



# Being popular or freak: how alien plants integrate into native plant-frugivore networks

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Received: 30 May 2018 / Accepted: 27 April 2019  
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**Abstract** The generalist diet of most frugivores opens a window of opportunity to the invasion of alien plants with fleshy-fruits. The outcome of the new relationships between alien plants and native frugivores depends both on traits of the invaders and of the mutualist partners in the recipient community. Two contrasting hypotheses attempt to explain the integration of alien species in native communities. “Darwin’s naturalization hypothesis” proposes that alien species more different from native species are more likely to

integrate in the community. The “similarity hypothesis” proposes the opposite, that alien species more similar to native species are more likely to integrate the native community. By comparing chemical and morphological traits of 12 alien and 48 native fleshy-fruited species, we tested both hypotheses as assembly rules of alien species in subtropical Andean forests. We did not find differences in most chemical or morphological traits between alien and native fruit species. The multidimensional variation of alien fruit traits was nested within that of native species. However, alien fruits tended to score high in the range of variation of native chemical traits. Accordingly, we propose the “fraction similarity hypothesis” as a main

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10530-019-01997-9>) contains supplementary material, which is available to authorized users.

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force that drive the assembly of alien species in mutualistic networks, i.e. alien species benefit from existing mutualistic interactions that involve fruit species with traits selected by the frugivores to invade native communities. The striking similarity in fruit traits between alien and native species highlights the potential role of seed dispersers as ecological filters to the invasion of alien plants. In turn, this similarity suggests that alien fruits can be functionally equivalent to native ones in terms of their interaction with fruit-eating birds.

**Keywords** Fruit traits · Invasive species · Darwin's naturalization hypothesis · Similarity hypothesis · Seed dispersal mutualism · Subtropical Andean forests

## Introduction

In the last centuries, human activity favoured the introduction of thousands of fleshy-fruited species into new ecosystems, where some of them (ca. 600 species only for trees and shrubs; Richardson and Rejmánek 2011) became invasive by interacting with the native biota and having the ability to grow and reproduce in the novel environments (Pantel et al. 2017). Interactions between fleshy-fruited plants and seed-disperser animals often result in the removal of plant diaspores ("fruits") as foraging animals reach part of their dietary requirements (Howe and Smallwood 1982). The outcome of these new relationships between alien plant species and native fruit-eating animals depends both on attributes of the invader and of the mutualist partners in the recipient community (Kueffer et al. 2009). Bearing fleshy-fruits dispersed by birds -the globally most diverse group of dispersers- might explain the invasiveness of many alien species around the world, especially of those with large crop sizes (Buckley et al. 2006; Giorgis et al. 2010; Gleditsch and Carlo 2011; Cronk and Fuller 2014). Thus, morphological and phytochemical traits seem to be important cues for fruit-eating birds (Blendinger et al. 2015). Moreover, although fruit traits could drive to the consumption of alien species, the role of these traits on the integration of alien species in native communities is poorly understood (Kueffer et al. 2009; Minoarivelo and Hui 2016; Hulme and Bernard-Verdier 2018).

Fruits show a variable combination of traits that allow them to interact with frugivores and promote seed dispersal, including morphological (colour, shape and size) and chemical (nutrients, water content, secondary compounds) traits (Schaefer and Ruxton 2011). Not all traits are of equal weight regarding foraging decisions by consumers, and the relative importance of a particular fruit trait or trait combination for seed dispersal could depend on idiosyncrasies of the frugivores (Blendinger et al. 2016; Bender et al. 2017). Bird selection of alien fruits seems to be influenced by the interaction between enhanced foraging efficiency and shared traits of alien with native fruits (Aslan and Rejmánek 2012). On the one hand, alien plant species with relatively higher crop size than native plants are presumed to attract more fruit-eating birds, which concentrate their foraging activity where resources are most abundant (Gleditsch and Carlo 2011; Mokotjomela et al. 2013a). On the other hand, the selection of fruits of alien species may be related to fruit traits, such as greater size and higher pulp-to-seed ratio, sugar concentration, and energy rewards (Kueffer et al. 2009; Mokotjomela et al. 2013b). Moreover, fruit traits found in a particular species may have been shaped through the interaction with the regional pool of seed dispersers (Schaefer et al. 2007; Valido et al. 2011; Guimarães et al. 2017), other fleshy-fruited plants (Schaefer et al. 2004; Stournaras and Prum 2015), and seed and fruit predators (Buchholz and Levey 1990; Cipollini and Levey 1997; Cipollini 2000). Altogether, these processes may have left an imprint in fruit traits through the evolutionary history of plant lineages. Consequently, fruit traits that have evolved in different dispersion contexts could be expected to vary among geographic regions.

Thus far, two main contrasting hypotheses aim to explain the integration of alien species into native communities. On the one hand, the 'Darwin's naturalization hypothesis' (DNH) states that a given alien species can better settle in novel environments when being more different from the native species in one or more traits (Traveset and Richardson 2011). The DNH assumes that it is easier to integrate to a given community when the putative competition is avoided by exhibiting different traits, either categorical or in terms of magnitude, compared to those of native species (Phillimore et al. 2008; Thuiller et al. 2010). On the other hand, assuming that the diversity of traits in native assemblages is moulded by the mutualistic

interactions in native communities (Guimarães et al. 2017; Pantel et al. 2017), the similarity of alien species with the existent native traits could promote the invasion (Traveset and Richardson 2011), as the hereafter referred to as the ‘similarity hypothesis’ (SH) argues. Specifically, SH proposes that in plant seed-disperser interactions, traits that define the interaction between novel flora and native seed-dispersers are determined by the interaction of native flora with native seed-dispersers. In consequence, the more similar the alien species traits to the receiver community, the more likely its integration to that community (Traveset and Richardson 2011). A third possible explanation is that alien plants share trait values with the native fleshy fruits more selected by frugivores. This explanation is partially similar to the SH mechanism, but it differs in that aliens are similar to a particular fraction of the native flora, rather than to the whole receiver community. We referred to this explanation as the ‘fraction similarity hypothesis’ (FSH). This idea is an expansion of the ‘limiting similarity hypothesis’ (LSH) proposed by MacArthur and Levins (1967). These authors conclude that limitations in trait variation are due to competition. Then, invasions are promoted under certain conditions in which trait values are not overlapped between species or when the overlap do not generate competitive exclusion (i.e. stable competition; MacArthur and Levins 1967). Thus, according to LSH, alien species are constrained to invade by niche partitioning assuming avoidance of competition (or a stable competition). A fundamental difference between FSH and LSH is that MacArthur and Levins (1967) assume competition between species. In the other hand, FSH stated that alien species benefit from existing mutualistic interactions that involve fruit species with traits selected by the frugivores to invade native communities.

Recently, Ng et al. (2019) highlights the need to consider data from phenotypic traits to test these hypotheses as predictive tools for community invasion. To date, explanations regarding how alien species overcome biotic filters imposed by native seed dispersers, and how they integrate into recipient communities are still scarce (Gurvich et al. 2005; Hulme and Bernard-Verdier 2018). In particular, whether a trait or combination of traits are responsible of such integration, and whether this is facilitated by similarities or differences with native species remains

unknown (Traveset and Richardson 2011, 2014; Aslan and Rejmánek 2012). In this study, we assess whether alien plants display novel values of fruit traits that are important for the interaction with seed dispersers (DNH); or if, instead, trait values shared with native flora (SH); or with a fraction of the native plant assemblage (FSH) prevail. To understand the ecological forces that might drive the integration of alien species in native plant-frugivore networks; we compare morphological and chemical fruit traits of 60 species of alien and native plants dispersed by birds in subtropical Andean forests.

## Methods

We conducted the study in subtropical Andean cloud forests known as Austral Yungas. In these forests, the native plant-frugivore mutualistic network includes at least 58 species of seed dispersers, belonging to 13 bird families and 7 mammal families, who feed regularly on fleshy-fruits of around 240 plant species of 61 families (Blendinger et al. 2015; Ruggera et al. 2016, PG Blendinger and NP Giannini unpubl.). We performed the field work in nine localities of Tucumán province (26°23′–27°40′ S, 64°55′–65°57′ W), north-west Argentina, over the entire range of vegetation elevation belts (ca. 500–1900 m a.s.l., Brown et al. 2001). Climate is subtropical, with dry winters (May to September) and wet summers (November to March). Average annual rainfall varies between 1100 and 1500 mm throughout the mountain range, with ca. 80% of rainfall occurring in summer. Average annual temperature is 19 °C (Hunzinger 1997). In the recent decades, at least 15 fleshy-fruited alien species became invasive in the area (Aragón and Morales 2003; Sirombra and Mesa 2012). These plants interact with native frugivores, which eventually disperse their seeds (Aragón 2000; Blendinger and Giannini 2010; Powell and Aráoz 2017). Most alien and native fruit species bear typical ornithochorous fruits, and it is known that birds eat them and disperse their seeds (Richardson and Rejmánek 2011; Ruggera et al. 2016; Ordano et al. 2017).

From 2013 to 2017, we collected fresh fruits of native and alien bird-dispersed plants throughout the year, for posterior chemical analyses. We collected fruits randomly from different plants of each species. We selected only ripe fruits without blemishes or

damage, we cleaned each fruit with distilled water, and freeze-dried them. Once freeze-dried, we removed the seeds from the pulp with forceps and needles. We stored freeze-dried seedless pulp samples at  $-20^{\circ}\text{C}$  until analysed. We were able to complete the dataset of chemical and morphological traits of 48 native and 12 alien plant species (Online resource1, Table S1). These species include the different growth forms (forbs, epiphytes, shrubs, vines and trees) which bear fleshy fruits dispersed by birds in the study area.

### Morphological traits

We considered a fleshy fruit according to its ecological role in mutualistic interactions, i.e. as the reproductive unit consumed by fruit-eating birds. We collected a minimum of 10 to 30 ripe fruits of the larger species (i.e.  $> 5$  g per fruit) and until reach 100 to 300 g for small fruits ( $< 5$  g per fruits), from different plants of each species. Variations in the amount collected depended on fruit availability and fruit mass inside both categories. We measured maximum fruit length and width with a digital calliper to the nearest 0.1 mm. We weighted the mass of the whole fresh fruit with a digital scale to the nearest 0.1 mg, and the mass of individual seeds with a precision lab scale to the nearest 0.01 mg. We then counted the number of seeds per fruit. With the raw data, we estimated the mean values of these, plus the mean value of fruit shape (fruit length/fruit width), total seed mass per fruit, and pulp-to-seed ratio (fruit mass/total seed mass).

### Chemical composition

We carried out sugar, and total phenolic determinations with ethanolic extracts (EE). Also, we extracted proteins with an aqueous extraction (AE). To prepare EE we first extracted fruit powder with  $96^{\circ}$  ethanol (0.071 g dry pulp/ ml of ethanol) for 24 h. Then, we filtered the extract with Whatman N $^{\circ}$  4 filter paper and we used the supernatant for chemical analysis. We performed the same procedure for AE, using distilled water instead of ethanol.

### Sugar determination

We determined total sugars on EE by the phenol-sulphuric acid method (DuBois et al. 1956). We took aliquots (0.8 ml) of different extract dilutions, and

measured the absorbance in an UV-visible Beckman-DU-650 spectrophotometer (490 nm). We performed a calibration curve using glucose as a standard and expressed the results as milligrams of glucose equivalents per gram of dry pulp mass (mg GE/g).

### Protein determination

We quantified total soluble proteins according to Bradford (1976) using bovine serum albumin as standard. We took aliquots (0.1 ml) of different EE extract dilutions and added 5 ml of dye solution (Coomassie Brilliant Blue G 250). We measured absorbance at 595 nm and performed a calibration curve with bovine serum albumin, expressing the results as milligrams of bovine serum albumin equivalents per gram of dry pulp mass (mg BSAE/g).

### Lipids

We extracted lipids with a Soxhlet extractor. We put 1 g of dried pulp in a cellulose cartridge, and then placed the cartridge in the extractor with 150 ml of petroleum ether  $60-80^{\circ}\text{C}$ , extracting lipids until exhaustion. We then evaporated the petroleum ether and weighted the extract using an analytic scale, assuming it is the lipid content. We expressed lipid content as milligrams of lipids per gram of dry pulp (mg/g).

### Mineral content

Once weighed (0.20 g), we mixed the lyophilized samples with sub-boiling  $\text{HNO}_3$  (8 mL) in a quartz glass and maintained it for 45 min in a microwave oven at  $280^{\circ}\text{C}$  and 75 bars. We then added Milli Q water until it reached a volume of 25 mL and filtered the disintegrated material through a 0.45- $\mu\text{m}$  filter. We determined the levels of Na, K, Ca, Fe and Mg of these solutions by inductively coupled plasma mass spectrometry (ICP-MS). We expressed the results as milligrams per 100 g of dry pulp mass (mg mineral/100 g).

### Water content

We determined water content by subtracting the dried fruit-pulp weight by fresh fruit-pulp weight. Then, we

transformed the weight value into a ratio, for better comparison between species.

### Total phenolics

Total phenolics were determined on EE extract using Folin–Ciocalteu’s reagent, following the description in Singleton et al. (1999), with certain modifications mentioned below. The reaction mixture contained different quantities of each EE, 100  $\mu$ L of Folin–Ciocalteu’s reagent and 400  $\mu$ L of sodium carbonate (15.9% w/v) and reached to 1500  $\mu$ L with distilled water. Total phenolic content was determined by the comparison with a calibration curve of gallic acid as a standard. We measured absorbance at 765 nm and expressed results as milligrams of gallic acid equivalents per gram of dry pulp mass (mg GAE/g).

### Tannins

We extract tannins using an acetone-distilled water 1:1 solution. We put 0.1 g of dried fruit pulp into an eppendorf tube, and then added 1.2 ml of extraction solution. We centrifuged at 10,000 rpm and filtered the extraction. We repeated the process until exhaustion, and subsequently dried the extractions. Then, we measured condensed tannins using 1% dimethyl-amino-cinnamaldehyde (DMAC) as reactive. We resuspended the samples with 1.5 ml of distilled water; and added 0.2 ml of the sample into an assay tube with 0.9 ml of DMAC. We left the solution at room temperature for 20 min and read absorbance at 640 nm. We expressed results as grams of procianidine-B2 equivalents/dry fruit grams (g PB2E/g).

### Statistical analysis

With the raw data we estimated the mean of each trait. We first independently compared the 19 fruit traits between groups (alien vs. Native) using GLMMs, with taxonomic order as random effect. We fitted a Gaussian distribution for all the comparisons, except for water content (beta distribution) and seed number (negative binomial distribution). Next, to avoid the usage of collinear variables, we performed a Pearson correlation analysis and dismissed one of two correlated variables whenever the Pearson correlation coefficient was larger than 0.7 (Online resource1, Fig.S1). Finally, we used the non-collinear variables to

analyse the multivariate space filled by alien and native bird-dispersed fleshy fruits. Since not all the trait data were available for all the species in order to perform the ordination analysis (Online resource 1, Table S1), we performed a paired comparison between species vectors containing trait values of each species - i.e. one vector by species- using Gower distances to estimate the dissimilarity.

The result of each vector comparison was used to build a dissimilarity matrix used to run a non-metric multidimensional scaling with 9999 permutations (NMDS; see methods in Giannini and García-López 2014). In this way, we avoided discarding entire species due to lacking of few measurements. We selected the number of axis as a compromise between stress, interpretation difficulty, and clarity in the detection of patterns. We then ran an analysis of similarities (ANOSIM) to test whether alien and native species could be grouped into discrete groups of species in the ordination space. Also, we performed a test (PERMDISP) to corroborate that the assumption of “multivariate homogeneity of group dispersions” of the ANOSIM be fulfilled (Oksanen et al. 2017). Finally, we fitted trait values to the NMDS to elucidate which traits were more important for the ordination (Oksanen et al. 2017). We used *lme4* package (Bates et al. 2015) to perform the GLMMs; basic commands of R (R Development Core Team 2016) to construct the matrix, and the *vegan* package for the dissimilarity distance calculation, NMDS, ANOSIM and PERMDISP analyses (Oksanen et al. 2017).

## Results

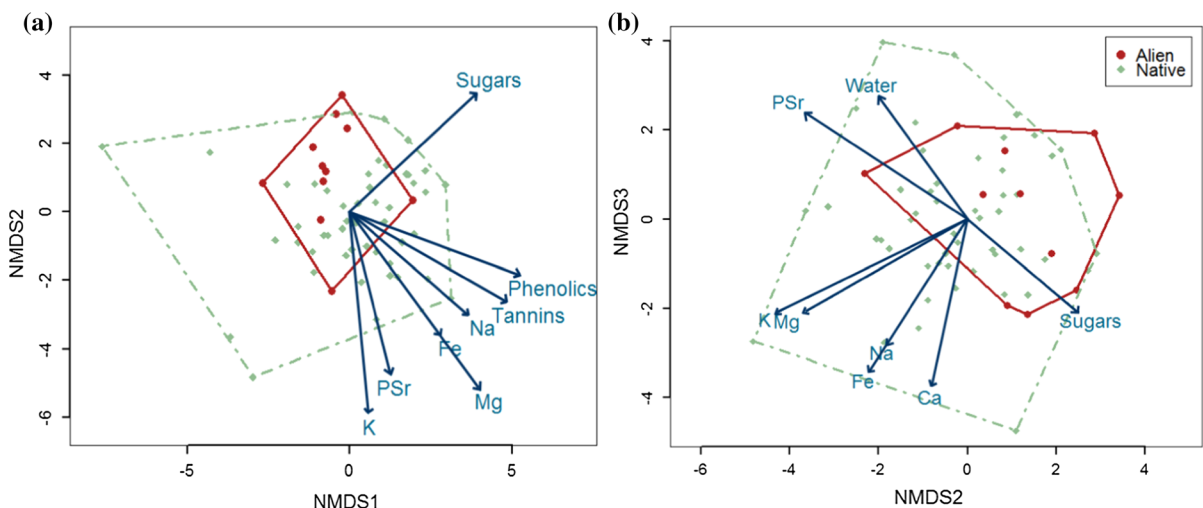
Of the 19 fruit traits analysed, K and Fe differed between alien and native fruit groups (GLMM,  $p < 0.05$ ; Table 1). The remaining traits did not differ between both groups of fruit species. Coefficients of variation were smaller in aliens than in natives for most fruit traits, except for sugars and tannins that showed similar values and pulp-to-seed ratio that was larger in aliens (Table 1).

After Pearson correlation analysis, we kept 15 non-collinear variables (Online resource1, Fig. S1) for the ordination analysis. Stress value of the NMDS was 0.18 for 3 dimensions. NMDS did not show a clear differentiation pattern between groups of native or alien plants (Fig. 1a, b). There was no difference

**Table 1** Comparison of fruit traits between alien and native fleshy-fruited bird-dispersed species

Trait	Alien (CV)	Native (CV)	<i>df</i>	<i>t</i>	<i>p</i>
Length	15.42 ± 9.17 (0.59)	13.97 ± 18.04 (1.29)	57.00	- 1.002	0.321
Width	11.63 ± 6.50 (0.56)	10.12 ± 6.69 (0.66)	53.32	- 0.834	0.408
Shape	1.33 ± 0.43 (0.32)	1.56 ± 2.54 (1.63)	56.33	- 0.793	0.431
Total mass	1.99 ± 3.04 (1.50)	1.46 ± 4.34 (2.96)	40.77	- 0.612	0.544
All seeds mass	0.39 ± 0.71 (1.83)	0.32 ± 0.91 (2.81)	48.44	- 0.717	0.477
One seed mass	0.34 ± 0.67 (2.02)	0.11 ± 0.36 (3.24)	56.98	- 1.083	0.283
Seed number	17.20 ± 29.79 (1.73)	63.02 ± 132.97 (2.11)	53.00	1.550	0.121
Pulp-to-seed ratio	11.19 ± 17.52 (1.57)	10.29 ± 11.68 (1.14)	56.00	0.635	0.528
Sugars	211.05 ± 138.76 (0.66)	143.39 ± 94.36 (0.66)	52.86	- 1.827	0.073
Lipids	0.039 ± 0.052 (1.33)	0.038 ± 0.088 (2.32)	24.11	- 1.171	0.253
Proteins	1.16 ± 0.51 (0.45)	0.52 ± 0.79 (1.51)	33.65	- 2.033	0.050
Water	77.52 ± 7.17 (0.09)	78.80 ± 11.87 (0.15)	32.14	0.667	0.509
Phenolics	2008.18 ± 1278.55 (0.64)	2841.96 ± 3226.86 (1.14)	54.37	0.934	0.355
Tannins	608.18 ± 1114.22 (1.83)	1101.21 ± 2024.42 (1.84)	49.73	1.466	0.149
Ca	592.81 ± 358 (0.60)	345.56 ± 302.15 (0.87)	30.03	- 1.798	0.082
Fe	6.65 ± 4.39 (0.66)	4.40 ± 25.06 (1.61)	53.00	2.008	0.049
Mg	122.85 ± 86.96 (0.71)	169 ± .42 ± 164.95 (0.97)	32.64	1.142	0.262
K	1418.46 ± 436.24 (0.31)	2536.33 ± 1412.65 (0.56)	52.49	2.015	0.049
Na	9.84 ± 5.29 (0.54)	20.54 ± 25.51 (1.24)	53.00	0.656	0.514

Alien and native columns indicate the mean ± standard deviation (coefficient of variation) of each group. Sugars, proteins and phenolics are expressed in equivalents of standard per dry pulp (mg GE/g, mg BSA/g, and mg GAE/g, respectively); minerals (Ca, Fe, K, Mg, Na) in mg/100 g of dry pulp; fruit mass in mg; water in %; pulp-to-seed ratio and fruit shape are non-dimensional. The last three columns report results of GLMM; between traits differences in degrees of freedom (*df*) are because of differences in sample size and in representation in different taxonomic groups when we compute the random effects (see “Methods” section for details)



**Fig. 1** NMDS plots of axis 1 and 2 (a); and axis 2 and 3 (b). Alien species in circles and native species in diamonds. Green and red lines connect species to the centroid of native and alien fruits respectively. Polygons contour the multivariate space

occupied by each group (natives: dot-dashed green line, aliens: continuous red line). Blue vectors are the fruit trait variables that better fit the ordination (*p* value < 0.05)

between alien and native fruits in the ordination space (ANOSIM test; R statistic = 0.068,  $p$  value = 0.253). The multivariate dispersion of alien and native fruits did not differ from homogeneity (PERMDISP;  $p$  value = 0.457).

Important variables that structured the NMDS ordination were pulp-to-seed ratio (PSr in Fig. 1), water, phenolics, tannins, sugars, Ca, K, Na, Fe and Mg (Fig. 1). As showed by polygons in Figs. 1a, b, alien plants (continuous line) are ordered inside native variation (dot-dashed line). Minerals structured the ordination as a whole, i.e. all mineral vectors increased in the same direction in the ordination planes. Besides, the centroid of alien plants was related to lower concentrations of minerals and phenolics (Fig. 1a, b). Figure S2 (Online resource 1) condenses the information of the previous analysis and shows the dispersion of values in each statistically significant trait important for the NMDS. We included proteins and sugars and lipids, because these three macronutrients are proposed as important traits for bird decisions (Aslan and Rejmánek 2012; Blendinger et al. 2015). K and Fe differed between fruit groups and were important for the ordination. As noted also by coefficients of variation (Table 1), most fruit traits showed less variation in alien than native fruits.

## Discussion

The comparison of fruit traits, both as a whole and separately, can provide insights about important traits that influence the invasion of fleshy-fruited plants (Gosper and Vivian-Smith 2010; Aslan and Rejmánek 2012). Our community-wide analysis highlight that native and alien plants dispersed by birds share many fruit traits, strongly suggesting that species assembly rules proposed by the similarity hypothesis (as opposed to Darwin's naturalization hypothesis) are the norm in subtropical Andean forests. Despite the similarity between groups of fruits of different geographical provenances, alien species differ from native species in certain particular chemical fruit traits (K and Fe content). This leads us to think that another mechanism different from the prevailing hypotheses could also be promoting the integration of alien species. It is likely that fruit-eating birds selectively promote the dispersal of alien species that display high values of native flora fruit traits selected by birds.

In line with other studies in subtropical climates (e.g. Gosper and Vivian-Smith 2010; Jordaan and Downs 2012), we did not find a clear differentiation between alien and native plant species in the multivariate space in terms of fleshy-fruit traits of morphological design or nutritional content. The diffuse nature of plant-seed disperser interaction positions the whole range of dispersers as selective agents (Guimarães et al. 2017). Thus, seed-dispersers assemblages could act as biotic filters for the settlement of novel species in native systems (Pantel et al. 2017). If plant species share functional partners in their natural range, and share a similar evolutionary history, it is expected for them to share traits that allow them to interact with similar mutualist partners in different environments (Pantel et al. 2017). Thus, fruit-eating birds affect plants with their selection idiosyncrasies, and by filtering them through their consumption of fruits (Blendinger et al. 2016; Pantel et al. 2017). This putative fruit trait convergence is a possible underlying SH and FSH mechanism. However, SH involves the similarity of the means of the traits (or the centroid of multiple traits), while FSH involves the similarity of a fraction of the total variability. In our study, alien species were less variable in most traits. They occupied a short range of variation nested within a portion of native plants variation. Trait-by-trait comparisons also showed the same pattern. The description of this pattern could be due to an unbalanced comparison -12 alien versus 48 native species- but considering the low taxonomical relationships between species and the differences found for some variables in the trait-by-trait comparison, we believe that is not a major issue when interpreting the results.

Certain chemical traits differed between native and alien fruit species in our study site, while morphological traits did not. Previous assessments of particular fruit traits at the community level showed some differences in the morphological traits (e.g. seed number) of native and alien species, and mostly in their chemistry (e.g. sugar and nitrogen levels, water and energy content), although with trends of variable sign among studies (Kueffer et al. 2009; Gosper and Vivian-Smith 2010; Jordaan and Downs 2012; Mokotjomela et al. 2013a, b). To understand the ecological importance of native and alien fruit traits, the variation of fruit traits at the community level should be compared in addition to the differences (Traveset and Richardson 2011; Hulme and Bernard-

Verdier 2018). Kueffer et al. (2009) were possibly the first to compare fruit trait variation at a regional scale, using a set of native and alien species of tropical oceanic islands. They found higher variation in alien than in native species, and native species in general scored lower in all traits they studied except water content. In contrast, alien fruit traits were narrower compared to those of native fruits in subtropical Andean forests, only sugars and tannins showing almost the same variation in alien and native species and pulp-to-seed ratio shows higher variation in aliens (Table 1). The apparent lack of consistency between these studies could be reflecting different mechanisms that play a relevant role in the invasion/colonization process. In less diverse communities, like oceanic islands, where frugivorous populations are more likely to be limited by resources, plants capable of adding more quantities of certain nutrients seems to be more likely to be selected by dispersers, and thus, to become invasive. On the other hand, in more diverse communities where the functional niche of fleshy fruits is widely occupied, alien species exploit the ecological space occupied by traits already chosen by seed dispersers (Pantel et al. 2017). In a receptive community, more potential mutualists occur when the functional and taxonomical diversity increase (Hui et al. 2016; Minoarivelo and Hui 2016). Thus, alien fruits that are functional equivalent with native fruits are more likely to integrate into native communities, leading to narrowing their ecological niche rather than to an expansion of the functional space in the community (e.g. Pigot et al. 2016). However, it is also likely that the wider range of traits displayed by native fruits in diverse communities hinder the occurrence of novelties originated in other communities with different evolutionary histories. Thus, a interesting challenge is to decouple if similarity of alien plants with native flora are due to the impossibility of being different because occurrence of all variation spectrum of traits or if similarity *per se* promotes invasion.

Interestingly, fruits of alien species tended to score in the upper range of variation of particular chemical traits of the native species in subtropical Andean forests. One possible explanation is that fruit-eating birds select alien species that display high values of the fruit traits selected in the native fruits. This has not been tested to date and may explain the apparent idiosyncrasy of responses across studies mentioned above. In subtropical Andes, fruit-eating birds have

strong preferences in the consumption of native fruit species (TN Rojas, in prep.), and select native fruit species that score high in pulp and chemical rewards (Blendinger et al. 2016). Whether alien species have similar nutritionally relevant fruit traits of the preferred native fruit species, or offer greater quantities of rewards that are low in native species, alien species could integrate into the communities through the complementarity of diet and fruit mixing behaviour of dispersers (Felton et al. 2009; Carlo and Morales 2016).

In summary, fruit traits are important in the invasion process, because they allow plants to interact with seed dispersers of the native communities (Schaefer et al. 2003; Gosper and Vivian-Smith 2010; Aslan and Rejmánek 2012). In diverse communities, alien plants are able to integrate to extant seed dispersal networks through similar trait combinations with native plants. We showed that the variability in alien fruit-traits is nested in the multivariate space of native fruits, suggesting that alien fruits are functionally equivalent to those found in the native community. This niche overlap suggests that invasive alien plants could exploit the already extant mutualisms and thus, settle in the native community. In this way, not all alien fruit species integrate a native community, but aliens are filtered by the preference and idiosyncrasies of seed-dispersers. In other words, alien plants overcome filters imposed by seed-dispersers when they are capable of offering similar signals and rewards as natives do. Empirical and theoretical studies using networks as a framework show similar interpretations (Hui et al. 2016; Minoarivelo and Hui 2016; Pantel et al. 2017). This highlights the need of integrating the information here generated with interaction information (e.g. consumption, networks) to get the full picture. Taking into account the evidence provided, we suggest not to discard the “fraction similarity hypothesis” as an important mechanism that favours the invasion of alien species in Andean forests. However, to test this hypothesis it is mandatory to further explore the influence of seed dispersers as ecological filters. We encourage the realization of studies that take consumption into account, to disentangle the effect of similarities and differences between alien and native fleshy-fruited plants in the invasion process.



**Acknowledgements** We are very grateful with Agustín Quaglia, Lucía Zarbá, Norberto Giannini and Sebastian Zeballos for helpful advises on methodology and Romina Chavez for valuable contribution in figures editing. We acknowledge funding by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET; PIP 2014-592) and Fondo para la Investigación Científica y Tecnológica (FONCYT; PICT 2013-1280).

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