Do frugivores exert selection on fruiting phenology? Potential scenarios across three plant populations of a Neotropical vine, *Passiflora caerulea*

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Abstract
Fruiting phenology is a critical aspect of plant fitness, as it is directly linked to the next-generation offspring delivery. Both abiotic and biotic factors presumably exert natural selection on plant phenology. Despite the role of climate in shaping fruiting phenology is well established, whether frugivores exert phenotypic selection on fruiting phenology has not yet been tested. We estimated the regime and magnitude of frugivore-mediated selection on fruiting phenology in three distant (> 500 km) populations of the Blue Passionflower (*Passiflora caerulea*) along one year. We measured phenological fruit traits (fruiting onset, fruiting peak, length of the fruiting season) and fruit crop size, and used animal fruit removal as a fitness component. We found highly variable fruiting phenologies between populations, yet phenological stages in lower latitudes were longer than in higher latitudes. One population showed a positive relationship between fruiting onset and fruiting peak among individuals, indicating that fruiting later in the season delayed the fruiting peak. Frugivores favored large fruit crop sizes in the three populations and early fruiting onsets in two populations. In two populations, frugivores selected favorable combinations of fruit crop size and fruiting peak (favoring plants with large crops and early fruiting peaks), as well as favorable combinations of fruiting peak and the length of the fruiting season (favoring plants with early fruiting peaks and extended fruiting seasons). Some degree of similarity in selection patterns among populations suggests that, despite strong geographic variation in climate and animal assemblage composition, some level of functional redundancy occurs in terms of phenotypic trait selection. Overall, our results show that fruiting phenology may be a highly variable life-history trait of plant populations, and support the idea that biotic interactors, conditional on heritable traits and selection pressures sustained over time, could potentially shape phenological fruiting characteristics.

Keywords Frugivore-mediated selection · Phenotypic selection · Plant-animal interactions · Seed dispersal · Selection gradients
Introduction

Phenology, defined as the timing of periodic biological activity, is a crucial life-history trait of plants since it strongly determines fitness through sexual reproduction (Fenner 1998). Despite its importance, phenology is often an overlooked aspect of plant trait evolution (Cleland et al. 2007). In recent decades, however, ecologists have shown a growing interest in phenological patterns, due to concerns in how changing climate could impact the timing of life cycles of plants (Cleland et al. 2007; Gordo and Sanz 2010; Wolkovich et al. 2012). In turn, this interest has given a lesser priority to the role of biotic interactions in shaping plant phenology, particularly fruiting schedule (Elzinga et al. 2007; van Schaik et al. 1993). Indeed, the vast majority of studies of selection on plant phenology has focused on flowering phenology and how pollinators exert selection pressures on flower traits (Elzinga et al. 2007; Munguía-Rosas et al. 2011; Austen and Weis 2015; Chapurlat et al. 2015; García et al. 2020). Although these studies have provided valuable knowledge about phenological components under pollinator-mediated selection pressures, later phenological stages of plant phenology, including fruit and seed production, have typically been neglected (González-Varo et al. 2019).

As previous studies in pollination systems have suggested (Rathcke and Lacey 1985; Parra-Tabla and Vargas 2004; Aizen and Vázquez 2006), the “competition avoidance hypothesis” (Snow 1965) has been advocated as the process influencing frugivore selection on fruiting phenology. This hypothesis has been a long-standing view in animal-fruit interactions, and states that co-fruiting plants compete for seed dispersers (Herrera 1981; Wheelwright 1985; van Schaik et al. 1993; Burns 2005; Rumeu et al. 2019). Therefore, fruiting plants sharing a common assemblage of frugivores should stagger their fruiting seasons to minimize competition for dispersers (Snow 1965). From an eco-evolutionary perspective, fruiting onset should be a critical phenological trait under phenotypic selection, which is expected to be selected against by frugivores. For instance, Wheelwright (1993) and Alcántara et al. (1997) found that early-ripening individuals of Ocotea tenera and Olea europaea, respectively, showed higher fruit removal than late-ripening trees. On the other hand, selection on the season length has shown idiosyncratic results, as long fruiting seasons could also promote facilitation by increasing visitation rates in less productive plants (Thompson and Willson 1979; Albrecht et al. 2015). These results suggest that a more comprehensive view of the mechanisms underlying the interaction between frugivores and fruiting phenology is still needed.

Therefore, at least three major factors should be taken into account to develop a broader perspective of animal-mediated selection on fruiting phenology (Fig. 1): (1) phenology is not a phenotypic trait itself, but several covarying traits define it (e.g., fruiting onset, fruiting peak, length of the fruiting season) and have different consequences for frugivore-mediated selection (Howe and Estabrook 1977), (2) fruiting phenology correlates with previous phenological stages, e.g., earlier flowering plants tend to fruit earlier (Eriksson and Ehrlén 1991; Lacey et al. 2003), and are both strongly linked to climatic factors (van Schaik et al. 1993; Cleland et al. 2007; Ting et al. 2008), and (3) the number of ripe fruits (fruit crop size) is a primary trait under selection, as it constrains resource allocation in plants (Austen et al. 2017) and it represents a strong visual cue for frugivores (Palacio and Ordano 2018; Schupp et al. 2019). So, the expected outcome of natural selection on a given phenological trait will depend on the combination of these three major factors. Often the first plants to produce ripe fruits attract many frugivores (Wheelwright 1985; Burns 2002), and competition for seed dispersers is the hypothesized mechanism influencing selection.
Variation in fruiting phenology

Selection regimes

Assumptions

(a) Competition without fruit trait covariation

(b) Facilitation without fruit trait covariation

(c) Competition with fruit trait covariation

(d) Facilitation with fruit trait covariation

Fig. 1 Hypothetical outcomes of frugivore-mediated selection on fruiting phenology. Left panels (‘Variation in fruiting phenology’) represent variation in fruit production between plants (individual curves) along a reproductive season in one population. Middle panels (‘Selection regimes’) represent selection exerted by frugivorous animals, in which a surrogate for fitness is often used (e.g., fruit or seed removal). Right panels (‘Assumptions’) represent assumptions on relationships between flower and fruit traits. The colors of the curves correspond with point colors in the middle and right panels.

(a) When plants face competition for dispersers by staggering their seasons and there are no covariations between fruit traits, frugivores should favor early fruiting onsets, short fruiting seasons and large fruit crops.

(b) If plants facilitate each other by overlapping their phenologies and there are no covariations between traits, frugivores should favor late fruiting onsets, long fruiting seasons, regardless of fruit crop size.

(c) Alternatively, if plants face competition and there is a covariation between fruiting earlier and producing less fruits, then selection should be stabilizing on fruiting onset, length of the fruiting season, and fruit crop size.

(d) If plants face facilitation with a covariation between fruiting earlier and producing less fruits, selection should favor late fruiting onsets, long fruiting seasons and large fruit crops. These four scenarios assume that fruiting covaries with flowering, which results in indirect selection on flowering onset (dashed lines) by frugivores on fruiting phenology. Therefore, selection should favor early-flowering, and consequently, early-fruiting plants with a short phenology and large fruit crop size (Fig. 1a; Howe and Estabrook 1977; Alcántara et al. 1997; Palacio and Ordano 2018). Alternatively, if facilitation is the mechanism driving frugivore-mediated selection on phenology, then selection should promote late-fruiting plants with long fruiting seasons, regardless of the number of fruits produced (Fig. 1b). These predictions assume that fruiting onset is independent of fruit crop size. If plants face a trade-off between fruiting earlier and producing less fruits...
as a result of having fewer resources to invest in reproduction (size-time trade-off; Austen et al. 2017), selection would favor either a stabilizing pattern on fruiting onset and length of the fruiting season (if plants compete, Fig. 1c; Elzinga et al. 2007), positive directional selection on fruiting onset and length of the fruiting season (if plants facilitate each other, Fig. 1d), or correlational selection on favorable trait combinations for animals (e.g., plants with large crops but late fruiting onsets and vice versa; Sobral et al. 2010).

To our knowledge, no study has assessed frugivore-mediated selection on phenological fruiting traits. Therefore, we estimated the regime and magnitude of phenotypic selection on fruiting phenology (fruiting onset, fruiting peak, and length of the fruiting season) on a South American endemic vine, the Blue Passionflower (Passiflora caerulea). To this end, we monitored flowering and fruiting phenology and quantified animal fruit removal of three plant populations from Argentina during a 1-year field study.

**Materials and methods**

**Study area**

The study was carried out in three study sites from central and northern Argentina, located at a minimum distance of 525 km (Fig. 2). The plants in each of these sites were thus considered as three distinct biological populations. The study sites are located in temperate (La Plata and Santa Fe) and subtropical (Tucumán; sensu Corlett 2013) urban and peri-urban areas in which two major habitat types can be recognized: (a) built-up areas including a built-up city center and residential areas with numerous gardens and tree avenues, and (b) parks distributed over the study area composed mainly of mature trees.

(1) La Plata (34°55′S, 57°57′W, 26 m a.s.l., 196,527 inhabitants), Buenos Aires province (hereafter “La Plata”). Main tree species are Jacaranda mimosifolia, Melia azedarach, Citrus ×aurantium, Platanus acerifolia, Tilia ×molteki, Acer negundo, and Ligustrum lucidum (Delucchi et al. 1993). The average annual rainfall is 1,007 mm, and the average annual temperature is 15.8 °C.

(2) “Reserva Ecológica de la Ciudad Universitaria U.N.L. El Pozo” (31°38′S, 60°40′W, 25 m a.s.l.), Santa Fe province (hereafter “Santa Fe”). This is a small nature preserve of 12 ha, located on the outskirts of Santa Fe city and represents a small fraction of the Paraná river floodplain (Cardozo et al. 2008). Main trees are Erythrina crista-galli, Sapient haematospermum, Salix chilensis, and Tessaria integrifolia, but there is also
a grassland with a few tree species, such as *Vachellia caven* and *Celtis tala* (Cardozo et al. 2008). The average annual rainfall is 977 mm, and the average annual temperature is 18.5 °C.

(3) San Miguel de Tucumán (26°49′S, 65°13′W, 431 m a.s.l., 694,327 inhabitants), Tucumán province (hereafter “Tucumán”). The main trees in the sampled area are *Handroanthus* spp., *Ligustrum lucidum*, *Morus* spp., *Jacaranda mimosifolia*, *Bauhinia variegata*, *Tipuana tipu*, *Peltophorum dubium*, and *Citrus ×aurantium* (Grau and Kort-sarz 2012). The average annual rainfall is 966 mm, and the average annual temperature is 19.3 °C (Minetti 2005; García et al. 2018).

**Study species**

The Blue Passionflower *Passiflora caerulea* L. (Passifloraceae) is a native vine from South America, 2–10 m in height, distributed through southeastern Brazil, Bolivia, Paraguay, Uruguay, Chile, and Argentina (Killip 1938; Deginani 2001). It grows in both xerophytic and wet forests, on modified, sandy, clayey, and rocky soils, from 0 to 1400 m a.s.l. (Deginani 2001). It spreads over other plants, wire and iron fences, light poles, and other human-made structures (Deginani 2001). It occurs in rural, peri-urban and urban areas, being more common and abundant in the latter two habitat types. It produces large conspicuous hermaphroditic flowers (Fig. 3), 40–90 mm radius, and is characterized as an insect-pollinated self-incompatible species (García and Hoc 1997; Torres et al. 2012; Varela et al. 2016). Fruits are large berries, orange when ripe, 43.1 ± 0.3 mm in length and 33.8 ± 0.2 mm in width (*n* = 365 fruits; Bandeira et al. 2016). Each fruit contains an average of 131.8 ± 72.2 seeds (*n* = 211 fruits; FX Palacio, unpubl. data), 4–5 mm in length, enclosed by red fleshy arils (Deginani 2001). Fruits and seeds are mainly consumed and dispersed by common and resident birds, including *Turdus rufiventris*, *Paroaria coronata*, *Zonotrichia capensis*,

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**Fig. 3** Phenological stages of *Passiflora caerulea*. a Flower bud, b flower, c unripe fruit, d ripe fruit, e dry fruit, and f pecked fruit
Saltator aurantiirrostris, S. coerulescens, and Thraupis sayaca (Palacio 2019; JF Cataudela, unpubl. data; Supplementary Table S1). Due to the large fruit size constraining fruit swallowing, all bird species peck the fruit ingesting both seeds and the peel, regardless of their typical fruit-handling behavior described in the literature (gulpers vs. mashers; Levey 1987). Therefore, those bird species typically considered gulpers (e.g., Turdus rufiventris) and mashers (e.g., Thraupis sayaca) presumably act as effective seed dispersers (sensu Schupp et al. 2017). Also, small mammals would potentially eat the fruit, as it has been observed in other members of the family (Williams et al. 2000; Beavon and Kelly 2015), and ancient people may have acted as seed dispersers (Gremillion 1989). Moreover, the large fruit size (>10 cm in diameter) and number of seeds (>100) suggest that the Blue Passionflower could have been related to an anachronic syndrome of dispersal by large extinct vertebrates (Guimarães et al. 2008; Pires et al. 2014). Blue Passionflower phenology has been poorly studied; it blooms and fructifies nearly all year round, with higher intensity between September and May (Deginani 2001; Eynard et al. 2017).

**Plant phenology and fitness measurement**

From Oct. 2018 to Oct. 2019, we monitored flowering and fruiting phenology on 17 (La Plata), 25 (Santa Fe), and 20 (Tucumán) focal plants at biweekly intervals. At each sampling day, we recorded five phenological stages (Fig. 3): (1) the number of unopened flower buds, (2) the number of open flowers (i.e., flower display), (3) the number of unripe (green) fruits (after fruit-set but before attainment of the characteristic hue color, shape, and consistency of ripe fruit), (4) the number of ripe (orange) fruits, and (5) the number of dry fruits (without the characteristic hue color and consistency of ripe fruits). To quantify animal fruit removal and use it as a fitness estimator in natural selection analyses (see Data analyses), we recorded the number of fruits with pieces of peel or pulp plus seeds removed (hereafter fruits consumed) at each sampling day (Fig. 3). All the pecked fruits recorded were mature fruits. Due to the size and conspicuousness of flowers (Fig. 3b) and to the fact that anthesis lasts around 24–48 h (Amela García and Hoc 1997), we could be sure that the number of flowers recorded per sampling day were only counted once. We therefore estimated the total number of flowers produced per plant by adding the number of flowers recorded along the season. It should be noted that this method likely underestimated the number of flowers, because we could have missed flowers that opened between sampling days. Fruits, in contrast to flowers, remain firmly attached to their stalks until the end of the fruiting season, and more rarely fall to the ground (Deginani 2001). Thus, the total number of ripe fruits per plant (i.e. fruit crop size) was estimated as the maximum number of ripe fruits recorded in the fruiting season. Fruit removal was estimated as the maximum number of fruits consumed in 1 year.

**Data analyses**

**Phenology description**

Due to the intrinsic periodic nature of plant phenology, it is more appropriate to use a circular instead of a linear scale (Morellato et al. 2010; Mendoza 2020). Classical circular statistics follow Mardia and Jupp (2009) (see Supplementary Methods S1). Given that the three populations showed two conspicuous flowering and fruiting annual peaks, seasonality
of phenological stages was tested using the Hermans-Rasson test, which outperforms the classical Rayleigh test in multimodal situations (Landler et al. 2019).

For each plant of each population, we described four phenological traits: (1) flowering onset, (2) fruiting onset, (3) fruiting peak, and (4) length of the fruiting season. Flowering and fruiting onset were quantified as the first sampling day in which at least one open flower and one mature fruit, respectively, were recorded. The fruiting peak was estimated as the modal angle (date) of fruit crop size (Morellato et al. 2010). The length of the fruiting season, an estimate of the fruit maturation period, was defined as one standard deviation around the mean fruiting time, weighted by the fruit crop size recorded in each sampling day (Burns 2005; Supplementary Methods S1).

To assess the relationship between phenology (flowering onset, fruiting onset, fruiting peak, and length of the fruiting season) and fruit crop size, we used several measures of correlations, according to the types of variables analyzed (linear–linear, linear-circular, and circular-circular correlations). Linear–linear correlations were computed using Pearson’s correlations. Linear-circular correlations were computed following Mardia (1976), and circular-circular correlations were calculated following Jammaladaka and Sarma (1988) using the functions circlin.cor() and circ.cor1(), respectively, in the R package Directional (Tsaigris et al. 2020).

Natural selection on fruiting phenology

We estimated the pattern and magnitude of frugivore-mediated phenotypic selection (understood as a consistent relationship between phenotypic variation and variation in fitness; Conner and Hartl 2004) on fruit fruiting phenology (fruiting onset, fruiting peak, and length of the fruiting season) and fruit crop size on each Blue Passionflower population. Fruit removal was used as a fitness measure in the context of animal-mediated selection. This is an early-stage plant fitness component widely used in the evolutionary ecology of seed dispersal (Wang and Smith 2002; Palacio and Ordano 2018; Palacio et al. 2020). By contrast, the number of seeds would be a better estimate of seed dispersal than fruit removal. However, in the particular case of the Blue Passion flower, fruits are not fully ingested as is the case of small berries, but rather are bitten (mammals) or pecked (birds), providing an indicator easier to record than quantifying the number of seeds dispersed (Forget and Wenny 2005). This proxy also estimated the overall contribution of frugivores to fruit removal after one fruiting season, regardless of the changes in the identity and contribution of different frugivores inherent to the temporal dynamics (González-Varo et al. 2019). Given that birds peck the fruit and remove the seeds without removing the whole fruit, fruit loss, which may partly determine the length of the fruiting season (Naoe et al. 2018), is largely independent of fruiting phenology. From the point of view of selection modeling, our fitness estimate assumes that at least one seedling survives in the next generation. In contrast, a fruit not pecked means that this probability is zero. In addition, we assumed that plants with a higher number of fruits removed increases the number of seed dispersed and the probability of reaching suitable sites for seed survival and recruitment (Siepielski and Benkman 2007; Palacio et al. 2020). Individual relative fitness was computed as each individual fitness divided by its population mean fitness, and traits were standardized to a mean of 0 and a variance of 1 before analyses (Palacio et al. 2019).

To assess the direction and strength of selection on a given trait independent of the indirect effect of other traits, we used a multivariate selection approach, following Morrissey and Sakrejda (2013). This method unifies multiple regression models to obtain selection
gradients (Lande and Arnold 1983) and spline-based estimations to obtain smooth functions of the relationship between fitness and phenotypic traits (Schluter 1988). Before analyses, fruiting onset, fruiting peak, and length of the fruiting season were converted to linear variables. To this end, we considered fruiting onset and fruiting peak as time series data (date converted to days) and treated the first visit of each population as the starting date (day 0). Then, we compared circular-circular correlations with their corresponding linear–linear correlations (Supplementary Table S2). All these correlations were very similar, indicating that these could be considered as linear variables. Significant linear gradients ($\beta_i$) indicate that total selection favors either a mean increase (if positive) or decrease (if negative) of a phenotypic trait. Significant non-linear selection gradients ($\gamma_{ii}$ and $\gamma_{ij}$) indicate total non-linear selection against extreme phenotypes (stabilizing selection), non-linear selection against intermediate trait values (disruptive selection), or correlational selection for trait combinations (Lande and Arnold 1983). Due to the low sample size per population and to prevent overfitting, we restricted the maximum number of knots per trait to four (an upper bound of six knots were used for fruiting peak in Santa Fe). Residuals plots and tests of the basis dimension choices indicated that these number of knots were adequate to not force, at the same time, oversmoothing ($p$’s for all covariates > 0.05, function gam.check in the mgcv package; Wood 2017). Count data (number of fruits consumed) were fitted using a Poisson error structure and log-link function for La Plata and Santa Fe, and a negative binomial error structure and log-link function for Tucumán to account for overdispersion. Standard errors and significance of selection gradients were estimated using 1,000 bootstrap replicates (Morrissey and Sakrejda 2013). Finally, we computed the opportunity for selection $I$ of each population as the variance in relative fitness (Moorad and Wade 2013).

All analyses were performed in R 4.0.2 (R Core Team 2020) using the packages Directional (Tsagris et al. 2020), mgcv (Wood 2017), gsg (Morrissey and Sakrejda 2014), and fields (Nychka et al. 2017), and the code to compute the Herman-Rasson test provided in Landler et al. (2019).

Results

We recorded a total of 514 (La Plata), 481 (Santa Fe), and 338 (Tucumán) data per phenological stage (e.g., number of unripe fruits), considering all the visits and plants of a given population. Fruit crop size varied substantially among the three populations (La Plata: mean $= 19.18 \pm 26.73$, range $= 1–110$, $N = 17$, Santa Fe: mean $= 30.32 \pm 35.66$, range $= 1–181$, $N = 25$, Tucumán: mean $= 22.55 \pm 16.92$, range $= 5–65$, $N = 20$), in contrast to the number of pecked fruits (La Plata: mean $= 10.65 \pm 12.68$, $N = 17$, range $= 0–41$, Santa Fe: mean $= 15.28 \pm 14.19$, range $= 0–69$, $N = 20$, Tucumán: mean $= 8.55 \pm 6.97$, range $= 1–23$, $N = 25$). The three populations showed similar peak dates in flower production and fruit crop size and had seasonally significant phenological stages, except in the case of dry fruits (Table 1). Most plants had two major flowering and fruiting peaks, in austral spring and autumn (Fig. 4). The autumn peak was of lesser intensity than the spring peak. Also, the length of each phenological stage was longer in lower latitudes (Table 1). In particular, the population in the lowest latitude (Tucumán) showed a very extended phenology relative to higher latitude populations, with individuals producing flowers or fruits throughout the year (Fig. 4). Flowering and fruiting onset was only correlated in Santa Fe ($r = 0.90$, $N = 25$, $P = 0.01$), whereas no significant correlations in La Plata ($r = 0.13$, $N = 14$, $P = 0.69$).
In La Plata, flowering peak was positively correlated with fruiting peak (\( r = 0.58, N = 20, P = 0.007 \)), indicating that plants flowering earlier brought forward the fruiting peak (Fig. 4). In Santa Fe, flowering peak was negatively correlated with fruiting peak (\( r = -0.40, N = 20, P = 0.04 \)), indicating that plants flowering later had smaller fruiting peaks (Fig. 4). In Tucumán, no significant correlations between flowering and fruiting peaks were found (Fig. 4).

Table 1: Circular statistics on flower and fruiting phenology of *Passiflora caerulea* populations

| Phenological stage       | Population | Modal date | SD (days) | HR     | N       | P       |
|--------------------------|------------|------------|-----------|--------|---------|---------|
| Budding peak             | La Plata   | 2018-10-10 | 36        | 2.77   | 109     | < 0.0001|
|                          | Santa Fe   | 2018-10-15 | 61        | 2.85   | 265     | < 0.0001|
|                          | Tucumán    | 2018-11-13 | 88        | 0.79   | 307     | 0.04    |
| Flowering peak           | La Plata   | 2018-10-10 | 25        | 4.48   | 43      | < 0.0001|
|                          | Santa Fe   | 2018-11-15 | 52        | 3.17   | 206     | < 0.0001|
|                          | Tucumán    | 2018-11-13 | 69        | 0.94   | 186     | 0.02    |
| Unripe fruiting peak     | La Plata   | 2018-12-06 | 27        | 4.32   | 105     | < 0.0001|
|                          | Santa Fe   | 2018-10-31 | 46        | 2.42   | 211     | < 0.0001|
|                          | Tucumán    | 2018-12-18 | 65        | 2.46   | 248     | < 0.0001|
| Ripe fruiting peak       | La Plata   | 2018-12-18 | 31        | 4.96   | 82      | < 0.0001|
|                          | Santa Fe   | 2018-11-16 | 53        | 1.15   | 164     | 0.007   |
|                          | Tucumán    | 2018-11-13 | 73        | 1.55   | 214     | < 0.0001|
| Fruit removal peak       | La Plata   | 2018-12-18 | 30        | 4.60   | 51      | < 0.0001|
|                          | Santa Fe   | 2018-11-16 | 56        | 0.87   | 147     | 0.03    |
|                          | Tucumán    | 2019-01-05 | 78        | 1.86   | 117     | < 0.0001|
| Dry fruiting peak        | La Plata   | 2018-12-18 | 53        | 0.28   | 52      | 0.45    |
|                          | Santa Fe   | 2018-12-03 | 58        | 0.51   | 70      | 0.16    |
|                          | Tucumán    | 2019-01-05 | 58        | 0.34   | 126     | 0.34    |

Peaks were computed by back-transforming modal angles and circular standard deviations to dates.

HR Hermans–Rasson test

Fig. 4: Flowering and fruiting phenology of *Passiflora caerulea* populations. a La Plata, b Santa Fe, c Tucumán. Rose diagrams depict the number of reproductive structures produced in each phenological stage along the year. Each bar represents the average number of reproductive structures produced per plant in a given month.

\( P = 0.89 \) or in Tucumán (\( r = -0.05, N = 19, P = 0.83 \)) were found. The number of flowers was positively correlated with fruit crop size in Tucumán (\( r = 0.58, N = 20, P = 0.007 \)), but not in La Plata (\( r = 0.37, N = 20, P = 0.15 \)) and in Santa Fe (\( r = -0.01, N = 25, P = 0.99 \)).

Fruiting peak was positively related to fruiting onset in Santa Fe, indicating that fruiting earlier brought forward the fruiting peak (Fig. 5). Fruit crop size was positively correlated to fruiting onset in Tucumán, indicating that plants fruiting later had larger fruit crop sizes (Fig. 5). By contrast, no significant correlations between phenological traits in La Plata were found (Fig. 5).
Three general patterns were found in selection analyses. First, frugivores selected fruit crop size and the length of the fruiting season in the three populations (Fig. 6). Second, selection favored large fruit crop sizes (positive directional selection in La Plata and Santa Fe, and non-linear selection in Tucumán) and showed the strongest intensity among all traits in the three populations (Table 2). Besides, selection intensity on this trait was lower in the lowest latitude, as well as the opportunity for selection ($I_{\text{La Plata}} = 1.42 \pm 0.04$, $I_{\text{Santa Fe}} = 0.86 \pm 0.02$, $I_{\text{Tucumán}} = 0.66 \pm 0.02$). Although significant disruptive selection gradients were found on fruit crop size in Santa Fe and Tucumán, visual inspection of the fitness functions indicated a positive directional selection on this trait (Fig. 6a). In addition, La Plata and Tucumán showed significant disruptive selection gradients on fruiting onset (Table 2), but visual inspection of the fitness function indicated negative directional selection patterns (Fig. 6b). We also detected positive directional selection and disruptive selection on fruiting peak in La Plata and Santa Fe (Fig. 6c). Disruptive selection gradients were also significant for the length of the fruiting season in the three populations (Table 2), although visual inspection of fitness functions showed positive directional selection on this trait in Santa Fe, negative directional selection in Tucumán, and disruptive selection in La Plata (Fig. 6d). We also detected significant correlational gradients in La Plata and Santa Fe. In both populations, we found selection on the combination of fruit crop size and fruiting peak, and on the combination of the length of the fruiting season and fruiting peak (Table 3). In particular, plants with large crops and early fruiting peaks had higher fitness (Fig. 6e-f). Also, plants with extended fruiting seasons and early fruiting peaks had higher fitness (Fig. 6g-h). Finally, we also found significant selection on the combination of fruit crop size and the length of the fruiting season in Santa Fe (Table 3), in which plants with large crops and slightly long fruiting seasons had higher fitness (Fig. 6i).

**Discussion**

Frugivores selected fruiting phenological traits (fruiting onset, fruiting peak, and length of the fruiting season) across three plant populations. Although numerous studies have focused on how pollinators exert phenotypic selection on flowering schedule (Gómez
1993; Hall and Willis 2006; Sandring and Ågren 2009; Munguía-Rosas et al. 2011; Weis et al. 2014) and how dispersers select different fruit traits (Janson et al. 1986; Russo 2003; Mello et al. 2005; Palacio et al. 2020), to our knowledge, no study has assessed frugivore-mediated selection on fruiting schedule. Therefore, this is the first evidence that biotic interactors (i.e., frugivores) have the potential, given a set of assumptions (see below), to shape fruiting phenology.

Two main contrasting hypotheses predict selection on phenological fruiting traits (Fig. 1). On the one hand, plant competition for seed dispersers predicts that selection will favor early-fruiting plants with a short phenology and large fruit crop size (Snow 1965; Howe and Estabrook 1977; Alcántara et al. 1997; Palacio and Ordano 2018). On the other hand, facilitation predicts that selection will favor fruiting plants with a long fruiting seasons, regardless of fruit crop size. However, our results do not fully agree with either of the two hypotheses. For instance, frugivores selected earlier fruiting peaks and large fruit crop sizes (suggesting competition), but also selected plants with extended fruiting seasons in two populations (suggesting facilitation). This evidence indicates that a more

Fig. 6 Frugivore-mediated selection on fruiting phenology and fruit crop size in Passiflora caerulea populations. a–d Generalized additive models (red=La Plata, green: Santa Fe, blue=Tucumán) between standardized (mean = 0, variance = 1) phenotypic traits (fruit crop size, fruiting onset, fruiting peak, length of the fruiting season) and fitness (number of pecked fruits), conditional on the mean of the remaining phenotypic traits (see Methods). Shaded areas represent 95% confidence bands. Dashed lines indicate non-significant relationships (P > 0.05). e–i Selection surfaces (thin-plate splines) for the number of pecked fruits (relative to their mean) as a function of standardized (mean = 0, variance = 1) fruit traits in La Plata (e and g) and Santa Fe (f, h, and i). Vertical bars depict predicted relative fitness and points represent observed data.
Table 2  Linear and quadratic multivariate selection on fruit crop size and fruiting phenology in three *Passiflora caerulea* populations

| Trait | La Plata | Santa Fe | Tucumán |
|-------|---------|---------|---------|
|       | $\beta_i$ | SE  | $P$ | $\gamma_{ii}$ | SE | $P$ | $\beta_i$ | SE  | $P$ | $\gamma_{ii}$ | SE | $P$ | $\beta_i$ | SE  | $P$ | $\gamma_{ii}$ | SE | $P$ | $\gamma_{ii}$ | SE | $P$ |
| FCS   | 0.93  | 0.16 | <0.0001 | 0.41  | 0.44 | 0.04 | 1.21  | 0.10 | <0.0001 | 0.90  | 0.22 | <0.0001 | 0.30  | 0.39 | 0.51 | **0.09**  | 0.28 | <0.0001 |
| FO    | -0.32 | 0.18 | 0.05   | **0.10** | 0.14 | <0.0001 | -0.11 | 0.12 | 0.36   | **0.01** | 0.03 | 0.01 | -0.35 | 0.70 | 0.53 | 0.22 | 1.51   | 0.15 |
| FP    | 1.56  | 0.40 | <0.0001 | 1.55  | 1.27 | 0.05 | **0.33** | 0.11 | 0.01   | **0.11** | 0.07 | <0.0001 | 0.26  | 0.40 | 0.49 | **0.07** | 0.35 | 0.01 |
| LFS   | 2.24  | 0.74 | <0.0001 | **9.41** | 6.70 | 0.02 | **0.13** | 0.07 | 0.03   | **0.02** | 0.02 | 0.002 | -0.27 | 0.51 | 0.55 | **0.07** | 0.56 | 0.004 |

Standardized directional selection gradients ($\beta_i$), stabilizing/disruptive selection gradients ($\gamma_{ii}$), and standard errors (SE) are shown. Significant gradients are shown in bold.

*FCS* fruit crop size, *FO* fruiting onset, *LFS* length of the fruiting season.
A comprehensive framework, rather than two mutually-exclusive mechanisms, is needed (Austen et al. 2017). We thus propose considering three main concepts when assessing phenotypic selection on fruiting phenology: (1) phenology is composed of several correlated traits, (2) flowering phenology impacts on fruiting phenology, and (3) fruit crop size strongly drives frugivore-mediated selection.

As we showed, frugivores exerted selection on energetic favorable trait combinations in two populations, consistent with optimal foraging behavior patterns (Sobral et al. 2010; Palacio et al. 2017a). In both La Plata and Santa Fe, frugivores selected plants with large crop sizes, early fruiting peaks and extended fruiting seasons (Table 2, Fig. 6), likely providing the greatest energy gain (Wheelwright 1993). From the plant’s perspective, these trait combinations would result in neither complete competition nor complete facilitation for seed dispersers. Instead, these selection patterns would reflect animal choices and trade-offs between plant traits (Forrest and Miller-Rushing 2010). Consequently, extended fruiting seasons would promote high overlap between conspecifics and seed dispersal facilitation, but large fruit crop sizes would then segregate frugivores, promoting a relaxed competition. This suggests that not only the spatial pattern of fruiting plants, but also the fruiting timing is relevant to understand the hierarchical decision-making process of fruit choice (plant patches, plants within patches, fruits within plants) made by frugivores (Palacio et al. 2017b).

We also found that fruiting phenology may depend on flowering phenology. This covariation would have strong implications from an evolutionary perspective, as both pollen and seed dispersal are the primary sources of gene flow in plants (Snell et al. 2019). In one population (Santa Fe), we found a positive correlation between flowering and fruiting onset, whereas in another (Tucumán), we found a positive correlation between the number of flowers and fruits (Fig. 5). This indicates that both flowering phenology and flower display can be also indirectly selected by frugivores or pollinators. In this sense, the correlation between flowering and fruiting schedules might be under selection in our system (e.g., favoring early flowering and fruit ripening), as both flowers and fruits are simultaneously produced, to ensure plant reproduction.

Fruit crop size is a crucial determinant of frugivore-mediated selection, as the number of fruits produced is a strong attraction signal in visually driven seed dispersal mutualisms (Snow 1971; Ordano et al. 2017; Palacio and Ordano 2018). Our results showed

| Trait          | La Plata | Santa Fe | Tucumán |
|----------------|----------|----------|---------|
| FCS×FO         | −0.29    | −0.14    | −0.10   |
| FCS×FP         | 1.29     | 0.39     | 0.08    |
| FO×FP          | −0.50    | −0.04    | −0.09   |
| FCS×LFS        | 1.01     | 0.16     | 0.08    |
| FO×LFS         | −0.71    | −0.01    | −0.08   |
| FP×LFS         | 4.28     | 0.04     | −0.07   |

Standardized correlational selection gradients ($\gamma_{ij}$) and standard errors (SE) are shown. Significant gradients are shown in bold.

$FCS$ fruit crop size, $FO$ fruiting onset, $LFS$ length of the fruiting season.
that fruit crop size was the most important selection target, as it showed the highest selection strength across the three populations (Table 2). It should be noted that fitness differences may be the result of larger crop sizes, rather than of selective removal. Although the debate of the role of frugivores in the evolution of fruit and seed traits remains contentious (Herrera 1985; Jordano 1995; Harrison et al. 2012), fruit crop size is one of the fruit traits frequently reported as a target of frugivore-mediated selection across populations of the same species (Ortiz-Pulido and Rico-Gray 2000; Sobral et al. 2013; Palacio and Ordano 2018), as well as across species (Izhaki 2002; Ordano et al. 2017). Although fruit crop size is not a phenological trait per se, fruit availability of a given plant changes through time (Fig. 4). Therefore, the average number of ripe fruits produced per plant in a given date along the season would be a more accurate proxy of fruit availability than the cumulative number of ripe fruits when quantifying animal-mediated selection on fruiting phenology. In our populations both proxies of fruit production were highly correlated ($r = 0.87–0.94$), suggesting that fruit crop size is partly explained by phenology (i.e., most productive plants tend to offer more ripe fruits than small productive plants at any given time).

In addition to the selection patterns found on fruiting phenology, phenological traits must have a genetic basis and selection should be sustained over time to drive an evolutionary response in fruiting phenology. Moderate to high heritabilities ($h^2$) have been documented in different phenological fruiting traits in fleshy-fruited crop species, including the number of days from fruiting to maturity ($h^2 = 63.1\%–90.0\%$; Nikolić 2006; Dossett et al. 2008; Rao et al. 2008; Muluken et al. 2016) and date of fruit ripening ($h^2 = 78.0–99.0\%$; Tancred et al. 1995; Yamada et al. 1995, de Souza et al. 1998). The lack of temporal replication of our study prevents predictions of the influence that seed dispersers might have on fruiting phenology over many generations. This is because both fruit trait values and frugivore assemblages can be highly variable from year to year (Jordano 1994; Herrera 1998) causing a great heterogeneity in the strength of phenotypic selection (Ortiz-Pulido and Rico-Gray 2000), thus casting doubt of the ability of seed dispersers to shape fruiting phenology. Despite these temporal fluctuations, plants can experience strong animal-mediated selection in infrequent years. For instance, selection on *Pinus albicaulis* cone traits by its main seed-predator disperser *Nucifraga columbiana* was negligible during common years of low seed abundance, but it was strong in years of high seed production (Siepielski and Benkman 2007). Although high heritability estimates in some plant species, along with the selection regimes found here on fruiting phenology, suggest a potentially strong response to selection, further studies with multiple selection episodes are needed to assess whether selection could drive adaptive evolution on fruiting schedules.

Despite geographic distance and strong variability in terms of climate and ecoregion between the three populations, some similarities in selection patterns were found. For instance, frugivores favored large crops in the three populations, with earlier fruiting peaks and extended fruiting seasons in two of them. The multivariate nature of reproductive plant phenology, as well as the low number of populations studied, challenges our possibilities to determine the causes of variation in selection regimes among populations. However, we suggest four factors that could account for variation in animal-mediated selection on reproductive phenology between populations. First, frugivores affect the genetic structure of populations through seed dispersal (Saastamoinen et al. 2018) and, consequently, phenological variability. In our study area, most frugivorous species are residents, and genetic variability would presumably mirror local adaptations (Tigano and Friesen 2016). Moreover, anthropogenic related dispersal would account for another source of gene flow, since humans often use Blue Passionflower as ornamental or medicinal species (Deginani 2001;
Eynard et al. 2017). This overlooked diplochory would increase the genetic variability both within and between populations, an issue not addressed yet.

Second, the large geographical variation in species composition of local assemblages and plant-animal interactions across the Blue Passionflower distribution would promote the occurrence of a geographic selection mosaic on reproductive phenology (Thompson 2005). Similarities between selection regimes suggest that frugivorous species could be functionally equivalent in terms of fruit trait selection (Blendinger 2017). Consequently, different assemblages would shape the phenological phenotype similarly regardless of geographic variation in abiotic and other biotic factors.

Third, other fruit traits not measured in this study (e.g., fruit size, seed size and number, nutrient content, fruit color) are known to be important targets of frugivore-mediated selection (Sobral et al. 2010; Palacio et al. 2017b, 2020). Phenotypic selection on these traits is thus expected to account for differences in frugivore-mediated selection on fruiting phenology, particularly if plants face compromises between fruit quantity and quality (e.g., large fruit sizes, high sugar concentration). It should also be noted that the number of seeds consumed and effectively dispersed by frugivores will be a better proxy for fitness than the number of fruits consumed. Although multiple studies support the idea that increased fruit and seed removal translates into increased probabilities of seed recruitment (Primack and Kang 1989; Jordano and Herrera 1995), later selection pressures could potentially counteract animal-mediated selection on fruit and seed traits (Gómez 2004; Martínez et al. 2007). Consequently, our results should be interpreted keeping in mind that fruit removal is an early-stage plant fitness component (Palacio et al. 2020).

Fourth, the opportunity for selection should promote geographic variation in selection intensity (Benkman 2013), because it sets an upper limit on the magnitude of selection (Crow 1958; Arnold 1986). Furthermore, the interaction strength (measured as the mean proportion of fruits consumed per population) is also expected to be negatively related to selection intensity in mutualisms, and by extension to the opportunity for selection (Benkman 2013; Trunschke et al. 2017). This is because the higher the proportion of individuals involved in the interaction, the higher the mean and the lower the variance in relative fitness (Benkman 2013). In our study system, however, selection strength was not apparently related to interaction strength, as the mean proportion of fruits consumed per population was similar across the three populations (La Plata = 0.48 ± 0.35, Santa Fe = 0.56 ± 0.25, Tucumán = 0.49 ± 0.36). Nevertheless, sample size limits our ability to assess the effects of interaction strength on selection intensity, and further studies including a higher number of populations are needed to effectively assess the relationship between interaction and selection strength.

Although phenology at the population level is ultimately a product of selection acting on phenological variation among individuals, the evidence of adaptive change based on selection pressures and trait heritabilities remains limited (Forrest and Miller-Rushing 2010). Overall, our results show a high between-population variability in fruiting schedules and support the idea that biotic interactors select phenological fruiting characteristics, underscoring the evolutionary potential of phenotypic trait variation in fruiting timing.

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