Flowering and Fruiting Phenology of Native and Non-Native Woody Species in a Semiarid Subtropical Forest

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Abstract

The timing of flowering and fruiting events has major implications for community assemblies in time and space, and is an important trait for explaining plant invasion. Wolkovich and Cleland proposed four phenological hypotheses to explain invasion success; however, in semiarid subtropical forests, where non-native woody species are highly invasive, these hypothesis have been poorly tested, with multiyear studies being even less scarce. We answered the following questions: 1) Which of the strategies proposed by Wolkovich and Cleland do non-native species exhibit in their flowering and fruiting phenology? 2) Does temporal variability in flowering and fruiting differ among individuals of native and non-native species? We measured the beginning and length of flowering and fruiting phenology of the most frequent native and non-native woody species during four consecutive reproductive periods. We found differences in the phenological patterns. Non-natives showed a delay in flowering and fruiting, coinciding with the Vacant niche hypothesis, and had a longer fruiting phenology, as predicted by the Niche breadth hypothesis. Many individuals of native species showed high temporal variability in flower and fruit production, with a sharp reduction or even absence of individuals with flowers or fruits in some periods. Contrarily, individuals of non-native species showed higher temporal stability in flower and fruit production. The different phenological strategies developed by non-native species generate different interactions and windows of opportunities that may explain invasion. These new strategies may also have profound consequences on ecosystem processes and functions.

Introduction

The period in which life history events occur has major implications for community assemblages in time and space (Ratche and Lacey 1985; Primack 1987; Morellato et al. 2016). As a consequence, plant phenology has received increasing attention in the last decades (Forrest et al. 2010; Morellato et al. 2016; Tang et al. 2016). More recently, phenology has emerged as a potential attribute to explain invasions by non-native plant species (Hulme 2011; Wolkovich et al. 2013; Zettlemoyer et al. 2019). In fact, Wolkovich and Cleland (2011) proposed an integrated framework for explaining how phenology may shape invasions. This framework was tested in a few studies, which were mainly focused on flowering phenology (Wolkovich et al. 2013; Zettlemoyer et al. 2019) and areas with temperate climate in the Northern Hemisphere (Chamber et al. 2013; Wolkovich et al. 2013). Seasonal ecosystems cover an important area of the world surface, particularly in the Southern Hemisphere (DRYFLOR et al. 2016; Kuemmerle et al. 2017). Those ecosystems are subject to invasion by several non-native woody species, which are modifying community composition and ecosystem functioning (e. g. Giorgis and Tecco 2014; Rejmanek 2014; te Beest et al. 2015; Giorgis et al. 2017). However, plant phenology has been scarcely studied in these seasonal systems, where flowering and fruiting are temporarily restricted to the warm and wet season. Moreover, long-term studies of plant phenology of native and non-native species are necessary to have a broader and more complete picture of the mechanisms underlying plant invasion success and chances of species coexistence.

As variability in space and time promotes coexistence, Wolkovich and Cleland (2011) proposed four important phenological hypotheses to explain invasion success. The Vacant niche (derived from Elton 1958) proposes that non-native species may benefit from using temporally available resources. The Priority effect hypothesis, a particular case of the Vacant niche one, predicts that flowering and fruiting phenology of non-native species occurs consistently earlier than in natives, implying an early access to resources for seedling establishment. The Niche breadth hypothesis proposes that non-native species may have longer phenological phases than natives, providing higher probabilities of encountering pollinators or seed dispersers. Finally, the Plasticity and climate hypothesis states that phenology of non-natives co-varies with climate. There is not a clear predominance of one hypothesis over the others, and studies testing them are very scarce, particularly in the Southern Hemisphere (Godoy et al. 2009; Wolkovich et al. 2013; Lediuk et al. 2014). Therefore, it is necessary to increase the number of phenological studies to test these hypotheses and identify the phenological windows used by non-native species.

The beginning and length of the flowering and fruiting periods may provide a different perspective that may help understand and manage invasions. For example, differences in flowering periods between native and non-native species may contribute to a better distribution of pollinators or/and abiotic resources over time, and therefore higher chances of non-native progeny production (Lake and Leishman 2004). Similarly, non-overlapping periods of fruiting between natives and non-natives may provide new sources of food for seed dispersers and better chances for seed dispersal and seedling establishment for non-natives (Vergara et al. 2016). Conversely, overlapping phenology between native and non-native species may lead to competition for pollinators and seed dispersers, affecting pollination and seed dispersal services (Wilke and Irwin 2010; Morellato et al. 2016). Previous studies comparing flowering of native and non-native species found evidence supporting a variety of strategies, i.e. non-natives might flower earlier or later than natives, or even at the same time (Lake and Leishman 2004; Pyšek and Richardson 2008; Godoy et al. 2009; Wolkovich et al. 2013; Lediuk et al. 2014; Durham et al. 2017). By contrast, studies comparing fruiting strategy between native and non-native species seem to support the same strategy of longer fruiting periods in non-natives than in natives (Lediuk et al. 2014; Durham et al. 2017). However, the evidence is scarce and more studies are needed to support this pattern.

In South America, studies of plant phenology are highly scarce and have been focused on native species from tropical humid forests (Chambers et al. 2013; Morellato et al. 2013). Moreover, phenological studies are usually carried out for short periods (but see Morellato et al. 2013), which hinders the analysis of changes among years in phenological strategies. The low-altitude slopes of Cordoba mountains (central Argentina) are covered by a semiarid subtropical forest subjected to two contrasting climatic periods, one with strongly coupled high temperatures and precipitations, defining a growing season of about seven months, (from October to April), and another period dominated by stressful conditions (i.e., cold, freezing days and drought). It is likely that this climatic condition has been the main driver modeling phenological evolution of native plants and, at the same time, it represents a filter that non-native plants must overcome in order to invade (Tecco et al. 2010). In this region, invasion by non-native species is one of the main ecological problems, together with forest fragmentation and the advance of agricultural and

urban frontiers (Gavier and Bucher 2004; Giorgis et al. 2017; Aguilar et al. 2018). In particular, many non-native woody species are highly invasive and are inducing multiple changes in the structure, biodiversity and ecosystem function in the area (Jobbagy et al. 2013; Furey et al. 2014; Giorgis et al. 2017; Milani et al. 2020; Withworth-Hulse et al. 2020; Segura et al. 2021). Previous studies on woody species in Córdoba mountains suggested that non-native species may use vacant niches for flowering and fruiting (Gurvich et al. 2005), but several other strategies are also likely (Tecco et al. 2013). None of the previous studies carried out in this semiarid subtropical forest have specifically tested the described hypotheses. Hence, the aim of this study was to conduct a multi-year flowering and fruiting phenological study including the native and non-native woody species most frequently occurring in a semiarid subtropical forest. We answered the following questions: 1) Which of the strategies proposed by Wolkovich and Cleland (2011) do non-native species exhibit in their flowering and fruiting phenology? 2) Does temporal variability in flowering and fruiting differ among individuals of native and non-native species?

Methods

Study area

The study was performed on the eastern slope of Córdoba mountains in central Argentina (31 ° 7'S and 64 ° 21'W) (Fig. 1a). The area belongs to the Chaco phytogeographic region and is characterized by a seasonal subtropical semiarid forest dominated by the tree *Lithraea molleoides* and *Celtis ehrenbergiana* (Giorgis et al. 2017; Cabido et al. 2018). Mean temperature is 22 °C in summer and 9 °C in winter (De Fina, 1992). Mean annual precipitation in the area is 956 mm (ranging from 570 to 1390 mm) with most rainfall concentrated in the warmest months, from October to April (unpublished data of climate record between 1960 and 2019 from J.J. Filardo and Unquillo and Río Ceballos Water Service Cooperatives). Conversely, the period from May to September is characterized by cold and dry conditions. By the end of August, temperature and wind frequencies increase; these conditions characterize the driest moment of the year, until the rainy period begins.

In this study, we considered July and June as the beginning and the end of each phenological period, respectively. We used this criterion because July is the coldest month; then, when temperature begins to rise, most native species of the area begin to flower (Torres and Galetto 2011; Giorgis et al. 2015). Finally, four reproductive periods were defined: 2015-2016, 2016-2017, 2017-2018 and 2018-2019 (Fig. 1b). The precipitation patterns differed among the four analyzed reproductive periods (Fig. 1b). The first (2015-2016) and fourth (2018-2019) periods were around the historical average, whereas the second (2016-2017) was a little dry and the third (2017-2018) represents the record of dry periods in the history of the study area since 1960 (unpublished data of climate records between 1960 and 2019 from J.J. Filardo and Unquillo and Río Ceballos Water Service Cooperatives).

The vegetation of the study area is composed of a mosaic of physiognomies from close to open native forest, including monospecific patches of woody non-native species, shrublands and grasslands (Gavier and Bucher 2004; Zeballos et al. 2014; Giorgis et al. 2017). The native woody community comprises 28

tree and 115 shrubs species (Giorgis et al. 2011), whereas non-native woody species amount to 40 (25 trees, 13 shrubs and 2 tree/shrubs; Giorgis and Tecco 2014).

Experimental design

We selected the most frequent native and non-native woody species (16 in total, 8 of each type) based on Zeballos et al. (2014), and more than 120 floristic surveys performed between 2004 to 2009 across the study area (Giorgis et al. 2017). For each species, we selected 10 reproductive individuals (individuals with flowers and/or fruits) and for dioecious species, we selected only female individuals, since only females set fruits (information about taxonomic status, origin, floral sexual expression, and fruit dispersal type for the studied plant species is given in Appendix S1). Individuals were separated at least 5 m from each other. Once a month, from July 2015 to June 2019, we observed each of the selected individuals to record its phenological stage: flowers or mature fruits. We considered that the individual belonged to a given phenological stage when at least 1% had flowers or fruits.

For each species and reproductive period, we obtained: a) number of days until the appearance of the first flowers and ripe fruits. This was calculated considering July 1° as day zero; b) Length of flowering and fruiting phases in months. For each species we considered that it fruited in a certain reproductive period when its fruiting began in that period, although fruiting length may extend over the next reproductive period. For example, *M. azederach* began its fruiting period in April (2016-2017) and extended it to November in the following period (2017-2018, see Appendix S2), accounting for a total of eight months of fruiting duration for the 2016-2017 reproductive period; c) Temporal predictability in the number of individuals with flowers or fruits. The number of individuals bearing flowers or fruits was counted each season. Temporal predictability in flowering and fruiting among individuals of each species was quantified by obtaining coefficients of variations ($CV = \text{standard deviation}/\text{mean}$) of the four reproductive periods. The higher the CV, the more variable (less predictable) the number of flowering and fruiting individuals of each species among reproductive periods.

Data analysis

The response variables “number of days until first flower/fruit” and “flowering/fruiting length” were analyzed using generalized linear mixed models (GLMM, glmer function from the lme4 package, Bates et al. 2015), including “species status” as fixed factor (i.e., native or non-native) and “species identity” as a random factor. In the models, Poisson error structure was used and overdispersion was checked following Zuur et al. (2009). When overdispersion was detected, quasi-Poisson error structure was used. All the analyses were performed with R 4.0.2.

Results

Flowering phenology

In all the studied reproductive periods, there was a consistent trend towards a higher number of days to produce the first flowers in non-native species than in native ones. This trend was significant for the first (2015-2016) and the last reproductive periods (2018-2019) (Fig. 2; Appendix S2). Flowering of non-native species began on average 34 ± 9.38 days later than flowering of native species. Flowering length tended to be longer in non-native species in some reproductive periods, but this trend was not significant in any of the studied periods (Fig. 3; Appendix S2). Flowering length was on average 1.7 ± 0.18 months for non-natives and 1.5 ± 0.13 for natives (Fig. 3).

Fruiting phenology

In all the studied reproductive periods there was a trend towards a later onset of the first fruits in non-native species than in natives. This trend was significant for the last reproductive period (2018-2019) and marginally significant for the third reproductive period (2017-2018) (Fig. 4; Appendix S2). Fruiting of non-native species began on average 55.7 ± 5.19 days later than fruiting of native species. Fruiting length showed a trend to be longer in non-native species in all the reproductive periods, which was significant for the second (2016-2017) and the last periods (2018-2019) (Fig. 5; Appendix S2). Fruiting of non-native species was on average 1.7 ± 0.37 months longer than fruiting of natives.

Temporal predictability in the number of individuals with flowers and fruits

Overall, in both groups of species, flowering was more predictable than fruiting (Table 1 and 2). Flowering and fruiting in the four reproductive periods were less variable among individuals of non-native species (range of coefficient variation 0-0.23 and 0-0.67, respectively) than among individuals of native ones (range of coefficient variation 0-0.82 and 0.20-1.15, respectively, Tables 1 and 2). It means that most non-native individuals showed flowers and fruits consecutively during the four reproductive periods analyzed. However, the flowering and fruiting of native species individuals was less predictable over time (Tables 1 and 2). The native *Condalia montana* was the least predictable and showed a very low number of reproductive individuals in the four reproductive periods. Similarly, *Lithraea molleoides* showed a low number of flowering and fruiting individuals in three reproductive periods, and *Ruprechtia apetala*, *Vachellia caven* and *Senegalia praecox* showed a low number of fruiting individuals in two reproductive periods. Among non-natives, *Lantana camara* was the only species with no individuals producing fruit during the 2016/2017 reproductive period; the remaining species did not show a remarkable variation in the number of flowering and fruiting individuals throughout the studied reproductive periods.

Table 1

Number of individuals in flower in each flowering period for non-native and native woody species of a seasonal subtropical semiarid forest in Central Argentina. Coefficient of variation for each species was calculated considering the four reproductive periods. Mean CV for native and non-native species is indicated in bold.

Species	Flowering periods				Coefficient of variation
	2015/2016	2016/2017	2017/2018	2018/2019	
Non-native					0.09
<i>Cotoneaster glaucophilus</i>	10	10	10	8	0.11
<i>Gleditsia triacanthos</i>	10	8	10	6	0.23
<i>Lantana camara</i>	10	6	10	10	0.22
<i>Ligustrum lucidum</i>	10	10	7	10	0.16
<i>Manihot grahamii</i>	10	10	10	10	0
<i>Melia azedarach</i>	10	10	10	10	0
<i>Morus alba</i>	10	10	10	10	0
<i>Pyracantha angustifolia</i>	10	10	10	10	0
Native					0.43
<i>Celtis ehrenbergiana</i>	10	10	10	10	0
<i>Condalia buxifolia</i>	10	10	10	10	0
<i>Condalia x montana</i>	0	1	2	1	0.82
<i>Lithraea molleoides</i>	10	0	5	5	0.82
<i>Ruprechtia apetala</i>	4	10	10	0	0.82
<i>Senegalia praecox</i>	10	6	10	10	0.22
<i>Vachellia caven</i>	10	5	10	10	0.29
<i>Zanthoxylum coco</i>	10	10	2	10	0.5

Table 2

Number of individuals in fruit in each fruiting period for non-native and native woody species of a seasonal subtropical semiarid forest in Central Argentina. Coefficient of variation for each species was calculated considering the four reproductive periods. Mean CV for native and non-native species species is indicated in bold.

Species	Fruiting periods				Coefficient of variation
	2015/2016	2016/2017	2017/2018	2018/2019	
Non-native					0.17
<i>Cotoneaster glaucophilus</i>	10	10	8	8	0.13
<i>Gleditsia triacanthos</i>	10	8	10	6	0.23
<i>Lantana camara</i>	10	0	10	10	0.67
<i>Ligustrum lucidum</i>	8	9	6	10	0.21
<i>Manihot grahamii</i>	10	10	10	10	0
<i>Melia azedarach</i>	10	9	10	8	0.1
<i>Morus alba</i>	10	10	10	10	0
<i>Pyracantha angustifolia</i>	10	10	10	10	0
Native					0.64
<i>Celtis ehrenbergiana</i>	6	7	6	9	0.2
<i>Condalia buxifolia</i>	3	10	10	10	0.42
<i>Condalia x montana</i>	0	1	1	0	1.15
<i>Lithraea molleoides</i>	10	0	2	5	1.02
<i>Ruprechtia apetala</i>	4	9	9	0	0.79
<i>Senegalia praecox</i>	4	4	10	10	0.49
<i>Vachellia caven</i>	3	5	10	6	0.49
<i>Zanthoxylum coco</i>	10	10	2	8	0.5

Discussion

Plant phenology is a central feature of community assembly (Ratche and Lacey 1985; Primack 1987) and an important trait involved in boosting the invasion of non-native species or in the resistance of the native community to their advance (Hulme 2011; Wolkovich et al. 2013; Zettlemoyer et al. 2019). Here we generated the first set of phenological reproductive data of native and non-native woody species for

multiple years in a seasonal semiarid subtropical forest (central Argentina, South America). Our study makes a remarkable contribution, considering that most studies of non-native phenology were conducted in the Northern Hemisphere for only few seasons and were focused mainly on forbs and grasses (Wolkovich et al. 2013; Godoy and Levine 2014; Durham et al. 2017; Zettlemoyer et al. 2019). We found that non-native species exhibit different phenological strategies from those of native species; we also observed distinct patterns in the temporal predictability of fruiting and flowering among their individuals. Those differences might underlie their invasion success and contribute important knowledge for their management (Wolkovich and Cleland 2011).

Flowering phenology

Flowering length of natives and non-native woody species was on average 1.4 months, but non-natives began to flower 1 month later; thus, there was a slight flowering overlapping between native and non-native woody species (Fig. 2-3; Appendix S2). Consequently, the flowering phenology of non-native woody species is explained by the Vacant niche strategy (Wolkovich and Cleland 2011). In general, previous studies have found that the expansion of non-native species is associated with early flowering (Chambers et al. 2013; Wolkovich and Cleland 2013; Zettlemoyer 2019). However, Godoy et al. (2009), observed that late flowering phenology of non-native species might be also responsible for the invasion; our findings are in line with the latter observation.

In our subtropical semiarid study area, we found that the beginning of flowering of native woody species coincides with the start of the growing period (i.e., spring). This is a period of climatic uncertainty, where late frosts may occur and there is a notable shift from drought to rainy and cold to warm days. This climatic variability may affect some flowering features, such as the number of flowers per individual and the quantity of floral rewards, which might depend on the amount of available resources, like water or soil nutrients (Leiss and Klinkhamer 2005; Thompson 2016; Waser and Price 2016). Moreover, such climatic uncertainty during spring may underlie the differences in flowering individuals among reproductive periods. In fact, the number of flowering individuals of native species showed higher temporal variability or less predictability than that of non-native species. On the other hand, non-native woody species flower on average one month later, when climatic conditions are more stable and the availability of pollinators is high. Moreover, the likelihood of competition for pollinators might be easily sorted out by non-native woody species, since they exhibited a higher and more predictable number of flowering individuals than natives. Indeed, as has been observed in other communities, a higher offer of flowers per individual or better floral reward by non-native species may have positive effects on pollinator attraction (Lopezaraira-Mikel et al. 2007; Aizen et al. 2008; Dietzsch et al. 2011; Zaya et al. 2021).

Finally, as in most of the studies in invasive species, some idiosyncratic responses were observed among native and non-native species (Tecco et al. 2013; Dyderski and Jagodzinski, 2019; Mazzolari et al., 2020). For example, the native *Ruprechtia apetala* is a late flowering species; thus, it behaves similarly to many non-native ones, whereas the non-native *Morus alba* flowered very early, simultaneously with many native

species (Appendix S2). Thus, even though we can describe a general pattern, there are clear exceptions showing other strategies.

Fruiting phenology

As flowering phenology, fruiting phenology of non-native species also showed a delay in the beginning of fruit production but, additionally, the fruiting period was longer in non-natives than in native woody species. These results support a Vacant niche plus a Niche breadth strategy for non-native species (Wolkovich and Cleland 2011). The delay in fruiting by non-natives implies the exposure of their mature fruits in autumn and winter, a period of scarce food resources for animals. Moreover, the length of the fruiting season is a defining factor in the number of interactions that species can establish (Morellato et al. 2016), with a longer fruit exposure providing non-native species with higher chances to explore interactions than shorter periods. Additionally, fruiting was temporarily more predictable in non-native species. Therefore, fruits produced by non-natives were offered for a longer time, but also in a more stable pattern among reproductive periods. Both a longer fruit exposure and a stable offer over the periods mean a higher propagule pressure by non-natives, and these strategies contribute to invasion. Fruit production late in the season was observed in non-native species in studies from other ecosystems (Lediuk et al. 2014; Jaryan et al. 2016; Durham et al. 2017) and may impact ecological interactions and ecosystem process. Indeed, Bellis et al. (2021) observed in Cordoba mountains that fruiting in winter by one of the non-native woody species here studied, the tree *Ligustrum lucidum*, modified the composition and abundance of bird communities. However, the study of Vergara-Tabares et al. (2016) also in Córdoba mountains, claims that the uncoupled fruiting phenology of the non-native *Pyracantha angustifolia* with natives is not a key attribute for its invasion. These authors did not find differences in the number of bird visits and fruit consumption in two invasive *Pyracantha* species, one with coupled phenology with natives and the other with a winter uncoupled phenology. Thus, they suggest that other attributes such as fruit characteristics (e.g., color, number), may be responsible for their invasion. Interestingly, in a recent work they found that the dominant native *L. molleoides* increases the number of dispersed fruits when its phenology overlaps with that of non-native *Pyracantha* species (Vergara-Tabares et al. 2021). Additionally, the provision of food during a period of regional resource scarcity might generate important changes in animal behavior and physiology (e.g., changes in food availability are linked to hormonal shifts; Gleditsch and Carlo 2011; Rojas et al. 2019). Finally, the differences in fruiting phenology (beginning and duration) might impact seed dispersal and seedling recruitment, generating particular windows for non-native recruitment (Morellato et al. 2016). However, the limited knowledge about the presence of seed dormancy and seed requirements for germination preclude associating phenology with seedling establishment.

Finally, as we mentioned for the flowering phenology, it is important to highlight that among non-native species, *Morus alba*, seems to be an exception to this general pattern, with an early and short fruiting phenology (Appendix S2). This species has a fruiting phenology even earlier than that of most native woody species, which could be considered a Priority effect strategy (Wolkovich and Cleland 2011).

Temporal predictability in flower and fruit production

The number of individuals bearing flowers and fruits was higher in non-native species in the four studied periods. Many native species showed a reduction or even absence of individuals with flowers or fruits in some reproductive periods. By contrast, non-native species had a reduction only exceptionally (e.g. *Lantana camara* fruiting). The higher stability of flower and fruit production in non-natives among years could be a consequence of the differences observed in the phenological patterns. That is, non-native species tend to produce their flowers under more stable and benign weather conditions than natives, which may decrease the chances of failures in flower production than flowering in more unstable climatic conditions. All in all, this different flower and fruit production among individuals might lead to a higher propagule pressure of non-native species, a key trait to trigger invasions (Simberloff 2009; Cassey et al. 2018).

Conclusion And Future Perspectives

Phenological studies are certainly scarce in South America (Chambers et al. 2013), with those including non-native species being even less scarce. Our study on woody species in a semiarid subtropical forest showed a differential and consistent phenological pattern between native and non-native species, regardless of the high climatic differences among the four studied periods. Flowering under more benign climatic and ecological conditions, fruiting longer, out of season, and temporally constant, may directly or indirectly (i.e., through differences in propagule pressure) trigger non-native species dominance and therefore their invasions success (Wolkovich and Cleland 2011; Cassey et al. 2018). In addition, those characteristics, probably boosted by other plant traits (Van Kleunen et al. 2010; Tecco et al. 2013), may favor their expansion to other areas where their invasion is still emerging (i.e., higher altitude mountains or drier areas, Giorgis et al. 2016). Moreover, the different strategies developed by non-native species and their higher temporal predictability may have consequences in the population dynamics of other functional groups (e.g., herbivores, pollinators, seed dispersers), in the transition probabilities between stages of the plant life cycle (e.g., from seed to seedling establishment) and in the rewiring of ecological interactions (Pearse et al. 2014; Vaughn and Young 2015; Morellato et al. 2016). The semiarid subtropical forest of South America is an area highly threatened by many anthropogenic pressures (de la Sancha et al. 2021). Thus, more phenological studies will help to understand the future of plant communities and the potential impact of non-native species, and they will also provide a solid background for effective management strategies.

Declarations

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Figures

Figure 1

a. Location of the study area in South America and Córdoba province in Argentina; **b.** Climatic diagram of the study region during the four studied reproductive periods, Dark gray: humid period when precipitation exceeded temperature. Light gray: dry Period when temperature exceeds precipitation. Abbreviations on axes: pp: precipitation, T: Temperature. Mean annual temperature and precipitation are given at the top of each reproductive period.

Figure 2

Boxplots showing the days to the first flower in native (light gray) and non-native (dark gray) woody species of a seasonal subtropical semiarid forest in Central Argentina. Four reproductive periods: **a.** 2015/2016; **b.** 2016/2017; **c.** 2017/2018; **d.** 2018/2019. The horizontal lines above and below the boxes

represent the maximum and minimum values within the range $1.5 * IQR$, where IQR is the interquartile range; the boxes represent the distance between the first and third quartiles. Horizontal lines inside the boxes correspond to the median values.

Figure 3

Boxplots showing the flowering length in native (light gray) and non-native (dark gray) woody species of a seasonal subtropical semiarid forest in Central Argentina. Four reproductive periods: **a.** 2015/2016; **b.** 2016/2017; **c.** 2017/2018; **d.** 2018/2019. The horizontal lines above and below the boxes represent the maximum and minimum values within the range $1.5 * IQR$, where IQR is the interquartile range; the boxes represent the distance between the first and third quartiles. Horizontal lines inside the boxes correspond to the median values.

Figure 4

Boxplots showing the days to the first fruit in native (light gray) and non-native (dark gray) woody species of a seasonal subtropical semiarid forest in Central Argentina. Four reproductive periods: **a.** 2015/2016; **b.** 2016/2017; **c.** 2017/2018; **d.** 2018/2019. The horizontal lines above and below the boxes represent the maximum and minimum values within the range $1.5 * IQR$, where IQR is the interquartile range; the boxes represent the distance between the first and third quartiles. Horizontal lines inside the boxes correspond to the median values.

Figure 5

Boxplots showing the fruiting length in native (light gray) and non-native (dark gray) woody species of a seasonal subtropical semiarid forest in Central Argentina. Four reproductive periods: **a.** 2015/2016; **b.** 2016/2017; **c.** 2017/2018; **d.** 2018/2019. The horizontal lines above and below the boxes represent the maximum and minimum values within the range $1.5 \times \text{IQR}$, where IQR is the interquartile range; the boxes represent the distance between the first and third quartiles. Horizontal lines inside the boxes correspond to the median values.

Supplementary Files

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