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Research article

Clade-specific responses regulate phenological patterns in Neotropical Myrtaceae

Vanessa G. Staggemeier[a,*], José Alexandre F. Diniz-Filho[a], Valesca B. Zipparro[b], Eliana Gressler[b], Everaldo Rodrigo de Castro[c], Fiorella Mazine[d], Itayguara Ribeiro da Costa[e], Eve Lucas[f], Leonor Patrícia C. Morellato[b]

[a] Departamento de Ecologia, ICB, Universidade Federal de Goiás, C.P. 131, 74001-970, Goiânia, GO, Brazil
[b] Departamento de Botânica, Laboratório de Fenologia, Grupo de Fenologia e Dispersão de Sementes, UNESP – Univ Estadual Paulista UNESP, CP 199, 13.506-900, Rio Claro, SP, Brazil
[c] Instituto Federal de Educação, Ciência e Tecnologia de São Paulo (IFSP), 14781-502 Barretos, SP, Brazil
[d] Universidade Federal de São Carlos, Campus Sorocaba, Rod. SP-264, Km 110, 18052-780, Brazil
[e] Departamento de Biologia, Universidade Federal do Ceará, Campus do Pici, 60455-760, Brazil
[f] Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, United Kingdom

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ABSTRACT

Understanding plant reproduction from an eco-phylogenetic perspective is essential because it allows us to predict how phenology could change in response to climatic changes. Unfortunately, reproductive patterns have been poorly explored in contemporary phylogenetic context until now. Closely related species are expected to reproduce in a similar ecological niche if phylogeny constrains the time of flowering and fruiting. In contrast, if climate determines phenology regardless of species affinities, species would randomly reproduce along favourable temporal axes. In this study, we used a clade of Neotropical Myrtaceae to test the influence of phylogenetic signal (PS) in phenology. Myrtaceae is the eighth largest angiosperm plant family in the world and the most speciose in the Atlantic rainforest. We reconstructed phylogenetic relationships among 57 Myrteae species plus an outgroup and quantified PS across three Atlantic rainforest communities: Saibadela, Cardoso and Picinguaba. Ecological factors were the main drivers of plant phenology. However, PS in plant reproduction was detected for flowering in Cardoso, suggesting a clade-specific response because flowering was conservative in the *Gomidesia* group. Fruiting in Saibadela also exhibited PS with phenological divergence between taxa with similar embryo shape and conservative fruiting time inside these groups, indicating that seed germination requirement can affect fruiting phenology. We suggest that investigation of PS in phenology should consider phylogenetic non-stationarity because evolutionary rates and ecological patterns are variable across taxa and often variable in short time scales. The identification of clades with conservative phenology, indicates the taxa most sensitive to climate change that can guide future conservation initiatives.

> "*Periodic and fluctuating patterns in physical and biological phenomena are interesting to biologists for many reasons, but particularly because of their importance as evolutionary constraints. . . . These regions* [very wet tropical environments] *should be particularly interesting because three important variables, light, water, and temperature, all vary minimally*."
>
> Hilty (1980).

1. Introduction

Darwin was the first to consider that related species share similar traits 'in a finest gradation' and, as a consequence, congeneric species would be expected to be more similar than unrelated species (for a complete transcription see Darwin notebook 'Transmutation of Species' in Barret, 1960). First attempts to understand shared responses in closely related species used a taxonomic approach through the study of variation of traits inside families, tribes or genera (e.g. Boulter et al., 2006; Harvey and Pagel, 1991; Johnson, 1992). The level of morphological and ecological similarity across taxa in relation to phylogenetic relationships or phylogenetic signal (PS) can now be tested by studying the pattern of trait

* Corresponding author.
E-mail address: v.staggemeier@gmail.com (V.G. Staggemeier).

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variation along evolutionary history, and the processes driving trait variation can be mapped over time.

Regardless of the method applied, PS has been detected in the morphology, demography and physiology of plants (Jordano, 1995; Morales, 2000), but remains underexplored for phenological traits such as flowering and fruiting time (but see Davies et al., 2013; Staggemeier et al., 2010). Phenology represents a key life history trait in plants, being primarily driven by climate and undergoing evolutionary selective pressures that define the timing, duration and intensity of any phenological event (Fenner, 1998). Thus, phenology has allowed researchers to monitor, predict and understand the response of organisms to climate change (Chambers et al., 2013; Rosenzweig et al., 2008). Indeed, many ecosystem properties are linked to species phenology and temporal changes such as biogeochemical cycles, population dynamics, and species interactions (Schwartz, 2013). As a result, identification of PS in key phenological traits might allow us to assess the impact of climate change on biodiversity. Changes in phenological patterns (i.e. earlier/later flowering/fruiting) can also culminate in cascade effects in plant-dependent guilds as well as their ecological interactions, e.g. herbivores, predators, pollinators and seed disperses (Burkle and Alarcón, 2011; Memmott et al., 2007), potentially leading to dramatic effects on communities. For instance, some plant clades have not been able to adjust their phenology to climate change and have declined dramatically in abundance (Willis et al., 2008).

While the ecological aspects of phenology have been extensively studied (Borchert et al., 2005; Morellato et al., 2000; Wright et al., 1999), evolutionary constraints on phenology are poorly understood. Although phylogenetic affinity has long been taken into account (Johnson, 1992; Kochmer and Handel, 1986; Wright and Calderon, 1995), phenological studies that consider phenology within an explicit phylogenetic framework are still scarce. Staggemeier et al. (2010) was the first to evaluate PS in flowering and fruiting times using a molecular phylogenetic hypothesis, and although that study detected a shared influence of ecology (reproductive niche) and phylogeny in Myrteae phenological responses, the climatic variables explained phenological variation better than phylogeny. However, the extent to which these local results are applicable to Myrtaceae at a larger scale or to other plant families is still unknown. More recently, attempts have been made to understand phylogenetic signal from a community perspective (Chang-Yang et al., 2013; Davies et al., 2013; for two recent examples); however, those authors did not address variation in phenology explained by species ecology.

South American Myrtaceae, represented by tribe Myrteae (Landrum and Kawasaki, 1997), offers an interesting system to test eco-evolutionary hypotheses (Smith-Ramirez et al., 1998; Staggemeier et al., 2010). Myrtaceae is represented by ca. 636 species in the Atlantic forest of Brazil (Stehmann et al., 2009), 515 of which are endemics that contribute substantially to high levels of diversity and endemism in this hotspot (Mori et al., 1983; Oliveira-Filho and Fontes, 2000). Members of this plant family also play a key role in the maintenance of trophic networks in this ecosystem (Gressler et al., 2006; VG Staggemeier unpublished results). These features coupled with a large variation in phenological patterns across taxa (Fig. 1) make Myrteae an excellent model in which to study patterns of evolution in plant phenology.

Here we shed light on the perennial question of whether phylogeny constrains plant phenology at a regional scale for one of the most important Neotropical plant families, Myrtaceae, for which a robust, species level phylogenetic hypothesis exists as well as detailed phenological observations of flowering and fruiting in the field. Specifically, we aim to disassociate the effects of ecological factors and phylogenetic constraints on the reproductive phenology of a Myrteae community in three Brazilian Atlantic rainforest localities. We seek to answer: (i) Is there phylogenetic signal in reproductive phenological responses? (ii) How has ecology and evolutionary history affect Myrteae reproduction? and (iii) What is the contribution of each method of measuring PS used here, to phenological research?

2. Material and methods

2.1. Study area: Atlantic rainforest

We selected three sites within São Paulo State parks encompassing some of the best-preserved, large areas of Atlantic rainforest (ARF) in Southeast Brazil (Fig. 2A). The first site is located at Núcleo Saibadela (Fig. 2B), Parque Estadual Intervales (total area: 48,000 ha), Sete Barras municipality; the vegetation was studied in detail by Guilherme et al. (2004) and Zipparro et al. (2005). The second site is a continental island (Fig. 2C), the Parque Estadual da Ilha do Cardoso (15,100 ha), in the municipality of Cananéia; the flora is described by Barros et al. (1991), Melo and Mantovani (1994), Pinto (1998) and Sugiyama (1998). The third site is located at Núcleo Picinguaba (Fig. 2D), Parque Estadual da Serra do Mar (7850 ha), in the municipality of Ubatuba. Detailed descriptions of the Picinguaba flora are available in Cesar and Monteiro (1995), Sanchez et al. (1999) and Joly et al. (2012). To facilitate identification of the three study sites in the text, figures and tables, hereafter we name them as follows: Saibadela, Cardoso and Picinguaba, respectively.

These regions are classified in accordance with the updated Köppen–Geiger system (Peel et al., 2007) as moist mid-latitude climates with mild winters, a typical warm temperate zone (Fig. 2A). Two main seasons are identified in the three study sites; the wet and less wet seasons. The wet season is long, warm and humid (from September to May) with monthly total rainfall over 100 mm; there is some regional differences in total rainfall during the short, colder and less wet season (from June to August) among the forest sites (Fig. 2B–D). However, there is no water restriction and mean monthly total rainfall never falls below 60 mm at any site, and the mean temperature is always around 20 °C (Fig. 2B–D). Climate data for the study period were obtained from local stations at Saibadela and Cardoso. When necessary we used supplementary data from the nearest meteorological station from the Departamento de Água e Energia Elétrica (DAEE) and the Instituto Agronômico de Campinas (IAC), respectively, where we also acquired the historical data; all data for Picinguaba are from the nearest IAC station (Table S1). Day-length for latitude 23°S–25°S follows Pereira et al. (2001). ARF phenology and specifically Myrteae flowering are mainly driven by day-length variations (Morellato et al., 2000; Staggemeier et al., 2010) and therefore we used an astronomical view of seasons to discuss Myrteae reproduction. Thus, two equinoxes and two solstice events divide the year into four periods: less rainy season (21 June to 23 September), early wet season (23 September to 21 December), middle wet season (21 December to 20 March), and late wet season (20 March to 21 June).

2.2. Phenological sampling and definition of peak date

Detailed phenological information for all three sites were collected from 1992 to 2009 as parts of different projects conducted by the UNESP Phenology Lab (Universidade Estadual Paulista), at Rio Claro, SP (Table 1). All studies used similar data collection protocols, observing marked individuals on a monthly basis. In total, 1525 adult individuals of 113 Myrteae species were observed over an average of 30 months (SD ± 12 months). We excluded 56 species (500 individuals) that presented fragmentary phenology data (see Supplementary material for details) or where molecular sequences were not available (Table S2). Therefore, our results are based on 57 species and 1025 individuals (Table S2). Thus 80% of species