Non-redundancy in seed dispersal and germination by native and introduced frugivorous birds: implications of invasive bird impact on native plant communities

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Non-redundancy in seed dispersal and germination by native and introduced frugivorous birds: implications of invasive bird impact on native plant communities

Valeria L. Martin-Albarracin[1] · Martin A. Nuñez[2] · Guillermo C. Amico[1]

Abstract

Seed dispersal by vertebrate animals is important for the establishment of many fleshy-fruited plant species. Different frugivorous species can provide different seed dispersal services according to their specific dietary preferences as well as behaviour and body traits (e.g. body size and beak size of birds). Our aim was to study redundancies and complementarities in seed dispersal and germination between the two main native seed disperser birds and the introduced silver pheasant *Lophura nycthemera* in the temperate Patagonian forests. For this, we collected fresh droppings from the studied species and analyzed seed content. We conducted germination trials for four plant species common in bird droppings; two native species (*Aristotelia chilensis* and *Rhaphithamnus spinosus*) and two invasive non-native species (*Rubus ulmifolius* and *Rosa rubiginosa*). Both native frugivorous birds and the silver pheasant dispersed fruits of non- native fleshy-fruited plants, but their roles were non-redundant in terms of species dispersed and effect on seed germination. The silver pheasant dispersed a proportionally high number of non-native seeds, while native birds dispersed a high number of native seeds. In addition, the effect of gut treatment in seed germination differed between seed dispersers. Native birds promoted the germination for the two native plant species studied, while the silver pheasant promoted the germination of one non-native plant. This suggests that seed dispersal by the silver pheasant may contribute to the spread of some invasive fleshy-fruited plants in the ecosystems that otherwise would not be dispersed by any other bird. The understanding of redundancies and complementarities on seed dispersal and germination between native and introduced birds will allow improving the management of fleshy-fruited non-native plants.

Communicated by David Westcott.

This article belongs to the Topical Collection: Invasive species.

✉ Valeria L. Martin-Albarracin
   valemartinalba@gmail.com

Extended author information available on the last page of the article

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Introduction

Endozoochory, or the dispersal of seeds through ingestion and subsequent regurgitation or defecation by animals, is a key process for the establishment of many fleshy-fruited plant species (Herrera 2002; Traveset et al. 2007). Functional consequences of plant-frugivore interactions depend on the effectiveness of seed dispersal, which includes both quantitative and qualitative components (Schupp et al. 2010). Quantitative components are those related to the number of visits and fruits consumed, and qualitative components involve other factors that can improve the quality of seed dispersal. In this aspect, seed dispersal can benefit plant establishment in several ways: promoting seed germination as a consequence of gut treatment (Yagihashi et al. 1998; Nogales et al. 2005; Traveset et al. 2007; Jordaan et al. 2011), increasing seedling growth rate through the fertilization of seeds (Traveset et al. 2001; Valenta and Fedigan 2009), depositing seeds in sites highly suitable for seed germination (Stevenson 2000), or taking seeds to areas with minor levels of interspecific competition (Herrera 2002).

The roles of different seed disperser animals in the dispersal network can be redundant or complementary. Two species are functionally redundant when they have a similar function for the ecosystem, in a way that, if one species becomes extinct, the other species would replace its function (Lawton and Brown 1994). In contrast, two species are functionally non-redundant or complementary when they play different roles on the ecosystem; thus, one species cannot replace the function of the other. Non-redundancy in seed dispersal is usually associated to differences in the set of interacting species, but it can also be reflected in differences in the quantitative and qualitative components of disperser effectiveness (Rother et al. 2016). For example, dispersers can be non-redundant in their seed dispersal function because they consume fruits from different substrates (i.e. fruits from the plant canopy or fruits fallen to the ground under the plant) (Christianini and Oliveira 2010), because they defecate seeds at different sites or distances (Spiegel and Nathan 2007; Lehouck et al. 2009; McConkey and Brockelman 2011; Escribano-Avila et al. 2014; Viswanathan et al. 2015), or because the effects of seed passage through disperser´s gut on germination are different (Jacomassa and Pizo 2010).

One consequence of the ongoing human-driven global change is the ecosystem gain and loss of species. The effect of those changes on ecosystem processes such as seed dispersal is currently a central issue in ecology (Wardle et al. 2011), and recent studies have addressed the impact of species loss on ecological function and seed dispersal processes (Bueno et al. 2013; Valiente-Banuet et al. 2015). The ecosystem effect of the addition of novel seed disperser species, however, remains understudied. The introduction of novel species in an ecosystem can cause the rise of new interactions, and the success of the introduced plants or animals to integrate into the native interaction network may influence their fitness and establishment success (Traveset and Richardson 2014).

The effects of alien seed dispersers on plant communities can be analyzed under degradation and meltdown scenarios or under rescue and recovery scenarios (Buckley et al. 2006). On the one hand, some studies have reported strong positive interactions between non-native plants and introduced seed dispersers, indicating that non-native dispersers can facilitate the establishment, spread and/or impact of non-native invasive plants (Bourgeois et al. 2005; Linnebjerg et al. 2009; Spotswood et al. 2012, 2013; Martin-Albarracin et al. 2015a). These interactions may support further invasions by exotic frugivores and plants, leading to a meltdown scenario. On the other hand, exotic dispersers may assist the movements and recruitment of native plants, leading to a recovery

scenario, particularly under a context of extinction of native seed dispersers (García et al. 2014). The raising of novel multispecies dispersal complexes incorporating native and exotic frugivores and plants may also facilitate native plant recruitment (Neilan et al. 2006). The impact of an introduced frugivorous species on the native community will be higher if its ecological role is non-redundant to that of native dispersers, because in this way it will be introducing novel functions to the ecosystem and thus resulting in a positive response in the seed dispersal function (Wardle et al. 2011; Schleuning et al. 2015).

In the temperate forests of Patagonia, approximately the 50% of woody plant species produce fleshy fruits (Aizen and Ezcurra 1998; Aizen et al. 2002). In addition, several non-native fleshy-fruited shrubs and trees were introduced and many of them are becoming invasive (Lediuk et al. 2014; Iglesias 2015). Some of these introduced species and their congeners develop a very aggressive behavior in different environments of the world and in Patagonia, such as *Rubus ulmifolius* (Baret et al. 2004; Rentería et al. 2012; Vargas et al. 2013a, b) and *Rosa rubiginosa* (Damascos and Gallopin 1992; Zimmermann et al. 2011). The assemblage of seed dispersers, on the other hand, is very simple. The main frugivorous birds are just two, the resident *Turdus falcklandii* (Turdidae, 23.7 cm body length and 7.4 mm gape width) and the migrant *Elaenia albiceps* (Tyrannidae, 13.7 cm body length and 4.3 mm gape width) (Amico and Aizen 2005). Other species, including *Scelorchilus rubecula* (Rhinocryptidae), *Xolmis pyrope* (Tyrannidae), *Patagioenas araucana* (Columbidae), *Curaeus curaeus* (Icteridae) and *Phytotoma rara* (Cotingidae) have been reported as facultative frugivores, but they are mainly granivorous, herbivores or insectivorous (Armesto and Rozzi 1989; Aizen et al. 2002; Amico and Aizen 2005; Amico et al. 2009). The role of other groups of vertebrate dispersers, like mammals or reptiles, is relatively unimportant for the dispersal of the majority of plant species, although a small endemic marsupial (*Dromiciops gliroides*, Microbiotheriideae) and the Andean fox (*Lycalopex culpaeus*, Canidae) have been reported as seed dispersers of several fleshy-fruited plants (Aizen et al. 2002; Amico et al. 2009).

The silver pheasant *Lophura nycthemera* (Phasianidae) was introduced as a game bird to Isla Victoria, Nahuel Huapi National Park, in the 1950 s, with the aim of promoting hunting tourism. Since then it became feral in the area and currently is very abundant there (Martin-Albarracin et al., 2015b). In its native habitat, *L. nycthemera* is omnivorous including fleshy fruits in its diet (Johnsgard 1986). Although there are no specific observations of foraging activity of pheasants on Isla Victoria, it has been frequently observed eating wild fruits near inhabited areas (e.g. the alien plants *Rubus ulmifolius* and *Prunus avium* and the native *Aristotelia chilensis*). *Lophura nycthemera* has a large body size in relation to native species (males measure ca. 90 cm length and females ca. 65 cm) and a bigger gape width (14.1 mm in males and 12.9 mm in females, Hennache et al. 2003). This species was found to use several different habitats in the area of introduction, mainly areas with a high level of disturbance like plantations of exotic trees and mixed shrublands near human settlements, but also natural areas like native shrublands and forest interior; so that it may generate a wide seed shadow (Martin-Albarracin et al. in press). As a consequence, the role of this introduced bird as seed disperser of fleshy-fruited plants in the temperate forest could be non-redundant in terms of species consumed and effect on seed germination. The objective of this work is to study the redundancy between *L. nycthemera* and native birds in their ecological role as seed dispersers of native and non-native fleshy-fruited plants. We predict that (1) the pheasant will eat a different set of plant species, including more non-native fruits and fruits bigger than those eaten by native birds; and (2) the germination capacity of seeds will differ between *L. nycthemera* and native species.

Methods

Study area

This study was conducted on Isla Victoria, located in the core of Nahuel Huapi National Park, in the northern Patagonian Andes, Argentina (40°57S, 71°33W). This island is located in the center of Nahuel Huapi Lake, a glacial lake with 557 km^2 surface that is located at an altitude of 770 masl. The island has a surface of 31 km^2 and a maximum altitude of 1050 masl. The climate is cold and temperate with a pronounced seasonality. The island is dominated by forests of native *Nothofagus dombeyi* (Nothofagaceae) and *Austrocedrus chilensis* (Cupresaceae) (Simberloff et al. 2003). The most common native fleshy-fruited plant species are *Aristotelia chilensis* (Elaeocarpaceae), *Rhaphithamnus spinosus* (Verbenaceae), *Berberis* spp. (Berberidaceae), *Luma apiculata* (Myrtaceae) and *Schinus patagonicus* (Anacardiaceae). Many non-native plant species were introduced to the island, beginning in the early 20th century, including at least 73 conifer species and 62 broadleaved trees (Simberloff et al. 2003). In addition, there are several introduced fleshy-fruited shrubs; among which *Rosa rubiginosa*, *Rubus ulmifolius, Prunus avium* (Rosaceae) and *Juniperus communis* (Cupressaceae) are the most common (Table 1).

The assemblage of terrestrial vertebrates in the island is dominated by non-native animals, mainly *Cervus elaphus* (red deer), *Dama dama* (fallow deer) and *Sus scrofa* (wild boar) (Martin-Albarracin et al. 2015b). There are no medium-sized animals like the Andean fox *L. culpaeus*, usually reported as a seed disperser. Among the small mammals we find native and introduced mice species (Contreras 1972; Daciuk 1978; Martin-Albarracin et al. 2015b) that are usually reported as seed predators. The small marsupial *D. gliroides* has a relatively low abundance (Rodriguez-Cabal and Branch 2011). For this reason, the main seed dispersers in the island are the native birds *T. falcklandii* and *E. albiceps* and possibly the introduced *L. nycthemera* (Martin-Albarracin 2016). Other facultative frugivores of the temperate forest are also present in the island: *S. rubecula*, *X. pyrope*, *P. araucana* (Martin-Albarracin, pers. obs.).

Table 1 Fruit traits and origin of the most common fleshy-fruited plant species in the study area

Species	Code	Fruit mass (g)	Number of seeds	Fruit color	Origin
Aristotelia chilensis	AC	0.222	2–6	Black	Native
Berberis darwinii	BER[a]	0.139	2–4	Violet	Native
Berberis microphylla	BER[a]	0.139	5–11	Violet	Native
Luma apiculata	LA	0.300	4–7	Black	Native
Maytenus boaria	MB	0.066	1–2	Red	Native
Rhaphithamnus spinosus	RS	0.405	2	Blue	Native
Schinus patagonicus	SP	0.040	1	Blue	Native
Juniperus communis	JC	0.080	1	Blue	Non-native
Prunus avium	PA	1.960	1	Red	Non-native
Rosa rubiginosa	RR	1.100	5–30	Red	Non-native
Rubus ulmifolius	RU	1.678	13–41	Black	Non-native

Species codes for the interpretation of Fig. 1 are given

[a]Seeds of *Berberis darwinii* and *Berberis microphylla* are very similar and could not be differentiated in the analyses of seed content of droppings

Sampling design

Seed dispersal

To study the set of fleshy-fruited plant species that are dispersed by *L. nycthemera* and by native birds (mainly *T. falcklandii* and *E. albiceps*), we collected fresh bird droppings and analyzed their seed content. Samplings were conducted in an area of ca. 400 ha on the central area of the island, where there is high abundance of fleshy-fruited plants (Martin-Albarracin et al. 2015b). To collect droppings of native birds, we placed seed traps under the canopy of plants of five abundant fleshy-fruited plant species during the complete fruiting season (since the emergence of the first unripe fruits until the removal, drop or wilting of all fruits in the plant). Between 28 and 30 seed traps were deployed per plant species, distributed under the canopy of 5–10 individuals per species (148 seed traps in total). This method was chosen to maximize the number of droppings collected. Plants included two native species (*Aristotelia chilensis* and *Rhaphithamnus spinosus*) and three non-native species (*Rubus ulmifolius*, *Prunus avium* and *Rosa rubiginosa*). Two of these species fruit during the summer season (*A. chilensis* and *P. avium*), so the droppings found in seed traps placed under their canopy belonged mainly to both *E. albiceps* and *T. falcklandii*. Two species fruit during the fall and winter season (*R. spinosus* and *R. rubiginosa*), period in which the migrant *E. albiceps* is absent, so droppings found in seed traps placed under their canopy belonged mainly to *T. falcklandii*. One plant species has an extended fruiting period that spans over several months (*R. ulmifolius*), so the droppings found in seed traps placed under their canopy belonged mainly to both *E. albiceps* and *T. falcklandii*. Seed traps were built using a mesh of mosquito net 50×50 cm deployed at a height of 40 cm to avoid rodent predation (García et al. 2011). Seed traps were checked every month and bird droppings were saved for later analysis. If any pheasant dropping was found in seed traps (pheasant droppings can be distinguished easily from droppings of other species), it was saved separately. Whole fruits (and pecked fruits) found in seed traps were discarded. Although this method does not allow identifying droppings of native birds at the species level, it makes possible to collect large quantities of bird droppings, having a representative sample of seeds dispersed by native birds. We considered that, although some post-dispersal seed loss probably occurred before collecting the samples, it is negligible as rodents—the main seed predators—are relatively scarce in the study area (Martin-Albarracin et al. 2015b). To look for *L. nycthemera* droppings, we conducted a direct search. Ten transects 100×30 m^2 located in areas with high abundance of fleshy-fruited plants were walked once a month looking for fresh droppings (i.e., droppings that looked intact and remained wet when collected). Droppings of *L. nycthemera* found were collected and saved for later analyses. Only fresh pheasant droppings were collected to minimize the exposure of seeds to post-dispersal seed predators and pathogens. All samples were dried at room temperature during 1 week. After that, samples were analyzed under magnifying glass and seeds were identified at the species level whenever possible using a reference collection.

Seed germination capacity

To study the germinability of seeds, we conducted germination trials in growth cabinets for four plant species, two native (*A. chilensis* and *R. spinosus*) and two non-native (*Rubus ulmifolius* and *Rosa rubiginosa*). We tested four treatments: (1) intact fruits, (2) hand-cleaned seeds,

(3) seeds defecated by *L. nycthemera* and (4) seeds defecated by native birds. For the first two treatments we collected mature fruits from several different plant individuals in the study area; seeds for the two last treatments were obtained from bird droppings collected on the field. The fourth treatment was not conducted with *R. rubiginosa* because we did not find seeds from this species in droppings of native birds.

Before starting the germination trials, we conducted a 40 days cold stratification (4 °C) of seeds. For germination trials we put 20 seeds of one species in a Petri dish 90 mm diameter. We conducted 10 replications of every treatment whenever the number of seeds available was enough. Seeds were placed on three layers of moistened blotting paper and every 15 days we added antifungal solution (FungoXAN® Punch Química S.A.). Growth cabinets were programmed with a photoperiod of 14 h light at a temperature of 18 °C and 10 h darkness at a temperature of 6 °C, which are conditions that resemble those common in the native forest during spring. Periodically (every 2 days during the first 20 days and every week thereafter) we recorded the number of seeds germinated in each Petri dish. Seedlings were removed after the formation of the first pair of leaves to reduce potential interspecific competition.

Data analysis

To conduct statistical analyses with data coming from seed traps, we used data from seeds of all plant species found in each trap, except seeds of the species under where the seed trap was located, to avoid biases towards that species. All analyses were conducted using R Statistical Software (R Development Core Team 2016). We compared the proportions of samples with non-native and native fleshy-fruited plants in *L. nycthemera* droppings and seed traps through a Chi Squared test. To compare the number of seeds dispersed by *L. nycthemera* and by native birds according to fruit size, we conducted a generalized linear model with number of seeds as the response variable; interaction between fruit mass and disperser group and plant origin ("native" vs. "non-native") as the fixed predictor variables; and plant species and sample as random variables. All continuous variables were log transformed and scaled. The global model was fitted assuming a Gaussian error distribution with the package "lme4" (Bates et al. 2017).

To determine if the passage of seeds through bird´s gut affects (positively or negatively) their germination rate, we conducted a factorial analysis of variances with repeated measures (Traveset et al. 2001) for weeks 6, 12, 18, 24 and 31. The response variable was the percentage of seeds germinated, and the predictor variables were treatment and week. Differences on percentage of germinated seeds through time between treatments were analyzed by a post-hoc Tukey test of multiple comparisons using the package "emmeans" (Lenth 2017). To know if the final percentage of seeds germinated differs between treatments, we compared it at the end of the experiment through a conventional analysis of variances. Differences between treatments were analyzed by a post-hoc Tukey test. All means are accompanied by their standard errors.

Results

Seed dispersal

We collected a total of 2800 seeds of fleshy-fruited plants in droppings of *L. nycthemera* (N = 224) belonging to nine species and 2355 seeds in droppings collected in seed traps

(N = 148) belonging to eight species. The most abundant seeds on seed traps, dispersed by native birds, were *R. spinosus* (18% of traps with seeds, 13.65 ± 5.33 seeds per trap), *A. chilensis* (16% of traps with seeds, 9.01 ± 2.94 seeds per trap), *Maytenus boaria* (16% of traps with seeds, 2.73 ± 0.72 seeds per trap) and the non-native species *R. ulmifolius* (16% of traps with seeds, 3.68 ± 0.92 seeds per trap) (Fig. 1a). The most abundant seeds in droppings of *L. nycthemera* were two non-native plants and one native. *Rosa rubiginosa* (35% of droppings with seeds, 7.59 ± 1.69 seeds per dropping) was the most abundant, followed by *R. spinosus* (24% of droppings with seeds, 5.68 ± 1.16 seeds per dropping) and *R. ulmifolius* (13% of droppings with seeds, 3.84 ± 1.34 seeds per dropping) (Fig. 1b).
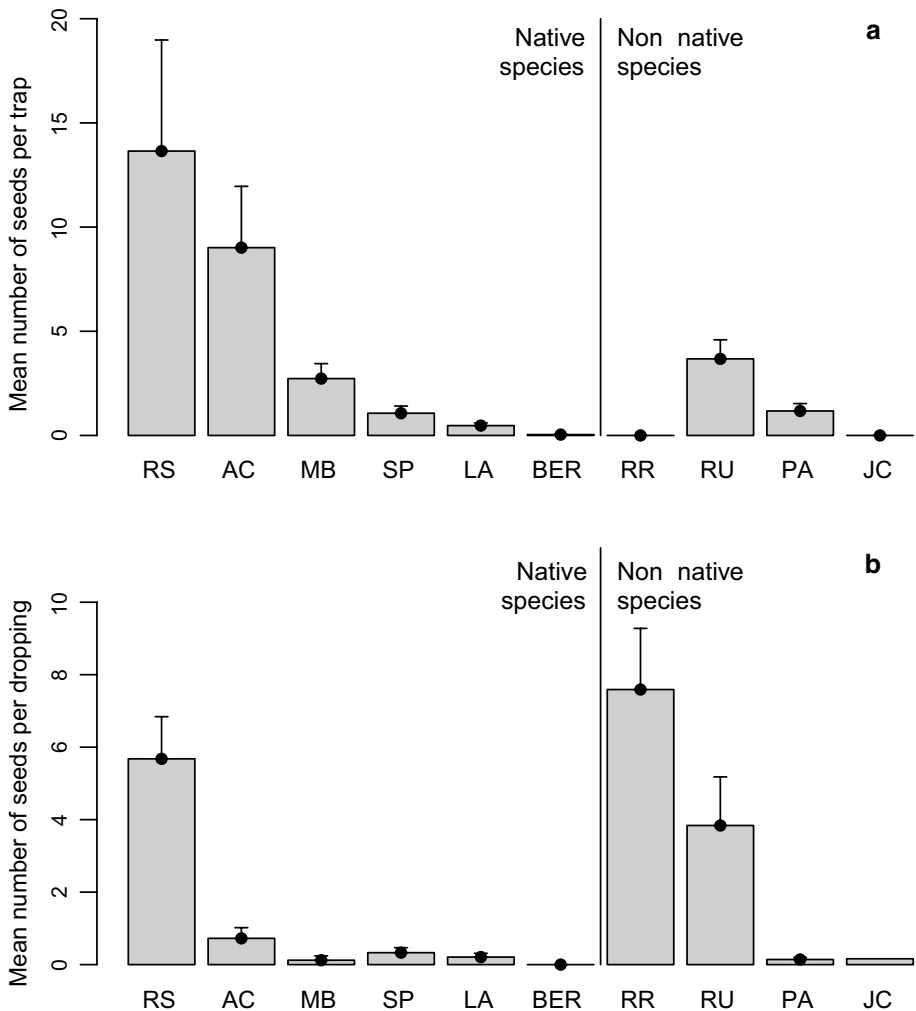

Fig. 1 Mean number of seeds found on **a** native bird droppings (data of all bird droppings collected per trap were pooled together; N = 89) and **b** droppings of *Lophura nycthemera* (N = 175) per plant species. Error bars show the standard error. Codes for plant species are detailed in Table 1

The proportion of droppings of *L. nycthemera* containing non-native seeds was bigger than the proportion of droppings containing native seeds. Conversely, the proportion of seed traps containing native seeds was bigger than the proportion of seed traps containing non-native seeds ($X^2 = 27.807$, df = 1, p < 0.001). The mixed model revealed that neither the interaction between fruit mass and disperser group nor the origin of the plant explained the number of seeds dispersed (p > 0.5 in both cases).

Seed germination capacity

Germination curves of *A. chilensis*, *R. rubiginosa* and *R. ulmifolius* became asymphthotic around the days 80, 100 and 200 of the experiment respectively; reaching final percentages of germination of ca. 75, 23% and 24% (Fig. 2a, c, d). Germination curves for *R. spinosus* did not become asymphthotic until the end of the experiment (day 219); and final percentages of germination were of ca. 9% (Fig. 2b). For *A. chilensis*, *R. spinosus* and *R. rubiginosa* we found significant differences in the percentage of seeds germinated for the interaction between week and treatment. *Rubus ulmifolius* showed differences in the percentage of seeds germinated by week, but not by treatment (Table 2).
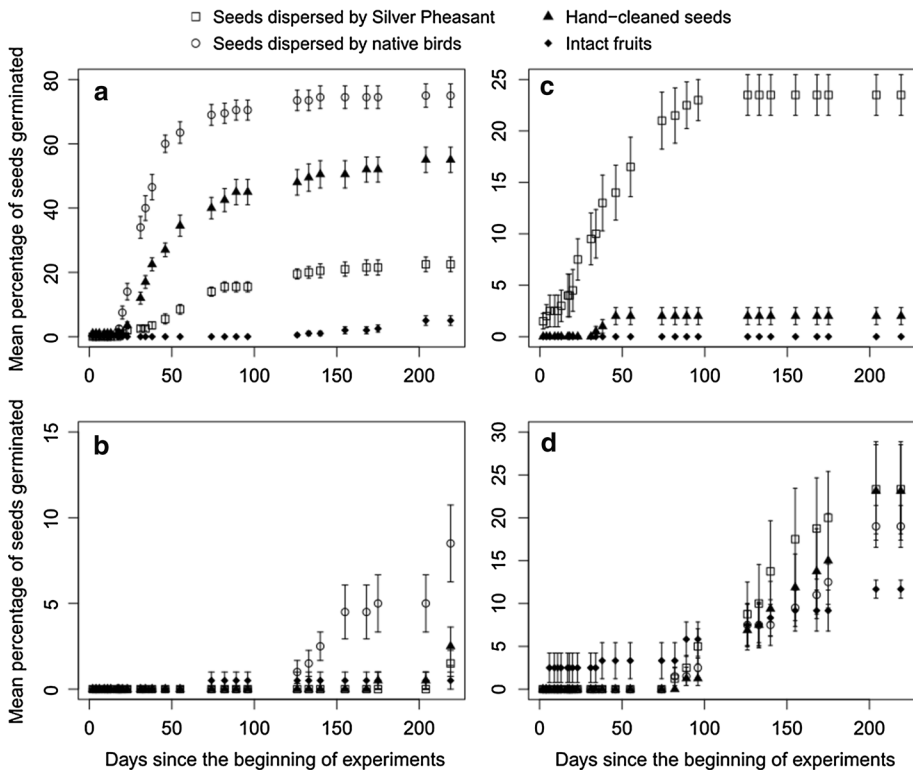

Fig. 2 Percentages of seeds germinated through time since the beginning of the germination trials for **a** *Aristotelia chilensis*, **b** *Rhaphithamnus spinosus*, **c** *Rosa rubiginosa* and **d** *Rubus ulmifolius*. We conducted 10 replications of every treatment whenever the number of seeds available was enough. Treatments used were: whole fruits (red points), hand-cleaned seeds (green points), seeds dispersed by native birds (black points) and seeds dispersed by *L. nycthemera* (blue points)

Table 2 Results of the factorial analysis of variance with repeated-measures for germination trials

Species	Week			Treatment			Week × treatment		
	F	df	p	F	df	p	F	df	p
Aristotelia chilensis	410.26	5	<0.001***	160.2	3	<0.001***	78.98	15	<0.001***
Rhaphithamnus spinosus	18.43	5	<0.001***	6.46	3	<0.01**	6.77	15	<0.001***
Rosa rubiginosa[a]	61.3	5	<0.001***	70.78	2	<0.001***	38.22	10	<0.001***
Rubus ulmifolius[a]	50.59	5	<0.001***	0.31	3	0.82	1.68	15	0.06

We included repeated measures for weeks 6, 12, 18, 24 and 31. The response variable was the percentage of seeds germinated, and the predictor variables were treatment and week

Significance levels: ***$p < 0.001$; **$0.001 \leq p < 0.01$; *$0.01 \leq p < 0.05$

[a]Non-native species

In the case of *A. chilensis*, germination rate until week 6 was increased for seeds dispersed by native birds. For *R. spinosus*, germination rate was increased for seeds dispersed by native birds between weeks 24 and 31. For *R. rubiginosa*, germination rate was highest for seeds dispersed by *L. nycthemera* between weeks 0 and 6. For *A. chilensis, R. spinosus* and *R. rubiginosa*, percentages of seeds germinated at the end of the experiment differed significantly according to treatment (K–W = 35.26, df = 3, $p < 0.001$; K–W = 16.10, df = 3, $p < 0.01$; K–W = 20.60, df = 2, $p < 0.001$ respectively). For *A. chilensis*, the percentage of seeds germinated was higher for seeds dispersed by native birds and hand-cleaned seeds than for seeds dispersed by *L. nycthemera* and whole fruits (Fig. 2a). In the case of *R. spinosus*, the percentage of seeds germinated was higher for seeds dispersed by native birds than for seeds dispersed by *L. nycthemera* and whole fruits (Fig. 2b). In the case of *R. rubiginosa*, the percentage of seeds germinated was higher for seeds dispersed by *L. nycthemera* than for hand-cleaned seeds and whole fruits (Fig. 2c).

Discussion

Both native frugivorous birds and *L. nycthemera* dispersed fruits of non-native fleshy-fruited plants, but their roles were non-redundant in terms of species dispersed (*R. rubiginosa* was only dispersed by *L. nycthemera*, possibly due to constrains of gape width in native birds) and effect on seed germination. *Lophura nycthemera* dispersed a greater proportion of non-native seeds than that of native seeds, while native birds dispersed a greater proportion of native seeds. In addition, the effect of gut treatment on seed germination differed between groups. The treatment of native birds promoted the germination for the two native plant species studied, while the treatment of *L. nycthemera* promoted the germination of the invasive *R. rubiginosa*. This suggests that seed dispersal by *L. nycthemera* may contribute to the spread of some invasive fleshy-fruited plants in the ecosystems that otherwise would not be dispersed by any other bird species.

In the studied area native birds incorporated fleshy fruits from introduced plants to their diet, a factor that can increase the invasive potential of plants (Gosper et al. 2005). In a similar way, the introduced *L. nycthemera* consumed fruits from native and non-native fleshy-fruited plants. This pattern was expected, as seed dispersal networks have low levels of specialization (Blüthgen et al. 2007). Due to constraints related to gape width, small

fruits are usually dispersed by both small and big frugivores, while big fruits are dispersed only by big frugivores (Gosper et al. 2005). Because of differences in gape width and body size between native birds and *L. nycthemera*, we expected that only *L. nycthemera* would disperse some non-native fleshy fruits bigger than native fruits in the area, and this was the case of *R. rubiginosa*. However, other species with big fruits like *P. avium* were dispersed by native birds also, showing a great ability to integrate into the native seed dispersal network. Aggregate fruits like *R. ulmifolius*, on the other hand, can be eaten in portions even though total fruit size is large; in fact direct observations revealed that *E. albiceps* remove individual drupes of this plant species (Martin-Albarracin, pers. obs.). The successful integration of novel plants into seed dispersal networks can also be associated to their fruiting phenology, only partially overlapped to native plants, constituting that way an attractive food source during periods of low offer of native fruits (Lediuk et al. 2014).

The effect of gut treatment on seed germination, on the other hand, differed between plant species. The dispersal of native seeds by native birds, as well as the dispersal of *R. rubiginosa* by *L. nycthemera*, facilitated germination. The germination of seeds dispersed by *L. nycthemera* was slightly improved in relation to fruits fallen from the trees in *A. chilensis*; and was not different to that of fallen fruits in *R. spinosus*. This means that, even when the gut treatment was not as good as the treatment from native birds, *L. nycthemera* could still contribute to the recruitment of native plants. This is because they can potentially move seeds away from the parent tree (presumably at relatively long distances, because time of seed passage through a bird´s gut is positively related to body size, Traveset and Verdu 2002; Jordano et al. 2007). In addition, *L. nycthemera* has frequently been observed consuming fruits fallen on the ground, so that it can be dispersing seeds that would not be dispersed by native birds (that usually forage on the crown of the trees, Martin-Albarracin, pers. obs.).

Non-redundancy in seed dispersal function between *L. nycthemera* and native birds can be attributed to morphological and behavioral differences existing among them. These differences, on the other hand, can reduce the interference competition between both groups (French and Smith 2005) and facilitate their coexistence, reducing the impact of *L. nycthemera* invasion on native bird communities. The result would be a community with a long-term enriched assemblage of seed dispersers and novel seed dispersal functions. In the studied area *L. nycthemera* seems to be a key seed disperser for *R. rubiginosa*, a species whose fruits are not ingested by native birds. It is known that *R. rubiginosa* can be dispersed by big mammals (Hatton 1989), so that in the studied area it could be dispersed by *C. elaphus*, *D. dama* or *S. scrofa*, but in preliminary analyses of feces of these mammals seeds appear damaged or destroyed and have low germination capacity (Barrios-Garcia and Simberloff 2013; Martin-Albarracin, pers. obs.). The effect of the introduction of seed disperser species with functions non-redundant to those of resident frugivorous in plant communities can be exacerbated in low-diversified communities like these on the temperate Patagonian forests.

Studying redundancies and complementarities in seed dispersal function between native and introduced dispersers allows discerning the role of each group in the overall process. As seed dispersal is a complex process including several steps since the removal of fruits to the recruitment of a seedling (Wang and Smith 2002), it is necessary to study the role of each disperser group at all stages. Taking this approach, here we studied redundancies and complementarities at two key stages—seed dispersal and germination—, which allowed us to have an approximation of the importance of each group studied for the dispersal of seeds of several native and non-native fleshy-fruited plants. Getting some spatial information on seed deposition and seed shadows of different bird species, as well as data on the effects of

gut passage on seed germination at the bird species level, would also help to better understand the role of each group. To get a complete picture of all the seed dispersal process other key stages should be analyzed, for example seed removal, seedling recruitment and survival. The understanding of redundancies and complementarities between native and introduced birds on seed dispersal will allow improving the management of fleshy-fruited invasive plants, focusing the efforts in key stages and interactions.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Affiliations

Valeria L. Martin-Albarracin[1] · Martin A. Nuñez[2] · Guillermo C. Amico[1]

[1] Laboratorio Ecotono, INIBIOMA, CONICET-Universidad Nacional del Comahue, Dirección postal: Quintral 1250, 8400 Bariloche, Río Negro, Argentina

[2] Grupo de Ecología de Invasiones, INIBIOMA, CONICET-Universidad Nacional del Comahue, Dirección postal: Av. de los Pioneros, 2350 Bariloche, Río Negro, Argentina