for forest-specialist species (Lehouck et al. 2009b).

The unique direct and significant effect of a habitat variable was the negative effect of the bamboo *Chusquea* on seed removal efficiency, suggesting a habitat-degradation effect rather than an effect of fragmentation per se. In continuous undisturbed forests, *Chusquea* grows in naturally created gaps in the forest interior, but this bamboo also occupies forest sites severely degraded by anthropogenic processes, such as logging and fire (Gonzalez et al. 2002). Similarly, as shown by other studies (e.g., Blendinger et al. 2008), fruit removal in unperturbed habitats could be constrained by natural heterogeneity of micro-habitat conditions. According to their interaction with crop size, patches

of *Chusquea* bamboo might reduce the ability of frugivores to discover fruiting trees, possibly by decreasing the conspicuousness of lingue fruits. On the contrary, we did not detect significant edge or fragment-size effects on frugivory despite larger fruit abundance at the edge and in large fragments (ESM Table S5).

We showed that at high levels of habitat degradation and fragmentation the increasing response of frugivore species to fruit availability was largely reduced (e.g., Fig. 3). Thus, a larger availability of fruit resources would not result in a sustained increase in seed dispersal rates. However, ecological factors other than habitat fragmentation could lead to those nonlinear effects, such as differences in territorial behavior between habitats (Tellería et al. 2008). Similarly, austral thrushes display intense despotic behavior that may result in dominant individuals monopolizing trees with large crop sizes in small-sized fragments, although according to their fruit abundance (ESM Table S5), small fragments would not represent high-quality habitats for frugivore birds unless they provide them with other alternative resources.

Nonlinear fruit abundance effects in degraded and fragmented habitats could be widespread in forested regions. Farwig et al. (2006) reported a positive response of frugivore species and individuals to crop size only in continuous forest, while the opposite effect occurred in isolated fragments. However, Farwig et al. (2006) also showed a steeper increase of species and individuals with increasing fruit abundance in highly disturbed sites relative to little disturbed sites. In another tropical forest, Kirika et al. (2008a) found that both the number of fruits removed and the number of frugivore species responded more strongly to fruit availability in continuous forest than in isolated fragments. We suggest that such nonlinear fruit abundance effects result from the link between the spatial scales over which frugivore birds sample resources and the spatial heterogeneity in fruiting resources caused by habitat fragmentation and degradation. The underlying assumption in making

such a prediction is that resources are not necessarily used by birds according to their availability but that their use depends on bird attributes, such as food searching efficiency, life-history traits, habitat-area requirements, dispersal capacity and social structure. Consequently, in tropical forests, it is probable that nonlinear fruit abundance effects respond directly to the difference in species attributes between habitat-specialist frugivore species and habitat-generalist frugivore species. Nonlinear fruit abundance effects could also emerge from intra-specific gradients in habitat use by habitat-generalist species across spatial scales. In fact, we demonstrated cross-scale interactions between fruit abundance and landscape-habitat variables in Chilean temperate forests.

Austral thrushes and fire-eyed ducons could spend more time searching for and foraging on fruits in large fragments than in the smaller ones as a positive response to the larger amounts of available fruiting resources. This fruit–fragment interaction can be explained in the context of the optimal foraging theory that predicts that residence time in a fragment should be positively related to its quality (e.g., Charnov 1976). Possibly, a similar explanation could be invoked for the increased response of frugivory to crop size in the more connected fragments, since birds using multiple connected fragments should remain less time in each fragment, resulting in a large number of fragments being visited by a bird. Furthermore, more fruits were removed in fragment networks harboring a larger number of fruiting trees compared to networks with few fruiting trees. In fruit-rich networks, frugivore birds can have the opportunity of selecting large-sized fragments, thereby avoiding the predation risk associated with the use of the matrix habitat (e.g., Vergara and Hahn 2009). In contrast, birds foraging in fruit-poor networks should have larger dispersal rates and distances as a means to obtain sufficient amounts of fruits for survival and, hence, their foraging decisions should be less influenced by fragment attributes such as size. Finally, we suggest that the effect of forest degradation and fragmentation, as addressed in our study, should be further assessed over longer time scales. It is evident that the temporal extent on which fragmentation effects should be studied will depend on the rate at which the spatial distribution of lingue trees changes in response to anthropogenic disturbances as well as the response of frugivore birds to such habitat and landscape modifications.

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