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Flowering Phenology in Relation to Adaptive Radiation

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ABSTRACT. The role of flowering phenology in ecological diversification is poorly understood, even though this variable may be an important determinant of fitness. While flowering schedules are readily evolvable, they also seem to be under phylogenetic constraint. I ask whether phenological change is a partner to adaptive radiation. Using examples from island and continental lineages, I show that habitat diversifications are not necessarily coupled with phenological change, whereas shifts in pollinator typically are so coupled. It all depends on whether alteration in flowering time is required to invade new habitats or exploit new pollinators. The coupling of ecological and temporal shifts is most evident in the evolution of autopolyploids. Stasis in the flowering times of some lineages more likely is due to stabilizing selection than to genetic constraints.

KEYWORDS: adaptive radiation, ecology, niche evolution, flowering phenology, pollinators.

Manifest and often rapid adaptive radiations in habitat tolerances have occurred in many lineages on islands (e.g., Hawaiian silverswords, Baldwin and Robichaux 1995; *Tetramolopium*, Lowrey 1995; *Echium*, Böhle et al. 1996; *Sonchus* Kim et al., 1996; *Argyranthemum*, Francisco-Ortega et al. 1996) and continents (e.g., *Cirsium*, Kelch and Baldwin 2003; *Phylica*, Richardson et al. 2001a; *Inga*, Richardson et al. 2001b; *Gaertnera*, Malcomber 2002; *Ehrharta*, Verboom et al. 2003; *Calochortus*, Patterson and Givnish 2004). Correlatively, many lineages, especially those in southern Africa, have experienced conspicuous radiations in the groups of pollinators exploited (e.g., *Gladiolus*, Goldblatt et al. 2001; *Sparaxis*, Goldblatt et al. 2000b; *Disa*, Johnson et al. 1998). Shifts in the habitats of lineages have been predicated by changes in growth form, morphology, and physiology. Movements into new pollinator niches typically were accompanied by changes in floral attributes.

Whereas much has been written about radiations in habitat and pollinator space, the literature is largely mute on the subject of phenological divergence. Even a readily observed attribute such as flowering time has received little scrutiny. This is surprising, because flowering period is an important determinant of population fitness (Rathcke and Lacey 1985; Reekie and Bazzaz 1987; Kozlowski 1992). The timing of flowering can substantially affect pollination success, seed production, and the level of seed and fruit herbivory (Dominguez and Dirzo 1995; Brody 1997; O'Neil 1997; Ollerton and Diaz 1999; Kelly and Levin 2000; Pilson 2000; Wright and Meagher 2003; Parra-Tabla and Vargas 2004; Stinson 2004). The timing of flowering and thus seed production also may affect progeny quality (Galloway 2002; Lacey et al. 2003).

I propose that within a genus, flowering time is a plesiomorphic trait that would remain in the ancestral state during ecological diversification, unless invasions of new niches would mandate temporal change. This idea is supported by the conservatism of flowering phenologies within temperate and within tropical phylads (Bell and Stephens 1984; Kochmer and Handel 1986; Johnson 1992). Wright and Calderon (1995) found that congeners had similar flowering times in 57 of 59 genera studied on Barro Colorado Island, Panama. Sister species and species within clades often have similar flowering periods, but differ temporally from species in other clusters (Mosseler and Papadopol 1989; Ferguson and Jansen 2002; Debussche 2004).

Ecologically divergent taxa have been documented in numerous lineages, and these taxa often have different flowering times (Heslop-Harrison 1964; Grant 1981; Levin 1978, 2000). Given that time is not a resource and that new times will not be ''invaded'' simply for their own sake, it follows that some niche shifts were predicated upon temporal change. For example, later flowering allowed the occupation of sand dunes in *Gilia capitata* (Grant 1952), *Viola tricolor* (Clausen 1926), and *Phlox pilosa* (Levin 1969) from races growing in richer substrates. In *Clarkia*, earlier flowering permitted mesophytic lineages to invade more xeric regions with their shorter growing seasons (Vasek and Sauer 1971; Moeller 2004). Alterations in flowering schedules also allowed populations to better exploit different groups of pollinators (Waser 1983; Goldblatt and Manning 1996, 2000; Johnson et al. 1998). For example, a shift to later flowering allowed *Ipomopsis* to better exploit hummingbirds (Price et al. 2005).

Flowering phenology may evolve relatively rapidly. Some weeds (e.g., *Camelina sativa*, Stebbins 1950; *Echinochloa crus-galli var. crus-galli*, Barrett 1983) have converged in flowering time on the crops that they grow amongst. Mine populations of *Agrotis tenuis* and *Anthoxanthum odoratum* flower earlier than their pasture counterparts (McNeilly and Antonovics 1968). Clinal variation in flowering time coincident with their northward and southward spread has evolved in invasive *Solidago altissima* and *S. gigantea* (Weber and Schmid 1998), *Impatiens glandulifera* (Kollmann and Banuelos 2004), *Abutilon theophrasti* (Warwick and Black 1986), *Amaranthus retroflexus* (Weaver et al. 1982), *Datura stramonium* (Weaver et al. 1985), and *Xanthium strumarium* (Tranel and Wassom 2001).

Given that flowering time is an important determinant of population fitness, and that many ecological shifts have been accompanied by phenological change, it is important to understand its involvement in adaptive radiations in the habitat and pollinator niches. Has flowering period evolution been a necessary partner of ecological diversification?

I will show that niche transitions are not necessarily coupled with new flowering schedules, although there are many cases of the latter. There are four possible scenarios involving flowering time and radiation in habitat and pollinator niches as follows: (a) major change in habitat, but little change in the temporal niche; (b) major change in habitat and temporal niches; (c) major change in pollinator and temporal niches; (d) major change in pollinator niche, but little change in the temporal niche. Examples from each category will be briefly discussed. The species compared below live in the same region.

The literature on flowering phenology is too sparse and anecdotal for meaningful quantitative comparisons between categories involving large numbers of genera, or for fine scale phylogenetic analyses. As seen in the examples below, differences between congeners may be much more than a month, thus conferring partial or complete temporal isolation. A substantial amount of the information presented was obtained by communicating directly with experts on different genera, who kindly provided their unpublished observations.

PATTERNS OF TEMPORAL CHANGE DURING ADAPTIVE RADIATION

Major Change in Habitat but Little Change in Temporal Niche. *Epilobium* flowering period has changed little in the face of extraordinary ecological diversification in New Zealand. This genus occurs in 13 distinctive habitats, including lowland moist and dry forests, rock cliffs and crevices, tussock grasslands, dry riverbeds, grasslands, alpine fellfields, and loose unstable scree slopes (Raven 1972). Yet, almost all of the species flower from December through January or February (Raven and Raven 1976). The rare exceptions, like *E. nummulariifolium*, flower from late summer into the winter.

North American members of *Cirsium* grow in a wide variety of habitats such as prairies, montane meadows, rocky desert canyons, seeps and streamsides, brackish marshes, forests, coastal dunes, and openings in chaparral. Molecular phylogenetic analyses indicate that ecological radiation was quite rapid (Kelch and Baldwin 2003). Nevertheless, in California for example, nearly each and every species flowers in June, July, and August (Baldwin, personal communication).

Lasthenia is another genus with many species in California. This genus comprises almost exclusively annuals and is thought to have undergone saltational radiation (Chan et al. 2001). The genus grows in a wide range of substrates, including alkaline flats, vernal pools, guano deposits, coastal bluffs, and serpentine outcrops (Rajakaruna 2003). However, nearly all species flower from March to June (Ornduff 1966). Similar flowering periods (April–July) also are had by species of *Calochortus*, in spite of its expansion into several habitat types in California (Munz and Keck 1959; Patterson and Givnish 2004). The evolution of the serpentine endemic, *Layia discoidea*, from the soil generalist, *L. glandulosa*, did not involve a shift in flowering time (Munz and Keck 1959; Gottlieb et al. 1985).

Thus far, consideration has been given to temperate genera. Genera with broader flowering periods may be found in regions with relatively little seasonal variation. *Tetramolopium* is one genus that has undergone extensive ecological radiation in the equable temperature regime of the Hawaiian Islands. Species reside in dry forests, subalpine woodlands, alpine deserts, cliffs, coastal shrubland, and grassy flats (Lowrey 1995). The species tend to occur in the dry, leeward parts of islands, and have largely synchronous and broad flowering periods. They flower whenever adequate moisture is available (Lowrey, personal communication).

The silversword alliance has undergone conspicuous ecological diversification in the Hawaiian Islands. Species occur in dry, mesic, and wet forests, subalpine shrublands and forests, alpine deserts and dry shrublands (Baldwin and Robichaux 1995). Sites differ in annual precipitation from less than 400 mm to over 12,000 mm. Nevertheless, each species flowers in the summer and fall, and rarely are species temporally isolated (Baldwin, personal communication).

Ecological diversification in *Argyranthemum*, a Canary Island endemic, has not been accompanied by temporal radiation. The genus has expanded into pine forests, arid lowland scrub, coastal deserts, heath belt, and laurel forests (Francisco-Ortega et al. 1997). All species flower from January to June (Humphries 1976).

Pericallis provides a striking example of ecological radiation in the Canary Islands, with species invading laurel forest, coastal desert, lowland scrub, pine forest, and high altitude desert (Panero et al. 1999). The woody habit evolved from herbaceous ancestors in some of these habitats. Most species flower from spring through early summer (Santos-Guerra, personal communication).

The evolution of the woody habit from an herbaceous ancestor also characterizes Canary Island *Echium* (Böhle et al. 1996). Its species are found in semi-desert habitats, laurel forests, semidesert habitats, and in the subalpine zone. Flowering in each species is largely confined to the spring and summer. Species show little temporal isolation (Santos-Guerra, personal communication). Other Canary Island genera sharing ecological diversification and the evolution of woodiness include *Aeonium* (Mes and Hart 1996; Jorgensen and Olesen 2001), and *Sonchus* (Kim et al. 1996). Once again, flowering is largely confined to the spring and summer (Santos-Guerra personal communication). In the three genera mentioned here, the species that do not flower in the spring and summer do so in the winter, and thus are reproductively isolated from the others.

Major Changes in Habitat and Temporal Niches. Like many other clades in the Hawaiian Islands, the *Alsinidendron-Schiedea* alliance has undergone extensive ecological diversification. Species occur in wet forests, mesic forests, dry forests, dry shrublands, and dry cliffs (Sakai et al. 1997). Unlike the Hawaiian lineages discussed above, this one has radiated in the temporal niche, as well as in the ecological. Species that occur in dry areas tend to flower early in the year after the winter rains, and then stop flowering by early summer. Species occurring in mesic and wet forests flower later. One alpine species that grows on dry cliffs flowers in the summer (Weller, personal communication).

Modest temporal radiation is associated with recent ecological differentiation in *Ehrharta*, which grows in the summer-arid zone of southern Africa (Verboom et al. 2003). The genus of annuals and perennials resides in fynbos, renosterveld, succulent karoo, dune scrub, and grasslands, with the minimum annual rainfall varying from 1000–1400 mm in forest and fynbos vegetation to 0–200 mm in succulent karoo. The more arid communities are inhabited by annual species. These species flower from July through November or December, whereas the perennials flower from September or October into December or January (Goldblatt and Manning 2000).

The evolution of tolerances to habitats with higher temperatures and less soil moisture often is accompanied by the evolution of earlier flowering times in order to complete reproduction prior to the onset of unfavorable growing conditions. For example, recurrent incursions of xeric habitats during the speciation process are well documented in *Clarkia* (Lewis and Lewis 1955; Sytsma et al. 1990; Gottlieb 2003). Selection for earlier flowering in habitats with ephemeral water sources has accompanied the reduction of protandry and the evolution of autogamy (Lewis 1973; Eckhart and Geber 1999).

The coupling of edaphic and temporal evolution is well illustrated in the derivatives of *Mimulus guttatus*, all of which are more xerophytic than this species (Macnair and Gardiner 1998). This species, which grows on normal soil, has given rise to the serpentine endemics *M. nudatus* and *M. pardalis*, and to the copper mine endemic *M. cupriphilus*. These taxa flower earlier than their orthodox parent, as does the copper mine ecotype of *M. guttatus*. A shift from outcrossing to partial self-fertilization also occurred during the evolution of *M. cupriphilus and M. pardalis* (Macnair and Gardiner 1998). *Mimulus guttatus* also has given rise to *M. nasutus*, which prefers sandy substrates and flowers earlier than its progenitor (Kiang and Hamrick 1978).

Major Changes in Pollinator and Temporal Niches. Many genera in southern Africa have undergone remarkable diversification in the pollination niche. Temporal shifts often were a prerequisite for moving into new pollinator niches, because pollinator abundance varies with the season. *Gladiolus* has one of the most diverse pollination systems in southern Africa, with species adapted to long-tongued bees, long-proboscid flies, nectarinid birds, night-flying moths, and satyrid butterflies (Goldblatt et al. 2001). In the winter-rainfall Cape Floristic Province, butterfly-pollinated species begin flowering in December and later, proboscis-fly pollinated species begin flowering earlier, and bee-pollinated species even earlier (August–September).

The orchid genus *Disa* has radiated into more pollination niches than any other genus, with species specializing on hawkmoths, wasps, short-tongued flies, long-tongues flies, butterflies, and bees (Johnson et al. 1998). This genus also is noteworthy because some of the floral syndromes associated with different pollen vectors have evolved more than once. In the Cape Floristic Province, bee-, wasp-, and long-tongued fly-pollinated species flower in the spring through mid-summer, although species pollinated by long-tongued flies are somewhat later in this time window. Moth- and butterfly-pollinated species flower from mid-summer or later into the fall (Goldblatt and Manning 2000).

Lapeirousa is another southern African genus with diversification in the pollinator niche (Goldblatt and Manning 1996). The genus has species specializing on bees, long-tongued flies, and moths, which flower in that sequence. Another member of the Iridaceae, *Ixia*, also has species that specialize on bees, beetles, long-proboscid flies and lepidopterans (Goldblatt et al. 2000a). Again, bee-pollinated species have earlier phenologies than fly-pollinated species, which are earlier than lepidopteran-pollinated species.

Not only may species diverge in flowering time within a year, they also may diverge in the time flowers are open during the day. This scenario has been documented in *Gaura*, where the dusk-flowering *G. longiflora* has given rise to the dawn-flowering *G. demareei* (Gottlieb and Pilz 1976). The former is pollinated by moths, and latter is pollinated by bees.

Major Change in Pollinator but Little Change in Temporal Niche. *Sparaxis*, a southern Africa endemic, exploits an unusual range of pollinators for a genus of 15 species (Goldblatt et al. 2000b). While some species attract generalists, others are visited by members of Coleoptera, Diptera, or Hymenoptera. Each and every *Sparaxis* species flowers from August to mid-September (Goldblatt and Manning 2000).

Watsonia laccata and *W. aletroides* are another southern Africa species pair with similar flowering phenologies. The former is pollinated by sunbirds, and the latter is pollinated by bees (Goldblatt et al. 1999; Goldblatt personal communication).

Discussion

The invasion of new pollinator niches tends to be dependent upon flowering time shifts. This can be explained by changes in abundances of alternate pollinator guilds throughout a year. Sometimes shifts in pollinators are unaccompanied by changes in flowering phenology, which is suggestive of sympatric speciation. However, species with little temporal isolation almost always have disparate habitat requirements and rarely occur in mixed populations. Diversification in the pollinator niche in large measure is preceded by diversification in the habitat niche (Goldblatt and Manning 1996; Goldblatt personal communication).

The invasion of new habitats is not typically coupled with phenological change. Why should this be the case? One possibility is that in some regions significant temporal change will not enhance fitness, and indeed may substantially diminish it. Consider, for example, the reproductive schedule of plants in California and South Africa where Mediterranean climates prevail. Flowering typically occurs in late winter through the early summer, prior to the depletion of soil moisture (Kummerow 1983; Johnson 1992; Le Maitre and Midgley 1992; Bosch et al. 1997; Dallman 1998; Thompson 2005). The window for growth, flowering, and fruiting may be too narrow for broad lineage diversification in their temporal schedules. Narrow flowering windows also are characteristic of genera that inhabit deserts (Beatley 1974; Solbrig et al. 1977; Mott 1979; Fox 1990).

Stasis in the temporal profiles of lineages ostensibly means that the microclimates and substrates in the new habitats are similar to those in the original habitats. Stabilizing selection presumably prevails. Whereas no one has documented the liabilities of accelerating or delaying flowering time in the genera with little temporal diversification, stabilizing selection has been demonstrated elsewhere many times (Dominguez and Dirzo 1995; O'Neil 1997; Ollerton and Diaz 1999; Kelly and Levin 2000; Pilson 2000; Wright and Meagher 2003; Parra-Tabla and Vargas 2004; Stinson 2004). I reject the notion that conservatism in flowering time within a genus can be explained by the absence or weak force of natural selection, as proposed by Ollerton and Lacey (1992). There is too much evidence that a change in the flowering schedule may substantially alter fitness.

Genetic constraints also could contribute to conservatism in flowering time in some lineages. It is difficult to gauge its importance relative to environmental constraints, which are much easier to measure. The evolution of new flowering schedules may be restricted by insufficient heritable variation (Bradshaw 1991). The evolution of phenological novelty also may be constrained by genetic correlations between flowering time and other temporal traits such as germination time and fruiting time (Rathcke and Lacey 1985; Primack 1987; Kelly 1993; O'Neil 1997). Genetic correlations also may occur between flowering times and ecophysiological attributes such drought tolerance, where increased drought tolerance is associated with later flowering (Geber and Dawson 1990, 1997; Craufurd 1991; White 1993; McKay et al. 2003). Selection for altered reproductive timing in *Arabidopsis thaliana* is constrained by a genetic correlation between this trait and plant size (Mitchell-Olds 1996; Baker et al. 2005).

Whereas some habitat transitions were not accompanied by temporal shifts, others were. This was not only so in cases of divergent evolution (as discussed above), but also where hybrid derivatives invaded sites not suitable for either parent. Consider two derivatives of *Helianthus annuus* (which grows in heavy clay soils) and *H. petiolaris* (which grows in sandy soils where precipitation is moderate). *Helianthus deserticola* grows in stabilized sandy soils on the desert floor; and *H. paradoxus* grows in brackish marshes. The former flowers several days earlier than either parent (Rosenthal et al. 2002), which is expected because desert annuals usually require heavy rains for seed germination and then reach reproductive maturity very quickly (Aronson et al. 1993; Clauss and Venable 2000). Conversely, *H. paradoxus* flowers several days later than either parent (Rosenthal et al. 2002). This is a function of slower growth, which is characteristic of halophytes (Flowers et al. 1986; Ishikawa and Kachi 2000).

Where phenological change is associated with habitat transitions, we would like to know whether both shifts occurred synchronously or whether one preceded the other. Fortunately, we can gain insights from an experiment reconstructing the origin of *H. deserticola*. Gross et al. (2004) planted second generation backcross hybrids between *H. annuus and H. petiolaris* (with the latter as the recurrent parent) in an *H. deserticola* habitat. An analysis of phenotypic selection revealed that flowering time did affect fitness. Unexpectedly, later-flowering was favored. The investigators proposed that early flowering may be advantageous only when the population shifts to the more rapid growth and higher reproductive effort characteristic of *H. deserticola*.

Ecological and temporal changes typically are coupled during the evolution of autopolyploids (Levin 2002). Autopolyploids typically occupy different habitats than their progenitors either in areas of sympatry and/or allopatry. Temporal differences between ecologically distinct cytotypes have been documented in numerous species including *Lotus corniculatus* (Gauthier et al. 1998), *Heuchera grossularifolia* (Thompson 1997), *Arrhenatherum elatius* (Petit and Thompson 1997), *Anthoxanthum alpinum* (Felber-Girard et al. 1996), *Plantago media* (Van Dijk and Biljsma 1994), and *Chamerion angustifolia* (Husband and Sabra 2003). Diploids flower earlier than tetraploids, but their flowering periods usually overlap. This difference reflects slower growth rates in the tetraploids.

Ecological radiation from a common ancestor begins in the absence of phenological isolation. The evolution of phenological differences between populations would facilitate their continued ecological divergence, because the incidence of interbreeding between them would be an inverse function of the phenological disparity. The ecological divergence of populations with similar flowering times strongly suggests that new habitats were spatially isolated from that originally occupied.

The ecological divergence of colonizers would be fostered if temporal assortative mating occurred *within* populations. By inflating the additive genetic variance in flowering time, assortative mating makes flowering time more sensitive to selection (Breese 1956; Kirkpatrick 2000; Fox 2003). Temporal assortative mating is ubiquitous in plants, as early bloomers tend to cross with other early bloomers and "lates" with "lates" (Weis and Kossler 2004; Weis et al. 2005). Kirkpatrick and Ravigne (2002) point to flowering time as a prime trait when they discuss how the action of disruptive selection on assorting traits may lead to reproductive isolation. Within the context of this paper, disruptive selection on flowering time would be coupled with at least partial spatial isolation.

Although flowering time differences are most likely to emerge as adaptations allowing the invasion of new habitat or pollinator niches, temporal differences between taxa also may arise from selection against hybridization. The products of adaptive radiation often are quite crossable and interfertile (Levin 2004). Models showing the efficacy of temporal character displacement have been formulated by Stam (1983) and Van Dijk and Bijlsma (1994). The reinforcement of temporal differences through artificial selection against hybridization has been demonstrated in maize (Paterniani 1969).

The reinforcement of temporal disparities has yet to be demonstrated in radiating angiosperm lineages. Perhaps displacement from the ancestral temporal niche is a greater liability than hybridization. Much of the discussion of character displacement in flowering phenologies has involved hummingbird-pollinated plants growing in the same community, which may or may not be related (Murray et al. 1987). Even at the community level, it is not clear that selection to reduce temporal overlap, and thus competition for pollinators, indeed has occurred.

The literature on flowering time differences within genera has focused on the reproductive isolation of sympatric species. Indeed, temporal isolation is a very important barrier to gene flow in a multitude of sympatric species pairs, while being less significant in numerous others. An important challenge for the future is to better understand the environmental factors that promote flowering-schedule differentiation within genera, whether lineages are responding to environmental opportunity in space (ecological speciation) or to gradual changes in time (geographical speciation). We also need to better understand the directions of phenological change within clades, which can be accomplished by mapping flowering phenologies onto phylogenetic trees.

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