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Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae



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ABSTRACT

We present an integrative model predicting associations among epiphytism, the tank habit, entangling seeds, C₃ vs. CAM photosynthesis, avian pollinators, life in fertile, moist montane habitats, and net rates of species diversification in the monocot family Bromeliaceae. We test these predictions by relating evolutionary shifts in form, physiology, and ecology to time and ancestral distributions, quantifying patterns of correlated and contingent evolution among pairs of traits and analyzing the apparent impact of individual traits on rates of net species diversification and geographic expansion beyond the ancestral Guayana Shield. All predicted patterns of correlated evolution were significant, and the temporal and spatial associations of phenotypic shifts with orogenies generally accorded with predictions. Net rates of species diversification were most closely coupled to life in fertile, moist, geographically extensive cordilleras, with additional significant ties to epiphytism, avian pollination, and the tank habit. The highest rates of net diversification were seen in the bromelioid tank-epiphytic clade ($D_{\text{crown}} = 1.05 \text{ My}^{-1}$), associated primarily with the Serra do Mar and nearby ranges of coastal Brazil, and in the core tillandsioids ($D_{\text{crown}} = 0.67 \text{ My}^{-1}$), associated primarily with the Andes and Central America. Six large-scale adaptive radiations and accompanying pulses of speciation account for 86% of total species richness in the family. This study is among the first to test *a priori* hypotheses about the relationships among phylogeny, phenotypic evolution, geographic spread, and net species diversification, and to argue for causality to flow from functional diversity to spatial expansion to species diversity.

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1. Introduction and conceptual framework

Bromeliaceae (58 genera, ca. 3140 species) is the largest of the 37 families of flowering plants found mostly or exclusively in the Neotropics (Stevens, 2013), and includes more epiphytic taxa than

any family worldwide except Orchidaceae (Gentry and Dodson, 1987; Benzing, 1987, 2000; Zotz, 2013). Bromeliads often impound rainwater and detritus in “tanks” formed by the overlapping bases of rosulate leaves, employ CAM photosynthesis, and bear absorptive trichomes on their leaf surfaces, providing the means to weather drought and absorb water and nutrients on rocks and epiphytic perches (Pittendrigh, 1948; McWilliams, 1974; Benzing, 1980, 2000; Crayn et al., 2004; Givnish et al., 2007, 2011; Schulte

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et al., 2009). Bromeliads constitute a large fraction of all species of vascular epiphytes in Neotropical forests, are especially diverse at mid-elevations and in areas of high rainfall and humidity, and display increasingly narrow endemism at higher elevations (Gentry and Dodson, 1987; Kessler, 2001; Kreft et al., 2004; Krömer et al., 2005; Linares-Palomino et al., 2009; Linares-Palomino and Kessler, 2009). They show little variation in chromosome number and have centers of diversity in four mountainous regions, including Central America, the Andes, the tepuis of the Guayana Shield, and the Serra do Mar and nearby coastal ranges of the Brazilian Shield in South America (Givnish et al., 2011).

Based on a fossil-calibrated phylogeny based on eight plastid regions, Givnish et al. (2011) concluded that Bromeliaceae arose in the Guayana Shield ca. 100 million years ago (Mya), with six of the eight subfamilies containing all but 2% of current species having diverged from each other over a relatively short period from 15 to 10 Mya, as bromeliads spread into the Andes, Amazonia, Central America, the Caribbean, and the Brazilian Shield. What functional traits did bromeliads acquire between 15 and 10 Mya that allowed them to invade mountainous or dry regions beyond the Guayana Shield and evolve the epiphytic habit? Which of these traits, or the habitats or adaptive zones invaded, helped trigger rapid rates of net species diversification? Did such traits evolve once or multiple times? Where did they evolve, and under what conditions? Which traits underwent correlated or contingent evolution, and why? Answers to these fundamental questions are now within reach, given the well supported, taxonomic ally and ecologically well-stratified phylogeny for Bromeliaceae provided by Givnish et al. (2011).

Several key innovations (*sensu* Simpson, 1944) – including epiphytism, the tank habit, water- and nutrient-absorptive leaf trichomes, CAM photosynthesis, and avian pollination – may have allowed bromeliads to invade new adaptive zones in rain- and cloud-forest treetops or arid regions and microsites and speciate extensively there (Schimper, 1888; Mez, 1904; Pittendrigh, 1948; McWilliams, 1974; Benzing, 1980, 2000; Givnish et al., 1984, 1997, 2004, 2007, 2010, 2011; Benzing et al., 1985; Gentry and Dodson, 1987; Smith, 1989; Kessler and Krömer, 2000; Crayn et al., 2004; Schulte et al., 2005, 2009; Givnish, 2010). Key landscapes (*sensu* Givnish, 1997) – including moist, fertile, dissected mountainous regions – may also have triggered adaptive radiation and pulses of speciation by offering a promising range of ecological possibilities. We propose that a complex of evolutionary forces (Fig. 1) can account for spatial and temporal patterns in the origin of critical bromeliad traits and the invasion of key landscapes; that this complex implies that these traits and landscapes should have undergone correlated and contingent evolution (*sensu* Pagel, 1994), associated primarily with orogenies of extensive, mineral-rich cordilleras; and that variation in these traits and landscapes –

across lineages and across time – can help explain patterns in the distribution and species diversification of the eight bromeliad subfamilies. Our rationale is as follows:

- Fertile, humid tropical montane habitats select for the epiphytic habit**, by favoring heavy rains and low evaporation rates at mid elevations (Gentry and Dodson, 1987; Grytnes and Beaman, 2006; Acharya et al., 2011) and a rich nutrient rain derived from leachate and shed parts from host trees, and possibly from animals or droppings derived ultimately from fertile soils (Janzen, 1974a,b, 1977; Benzing, 2000; Gentry and Emmons, 1987; Romero et al., 2006, 2010; Benner and Vitousek, 2007).
- Epiphytism and fertile, humid montane habitats favor the tank habit** – Many bromeliads impound rainwater and detritus in “tanks” formed by tightly overlapping leaf bases. Tanks can provide epiphytes with a source of water and nutrients tapped by absorptive leaf trichomes or adventitious roots (McWilliams, 1974; Benzing, 1980, 2000). However, young tank epiphytes are vulnerable to desiccation given their high ratio of evaporative surface to water volume, and are unlikely to survive in lowlands with unpredictable rainfall and high temperatures and evaporation rates (Krömer et al., 2006; Zotz et al., 2011). Tanks should thus be more common in montane areas with higher rainfall, greater humidity, and lower seasonality and in larger species and individuals, and uncommon in small-bodied species and arid areas. By capturing nutrients from falling debris, tanks should be favored in areas with richer substrates.
- Epiphytism should favor the evolution of “entangling seeds” that permit ready attachment to twigs and branches, and vice versa** – Epiphytes must be able to attach their seeds to hosts (Schimper, 1884). Bromeliads have evolved three mechanisms of seed dispersal, involving finely divided appendages (comas) in subfamily Tillandsioideae, fleshy berries in subfamily Bromelioideae, and wing-like appendages in the remaining six subfamilies (Givnish et al., 2010). Of these, the first two can entangle seeds with the substrate via wetted comas, or sticky regurgitates or droppings.
- Epiphytism or dry terrestrial sites favor the evolution of CAM photosynthesis** – CAM photosynthesis and leaf succulence reduce transpiration and prolong the period over which carbon uptake can be maintained following the onset of drought, albeit at the cost of low photosynthetic capacity (Medina, 1974; Winter and Smith, 1996a,b). CAM should thus be associated with atmospheric *Tillandsia* that absorb water and nutrients solely via absorptive trichomes, given their exposure, small body size and virtually absent water

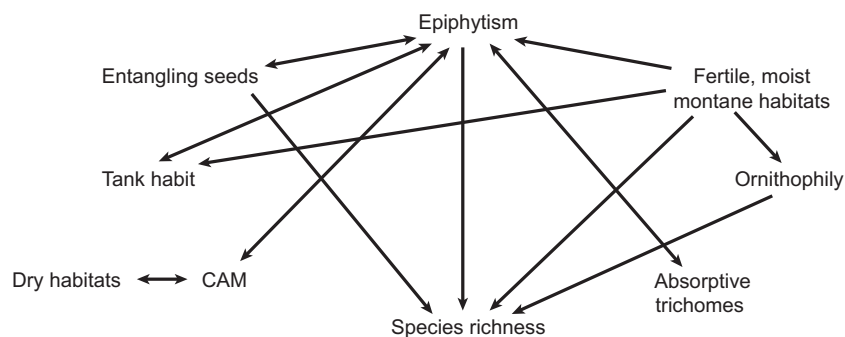


Fig. 1. Proposed schema of ecological and evolutionary forces driving the evolution of various traits in the family Bromeliaceae. One-way arrows indicate a single direction of causality; two-way arrows, bi-directional causality. Although not every trait is expected to affect all others directly, the complex of causal drivers could indirectly tie together many traits shown that are shown as unlinked.

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