



Aliens will provide: avian responses to a new temporal resource offered by ornithocorous exotic shrubs

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Abstract

Frugivorous birds are able to track spatiotemporal changes in fruit availability. Food resource fluctuations, characteristic of seasonal environments, can be affected by the naturalization of exotic ornithocorous plants. In the mountain forest of central Argentina, invasive shrubs of the genus *Pyracantha* provide a new temporal resource that modifies fluctuations of natural resource availability because the invasives fructify in autumn–winter (largely uncoupled with the fruiting of native species). The contrasting patterns of resource fluctuation between non-invaded and invaded areas throughout the year provide a good study system to test predictions of the fruit-tracking hypothesis, and to understand the relationship between food resources offered by fleshy fruited invasives and abundances of avian trophic guilds. By means of point counts conducted during five time periods at invaded and non-invaded sites we found that the presence of *Pyracantha*, and time periods, significantly affected frugivorous bird abundance, which in autumn–winter was greater in invaded sites and in spring–summer similar between invaded and non-invaded sites. On the other hand, granivores and insectivores did not show a significant relationship with the presence of *Pyracantha*. Abundances of the most common seed disperser were significantly affected by the interaction between time period and presence of *Pyracantha*. These results indicate that the abundances of birds that legitimately disperse *Pyracantha* seeds are temporally and spatially associated with fruit abundance provided by this exotic plant. This underscores fruit availability as an important ecological factor affecting frugivorous bird abundance, and suggests that *Pyracantha* seed dispersers are capable of detecting changes in the availability of its fruit, likely contributing to the effectiveness of its dispersal.

Keywords Asynchronous fruiting · Fleshy fruited plants · Frugivorous birds · *Pyracantha* · Seed dispersers

Introduction

Biological invasions are currently recognized as one of the main causes of biodiversity loss (Gilbert and Levine 2013). Traditionally, searches for the causal mechanism of plant

invasions have focused on negative interactions that occur between invasive plants and resident biota (i.e., herbivory, competence, parasitism, and predation). During the last 20 years there has been an enormous increase in studies analyzing such processes (Ricciardi and MacIsaac 2008; Lowry et al. 2013), shifting the focus to positive interactions as promoters of biological invasions (Richardson et al. 2000). Theoretical models and empirical evidence demonstrate that positive interactions are important drivers of community structure (Bruno et al. 2003; Bulleri et al. 2008; Carlo and Tewksbury 2014), and hence, of invasion success (Richardson et al. 2000). Particularly, seed dispersal by animals represents a mutualistic relationship that has profound effects on plant population dynamics and/or community structure (Herrera and Pellmyr 2009; Bond 1994). A vast amount of evidence for these effects comes from native systems, and there are currently several examples of the influence of frugivorous animals on the dispersal of invasive plants

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(Gosper et al. 2005; Jordaan et al. 2011). However, knowledge regarding the influence of invasive plants on mutualistic organisms that disperse their seeds is much more limited (e.g., Gleditsch and Carlo 2011; Spotswood et al. 2012).

The system most investigated regarding mutualistic patterns and processes of seed dispersal is the interaction between fleshy fruited plants and frugivorous birds (Moenburg and Levey 2003). The evolutionary and ecological consequences of this interaction are assumed to give positive spatiotemporal correlations between fruit availability and bird abundance that guarantee effective seed dispersal (Herrera et al. 1998; Levey and Benkman 1999). Consequently, the proposed mechanism for the maintenance of this interaction in space and time is that birds are able to detect and respond to changes in fruit availability in their habitat, which has been evidenced by covariation between bird abundance and fruit availability (Herrera 1985; Ortiz-Pulido et al. 2000; Jordano and Godoy 2002). This mechanism, commonly referred to as “fruit tracking” by birds, has been demonstrated through robust observational and experimental approaches (Rey 1995; Saracco et al. 2004). For example, García and Ortiz-Pulido (2004) detected a correlation between fruit availability and the number of plant-frugivorous bird interactions in a Mediterranean system. Similarly, Rey (1995) detected a spatiotemporal relationship between fruit availability and frugivorous bird abundance in olive orchards where he experimentally modified fruit availability. This work represents one of very few experimental case studies undertaken at different scales to evaluate the relationship between fruit and bird abundance. Although this relationship has been tested with native species as protagonists in the interaction, only few studies (e.g., Gleditsch and Carlo 2011) have explored such relationships in the context of plant invasion. However, to the best of our knowledge, no study has yet used as its framework the fruit-tracking hypothesis.

A common observation for ecosystems in temperate latitudes is that fruit availability temporally fluctuates (Jordano 2000). A vast amount of evidence supports the idea that the abundance of frugivorous birds positively responds to temporal and spatial fluctuations of fruit resources (e.g., Guitián and Munilla 2008). This initially inspired the creation and testing of the fruit-tracking hypothesis (Wiens 1989). Hence, in fluctuating environments, the invasion of fleshy fruited plants may alter the temporal and/or spatial variations of fruit availability in otherwise “natural” systems (Tecco et al. 2013; Vergara-Tabares et al. 2016). Such alterations in fruit availability, it is hypothesized, may affect the abundance of frugivorous avian species. For example, if invasive species fructify synchronously with native species, fluctuation in fruiting should be exacerbated (e.g., Gleditsch and Carlo 2011), resulting in a pronounced difference in food availability between fruiting and non-fruiting periods. On the

other hand, if the invasive plants fructify asynchronously with the native species, fruit fluctuations should be attenuated, as natives and invasive plant species complement each other across seasons. From a community ecology point of view, in the last scenario the fruit provided by the invasive would represent a new temporal axis of resources in the community niche.

In some areas of the Chaco Mountain Woodland of central Argentina, invasive plants provide several novel resources for birds including nesting sites (Vergara Tabares and Peluc 2013) and fruit resources during a period of food shortage (Tecco et al. 2013; Vergara-Tabares and Rojas 2016). The majority of these fleshy fruited invasive plants (e.g., *Ligustrum* sp. and *Pyracantha* spp.) have a fruiting period (autumn–winter) asynchronous with the fruit production of native fleshy fruited plants [summer (Vergara-Tabares et al. 2016)], which suggests that current fluctuations of fruit availability may be reduced. Given that the invasion by fleshy fruited alien plants provides a new temporal food resource for frugivorous birds, and that in some areas such an invasion is still relatively moderate [i.e., there are easily distinguishable invaded and non-invaded sites (Giorgis et al. 2011)], we can use such study systems as comparative scenarios to evaluate how frugivorous birds respond to changes in food fluctuation. Such scenarios also allow us to assess the effect of the presence of a new temporal resource on bird abundance and, specifically, on the abundance of seed dispersers, which are likely linked to the spread of the invasive plants.

We tested predictions regarding the relationship between fruit availability and abundance of frugivorous birds by comparing bird abundance throughout the year between sites both invaded and non-invaded by *Pyracantha* spp. In the Chaco Mountain Woodland of central Argentina, non-invaded areas undergo a remarkable seasonal fluctuation of fleshy fruits produced by native flora [with fruit availability concentrated in the spring–summer seasons and drastically decreased during autumn–winter (Tecco et al. 2013; Vergara-Tabares et al. 2016)]. Yet, in areas invaded by *Pyracantha* spp., seasonal fruit fluctuation seems to be reduced, with fruit availability extending into autumn–winter months. Under these circumstances, and as predicted by the fruit-tracking hypothesis, we expected to observe an increase in the abundance of frugivorous birds at invaded sites and a reduction in their abundance at non-invaded sites between summer and autumn–winter. Additionally, invaded and non-invaded sites were expected to have similar frugivorous bird abundances during the summer, given the comparable fruit availability of native plants in all sites.

This study uses a natural experimental design that exploits invaded sites as the experimental treatment, and non-invaded sites as the experimental control. Additionally, our design intentionally separates out and minimizes

the effects of factors other than fruit availability that might influence bird abundances. For example, treatment sites used in our study contained relatively low densities of *Pyracantha* spp. and had floristic compositions similar to our control sites (Fig. S1, Supplementary material). We chose these sites in an attempt to reduce the confounding effects of changing habitat structure resulting from the invasive plant on avian abundance (e.g., Ayup et al. 2014). As such, if we can presume that moderate population densities of the invasive *Pyracantha* spp. do not substantively affect overall habitat structure, and thus, any observed changes in avian abundance reflect factors other than habitat structure (e.g., fruit availability), we would expect to see only increases in frugivorous birds, while other trophic guilds (sensu Yodzis 1982), such as granivores and insectivores, should remain the same. Therefore, our design includes counts of granivores and insectivores (that do not interact with *Pyracantha* spp. in any relevant way) as additional experimental controls.

Finally, changes in frugivorous bird abundance may have implications for seed-dispersal effectiveness of invasive shrubs. For example, if an increase in frugivorous birds during fruiting of *Pyracantha* spp. occurs due to an increase in abundance of legitimate seed dispersers, this may entail greater consumption of fruits from and greater seed dispersal of the invasive. Therefore, we additionally evaluated if the abundance of the dominant and common frugivores associated with *Pyracantha* spp. (Vergara-Tabares et al. 2016) increased during the fruiting season of these invasive shrubs.

Materials and methods

Study area

The study was carried out on the western slopes of the Sierras Grandes and Sierras de Comechingones between 900 and 1300 m a.s.l., Córdoba Province, Argentina. The plant community in the area corresponds to Chaco Serrano Woodland (Luti et al. 1979). Mean annual precipitation in the area is 700–800 mm (concentrated in the summer) and mean annual temperature is 17.5 °C [data retrieved from the station La Ventana (Acosta et al. 1992)]. The dominant tree species is *Lithraea molleoides* (Anacardiaceae), and common trees are *Acacia caven* (Fabaceae), *Celtis ehrenbergiana* (Celtidaceae) and *Bougainvillea stipitata* (Nyctaginaceae). Dominant shrub species are *Heterothalamus alienus* (Asteraceae), and species of the genera *Flourensia* and *Baccharis* (Cabido et al. 1998).

In the area, we selected six sites with similar topography, characterized by ravines with permanent streams, yet with contrasting plant invasion situations. Three of the sites (Las Calles, San Javier, and Los Hornillos) have been invaded

(hereafter, termed “invaded sites”) by *Pyracantha angustifolia* (Rosaceae) and *Pyracantha atalantoides*, which are fleshy fruited plant species native to eastern Asia that established mainly on stream margins but rarely on ravine slopes (personal observation). *P. atalantoides* produces fruit during early autumn to early winter and *P. angustifolia* produces fruit during mid autumn to late winter when fruit resources from native plant species are scarce or absent (Vergara-Tabares et al. 2016). Both species of *Pyracantha* (hereafter “*Pyracantha* spp.”) have the same architecture and other attributes as some native plant species such as *Condalia* spp. and *Schinus fasciculatus* (Tecco et al. 2006; Giantomasi et al. 2008). The other three sites selected (Las Rabonas, Travesia and Luyaba) have not yet been invaded by *Pyracantha* spp. (hereafter, termed “non-invaded sites”).

In order to control for additional factors that may affect the presence or abundance of birds, we selected the study sites within the same altitude (between 900 and 1100 m a.s.l.) and with similar plant community assemblages (mountain forests dominated by *L. molleoides*; Fig. S1, Supplementary material). Also, because of the close proximity of the study sites (i.e., the distance between the northernmost and southernmost sites is approximately 60 km) we assumed similar climatic conditions (precipitation and temperature) at all sites.

Bird surveys

We conducted a minimum of 20 point counts during five time periods during 2015 (6–11 January, 28 March–2 April, 29 July–4 August, 10–15 October, and 26–31 December) at each of the six study sites (a total of 772 point counts). Locations of point counts were established randomly, yet were separated by at least 150 m to avoid double counting between neighboring points. At each point, we waited 5 min as a settling down period before starting counting (Bibby et al. 2000), after which we recorded all individuals heard or seen within a 40-m fixed radius during 10 min. Surveys were conducted only under favorable weather conditions, within a 4-h period after sunrise.

Fruit abundance

To provide evidence of the different patterns of fruit resource fluctuation between invaded and non-invaded sites, we estimated fruit availability (i.e., from the fleshy fruited species that are effectively consumed by birds) in both invasion situations. At each site and during the same sampling periods described above, we established five 20 × 50-m plots where we counted the total number of fruits per plant for all the plant species with fleshy fruits (including trees, shrubs, vines and herbaceous species). When fruit abundance per plant was high (e.g., *Pyracantha* spp. or *L. molleoides*), we

estimated the amount of fruit produced per individual by multiplying the average number of fruits on three representative branches by the total number of branches with fruit in that plant (Ferrerias and Galetto 2010). Fruit abundance is expressed as the mean number of fruits per plot per invasion situation and per period.

Categorization of trophic guilds

Given that in the study area all frugivorous species consume not only fruits from native plants, but may also include either insects or seeds in their diets, we provide a table detailing a more precise categorization of each species' diet according to feeding guilds (Tables S2–4, Supplementary material). In this study, we considered members of the frugivorous guild all species that consume fruits of native and invasive plants, including all frugivorous birds known to consume fruit of *Pyracantha* spp. in the study system (described in Vergara-Tabares et al. 2016). This group is composed of Chiguanco Thrush (*Turdus chiguanco*), Creamy-bellied Thrush (*Turdus amaurochalinus*), Rufous-bellied Thrush (*Turdus rufiventris*), Slaty Thrush (*Turdus nigriceps*), Spotted-winged Pigeon (*Patagioenas maculosa*), Monk Parakeet (*Myiopsitta monachus*), Gray-hooded Parakeet (*Psilpsiagon aymara*), Golden-billed Saltator (*Saltator aurantirostris*), Blue-and-yellow Tanager (*Pipraeidea bonariensis*), Hepatic Tanager (*Piranga flava*), Golden-breasted Woodpecker (*Colaptes melanochloros*), Brown Cacholote (*Pseudoseisura lophotes*), Chalk-browed Mockingbird (*Mimus saturninus*), and White-banded Mockingbird (*Mimus triurus*). In our reported findings, we have purposely excluded migrant species from the frugivorous guild because the presence of these species could alter abundance patterns due to idiosyncratic factors associated with the species other than the availability of fruit resources. That said, an analysis with the inclusion of migratory birds did not affect the observed patterns (Table S6, Fig. S2, Supplementary material). In addition, by confining the frugivorous group to species for which we are certain about their consumption of *Pyracantha* spp. fruit, we are able to use the term “resource availability” instead of using less precise terms such as “fruit abundance” (Wiens 1989). Finally, we categorized birds within the granivorous and insectivorous trophic guilds based on bibliographic citations (Blendinger and Ojeda 2001; Malizia 2001; De la Peña 2005; Dardanelli et al. 2006; Marone et al. 2008; Salvador et al. 2017) and personal observations and, similarly, only considered resident species. The latter trophic guilds comprise the following species: granivores—Rufous-collared Sparrow (*Zonotrichia capensis*), Black-and-chestnut Warbling Finch (*Poospiza nigrorufa whiti*), Saffron Yellow Finch (*Sicalis flaveola*), Hooded Siskin (*Spinus magellanicus*), Band-tailed Seed-eater (*Catamenia analis*), Ultramarine Grosbeak (*Cyanocompsa brisonii*), Many-colored Chaco

Finch (*Saltatricula multicolor*), and Stripe-capped Sparrow (*Rynchospiza strigiceps*) (see Table S3, Supplementary material for details about the abundance of each species); and insectivores—House Wren (*Troglodytes aedon*), Brown-capped Redstart (*Myioborus bruniceps*), Stripe-crowned Spinetail (*Cranioleuca pyrrophia*), Masked Gnatcatcher (*Polioptila dumicola*), Sooty-fronted Spinetail (*Synallaxis frontalis*), Variable Antshrike (*Thamnophilus caerulescens*), Greater Wagtail Tyrant (*Stigmatura budyoides*), Tyrannulets (*Serpophaga* spp.), Short-billed Canastero (*Asthenes baeri*), Masked Yellowthroat (*Geothlypis aequinoctialis*), Southern Beardless Tyrannulet (*Camptostoma obsoletum*), Chaco Earthcreeper (*Tarphonomus certhioides*), and Pearly Vented Tody Tyrant (*Hemitricus margaritaceiventer*) (see Table S4, Supplementary material for details about the abundance of each species).

Statistical analysis

To examine patterns of fruit fluctuation between invaded and non-invaded sites, we used a generalized linear mixed model (GLMM). Factors included in the model were invasion situation (invaded and non-invaded), time period (January, March–April, July–August, October and December) and their interaction. As a response variable, we included fruit number per plot, and sites were included as random factors. We assumed a negative binomial distribution of the error (Zuur et al. 2009).

We used a GLMM to analyze the effect of *Pyracantha* fruit availability on the abundance of trophic guilds (i.e., frugivorous, granivorous and insectivorous birds) and of dominant or common frugivorous species associated with *Pyracantha* spp. (i.e., Chiguanco Thrush, Creamy-bellied Thrush, Spot-winged Pigeon and Golden-billed Saltator). Factors included in the model were invasion situation (invaded and non-invaded), time period (January, March–April, July–August, October and December) and their interaction. In addition, the sites were included as a random factor in the model in order to account for repeated measures in the same sites during different time periods. Because in all of the cases the response variable refers to counts, we assumed a negative binomial distribution of the error to model the over-dispersion (Zuur et al. 2009). The package glmmADMB (Skaug et al. 2012) allowed us to develop all GLMM analyses using R (R Core Team 2014).

Results

Fluctuation in fruit availability

Abundance of fleshy fruits available to birds was significantly affected by the interaction between invasion situation

and time period ($\chi^2_{4146} = 48.32$; $P < 0.001$). Fruit abundance was similar between invasion situations during January and December, when all the fruit in the system was produced by native plants (see Table S1, Supplementary material). During autumn–winter, fruit abundance was virtually zero at non-invaded sites (Fig. 1a) but remained at about 20,000 fruits/plot in invaded sites.

Fluctuation in bird abundance

Of the 772 point counts conducted during this study, we recorded a total of 11,503 individuals representing 106 species (see Tables S2–S5, Supplementary material for details about the abundance of each species). We classified 5364

individuals in the frugivorous trophic guild (46.6% of all counted birds). The most abundant species throughout the year, considering all study sites, was the Chiguanco Thrush (1625 individuals, 14.1% of all individuals recorded). This species is a legitimate seed disperser of *Pyracantha* spp. and of other fleshy fruited native plants (e.g., Vergara-Tabares et al. 2018). The number of individuals in insectivorous and granivorous trophic guilds totaled 2026 (17.6%) and 1454 (12%), respectively.

Regarding the trophic guilds, the interaction between invasion situation and time period significantly affected the abundance of frugivorous birds ($\chi^2_{4768} = 71.57$; $P < 0.001$). The abundance of frugivorous birds did not vary throughout the year at non-invaded sites, whereas at invaded sites, the abundance of frugivorous increased towards autumn–winter.

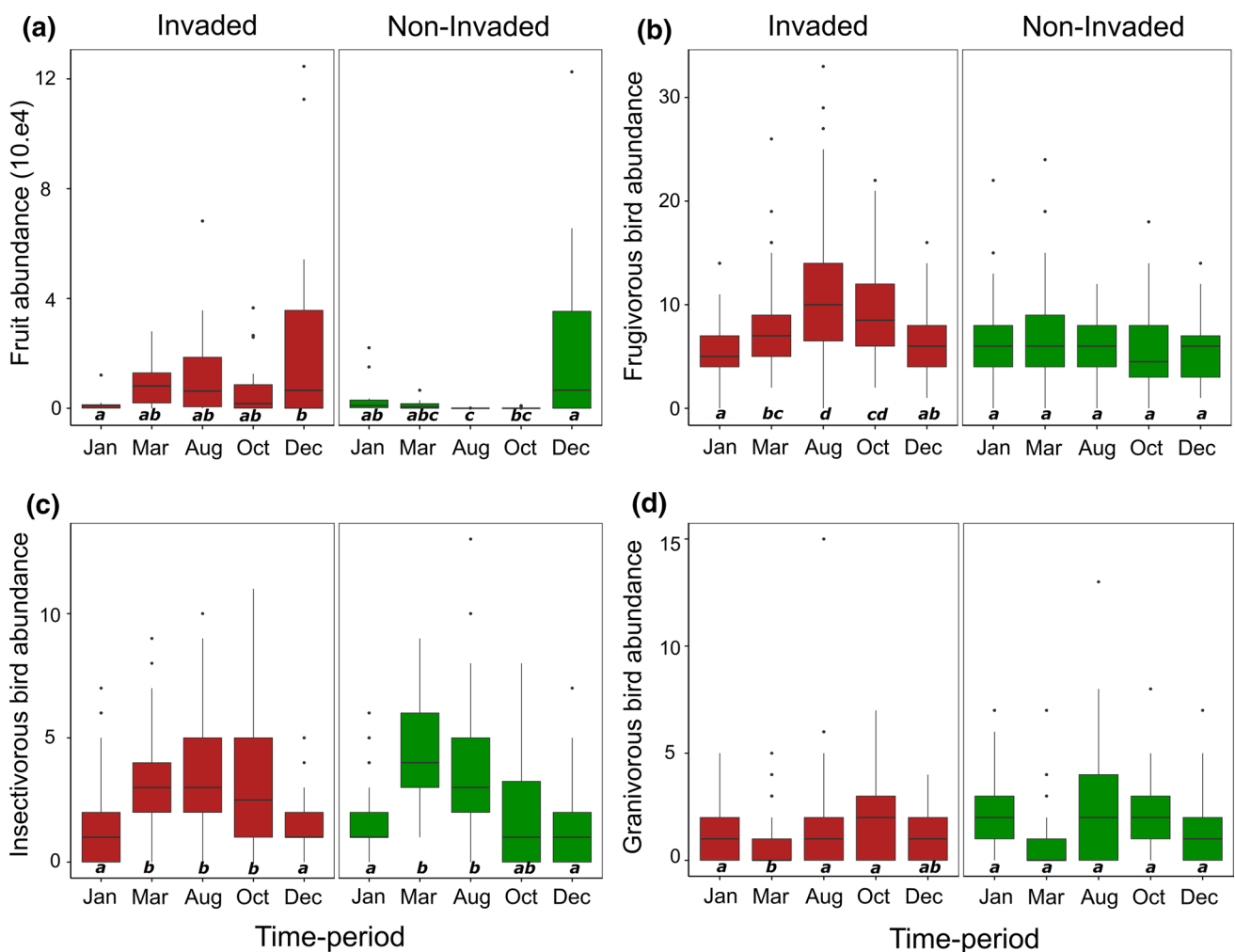


Fig. 1a–d Spatiotemporal fluctuations over five periods of three bird feeding guilds and fruit resources at three sites invaded by *Pyracantha* spp. (red) and three non-invaded sites (green) in mountains of central Argentina. **a** Fleshy fruit abundance per plot, **b** frugivorous bird abundance per point count, **c** insectivorous bird abundance per point count, and **d** granivorous bird abundance per point count for

each period and situation. The 1-year study period started in January 2015. Lines in boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range, and circles are outliers. Different lowercase letters indicate significant differences between periods for each situation (color figure online)

During spring–summer the abundance did not differ between invasion situations (Fig. 1b), yet during autumn–winter the abundance of frugivorous was significantly greater at invaded sites.

In contrast, the abundance of granivorous birds was significantly affected by the time period ($\chi^2_{4768} = 17.11$; $P = 0.002$), but not affected by the invasion situation or the interaction of these factors ($\chi^2_{4768} = 3.44$; $P = 0.064$ and $\chi^2_{4768} = 1.47$; $P = 0.83$, respectively). The abundance of granivorous birds was similar between invasion situations in the majority of periods, except during July–August when the abundance was higher at non-invaded sites (Fig. 1d).

Finally, the abundance of insectivorous birds was affected by the interaction between invasion situation and time period ($\chi^2_{4768} = 11.38$; $P = 0.023$). During spring–summer, the abundance of insectivores mildly decreased but did not show a clear pattern associated with invasion situation (Fig. 1c).

To gain more insight into the effect of *Pyracantha* fruit availability on the frugivorous birds, we focused on the dominant and most common bird species that consume the invasive fruit (Fig. S3, Supplementary material for methodology of categorization and results), which represented 70% of the total frugivorous abundance (3763 individuals from 5364). Within this group, two species are legitimate *Pyracantha* spp. seed dispersers (Chiguanco Thrush and Creamy-bellied Thrush), one is a seed predator (Spot-winged Pigeon) and the other considered a pulp consumer and/or seed predator (Golden-billed Saltator). The abundance of the Chiguanco Thrush, the dominant species in the system, was significantly affected by the interaction between invasion situation and time period ($\chi^2_{4768} = 111.68$; $P < 0.001$). The highest abundance of this species occurred during July–August at invaded sites and did not differ between invasion situations during spring–summer (Fig. 2a). Creamy-bellied Thrush abundances showed a similar pattern ($\chi^2_{4768} = 12.57$; $P = 0.013$), but were lower (Fig. 2b). Regarding the seed predator and pulp consumer Golden-billed Saltator, its abundance was affected by the interaction between invasion situation and time period ($\chi^2_{4768} = 11.75$; $P = 0.019$), with a similar abundance pattern between invasion situations and time periods, except during October when the abundance was higher at invaded sites (Fig. 2d). Finally, the seed predator the Spot-winged Pigeon, was not affected by the invasion situation ($\chi^2_{1768} = 0.30$; $P = 0.582$), or by the interaction between invasion situation and time period ($\chi^2_{4768} = 8.73$; $P = 0.068$), and only the time period showed a significant effect on its abundance ($\chi^2_{4768} = 59.41$; $P < 0.001$; Fig. 2c).

Discussion

This study represents, to the best of our knowledge, one of the few contributions to an understanding of the effects of fruiting plants community structuration—which is a result

of plant invasion—on the temporal dynamics of frugivorous and seed-disperser bird species (Gleditsch et al. 2017). The ecological scenario analyzed here, which depicts asynchronous fruiting between native and invasive fleshy fruited plants, provided a novel approach for the assessment of fruit tracking by birds and the effect of fleshy fruited invasive plants on the abundance of their seed dispersers. Moreover, this approach contrasts with previous attempts to analyze the effects of plant species introductions, which mostly focused on seed-dispersal networks or plant species that fructify synchronously with native plants (Traveset and Richardson 2006; Gleditsch and Carlo 2011; Gleditsch et al. 2017).

The results presented here indicate that the abundance of frugivorous birds changes in response to the availability of a new temporal resource provided by an invasive fleshy fruited plant in the early stages of invasion. We show that the abundance of frugivorous birds did not differ between invaded and non-invaded sites during spring–summer, which are periods of similar fruit availability (provided only by native plants). Yet, during autumn–winter, frugivore abundance increased at invaded sites (coinciding with high fruit availability provided by the invasive *Pyracantha* spp.), whereas it did not change at non-invaded sites. Contrary to what we observed for the frugivorous guild, as expected, granivorous and insectivorous birds did not show a pattern clearly associated with fruit availability (interaction between time period and invasion situation) or with the presence of the invasive *Pyracantha* spp. These findings suggest that changes in frugivore abundance may be attributable to changes in food resources and not potential changes in habitat structure resulting from the plant invasion. Among the dominant or common frugivores, we observed an increase in the abundance of only the legitimate seed dispersers (Chiguanco and Creamy-bellied thrushes), which increased in response to changes in *Pyracantha* fruit availability.

These patterns taken together suggest that modification of the natural fluctuation of fruit availability affects the abundance of frugivorous birds that are able to track fruit variation (at least as evidenced at the invaded sites). Also, the abundance of legitimate seed dispersers of the invasive *Pyracantha* spp. was positively associated with its fruiting, which may have contributed to the effectiveness of its seed dispersal. It is possible that the asynchronous phenology of *Pyracantha* and its abundant fruit production relative to fleshy fruited plants in the native community (Vergara-Tabares et al. 2016) influence frugivore abundance even at low invasive plant densities. In addition, fruit tracking by seed-disperser birds may be one of the causal mechanisms contributing to the spread of this exotic plant, promoting its invasion.

Non-invaded sites in our study system, similar to temperate systems and seasonal tropical forests, show a unimodal pattern of fruit fluctuation (Fenner 1998). At

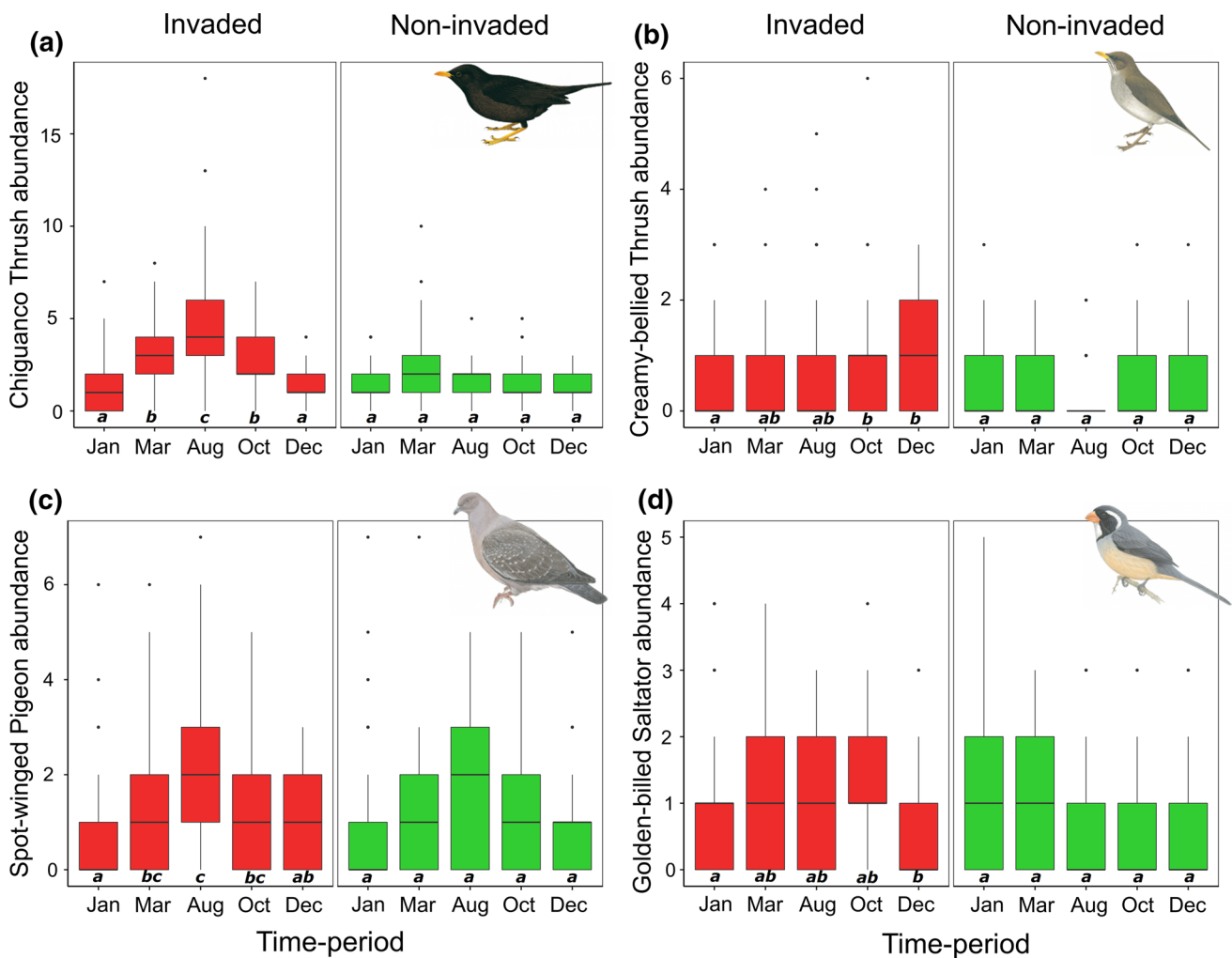


Fig. 2a–d Spatiotemporal fluctuations over five periods of dominant and common bird species belonging to a frugivorous assemblage at three sites invaded by *Pyracantha* spp. (red) and three non-invaded sites (green) in mountains of central Argentina. **a** Seed disperser Chiquanuco Thrush abundance per plot, **b** seed disperser Creamy-bellied Thrush abundance per point count, **c** seed predator Spot-winged Pigeon abundance per point count, and **d** pulp consumer Golden-

billed Saltator abundance per point count for each period and situation. The 1-year study period started in January 2015. Lines in boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range, and circles are outliers. Different lowercase letters indicate significant differences between periods for each situation (color figure online)

non-invaded sites, fruit availability was virtually zero during autumn–winter. During summer, we observed an increase in fruit availability under both invasion situations, primarily due to high fruit production of the native dominant tree *Lithraea molleoides*. Other studies have demonstrated the fluctuation of fruit resources in seasonal environments, as well as seasonal fluctuations of avian frugivore abundances in those environments (e.g., Varela 2003; Codesido and Bilenca 2004). However, such variation in bird abundance has been attributed to the total or partial migration dynamics of avian species, whereas in our study we excluded migratory birds from the analysis specifically to focus on resident species (although the

inclusion of migratory birds did not affect the reported patterns; Table S6, Fig. S2, Supplementary material).

We confirmed that fruiting by *Pyracantha* spp. can modify the seasonal fruit fluctuation of the resident plant community. Our results at invaded sites suggest that resident frugivorous may be capable of detecting changes in fruit availability and respond positively to increments of this kind of resource during periods of food shortage (autumn–winter). On the other hand, the pattern observed at non-invaded sites, characterized by a stable abundance of frugivorous birds throughout the year, does not seem to provide support for the fruit-tracking hypothesis, as it predicts a reduction in frugivorous bird abundance during periods of fruit shortage.

However, the stable population values may be explained by the capacity of these birds to shift their diets in response to changing resource availabilities. In other words, these birds should be adapted to resource fluctuations by eating a broad diet (Witmer and Van Soest 1998; Jordano 2000; Carnicer et al. 2008; Lehouck et al. 2009). In fact, many of the species that comprise the frugivorous assemblage may consume fruits or arthropods. For example, Chiguanco Thrush feeds on arthropods during autumn–winter at non-invaded sites (De la Peña 2005; Rojas et al. 2015). Taking into account the patterns of frugivorous abundance at invaded and non-invaded sites, one can infer that the flexibility of these populations could make them resilient in the face of global climate change (Mulwa et al. 2013).

Many studies that have evaluated the relationship between fruit availability and frugivorous abundance refer to idiosyncratic species' responses to fruit availability (e.g., Malizia 2001; Guitián and Munilla 2008; Blendinger et al. 2012; Mulwa et al. 2013). Studies undertaken in the Mediterranean region or South America reported that abundances of species of the Turdidae family were directly associated with fruit availability (Guitián and Munilla 2008 and references therein). By disentangling the pattern observed here for frugivorous abundance, we found that only some species, including two *Turdus* species, positively responded to changes in the abundance of fleshy fruits provided by *Pyracantha* spp., whereas other common species were not associated with the availability of the fruits of invasive species. The most notorious case of this was the Chiguanco Thrush, the abundance of which was five times greater during July–August at invaded sites than at non-invaded sites. The abundance of the Creamy-bellied Thrush also changed in relation to the availability of fruit of *Pyracantha* spp. (although its abundance increased at a lower magnitude than that of the Chiguanco Thrush). The lack of association between the abundance of some frugivorous species that destroy seeds and *Pyracantha* spp. fruit availability (Fig. 2c) may be due to the capacity of these species to feed on or to select other kinds of resources, such as seeds or arthropods (Freeland 1973; Beltzer et al. 1997; Linz and Hanzel 1997). This lack of association indicates that patterns of abundance observed for the entire frugivorous assemblage may be due to abundances of *Turdus* species. The association between these thrushes and abundance of invasive fruits is remarkable because it has direct implications on qualitative and quantitative elements of the invasive *Pyracantha*'s effective seed dispersal (Vergara-Tabares et al. 2016; Vergara-Tabares 2017).

The relationship between the availability of fruit produced by the invasives and frugivore abundance may affect the recruitment of these plant species, depending on which functional frugivorous group prevails in this association. Assuming that the abundance of common frugivores that

consume fruit of a given plant species is directly related to seed-dispersal effectiveness, it is plausible that in our study system an increase in thrush abundance contributes quantitatively to seed dispersal of *Pyracantha* spp. Given that frugivores are easily satiated and typically disperse only a proportion of the available seed pool (García et al. 2001), the increase in the abundance of seed-disperser birds may lead to a decrease in the satiation of the bird population, or, in other words, an increase of the proportion of dispersed seeds (Hampe 2008). For example, disperser satiation due to the high fruit offer of *Pyracantha* spp. (Vergara-Tabares et al. 2016; Table S1, Supplementary material) is conceivable. If this phenomenon actually occurs in our study system, in a hypothetical scenario in which seed disperser abundance does not increase during *Pyracantha* spp. fruiting, disperser satiation should increase (Hampe 2008), which should lead to a decrease in seed-dispersal effectiveness for *Pyracantha* spp. Based on the increase of seed disperser abundance observed in this study during *Pyracantha* fruiting, disperser satiation should be at a higher threshold leading to higher fruit consumption and seed dispersal of these invasive plants. Although frugivores are quickly satiated when consuming abundant fruiting species, some recent findings suggest that they still eat a variety of other fruits, especially from infrequently available plant species (Carlo and Morales 2016; Morán-López et al. 2018). Despite the fact that the great fruit abundance of *Pyracantha* spp. may lead to the satiation of seed dispersers, the increase in seed disperser abundance during the fruiting of invasives may promote the seed dispersal of other native fleshy fruited plants (e.g., *Ligaria cuneifolia* and *Jodinia rombigolia*). This may occur if anti-apostatic mechanisms of seed dispersal are operating, for example, in our study site (Carlo and Morales 2016).

Finally, the observed changes in abundance for specific guilds and some particular species linked to fruit production of invasive shrubs may have consequences for higher organizational levels. From the perspective of community ecology, it is arguable that the temporal availability of fruit of invasive plants induces changes in the bird assemblage. If fruit availability affects mainly the abundance of frugivorous species, including the most abundant species, but does not affect other trophic guilds, it is plausible that the avian community decreases in evenness during the period of *Pyracantha* spp. fruiting in invaded sites (e.g., López de Casenave and Marone 1996). In such cases, the new temporal resource provided by the invasive *Pyracantha* would act as a bottom-up bird community structurer (Ostfeld and Keesing 2000). This pattern would indicate the strength of the effects of positive interactions on community structuration.

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