Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

Vulnerability of phenological progressions over season and elevation to climate change: *Rhododendrons* of Mt. Yulong

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A B S T R A C T

Seasonal timing (phenology) of reproduction is a critical dimension of life-history, affecting ecological and evolutionary processes including individual fitness, community interactions, species boundaries and climate change adaptation. Staggered phenological sequences, or progressions, of flowering in plants have long been a topic of interest. Less well studied are multi-dimensional progressions across seasonal time and elevational space, which may be especially vital to understanding montane and alpine environments that are among the ecosystems most vulnerable to climate change.

To further our understanding of how phenological progressions are structured and to predict how they may respond to climate change, we collected data from an assemblage of ten co-occurring Himalayan *Rhododendron* species on Mt. Yulong, China, through two years of phenology monitoring in transects spanning a 1400 m elevation gradient, greenhouse experiments, and in comparison with the results of long-term models of species phenological responses to temperature derived from herbarium specimens. We asked whether we could quantitatively support flowering as a multi-dimensional progression in Mt. Yulong *Rhododendron* species, whether species that are part of this progression show differential phenological responses to changes in temperature, and how these responses impact reproductive success.

We found evidence for a progression of flowering, with *Rhododendron* species significantly overdispersed in elevation and flowering time and showing significantly less inter-species overlap in flowering time-space niche (2.9%) than expected by chance (8.5%). As a whole, the progression responded to changes in weather (-2.4 days / °C) and to experimentally increased greenhouse temperatures (-9.3 days / °C). However, individual species responses varied in their response (from $-26 - 2$ days / °C). Models derived from historical herbarium specimens predicted contemporary observed flowering well ($> 95\%$ of plants flowering within prediction intervals) and showed corresponding species differences. Reproductive output was affected by phenology, with the quantities of flowers and fruits greater in plants which flowered slightly earlier than their population mean (flowers $p < 0.05$; fruits $p < 0.01$), and in plants that responded to warmer weather with commensurately earlier flowering (flowers $p < 0.01$; fruits $p < 0.001$).

The elaborately sequenced progression of flowering over season and elevation in Himalayan *Rhododendron* highlights the intricacy of species assemblages in time and space. Varying phenological responses among species and the associated reproductive impacts make this progression, like other staggered phenological sequences, vulnerable to disruption with ongoing climate change.

1. Introduction

Phenology is a critical dimension of natural history. The timing of key life history stages determines much about the environments to which they are exposed. In plants, reproductive phenology is particularly important, affecting gene flow, population persistence, and species boundaries (Antonovics, 2006; Kameyama and Kudo, 2009; Devaux and Lande, 2009; Ladinig et al., 2013). The staggered sequence of flowering

and fruiting among species assemblages has long been a topic of interest (Clarke, 1893; Robertson, 1895). The community implications of such phenological progressions may include resource partitioning and the continuous provisioning of pollinators (Stiles, 1977; Waser and Real, 1979; Kochmer and Handel, 1986; Sherry et al., 2007) and dispersers (Wheelwright, 1985; González-Castro et al., 2012). In species assemblages that span elevational gradients, staggered flowering phenologies may be seen as multi-dimensional progressions across seasonal time

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and elevational space. However, phenological observations explicitly integrating elevational gradients remain limited to a few sites (Inouye, 2008; Wolkovich et al., 2012; Cornelius et al., 2013), despite the salience of phenology to alpine environments where late spring and early fall bracket a short period for growth and reproduction (Levesque et al., 1997; Körner, 2003).

Phenology is one of the earliest and most noticeable traits by which organisms respond to climate change (Parmesan and Yohe, 2003; Bertin, 2009; Wolkovich et al., 2014). Across the globe, reproductive phenologies have advanced with warming temperatures (Cleland et al., 2007; Wolkovich et al., 2012; Ellwood et al., 2013). However, certain species may not have sufficient plasticity or rate of adaptation to keep pace with changing climate (Visser et al., 2010; Cook et al., 2012), which may lead to species declines (Willis et al., 2008, 2010). Further, the amount and direction of phenological response may vary among species, depending on phylogenetic history (Levin, 2006; Lessard-Therrien et al., 2014) or other plant traits (Polgar and Primack, 2013; Ellwood et al., 2013). Mechanistically, different species respond to different physiological cues, including growing season temperatures, chilling requirements (Schwartz and Hanes, 2010; Cook et al., 2012), photoperiod (Amasino, 2010; Keller and Körner, 2014) and snowmelt (Inouye and McGuire, 1991; Price and Waser, 2008). These differential responses may lead to the disruption of plant flowering progressions, much as they threaten mismatches among plants and animal pollinators, seed dispersers or herbivores (Parmesan, 2006, Post et al., 2008, Forrest et al., 2010).

Seasonal gradients also may affect phenological responses to climate change, with differing responses in spring and fall phenologies or in components of phenology such as the beginning and ending of life-history events (Sherry et al., 2007; Fridley, 2012; Hart et al., 2016). These contrasts are only visible in studies that prioritize whole-season measures of phenology rather than relying solely on first flowering date (Miller-Rushing et al., 2008; CaraDonna et al., 2014). They remain less explored in phenological research (Polgar and Primack, 2013; Laube et al., 2014).

To further our understanding of how phenological progressions are structured and to predict how they may respond to climate change, we collected data from an assemblage of *Rhododendron* species on Mt. Yulong, China, near the center of distribution for *Rhododendron*. On Mt. Yulong, as elsewhere in the eastern Himalaya, *Rhododendron* species flower across broad ranges of elevation and season, are ecologically and ethnobotanically salient, and are well represented in historical herbarium collections (Hart et al., 2014; Hart and Salick, 2017; Hart and Ranjitkar, 2018). With two years of phenology data gathered across transects spanning a 1400 m elevation gradient, experimental warming treatments in high-altitude greenhouses, and comparison with the results of long-term models of phenological responses to temperature derived from these herbarium specimens (Hart et al., 2014), we asked whether we could quantitatively support flowering as a multi-dimensional progression in Mt. Yulong *Rhododendron* species, whether species or phenological components that are part of this progression show differential phenological responses to temperature, and how these responses impact reproductive success.

2. Materials and methods

2.1. Study site

At the far eastern edge of the Himalaya, Mt. Yulong (玉龙雪山 27.0 °N, 100.1 °E) occupies a geographcal nexus of the tropical lowlands of SE Asia, the subtropical and temperate vegetation of China, and the alpine Tibetan Plateau (Fig. 1A). It is the southernmost glaciated mountain in Eurasia and is located within the 'Mountains of Southwest China', a global hotspot of biological diversity (Mittermeier et al., 2005). This area is among the world's richest in temperate plant species (Kier et al., 2005) and is the center of diversity for many plant genera

(Wen et al., 2014) including *Rhododendron* (Fig. 1A). More than 30% of the world's *Rhododendron* species occur in the area and half of them are endemic (Wu et al., 2005), with species richness further concentrated in northwest Yunnan and adjoining areas (Shrestha et al. 2017). Mt. Yulong (Fig. 1B, C) and the other ranges in this area (collectively called the Hengduan Mountains) are separated by deep gorges carved by the Yangtze, Mekong, and Salween Rivers. The resulting biogeographic isolation creates the high beta-diversity (Salick et al., 2004; Wen et al., 2014) that is an important component of the area's species richness. Mt. Yulong was a center of collection for the plant-hunters George Forrest and Joseph Rock (Mueggler, 2011), whose collections, along with those of later botanists, provide an exceptionally strong and well documented historical context (Hart et al., 2014).

Elevation structures vegetation communities on Mt. Yulong (Fig. 2). Above the highest agricultural fields, lower elevations (~2700 – 3300 m asl) consist mostly of pine-oak forest. With increasing elevation, vegetation grades to oak scrub (~3300 – 3700 m asl), alpine meadows (~3700 – 4100 m asl), and finally rock cliffs and retreating glaciers (Wang et al., 2007; Kong et al., 2009). At all elevations, *Rhododendron* species make up a substantial portion of the plant communities. *Rhododendron* life-forms vary depending on elevation and species: shrub understory in forest, small-tree canopy at middle and higher elevations, and dwarf shrub patches in open alpine areas and on rock outcrops.

2.2. Transect structure

We sampled *Rhododendron* populations along the elevational gradient in a stratified random pattern. We laid two transects on the eastern slopes of the mountain and two transects on the western slopes from the lowest elevation forests at the edge of cultivated land (2760 m asl on the east and 3060 m asl on the west) to the local elevational limit of *Rhododendron* species (4060 m asl). At every 100 m of elevation along each of the four transects, we set two transect points, one directly north and one directly south. Each transect point was offset a random distance between 5 and 20 m from the ascents. This produced 60 transect points on the east slopes and 44 transect points on the west slopes (Fig. 1C), at 15 elevations. From each transect point and for each *Rhododendron* species present (Table 1), we calculated plant density (as described below), monitored phenology, and recorded fruit-set. Below, we refer to the collective individuals of one species monitored around one transect point as a 'population'.

To calculate density, we used the variable area transect method (Parker, 1979), a powerful and efficient plotless density estimator which performs well with spatially aggregated distributions (Engeman et al., 1994) such as *Rhododendron* populations. From each transect point, we continued directly north or south (approximately along the elevational contour), demarking a 1.5 m wide subtransect of variable length. For the first four plants of each *Rhododendron* species encountered, we measured: distance along the subtransect, height and maximum horizontal canopy cover. The density of a given species (plants / m^2), was calculated as $D = (nr - 1) / (w \Sigma l_i)$, where n is the number of subtransects, r is the nth plant (here, 4), w is the search width (here, 1.5 m), and Σl_i is the sum of lengths (distances from the transect point) to the rth (4th) plant. If 50 m along the subtransect was searched encountering 1–3 plants of a species, the species was recorded as low density (which we quantified as $D = 0.005$ for the purposes of aggregation), and if no plants were encountered, the species was recorded as absent. Species were identified in the field according to the local plant checklist (Wang et al., 2007). We collected voucher specimens of each species to confirm identification with reference to the Flora of China (Wu et al., 2005) and deposited specimens at the herbaria of the Kunming Institute of Botany-Chinese Academy of Sciences (KUN) and the Missouri Botanical Garden (MO).

For phenological monitoring of *Rhododendrons* at each point, we tagged the nearest 12 plants of each species present for repeat monitoring. For the entire flowering period (February to August) in 2012