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ORIGINAL PAPER

Plant origin and fruit traits shape fruit removal patterns by native birds in invaded plant communities

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Abstract Biotic interactions and mutualisms in particular have an important role in ecosystem structure and functioning as well as in the maintenance of biodiversity. Understanding how communities respond to the introduction of non-native species and what determines the establishment of novel interactions between native and introduced species will help in determining the potential impacts of biological invasions. The aims of this work were to assess patterns of frugivory and fruit removal in environments with invasion of non-native fleshy-fruited plants and to evaluate whether novel associations between native frugivores and non-native plants are determined by fruit traits. For this we selected eight study sites in areas with different degrees of invasion of non-native fleshy-fruited plants. In each site, we measured fruit availability and fruit traits of native and non-native plants. In addition, we conducted direct frugivory observations. We found that native and non-native fruits differed based on morphological trait variables, such as fruit weight and dimensions. Only two birds, *Elaenia albiceps* (smaller and migrant) and *Turdus falcklandii* (bigger and resident), are the main frugivorous present in the area. At the scale of the community of frugivores, neither visit nor fruit removal rates differ between natives and non-natives. However, at the species scale, while *E. albiceps* preferentially foraged on native plants, *T. falcklandii* preferred non-natives. Thus, some generalist frugivorous species like *T. falcklandii* can play a key role in promoting the invasion of non-native plants.

Keywords Biological invasions · Fruit trait · Frugivory · Interaction networks · Seed dispersal · Patagonia

Introduction

Biotic interactions and mutualisms in particular have an important role in ecosystem structure and functioning as well as in the maintenance of biodiversity (Stachowicz 2001; Bascompte et al. 2006; Valiente-Banuet et al. 2015). Mutualistic species interact with each other forming complex interaction networks that support key ecological processes like pollination and seed dispersal (Bascompte and Jordano 2014). A rapid global environmental change is taking place as a consequence of anthropic activity (Millennium Ecosystem Assessment 2003), and understanding how the main drivers of this global change—habitat loss and fragmentation, climate change, air and water pollution and biological invasions—affect ecological interactions has become of great interest in recent

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years (Tylianakis et al. 2008; Valiente-Banuet et al. 2015).

Biological invasions, in particular, can be mediated by mutualisms and in turn can influence native mutualisms (Traveset and Richardson 2014). Endozoochory—the dispersal of seeds via ingestion by vertebrate animals—can be affected by the introduction of non-native dispersers, non-native plants, or both (Traveset and Richardson 2006). As seed-dispersal systems usually have a high level of generalism (Bascompte et al. 2003), alien dispersers or plants often establish effective interactions with native species (Traveset and Richardson 2006). The integration of non-native species to plant–disperser mutualisms may have consequences that range from scenarios of degradation and meltdown to scenarios of rescue and recovery. In the first case, invasion increases through time helped by mutualisms; while in the second case, the establishment of mutualisms between native and non-native species contribute to the maintenance or recovery of native biodiversity (Buckley et al. 2006). Understanding what factors determine the successful integration of non-native species to seed-dispersal networks would be useful to predict the outcomes of species introductions in terms of novel interactions and community-level consequences.

The successful establishment of novel seed-dispersal interactions between non-native plants and local frugivores will depend on the capacity of frugivorous animals to incorporate the novel fruits into their diet (García et al. 2014). Although seed-dispersal interactions are considered generalized, there are some traits of the non-native fruits and/or the recipient frugivore community that could determine the occurrence or not of specific interactions. For example, high generalization and abundance in birds are associated with the ability to disperse non-native plants (García et al. 2014; Bitani et al. 2020). Trait matching is another factor that facilitates the occurrence of interactions between birds and non-native plants (Peralta et al. 2020). Bill dimensions can limit the size of fruits that birds are able to swallow, so not all fruits available are potential food sources (phenotypic trait matching, Jordano 1995; González-Castro et al. 2015). As a consequence, smaller fruits can be consumed by a greater number of frugivorous species than bigger fruits (Kitamura et al. 2002; Sebastián-González 2017). Seed size is another trait predicted to contribute to the effective seed dispersal of non-native plants (Bitani et al. 2020). In addition, birds may show preference for non-native fruits that resemble native fruits (Aslan and Rejmanek 2012). Fruit crop size, or the number of ripe fruits displayed by plants, is a strong predictor of bird fruit consumption (Palacio and Ordano 2018). As a consequence, non-native plants with big crop sizes could be consumed to a high degree by frugivorous species, increasing their invasive potential. Fruiting phenology can also influence fruit consumption by local frugivores, because non-native plants fruiting asynchronously to native plants could be seen as an attractive resource in times of scarcity (Vergara-Tabares et al. 2018).

In the temperate forest of Patagonia, the prevalence of mutualisms of seed dispersal by endozoochory is very high, and 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). These plants were usually introduced for ornamental purposes or because they produce edible fruits. They are characterized by having high loads of showy, bright-colored fruits, presumably consequence of anthropic selection (Rovere et al. 2013; Iglesias 2015). On the other hand, the assemblage of vertebrate seed dispersers is relatively simple (Aizen et al. 2002). Birds represent the main group of frugivorous animals, with *Turdus falcklandii* (Turdidae) and *Elaenia albiceps* (Tyrannidae) as the key seed dispersers (Amico and Aizen 2005). These species differ in body size, bill gape and residence period in the area (Amico and Aizen 2005; Reid and Armesto 2011). Thus, we could expect that their role as seed dispersers of non-native plants will also be different.

The aims of this study were (1) to evaluate the topological differences in plant–frugivore interaction networks between areas with and without invasion of non-native fleshy-fruited plants, (2) to explore morphological differences between native and non-native fleshy-fruits in the temperate forest of Patagonia and (3) to evaluate whether native and non-native plants are preferentially consumed by (i) the community of frugivores or (ii) specific frugivorous species. Specifically, we studied patterns of fruit consumption of native and non-native plants by local frugivores in several areas with different degree of invasion of fleshy-fruited plants. We expect that frugivory will differ between native and non-native plants, and that these differences will be associated with fruit traits and body and beak size of frugivorous birds.

Methodology

Study area

Fieldwork was conducted in two protected areas within the northern region of the temperate forest of Patagonia: Nahuel Huapi National Park (40° 58´ S, 71° 30´ W, 710,000 ha) and Llao Llao Municipal Park (41° 02´ S, 71° 33´ W, 1226 ha). Mean annual temperature ranges between 5 and 8 °C. The rainfall regime is strongly seasonal, with mean annual precipitation ranging between 1000 and 1200 mm, mainly concentrated between April and August (Mermoz and Martin 1987). Most of the area is covered by evergreen forest dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis*. The shrub stratum is dominated by the endemic bamboo *Chusquea culeou* and several fleshy-fruited plant species; the most common are *Aristotelia chilensis*, *Ribes magellanicum*, *Maytenus boaria*, *Azara microphylla*, *Luma apiculata*, *Rhaphithamnus spinosus*, *Schinus patagonicus, Berberis darwinii* and *Berberis microphylla*. Several areas are invaded by non-native fleshy-fruited plants such as *Rubus idaeus*, *Rubus ulmifolius*, *Prunus avium*, *Prunus cerasus* and *Sorbus acuparia*. Most of these species fruit during the summer (Amico and Aizen 2005; García et al. 2010; Iglesias 2015).

The seed-dispersal interaction network in this system is very simple, with a small assemblage of seed dispersers mostly composed of birds and mammals. The main frugivorous birds are the resident *T. falcklandii* (24 cm body length, 7.2 mm bill gape) and the migrant *E. albiceps* (13 cm body length, 4.3 mm bill gape), present in the area only during the spring–summer season (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 eventual frugivores, but their diet is predominantly granivorous, herbivore or insectivorous (Armesto and Rozzi 1989; Amico and Aizen 2005). A small endemic marsupial (*Dromiciops gliroides*, Microbiotheriideae) and the Andean fox (*Lycalopex culpaeus*, Canidae) have also been reported as seed dispersers of several fleshy-fruited plants (Aizen et al. 2002; Amico et al. 2009). The role of other groups of vertebrate dispersers like reptiles is relatively unimportant for the dispersal of the majority of plant species (Aizen et al. 2002).

We selected eight study sites: four in areas without invasion of non-native fleshy-fruited plants and four in areas with invasion (Online Resource 1). The sites selected had different compositions of fleshy-fruited plant species, although most species (73%) were present in two or more sites. We established one plot 100 × 30 m at each study site, including as many fleshy-fruited plant species as possible. A total of seven native plant species and four non-native species were found across all plots (Table 1), with a mean (± SE) of 5 ± 0.85 species per plot (Online Resource 2). Sites were distanced from each other by at least 2 km. A complete description of study sites is available in Online Resource 2.

All adult fleshy-fruited plants present at each plot were individually identified and georeferenced using GPS. We measured the availability of ripe fruits of each individual plant, fruit traits of all species, and conducted frugivory observations. Samplings were conducted in the summer, between December 2016 and March 2017; where the majority of plants fructify. Sampling periods varied according to the fruiting phenology of each particular plot and were defined trying to maximize fruit availability in terms of number of species and fruit abundance.

Interaction networks

To visualize the global structure of interaction networks, a bipartite network approach was used (Spotswood et al. 2012). The number of fruits removed by birds (see below) in each plant species was used as the measure of interaction strength. Two interaction networks were constructed, one for areas without invasion of fleshy-fruited plants and other for areas with invasion. For this, fruit removal data from the four sites in each category were pooled.

Fruit availability

The fruit availability per individual plant was estimated once, at the beginning of frugivory observations

Table 1 Fleshy-fruited plant species present in the study area. For each species we indicate the family, geographical origin, fruit color, fruiting season and number of sites in which it is present

Plant species	Family	Origin	Fruit color	Fruiting season	N sites
Aristotelia chilensis	Elaeocarpaceae	Native	Black	Summer	8
Azara microphylla	Salicaceae	Non-native	Brown	Summer	4
Berberis darwinii	Berberidaceae	Native	Blue	Summer	3
Berberis microphylla	Berberidaceae	Native	Blue	Summer	1
Maytenus boaria	Celastraceae	Native	Red	Summer and fall	7
Prunus avium	Rosaceae	Non-native	Red	Summer	4
Prunus cerasus	Rosaceae	Non-native	Red	Summer	1
Ribes magellanicum	Grossulariaceae	Native	Black	Summer	2
Rubus idaeus	Rosaceae	Non-native	Red	Summer	2
Rubus ulmifolius	Rosaceae	Non-native	Black	Summer and fall	1
Schinus patagonicus	Anacardiaceae	Native	Blue	Summer	7

periods (see below). Whenever possible, we directly counted the total number of ripe fruits per plant. In cases where the fruit load was too large as for a direct count, we selected a representative branch and counted the number of ripe fruits there. Then, we counted the total number of branches bearing fruits and multiplied it by the number of fruits in the selected branch to get an estimation of the total number of ripe fruits per individual (Vollstädt et al. 2017).

Fruit traits

We collected between 15 and 20 ripe fruits per species from at least five different individuals and two different sites to measure fruit traits. We visually recorded the fruit color at maturity of each plant species (Table 1). We weighted fresh fruits on a precision scale (model METTLER AJ150) and measured length from the base of the pedicel to the apex (*L*) and diameter (*D*) using a caliper to the nearest 0.1 mm. In addition, the ratio between length and diameter (*L*/*D* ratio) was used as an index of fruit shape (globose fruits, $L/D = 1$; elongated fruits, $L/D > 1$; depressed fruits, $L/D < 1$; Pizo 2002). Then, we separated seeds from pulp, recorded the number of seeds per fruit and weighted pulp and seeds. After that we estimated the ratio between pulp (*P*) and seed (*S*) weight (*P*/*S* ratio). Fruit material was dried in an oven at 50 °C during one week and then flesh and seeds were weighted. Using these data, we estimated the water content of fruits as the difference between the fresh and dry weight and the water percentage of fruits as the percentage difference between dry and fresh fruit weight. For each trait we calculated a mean value per plant species (Online Resource 2). In the case of *R. ulmifolius* and *R. idaeus* traits were measured for the cluster of drupelets, because these structures are the ones that result visually attractive for dispersers. However, birds can remove individual drupelets instead of clusters, especially smaller birds.

Frugivory observations

To study the removal of fruits and seeds by birds, we conducted 20 h of observation of frugivory activity per plot. Observations were conducted in the morning (from 6:30 to 11:30) and each plot was visited four times in a period of two weeks, short enough to avoid large phenological variations in fruit availability. One observer walked slowly through the plots to detect frugivore activity and recorded every event of frugivory using binoculars (8 × 42). Observations were conducted by two observers that alternated days and sites. All frugivores foraging on fruiting plants were identified to species level. We recorded for every visit the number of fruits consumed, dropped or carried away. In the cases of *R. idaeus* and *R. ulmifolius*, we recorded the number of individual drupelets removed from each aggregated fruit and then calculated the proportion of the fruit removed based on the average number of drupelets per fruit. For bird groups feeding on one plant, we counted the number of individuals and randomly selected one to record the number of fruits handled. Then, we extrapolated the total number of fruits consumed by this individual to the rest of the birds of the group.

Statistical analyses

General network metrics (number of species, connectance and web asymmetry) were calculated to make a general description of the interaction networks; and group-level metrics (generality and niche overlap) were calculated to describe functional differences between networks with and without invasion. All metrics were calculated with the package "bipartite" (Dormann et al. 2008) in R statistical software (R Development Core Team 2017).

To explore morphological traits in native and non-native fruits (Table 1), we conducted a principal component analysis (PCA). Variables included were length, diameter, L/D ratio, fruit weight, seed weight, P/S ratio, number of seeds, water content and water percentage. The two first principal components were plotted in two-dimensional PCA scatter plots and species were clustered based on their geographical origin (native and non-native). Values of the first principal component of the analysis for each fruit species were saved for further inclusion in mixed models. The PCA analysis was conducted using the packages "pcaMethods" and "factoextra" (Stacklies et al. 2007; Kassambara and Mundt 2017) in R statistical software (R Development Core Team 2017).

To assess the activity of the community of frugivores (number of visits and mean number of fruits removed per visit) associated to plant species and origin (native vs. non-native), we used linear mixed-effect models fitted by maximum likelihood. First, we analyzed the number of frugivore visits per plant individual as a function of (1) plant species or (2) plant origin. For this, the feeding visits of all frugivorous bird species at an individual plant were pooled together and this total number of visits was the response variable. We considered only the plant individuals that received at least one visit (i.e., there were no zeros in the dataset). Thus, fixed effects included in the models were (1) plant species or (2) plant origin; site was included as a random effect. As fruit availability is usually a strong predictor of frugivore activity, it was included in the models as a fixed effect. The same analyses were conducted using the mean number of fruits removed per visit per plant individual as the response variable. All numerical variables were log-scaled prior to analyses. Linear mixed-effects models were conducted using the package "lme4" (Bates et al. 2015) in R statistical software (R Development Core Team 2017).

We investigated whether differences in the activity of the two main frugivorous birds present in the area (*E. albiceps* and *T. falcklandii*) depended on plant origin and fruit traits. To evaluate whether (1) the number of visits and (2) the total number of fruits removed differ between *E. albiceps* and *T. falcklandii* in native and non-native plants, we conducted Pearson's Chi-squared tests followed by pairwise comparisons. Expected values were estimated by multiplying the number of interactions of each bird species by the number of interactions of each plant category and dividing this by the total number of interactions. For these analyses we used the package "RVAideMemoire" (Hervé 2018) in R statistical software (R Development Core Team 2017).

To assess whether the activity of different frugivore species is associated to fruit traits, we used linear mixed-effect models fitted by maximum likelihood. First, we analyzed whether the number of visits per plant individual differs between bird species in function of fruit traits. We considered only the plant individuals that received at least one visit (i.e., there were no zeros in the dataset). Thus, fixed effects included in the model were the interaction between bird species and the value of the first component of the PCA; site was included as a random effect and fruit availability as a fixed effect. The same analysis was conducted using the mean number of fruits removed per visit per plant individual as the response variable. All numerical variables were log-scaled prior to analyses. Linear mixed-effects models were conducted using the package "lme4" (Bates et al. 2015) in R statistical software (R Development Core Team 2017).

Results

A total of six frugivorous bird species and 756 interactions of frugivory with 1510 events of fruit removal were recorded across all plots. *E. albiceps* and *T. falcklandii* were the most abundant species, accounting for 96% of the records. The other four species were *Colorhamphus parvirostris*, *Curaeus curaeus*, *Lophura nycthemera* (introduced species) and *Patagioenas araucana*. The interaction network in areas without invasion was made up of five bird species and four plant species, while in areas without invasion it was made up of four bird species and ten plant species (Table 2). In areas without invasion, *E. albiceps* removed 93% of fruits and interacted with four plant species, while *T. falckandii* removed 2% of fruits and interacted with two plant species (Fig. 1a). In areas with invasion, *E. albiceps* removed 80% of fruits and interacted with eight species (6 native and 2 non-native), while *T. falcklandii* removed 17% of fruits and interacted with seven species (four non-native and three native, Fig. 1b). Network metrics for areas with and without invasion are listed in Table 2. Areas with invasion had more plant species. In these areas the asymmetry of interaction networks was − 0.42, while in areas without invasion it was 0.11. The connectance was similar in areas with and without invasion, while there were more than twice as many interactions in areas with invasion.

Fruit availability varied between individuals, plant species and sites, ranging from 1 to 275,850 fruits per individual and from 8967 to 828,571 total fruits per plot. Mean fruit availability was highest in *A. microphylla* (36,979 fruits per individual) and lowest in *B. microphylla* (2 fruits per individual). The abundance of non-native plants differed between sites, being absent in some plots and dominant (85.69% of fruit availability) in others (see Online Resource 1).

Principal component analysis clearly differentiated native and non-native fruits based on morphological trait variables included (Fig. 2). The first principal component explained a 65% of the variance and the second principal component explained an 18%. Contributions of each variable to the first two factors of the PCA are shown in Table 3. PC1 represents larger fruit (fruit diameter, fruit length, water content and fruit mass are the variables that most contribute to this axis). Axis 2 represents fruit with lower number of seeds and lower water percentage. The arrangement of plant species along the PC1 shows that non-native plants have larger fruits than native ones. The fruit color was also different between native and non-native plants. Most non-native fruits were red (three of the four species), while the native fruits were blue ($n = 3$), black ($n = 3$) brown ($n = 1$) and red ($n = 1$).

Table 2 Metrics of interaction networks in areas with and without invasion

	Without invasion	With invasion
Total number of species	9	14
Number of bird species	5	4
Number of plant species	4	10
Number of interactions	425	1085
Connectance	0.50	0.45
Web asymmetry	0.11	− 0.42
Generality (birds)	2.31	4.00
Niche overlap (birds)	0.80	0.30

Fruit availability per plant individual was positively related to the number of visits and to the number of fruits removed per visit in all mixed-effect models. The total number of frugivore visits did not differ among plant species ($p > 0.05$ in all cases, Fig. 3a) or between native and non-native plants (estimate = 0.11, $p = 0.51$). The number of fruits removed per visit was higher for two native species, *A. microphylla* (estimate = 0.83, $p = 0.02$) and *S. patagonicus* (estimate = 1.33, $p < 0.01$) (Fig. 3b). The number of fruits removed did not differ by plant origin (estimate = 0.19, $p = 0.39$). The complete reports of linear mixed models are available in Online Resource 3.

The activity of the two main frugivorous birds present in the area (*E. albiceps* and *T. falcklandii*) differed according to plant origin (Fig. 4). The number of visits (*X*-squared = 383.2, df = 1, $p < 0.001$) and the total number of fruits removed (*X*-squared = 629.1, df = 1, $p < 0.001$) differed from expected values (Fig. 4a). Pairwise comparisons revealed that *E. albiceps* visited native plants 15% more frequently than expected (Fisher test, $p < 0.001$), while *T. falcklandii* visited non-native plants 457% more frequently than expected (Fisher test, $p < 0.001$, Fig. 4b).

The effect of fruit size (represented by the first component of the PCA) on the number of visits was different between *E. albiceps* and *T. falcklandii* (estimate = 0.24, $p = 0.02$). The number of visits of *T. falcklandii* increased with fruit size, while that of *E. albiceps* decreased (Fig. 5). The effect of fruit size on the number of fruits removed per visit was also different between bird species (estimate = − 0.37, $p < 0.01$), being negative in *T. falcklandii* and near zero in *E. albiceps* (Fig. 5). The complete reports of

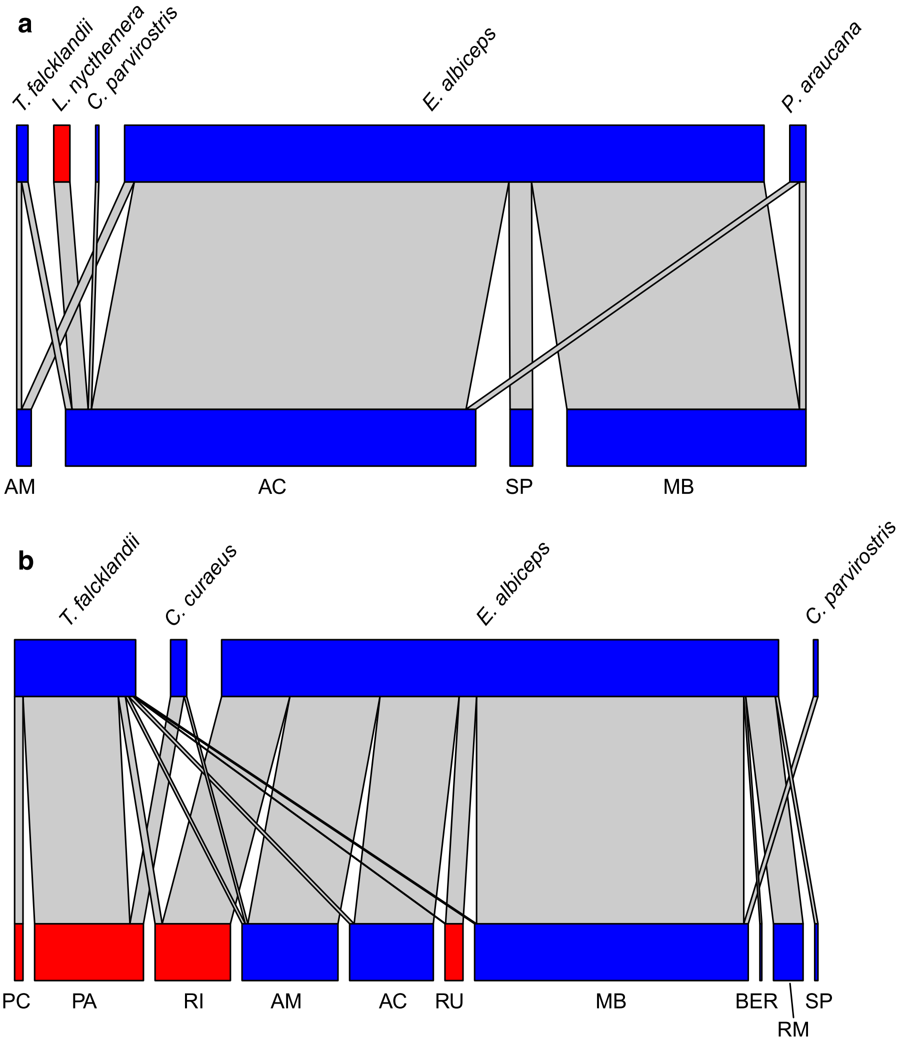

Fig. 1 Seed-dispersal network in **a** areas without invasion of fleshy-fruited plants and **b** areas with invasion. Native species are colored in blue and non-native species in red. The strength of interaction is measured as the number of fruits removed and is indicated by the width of interaction bars

linear mixed models are available in Online Resource 3.

Discussion

This study contributes to the understanding of how frugivore communities respond to the introduction of non-native fleshy-fruited plants, associating patterns of fruit removal to plant species and fruit traits. The successful integration of non-native plants into interaction networks suggests that generalist frugivores can play a key role in promoting the invasion of non-native plants; in particular in ecosystems with small assemblages of seed dispersers. This is the case of the temperate forest of Patagonia, where *E. albiceps* and *T. falcklandii* are two generalist species responsible for the dispersal of most of the seeds, and that also disperse non-native plants.

Interaction networks

We found that areas with invasion had more plant species, which increased the asymmetry of interaction networks (− 0.42 in areas with invasion vs. 0.11 in areas without invasion). However, the number of interactions also increased in areas with invasion, and connectance remained similar, reflecting a good integration of non-native plants into interaction networks. Previous studies agree that non-native species can become integrated into novel interaction networks, which makes the restoration of native

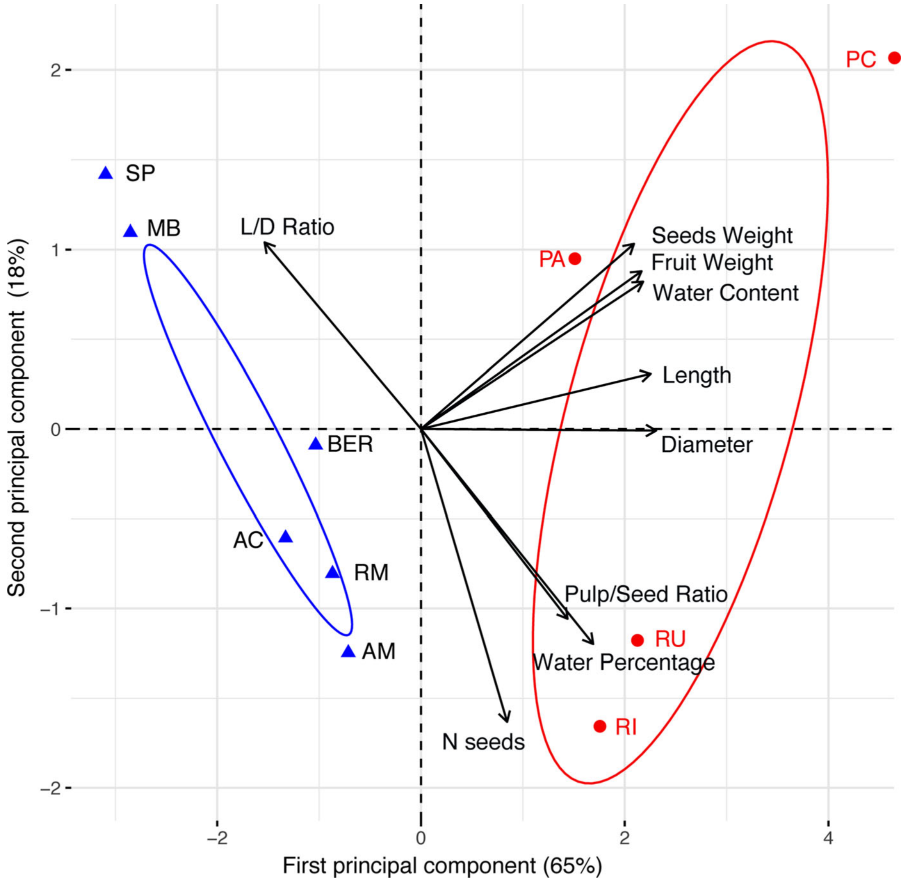

Fig. 2 Two-dimensional scatterplot showing the distribution of fruit species along the two first components of the PCA. Blue triangles are native species, and red circles are non-native species. The arrows indicate the contribution of each variable. Each point represents one species: AC = *Aristotelia chilensis*, AM = *Azara microphylla*, BER = *Berberis darwinii* and *Berberis microphylla*, MB = *Maytenus boaria*, PA = *Prunus avium*, PC = *Prunus cerasus*, RI = *Rubus idaeus*, RM = *Ribes magellanicum*, RU = *Rubus ulmifolius*, SP = *Schinus patagonicus*. Concentration ellipses at a 0.95 confidence are shown

ecosystems very challenging (Spotswood et al. 2012; Vizentin-Bugoni et al. 2019). Generality and niche overlap values for the high level, on the other hand, indicate that birds incorporate non-native fruits into their diets, but there is a segregation of interaction patterns among bird species. This segregation seems to occur because bird species have different fruit preferences, mainly driven by fruit traits (see “Patterns of fruit consumption by bird species” later).

Fruit traits

Fruits of non-native plants were different to native fruits based on the morphological traits measured. The clearest difference is fruit size, showing that non-native fruits are bigger than native fruits. Most studies that analyzed differences between native and non-native fleshy-fruited plants have focused on phenological differences, but there are few studies that analyzed morphological and nutritional traits of native and non-native plants and their possible consequences for frugivory and seed dispersal, arriving to contrasting results. A previous work conducted in Australia found that non-native fruits were small and have smaller seeds than native fruits (Gosper and Vivian-Smith 2010). Another study conducted in the oceanic island Mahé (Seychelles, Indian Ocean) found that the range of fruit traits differ between native and non-native plants; and the authors suggest that gaps in the native fruit trait spectrum might be considered as empty niches that can be exploited by non-native plants (Kueffer et al. 2009). This could be the case in

Table 3 Relative contribution of each fruit trait variable to the first two components of the PCA, their corresponding eigenvalues and cumulative variance explained

Variables	PC 1	PC 2
Length	0.96	0.13
Diameter	0.98	− 0.01
Fruit weight	0.92	0.37
Length/diameter ratio	− 0.65	0.44
Seed weight	0.89	0.44
Pulp/seed ratio	0.61	− 0.45
Number of seeds	0.36	− 0.69
Water content	0.93	0.35
Water percentage	0.72	− 0.51
Eigenvalue	5.85	1.62
Cumulative variance %	65.02	82.99

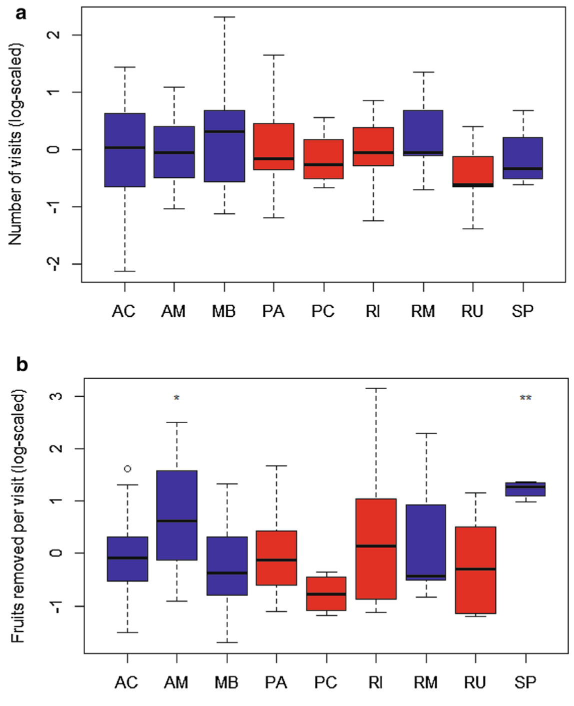

Fig. 3 Boxplots showing **a** the log-scaled number of visits and **b** the log-scaled number of fruits removed per visit (partial residuals of the mixed-effects model) as a function of plant species. Native species are colored in blue and non-native species in red. Significance levels: $**0.01 \leq p < 0.01$ $*0.01 \leq p < 0.05$. Codes for species are detailed in the legend of Fig. 2

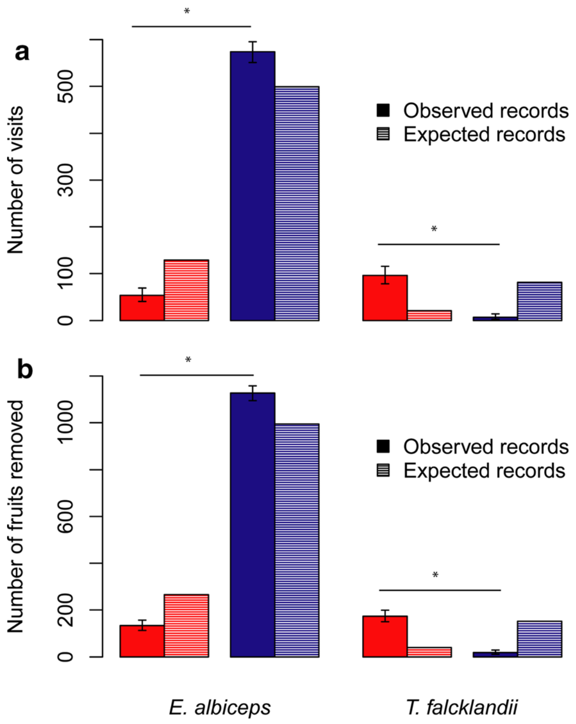

Fig. 4 Barplot comparing the observed and expected **a** number of visits and **b** number of fruits removed for *E. albiceps* and *T. falcklandii* visiting native and non-native plants. Native species are colored in blue and non-native species in red. Error bars show the 95% confidence interval for each observed number of records

our study system, since although non-native fruits are so different from the native ones, they are well integrated into the dispersal networks. Moreover, bigger, bright-colored fruits and large crop sizes can make non-native plant species particularly attractive to dispersers (Aslan and Rejmanek 2012). In accordance with our results, in communities of northern Patagonia, Lediuk et al. (2014) found that two non-native plants differ in phenology and fruit traits to native plants: they have a longer fruiting period and bigger, fleshier fruits than native plants. Fruit traits of plants found to be invading the temperate forest in our study system are probably the result of anthropogenic selection, because the four species are widely cultivated in gardens and eaten by people or used for the production of preserves and jams (Riádigos and Martínez 1994; Rovere et al. 2013; Iglesias 2015; Bravo et al. 2019).

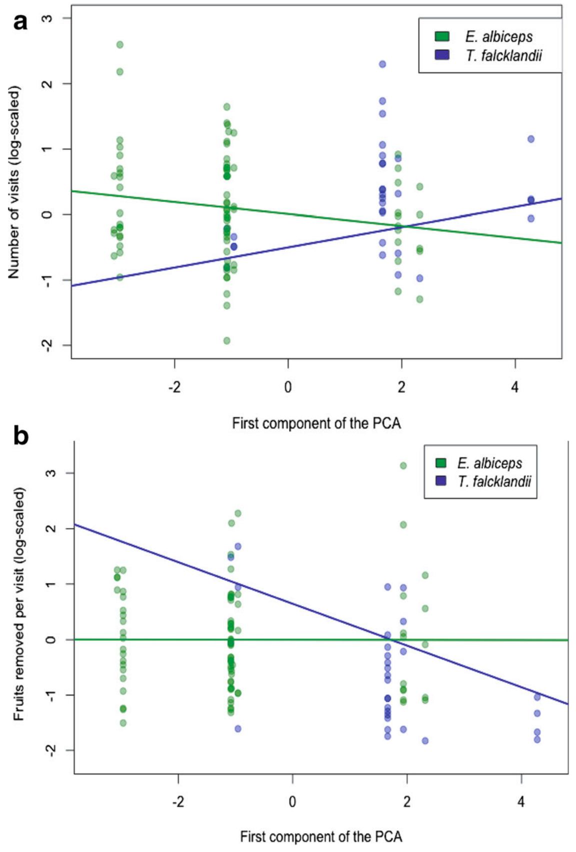

Fig. 5 Scatterplots showing the effect of the interaction between the two main frugivorous bird species and fruit size (represented by the first component of the PCA of Fig. 2) on **a** the number of frugivore visits and **b** the number of fruits removed per visit. Native species are located to the left of zero (small-sized fruits) and non-native species are located to the right of zero (big-sized fruits) along the horizontal axis. Each point represents one plant individual. Regression lines for each bird species are drawn. Values from *y*-axes correspond to the partial residuals of mixed-effects models for each response variable

Patterns of fruit consumption by the community of frugivores

Despite differences between native and non-native fruits, the total number of frugivore visits did not depend on plant species and origin. This, added to network analysis (see above), shows that the community of disperser birds successfully incorporated non-native fruits to their diets. These results agree with several previous works that demonstrate that non-native plants are dispersed by resident frugivores (e.g., Bartuszevige and Gorchov 2006; Spotswood et al. 2012; Heleno et al. 2013). Birds removed more fruits per visit for two native plant species (*Azara microphylla* and *Schinus patagonicus*). This may be partly because those fruits are small and birds need to consume a greater amount to be satiated; but fruits could also be selected by their nutritional content (Schaefer et al. 2003; Blendinger et al. 2016; Morán-López et al. 2018), not explored in this study. The nutritional content of fruits can determine the selection by frugivorous birds, structuring the composition and spatial patterning of plant communities (Morán-López et al. 2018).

Previous studies showed that native birds are legitimate seed dispersers of several alien fleshy-fruited plant species (Martin-Albarracin et al. 2018); thus, the integration of non-native plant species to the resident interaction network can facilitate plant invasion. Previous works have found contrasting results regarding the preference of native or non-native fruits by resident birds. For example, a study conducted in the South African Mediterranean climate region found that several bird species exhibited higher visitation frequency indices on fruits of alien shrub species (Mokotjomela et al. 2013). Conversely, native birds preferred native fruit species in northern California (Aslan and Rejmanek 2012). However, there is strong evidence that fruits of non-native plants are important food items for native birds in different parts of the world (Smith et al. 2013; Gleditsch and Carlo 2014; Rojas et al. 2019), and that non-native fruits do not need to resemble native fruits to be dispersed by frugivores, but that generalist non-native plants can easily establish seed-dispersal interactions with generalist frugivores (Peralta et al. 2020). Our work shows that even in a very simple system, in which differences between native and non-native fruits are so marked, non-native plants integrate successfully to the interaction network. It is very expected that this pattern is also observed in more diverse systems, with more disperser species having diverse morphological traits.

Patterns of fruit consumption by bird species

Seed-dispersal interactions can be shaped by associations between fruit and seed dimensions and frugivore´s body size and bill gape (Wheelwright 1985; Donatti et al. 2011). Thus, although both *E. albiceps* and *T. falcklandii* are legitimate dispersers of native and non-native plants (Lediuk et al. 2014; Iglesias

2015; Martin-Albarracin et al. 2018), they could play different roles in the dispersal of seeds of different plant species. When analyzing frugivory by bird species, we found clear differences between native and non-native plants (Fig. 4). *E. albiceps* visited native plants more than expected and also removed more fruits than expected, showing that this migrant bird is selecting native plants. *T. falcklandii*, on the other hand, visited non-native plants more than expected and also removed more fruits than expected, so it is selecting non-native fruits. These differences could be explained by constraints imposed by bill gape and fruit size. *E. albiceps* has a smaller gape width that prevents it from eating large fruits (Amico and Aizen 2005; Burns 2013), while *T. falcklandii* has a large bill that allows ingest bigger fruits. *T. falcklandii* is also an opportunistic species and may be particularly attracted by non-native fruits; that are bigger than native fruits, and have different color than natives (Iglesias 2015). In this work we found that most non-native fruits are red, while this color is rare between native fruits (1 of 8 species). Behavioral and morphological differences between *T. falcklandii* and *E. albiceps* can influence their seed-dispersal effectiveness (Schupp et al. 2010). For example, as *T. falcklandii* frequently feeds in forest gaps, it can benefit non-native plants that perform better in disturbed areas, such as *R. ulmifolius* (Vargas et al. 2013a), by depositing their seeds in microsites suitable for germination.

Although *E. albiceps* is present in the area only during the summer season, it is very abundant and has a key ecological role in the dispersal of seeds in the temperate forest of Patagonia (Amico and Aizen 2005; García et al. 2010; Martin-Albarracin et al. 2017). Because of its great abundance, this species may still cause issues, even though they visit non-native fruits less than expected. Further, it could contribute to the long-distance dispersal of seeds during migration periods (Viana et al. 2016).

On the other hand, *T. falcklandii*, although not as abundant as *E. albiceps*, eats a greater proportion and diversity of non-native fruits. Other studies found that *T. falcklandii* and other *Turdus* species are important dispersers of seeds of non-native plants in temperate ecosystems (Bartuszevige and Gorchov 2006; Williams 2006; Burns 2012; Smith-Ramírez et al. 2013; Díaz Vélez et al. 2018). In addition, as *T. falcklandii* is resident in the area, it could disperse seeds of non-native plants that fruit in other seasons like *Sorbus aucuparia* and *Crataegus monogyna* (Iglesias 2015; Lediuk et al. 2016). Other studies agree that generalist birds have an important role in the dispersal of seeds of non-native plants (Bartuszevige and Gorchov 2006; Jordaan et al. 2011; Vergara-Tabares et al. 2018).

Implications for the community of fleshy-fruited plants in the temperate forest of Patagonia

Although seed-dispersal systems are usually associated to a wide spectrum of disperser animals, there are examples in which non-native plants reliant on one or few seed dispersers become invasive (Gosper et al. 2005). This could be the case in the temperate forest of Patagonia, where most seed dispersal relies on two bird species. In addition, the fact that these birds incorporated non-native fruits to their diet demonstrates that they have some degree of dietary flexibility.

Some of these introduced plant species and their congeners develop a very aggressive behavior in different environments of the world as in Patagonia, such as *Rubus ulmifolius*, *Rubus niveus* (Baret et al. 2004; Rentería et al. 2012; Vargas et al. 2013b, a), *Prunus serotina* and *Prunus mahaleb* (Deckers et al. 2008; Amodeo and Zalba 2013). This makes it important to know the main factors that contribute to their spread, in particular their dispersal agents. Moreover, beyond plant invasion, the availability of non-native fruits may indirectly affect seed dispersal of native plants. As *T. falcklandii* is the main disperser of native fleshy-fruited plants during winter (when *E. albiceps* is absent), those plants may be highly dependent on *T. falcklandii* for seed dispersal; thus, changes in the diet of this species will particularly affect them.

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