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Decreased frugivory and seed germination rate do not reduce seedling recruitment rates of *Aristotelia chilensis* in a fragmented forest

Carlos E. Valdivia · Javier A. Simonetti

Abstract Habitat fragmentation reduces frugivorous bird abundance. Such a reduction may lead to a reduction in seed dispersal, thereby compromising seedling recruitment rate with far reaching consequences for plant population persistence. We assessed frugivory, seed germination, and seedling recruitment rates in a fragmented forest of central Chile by comparing a continuous forest with four forest fragments surrounded by pine plantations. Frugivory was 2.4 times higher in continuous forest than in forest fragments. Seeds eaten by birds germinated 1.7 and 3.7 times higher than non-eaten seeds from continuous forest and fragments respectively. Non-eaten seeds from continuous forest germinated 2.2 times higher than those from forest fragments, suggesting inbreeding depression. However, seedling recruitment rates at forest fragments were far higher than in continuous forest where no seedling recruited in the five years analysed. Therefore, despite forest fragmentation negatively affected frugivory, it did not translate into a decreased fitness of plants, thus highlighting the importance of considering the overall processes leading the reproductive success of plants following anthropogenic disturbances.

Keywords Forest fragmentation · Avian frugivory · Seed quality · Seedling recruitment rates

Introduction

Habitat fragmentation can have profound effects on frugivory and seed dispersal with negative consequences for plant fitness (Santos and Telleria 1994; Galetti et al. 2003; Şekercioğlu et al. 2004). The reduction in habitat size and increment in isolation can reduce the diversity and abundance of the remaining frugivores. Such reductions may lead

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to a reduction in the intensity of frugivory, and consequently, in seed dispersal and upon seedling recruitment (Galetti et al. 2003; Cordeiro and Howe 2001, 2003; Traveset and Riera 2005).

Small patches of fruiting plants may be less attractive to frugivores as they offer a lower food reward (Saracco et al. 2004). Because sugar concentration of pulp fruits depends on environmental conditions (Ito et al. 1999), forest fragmentation might then affect the attractiveness of plants to frugivores by increasing sugar concentration given the lower environmental humidity of forest fragments. Frugivores prefer concentrated pulps, which may in turn trigger an increased frugivory rate (Stanley et al. 2002). Because habitat fragmentation reduces atmospheric humidity (Camargo and Kapos 1995), the attractiveness of fruits, in terms of sugar concentration, might be higher in fragmented populations. Therefore, habitat fragmentation could lead to contrasting tendencies: a reduction of frugivory, since small and isolated patches are less attractive and harbour a depauperated fruit-feeding animal abundance; or increased frugivory rates, because fruits in fragments might produce more concentrated pulps, leading to some sort of compensation, or even overcompensation, of the lowered population sizes, and hence similar rates of frugivory in continuous forests and forest fragments.

A failure in seed dispersal triggered by a lowered frugivory might lead to a clumped pattern of tree recruitment which may in turn favour a higher mating ratio among close relatives (Bleher and Böhning-Gaese 2001). Therefore, failures in frugivory coupled to a reduction in plant population size and increased isolation triggered by habitat fragmentation may lead to inbreeding depression (Barrett and Khon 1991; Young et al. 1996). Inbreeding depression in turn, may produce a reduction in seed quantity i.e., seed per fruit) and seed quality (i.e., germination rate) (Barrett and Khon 1991; Young et al. 1996; Henríquez 2004). Certainly, the reduction in frugivory coupled to the lowered fitness of plants in terms of the seed quality and quantity may reduce the seedling recruitment rates, which might compromise the long-term population persistence (Barrett and Khon 1991; Galetti 2003).

Although frugivorous vertebrates are rather scarce in the temperate rainforests of southern Chile, the proportion of vertebrate seed dispersal is roughly comparable to tropical forests (Armesto and Rozzi 1989; Willson 1991). In these temperate forests, birds are the most important frugivores being more than three-quarters of the whole vertebrate dispersers (Willson 1991; Aizen et al. 2002). Therefore, changes in frugivorous birds may lead to a changes in frugivory.

Currently, the southern temperate rainforest is severely fragmented which may affect animal-dispersed plants (Bustamante and Castor 1998; Bustamante et al. 2005). In these forests, assessments on the effects of forest fragmentation on birds have only recently been considered, reporting negative effects on richness and abundance of fruit-feeding birds (e.g., Willson et al. 1994; Vergara and Simonetti 2004). Despite this fact, however, there is a great knowledge vacuum concerning the potential effects of such reductions on seed dispersal and seedling recruitment rates. Here, we assess the effect of forest fragmentation on avian frugivory, seed quality, and seedling recruitment rates on the bird-dispersed tree *Aristotelia chilensis* (Elaeocarpaceae), a broadly distributed understory tree in temperate forest of southern South America (Rodríguez et al. 1983). If forest fragmentation negatively affect the frugivorous assemblage, we expect a negative effect on frugivory at the forest fragments with regard to continuous forest. Similarly, because forest fragmentation may also negatively affect seed quality, we expect a lower germination rate of seeds from forest fragments than from continuous forest. Therefore, because we expect a lowered seed dispersal rate coupled to a lowered seed quality, it is reasonable to expect a lowered seedling recruitment rate in fragments than in the continuous forests.

Materials and methods

Study site and species

The study was conducted in Maulino forest in the northernmost zone of the Southern temperate rainforest (35°59′S, 72°41′W; San Martín and Donoso 1996). Specifically, we worked in Los Queules National Reserve and four neighbouring forest fragments. Distance between continuous forest and fragments, and between fragments, ranges from 1 to 4 km (see Donoso et al. 2003 for a map). Los Queules is a protected area of 145 ha embedded in a large tract of 600 ha of continuous forest. Forest fragments, ranging from 1 to 6 ha, are patches surrounded by commercial plantations of *Pinus radiata*. Both in the forest fragments and in the continuous forest composition and abundance of adult trees are similar, the most abundant trees being *Aetoxicon punctatum, Cryptocarya alba, Gevuina avellana*, and *Persea lingue* among others (Bustamante et al. 2005).

   Aristotelia chilensis (Elaeoearpaceae) is a dioecious tree of up to 4 m tall that inhabits the southern temperate rainforests (Rodríguez et al. 1983). While the adult abundance is roughly the same at both continuous forest and forest fragments, seedling abundance is higher at forest fragments (Bustamante et al. 2005). It bears black-coloured fleshy berries which are eaten and dispersed by fruit-feeding birds. Fruiting occurs from October to December, while fruit ripeness and seed dispersal occur from mid-December to January in the austral spring-summer season (Rodríguez et al. 1983). In the Maulino forest, potential dispersers are *Anairetes parulus, Elania albiceps, Xolmis pyrope* (Tyrannidae), *Aphrastura spinicauda* (Furnariidae), and *Turdus falklandii* (Muscicapidae) (Vergara and Simonetii 2004). In the study site, *A. parulus, E. albiceps* and *X. pyrope* are less abundant in forest fragments than in continuous forest, whereas *A. spinicauda* and *T. falklandii* are equally abundant in both forest fragments and continuous forest (Vergara and Simonetti 2004; González-Gómez 2004).

Fruit characteristics

To determine fruit characteristics, in January 2002, we randomly selected trees and branches and then collected ripe fruits ($n=30$ fruits from six trees in the continuous forest, $n=35$ fruits from six trees in the forest fragment, 1–2 trees per fragment) for assessing fruit size, quantity of seeds, and sugar concentration. Fruit size was estimated as the diameter of each fruit, while sugar concentration (mass percentage) was assessed with a hand-held temperature-compensated refractometer. All measurements were made in fresh fruits immediately after being collected.

Frugivory

The intensity of frugivory was experimentally assessed. We mimicked fruits making red-coloured wire branches bearing nine black-coloured plasticine fruits ($n=96$ branches with 864 fruits placed in the continuous forest, $n=100$ branches with 900 fruits in the forest fragments). The artificial infructescences were attached to individual fruiting trees (2–8 wire branches per tree depending on tree size; $n=16$ trees at continuous forest, $n=16$ trees at forest fragments, four per fragment) leaving them for the action of fruit-feeding birds during 30 days, from December 2001 to January 2002, coinciding with the period of seed dispersal. The only dispersers known for *A. chilensis* are fruit-feeding birds; hence, fruits

removed from infructescences were considered as dispersed by frugivorous birds, assumption reinforced by bill impressions on the picked fruits. This experimental array, mimicking natural infructescences of *A. chilensis*, allowed for a control of numerous traits which might otherwise bias the fruit-feeding animal choice, and thus the effect of forest fragmentation on frugivory (see Alves-Costa and Lopes 2001 on methodological details).

Seed germination

To determine the effect of consumption on seed germination, we placed for germination seeds randomly collected in January 2002 from faeces placed on the ground in the continuous forest and forest fragments (*n*=150 seeds from ca. 100 faeces), together with seeds collected from ripe fruits on trees (*n*=150 seeds from six trees in the continuous forest, and *n*=150 seeds from six trees in the forest fragments, 1–2 trees per fragment). This experimental design allowed to assess the effect of frugivores (eaten versus non-eaten seeds) as well as the origin of seeds (continuous forest versus forest fragments) on the seed germination rate.

Germination trials were carried out through a common garden experiment. Because we were incapable of assigning bird-eaten seeds to a specific site, they were only considered as dispersed seeds with mixed origin (i.e., from both continuous forest and forest fragments), thereby rendering conservative the comparisons with non-dispersed seeds from both types of sites. Seed germination was carried out during 250 days by placing 10 seeds from all individual trees into Petri capsules (*n*=15 capsules per treatment) placed inside germination chambers. Photoperiod of germination chambers was 12-h day/12-h night throughout all time of seed germination, whereas the temperature was modified according to the month when germination naturally occurs, thus mimicking natural conditions for germination (monthly temperature from March to November: 13.3, 10.9, 9.7, 8.5, 8.6, 8.8, 10.6, 12.3, and 13.6°C). Seeds were weekly irrigated with water. We considered a seed as germinated when the emerged root presented 2 mm elongation.

Seed rain and seedling recruitment rates

Forty seed traps were erected within the continuous forest, while other 40 seed traps were placed in forest fragments (10 at each fragment). Each trap consisted of a 0.25 m^2, open-topped, 1 mm wire-mesh bag held 0.8 m above the ground on a PVC frame. All seeds falling into the traps were counted and identified to the species level each month from January 2002 to December 2002. Because we were incapable of determining if seeds corresponded to bird-dispersed seeds or not, they were only considered as seed rain remaining the dispersal mechanism unknown.

To assess seedling recruitment rates we randomly placed plots of 2 m^2 (*n* = 20 in the continuous forest, and 20 in forest fragments, five per fragment). In these plots, we registered all woody plant less than 50 cm height (hereafter seedlings). Each seedling was individually tagged and identified to the species level from 1998 to 2004. Sampling was performed in September of each year, and survivors were recorded in January of the next year for registering all new recruits of the same recruitment season.

At both continuous and forest fragments, we placed two seed traps 2-m away from each plot. Thereafter, each plot and its two adjacent seed trap constituted a census station. Census stations were roughly linearly arranged at each site. The average distance (±1 SE) from each census station to the next census station was 21.13±2.14 m at continuous forest,

Table 1 Fruit characteristics of *Aristotelia chilensis* in the continuous forest and forest fragments (Mean ± 1se)

Fruit characteristics	Continuous forest	Forest fragments
Fruit size (mm)	5.8±0.1[a]	6.2±0.1[a]
Number of seeds per fruit	2.9±0.2[a]	2.9±0.2[a]
Sugar concentration (%)	15.4±1.5[a]	11.0±0.7[b]

Different letters depict significant differences (*P*<0.05)

and 20.83±3.14 m at forest fragments, which did not differ significantly (Mann–Whitney test: *U* =121, *P* = 0.305).

At each census station we determined the seedling recruitment rate as $r = (N_t/N_0)^{1/t}$, where N_0 is the number of seedlings at the beginning of the interval, N_t is the number of seedlings at the end of the interval, and t is the number of years (Sheil et al. 1995). The time interval assessed was five years, from 1998 to 2004, thus diminishing a possible overestimation of seedling recruitment rate associated to a narrow time interval (Lewis et al. 2004).

Results

Fruit characteristics

Fruit size was marginally bigger at forest fragments than at continuous forest (Mann–Whitney Test: *U* = 387.5, *P* = 0.07; Table 1). The number of seeds per fruit did not differ between both types of sites (*U* = 520.0, *P* = 0.948; Table 1). Nevertheless, sugar concentration of fruits was 1.4 times higher in the continuous forest than in the forest fragments (*U* = 327.5, *P* = 0.047; Table 1).

Frugivory

Frugivory was 2.4 times higher in the continuous forest than in forest fragments (Mean ± SE: 0.47±0.05 fruits preyed/infructescence in the continuous forest, 0.20±0.04 fruits preyed/infructescence in the forest fragments; *U* = 3510.0, *P*= 0.001; Fig. 1b). Such a reduction was 2.2 times greater than the reduction in frugivorours bird abundance previously reported by Vergara and Simonetti (2004) (Fig. 1a).

Seed germination

Overall, both consumption by birds and the origin of seeds (i.e., continuous forest and forest fragments) affected seed germination rate (Table 2). In fact, dispersed seeds germinated 1.7 (Tukey HSD test for balanced data: *P*<0.01) and 3.7 (*P*<0.01) times higher than non-dispersed seeds from continuous and forest fragments respectively, while seeds from continuous forest germinated 2.2 times higher than seeds from forest fragments (*P*=0.02) (Fig. 2).

Seed rain and seedling recruitment rates

Seed rain was 5.4 times higher in the forest fragments than in the continuous forest (*U* = 54, *P*<0.001; Fig. 3a). At forest fragments, 21 seedlings were tagged at the onset of the

Fig. 1 Frugivore abundance (**a**) (modified from Vergara and Simonetti 2004) and frugivory (**b**) of *Aristotelia chilensis* in a continuous forest and forest fragments (Mean ± 1se)
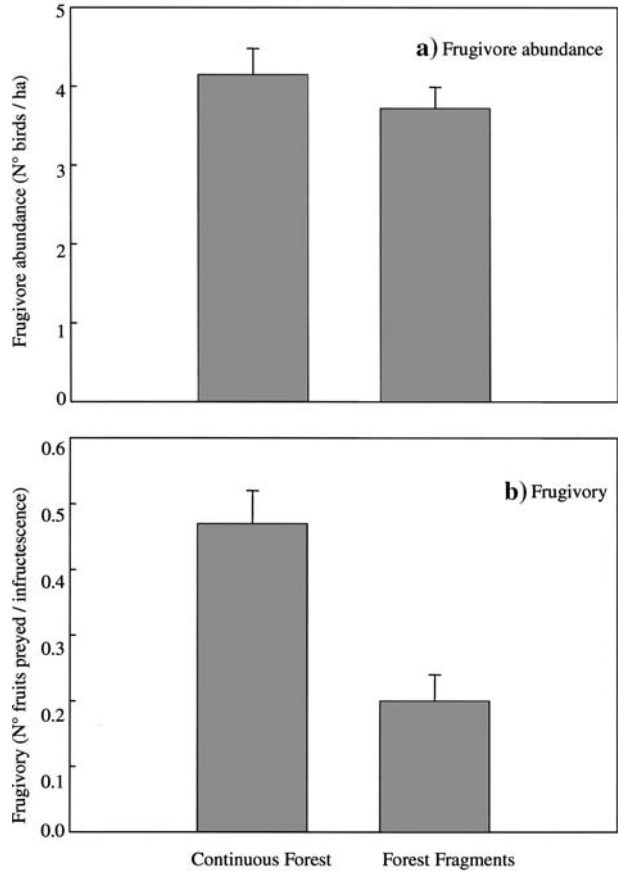

Table 2 Summary of repeated measures ANOVA testing the effect of seed type (non-eaten seeds from continuous forest and from forest fragments, and eaten seeds from both continuous forest and forest fragments) and time on the seed germination of *Aristotelia chilensis*

Source	df	MS	F	P
(a) Within-subjects:				
Type of seeds	2	169.39	12.39	<0.001
Error	42	13.67		
(b) Between-subjects:				
Time	36	44.73	70.13	<0.001
Time × type of seeds	72	6.69	10.49	<0.001
Error	1512	0.64		

experimental assessment. Of these, only one stayed alive until 2004. On the contrary, at continuous forest no seedling was recorded neither at the onset of the experimental assessment nor in the time interval evaluated (1998–2004). Consequently, the seedling recruitment rate was far higher at the forest fragments with respect to continuous forest (Fig. 3b).

[24]

Fig. 2 Effects of bird consumption and forest fragmentation on seed germination rate of *Aristotelia chilensis* (points correspond to Mean ± 1 SE and are presented at fortnight intervals)
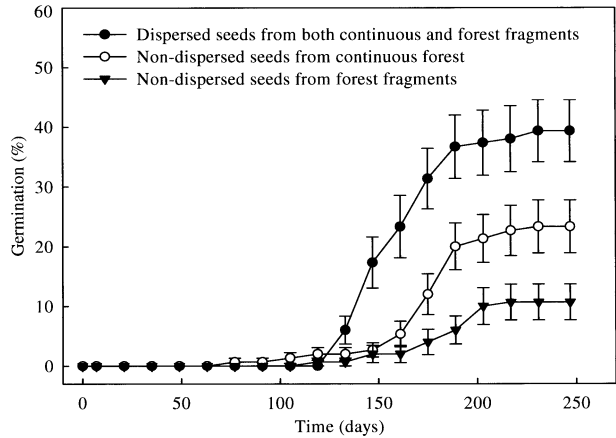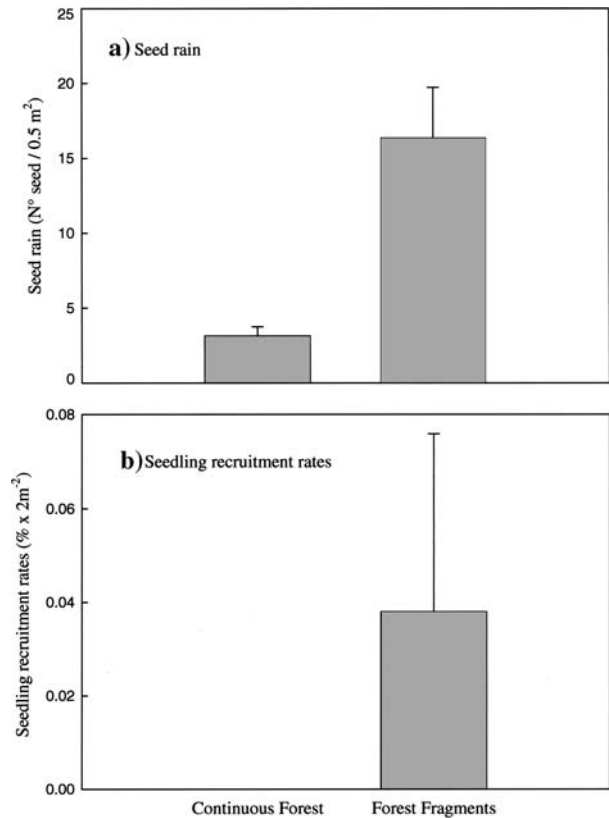

Fig. 3 Seed rain (**a**) and seedling recruitment rates (**b**) of *Aristotelia chilensis* in a continuous forest and forest fragments (Mean ± 1SE)

Discussion

Aristotelia chilensis faces a seemingly contradictory scenario in the fragmented Maulino forest. It faces a lowered frugivory and consequently a reduced probability for seed dispersal, yet higher seedling recruitment rates as the final outcome. Forest fragmentation

significantly reduced frugivory coupled to the lower abundance of frugivorous birds (Vergara and Simonetti 2004). Contrary to our expectations, forest fragmentation reduced sugar concentration of fruits. However, because we used artificial fruits for the frugivory assessments, thus avoiding the effects of sugar concentration, the lowered frugivory at fragments herein reported may be even more reduced regarding that furgivores prefer more concentrated nectar (Stanley et al. 2002).

A failure in seed dispersal triggered by a lowered frugivory may lead to a clumped pattern of tree recruitment which may in turn favour a higher mating ratio among close relatives, and hence to a likely frugivore-mediated inbreeding depression (Bleher and Böhning-Gaese 2001; Şekercioğlu et al. 2004). Frugivores in the forest fragments, besides providing a lowered seed dispersal service, might carry also seeds with a reduced germination rate, suggesting a likely evidence for inbreeding depression. In fact, perennial and dioecious plants may suffer most strongly the effects of forest fragmentation, in term of inbreeding depression, on account of these reproductive traits (sensu Murcia 1996). Because *A. chilensis* is pollinated by the small-sized bees *Cadeguala albopilosa* and *Ruizantheda mutabilis* (Aizen et al. 2002), which may be strongly restricted for moving across fragments, the possibility of inbreeding depression in *A. chilensis* is indeed to be expected. For instance, in the same forest, the self-compatible vine *Lapageria rosea*, despite exhibiting a suite of traits that render less prone to express inbreeding depression of compared with *A. chilensis*, exhibits a lowered genetic diversity which has triggered inbreeding depression expressed through a lower pollen quality and seed germination capability (Henríquez 2002).

Therefore, the lowered seed dispersal service coupled to a reduced germination rate should lead to *A. chilensis* towards a lowered seedling recruitment rate, and hence towards a likely threat in the long-term population persistence in fragments. Nevertheless, seedling recruitment rates were far greater in fragments than in continuous forest. This fact may be a result of the great number of seeds falling into the fragments, which could exert a ''mass effect'', overcompensating the lowered seed quality and reduced possibilities for seed dispersal. Even though we were incapable of determining the exact origin of the seed rain, the great number of seeds falling into the fragments may be a consequence of the in situ seed production further those seeds produced outside. In fact, the Maulino forest fragments seem to be part of a source-sink system, where there would be an active colonisation process by bird-dispersed trees, since birds would be able of moving across sites with no restriction (sensu Bustamante et al. 2005).

A second aspect to be considered deals with the latter mechanisms leading the seedling recruitment following the seed rain. Population of *A. chilensis* inhabiting the remaining forest fragments do not exhibit the negative density-dependent mechanisms for seedling recruitment exhibited by a great proportion of trees in the continuous forest (Valdivia 2004). For this reason, the high number of seeds falling into the fragments would be not under the mechanisms for population regulation, which increases the probability for seedling recruitment (Valdivia 2004; Bustamante et al. 2005).

Additionally, *A. chilensis* is a short-lived tree with a great phenotypic plasticity being capable to survive in forests with a great variability of environmental light (Lusk and del Pozo 2002). However, *A. chilensis* exhibits a higher rate of growth in light than in darkness of compared with other species of the temperate rainforest of Chile (Lusk and del Pozo 2002). Because light is higher in fragments than in continuous forest (Simonetti, to be published), fragments would be a more suitable habitat for *A. chilensis* regarding the continuous forest, which in turn would increase the likelihood of growth and survival.

   As far as seed dispersal by birds is concerned, the scenario faced by *A. chilensis* may be representative of numerous other bird-dispersed trees of the highly fragmented temperate rainforest of South America, as for instance, *Aetoxicon punctatunn, Amomyrtus luma, Drymis winteri*, and *Raphithamnus spinosus*, all of them occurring at the Maulino forest as well (Armesto and Rozzi 1989; Aizen et al. 2002). Concerning the niche regeneration and probabilities for recruitment, however, the same species might respond in many different ways (Lusk and del Pozo 2002; Bustamante et al. 2005). Therefore, several functional responses are to be expected in trees inhabiting the temperate rainforest of southern South America after suffering anthropogenic disturbances such as forest fragmentation. Accordingly, despite some reports have provided evidence that disrupted mutualisms may lead to an almost irrevocable decline in populations (e.g., Cordeiro and Howe 2001, 2003; Traveset and Riera 2005), our report points to consider the importance of assessing the overall mechanisms leading the long-term population persistence of trees, and thus the fate of such forests, before rigorous biological interpretations can be offered.

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