



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



Thomas J. Givnish<sup>a,\*</sup>, Michael H.J. Barfuss<sup>b</sup>, Benjamin Van Ee<sup>c</sup>, Ricarda Riina<sup>d</sup>, Katharina Schulte<sup>e,f</sup>, Ralf Horres<sup>g</sup>, Philip A. Gonsiska<sup>a</sup>, Rachel S. Jabaily<sup>h</sup>, Darren M. Crayn<sup>f</sup>, J. Andrew C. Smith<sup>i</sup>, Klaus Winter<sup>j</sup>, Gregory K. Brown<sup>k</sup>, Timothy M. Evans<sup>l</sup>, Bruce K. Holst<sup>m</sup>, Harry Luther<sup>n</sup>, Walter Till<sup>b</sup>, Georg Zizka<sup>e</sup>, Paul E. Berry<sup>o</sup>, Kenneth J. Sytsma<sup>a</sup>

<sup>a</sup> Department of Botany, University of Wisconsin-Madison, Madison, WI 53706, USA

<sup>b</sup> Department of Systematic and Evolutionary Botany, Faculty of Life Sciences, University of Vienna, Vienna A-1030, Austria

<sup>c</sup> School of Natural Sciences, Black Hills State University, Spearfish, SD 57799, USA

<sup>d</sup> Real Jardín Botánico, CSIC, Plaza de Murillo 2, Madrid 28014, Spain

<sup>e</sup> Department of Botany and Molecular Evolution, Research Institute Senckenberg and J.W. Goethe University, Frankfurt am Main D-60325, Germany

<sup>f</sup> Australian Tropical Herbarium, James Cook University, Cairns, QLD 4878, Australia

<sup>g</sup> GenXPro, Frankfurt am Main 60438, Germany

<sup>h</sup> Department of Biology, Rhodes College, Memphis, TN 38112, USA

<sup>i</sup> Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, United Kingdom

<sup>j</sup> Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama

<sup>k</sup> Department of Botany, University of Wyoming, Laramie, WY 82071, USA

<sup>l</sup> Department of Biology, Grand Valley State University, Allendale, MI 49401, USA

<sup>m</sup> Marie Selby Botanical Gardens, Sarasota, FL 34236, USA

<sup>n</sup> Gardens By The Bay, National Parks Board Headquarters, Singapore 259569, Singapore

<sup>o</sup> Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

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### ABSTRACT

We present an integrative model predicting associations among epiphytism, the tank habit, entangling seeds, C<sub>3</sub> 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

\* Corresponding author. Fax: +1 262 7509.

E-mail address: [givnish@wisc.edu](mailto:givnish@wisc.edu) (T.J. Givnish).

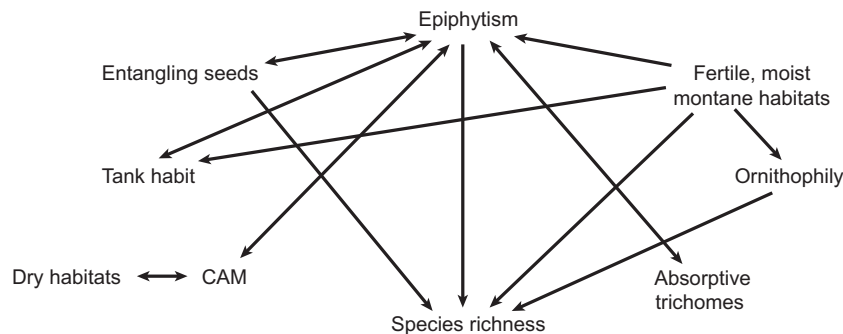
et al., 2009). Bromeliads constitute a large fraction of all species of vascular epiphytes in Neotropical forests, are especially diverse at mid-elevations and in areas of high rainfall and humidity, and display increasingly narrow endemism at higher elevations (Gentry and Dodson, 1987; Kessler, 2001; 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.

storage (Benzing and Renfrow, 1974), and to a lesser extent with tank epiphytes. Dry conditions should also favor CAM in terrestrial bromeliads, at low elevations or above cloud and elfin forests at high elevations. Low atmospheric CO<sub>2</sub> in the past would have also favored CO<sub>2</sub>-concentrating mechanisms like CAM (Arakaki et al., 2011).

5. **In bromeliads, epiphytism favors absorptive leaf trichomes and vice versa** – Epiphytes lack access to reliable supplies of water and nutrients in the soil, and their roots are often reduced to holdfasts (Pittendrigh, 1948; Benzing, 1990). Trichomes on the leaf bases of tank and atmospheric bromeliads provide an alternative means of absorbing water and nutrients (Mez, 1904; Benzing, 2000).
6. **Fertile, humid montane habitats favor avian pollination** – Cool, wet conditions select for thermoregulating pollinators, often hummingbirds in the Neotropics (Cruden, 1972; Maberley, 1975; Feinsinger, 1983; Bawa, 1990; Givnish et al., 2009). Floral nectar often lacks critical amino acids, so avian pollinators must consume substantial amounts of insects as well (Brice and Grau, 1991; Martínez del Rio, 1994; Fleming and Nicolson, 2003; Yanega and Rubega, 2004). Extremely infertile substrates should thus work against avian pollination, because such substrates favor heavy chemical defenses in plants that, in turn, reduce the density of herbivorous insects (see Janzen, 1974a,b, 1977).
7. **Fertile, humid montane habitats in extensive cordilleras favor high rates of net species diversification in epiphytic lineages** – Extensive shifts in ecological conditions over short horizontal and vertical distances in montane regions can foster rapid speciation in epiphytes (Gentry and Dodson, 1987). More extensive cordilleras have more geographic barriers for species specialized on particular habitats, and thus, a greater potential for species diversification rate and total species richness. Species at higher altitudes should face more habitat barriers (e.g., valleys), fostering narrower ranges for individual taxa (Ibisch, 1996; Kessler, 2002a,b) and partly reversing the trend for species richness to decline with elevation. As argued above, extremely infertile substrates should work against epiphytic diversity. Net rates of species diversification should be especially high for recently uplifted, ecologically unsaturated areas (Gentry, 1982; Gentry and Dodson, 1987; Benzing, 1990; Linder, 2008; Givnish, 2010).
8. **Epiphytism favors high net rates of species diversification** – Epiphytism offers more impetus for speciation by providing a more diverse range of microsites than forest floors, over a larger, better lit, more fragmented, more dynamic surface (Gentry and Dodson, 1987; Benzing, 1990; Gravendeel et al., 2004). Selection for short generation times in twig specialists may favor high speciation rates in some lineages (Benzing, 1990, 2000; Gravendeel et al., 2004; Richter et al., 2009).
9. **Entangling seeds favor higher net rates of species diversification** – Entangling seeds characterize Tillandsioideae (coma-like flight apparatus) and Bromelioideae (fleshy berries), and should result in greater dispersal ability than the winged or unappendaged seeds of other subfamilies. Increased seed movement might increase overall speciation in epiphyte line ages by facilitating occasional long-distance dispersal, colonization, isolation, and parallel bouts of speciation along the length of extensive cordilleras (Gentry, 1982; Gentry and Dodson, 1987; Benzing, 1990; Givnish et al., 2004, 2007; Gravendeel et al., 2004).
10. **Avian pollination should favor higher species richness and rates of species diversification** – Coevolution with more than 300 hummingbird species spawned by the recent

uplift of the northern Andes may have accelerated bromeliad speciation (Gentry, 1982; Graham, 1997; Kay et al., 2005). Hummingbirds may have also accelerated speciation by favoring gullet-shaped flowers. Once such exclusionary blossoms evolve, their length and shape could easily shift to attract species with different bill lengths and shapes, providing a rapidly evolved means of plant premating isolation (Givnish, 2010).

Our model (Fig. 1) predicts that epiphytism should exhibit patterns of correlated and contingent evolution with entangling seeds, the tank habit, CAM photosynthesis, ornithophily, absorptive trichomes, and fertile, moist montane habitats. It also implies that these characteristics should, directly or indirectly, result in higher aggregate levels of species richness and species diversification associated with radiation into the epiphytic adaptive zone and dry terrestrial microsites. Here we test these hypotheses by (1) overlaying key traits on the most recently derived bromeliad phylogeny as a function of time and spatial location; (2) testing whether these traits exhibit predicted patterns of correlated and contingent evolution; and (3) assessing whether the such traits are correlated with species richness and net rates of species diversification within Bromeliaceae. Our conclusions have broad implications for the evolution of epiphytism and the impact of individual traits and ecological conditions on the genesis of plant diversity (Givnish, 2010). They also illustrate how phylogeny, ecology, physiology, and biogeography can be integrated to develop and test *a priori* hypotheses about the relationships among phenotypic innovation, geographic spread, and species diversification of a major group.

## 2. Methods

### 2.1. Taxon sampling

We used a placeholder approach in this study and our preceding analysis of phylogenetic relationships and historical biogeography in Bromeliaceae (Givnish et al., 2011). We employed 90 species stratified across 46 of 58 bromeliad genera – which collectively include >97.5% of all described bromeliad species – to represent a family of ca. 3140 species. We believe that this approach is justified, based on the high degree of uniformity within genera (and often within subfamilies) for most of the character-states under study (see Smith and Down, 1974, 1977, 1979; Crayn et al., 2004; Schulte et al., 2009), and based on a general presumption of phenotypic conservatism across close relatives (Webb, 2000; Donoghue, 2008). Where variation in key traits under study occurs within genera (e.g., presence/absence of the tank habit in *Brocchinia*, or of CAM in *Puya* and *Tillandsia*), we attempted to include species representing the taxonomic extent of alternative character-states based on published phylogenies for those groups (e.g., Givnish et al., 1997; Barfuss et al., 2005; Schulte et al., 2009; Sass and Specht, 2010).

### 2.2. Phylogenetic analyses

Character-state reconstructions, tests of correlated and contingent evolution, estimates of net rates of diversification, and assessments of character determinants of speciation used phylogenetic trees for Bromeliaceae derived by Givnish et al. (2011) from 9341 aligned plastid nucleotides from the 90 bromeliad species and four outgroups from Typhaceae, Rapateaceae, and Arecaceae. Very few natural hybrids have been detected among bromeliads via comparisons of nuclear vs. plastid trees, justifying the use of a plastid phylogeny alone to infer evolutionary relationships (see Schulte et al.,

2009; Jabaily and Sytsma, 2010; Sass and Specht, 2010). Trees used were generated based on maximum likelihood (ML) (Givnish et al., 2011) and Bayesian inference (BI) using BEAST v 1.7.4 (Drummond and Rambaut, 2007; Drummond et al., 2012a). *Vriesea espinosae* in Givnish et al. (2011) is here considered *Tillandsia* sp. A; this taxon is embedded in a large clade of Mexican *Tillandsia* based on *matK* and *rps16* sequences (M. Barfuss, pers. comm.).

Simultaneous estimations of phylogeny and divergence times were executed in BEAST under a Yule tree prior (Yule, 1925) and unlinked clock models, using the GTR + G + I model of evolution suggested by the Akaike information criterion (Akaike, 1974) obtained in ModelTest v3.7 (Posada and Crandall, 1998). Calibration dates for the root (Poales:  $100 \pm 1.0$  My (mean  $\pm$  s.d.)), Typhaceae (*Typha* + *Sparganium*):  $69.5 \pm 1.5$  My, and crown Bromeliaceae:  $19 \pm 2.0$  My) were obtained from the monocot-wide analysis of Givnish et al. (2011). In all analyses, we constrained *Puya* to be monophyletic (Jabaily and Sytsma, 2010). BEAST analyses were run for 40 million generations, with samples taken every 2000 generations. The first two million generations were discarded as burn-in, and we then interpreted the trees in TreeAnnotator v. 1.7.4 prior to visualization in FigTree v. 1.4. Log files were analyzed in tracer (Rambaut and Drummond, 2007), and the effective sample size values (ESS) were over 300 for all parameters. A random subset of 100 prior probability trees was also saved for additional analyses (see below).

### 2.3. Character coding

We obtained data on the taxonomic distribution of the states of seven key functional and distributional characters from the literature. Binary character states were assigned for **habit** (terrestrial vs. epiphytic), **growth form** (tank vs. non-tank), **seeds** (winged/unappended vs. entangling), **photosynthetic pathway** ( $C_3$  vs. CAM), **pollination syndrome** (avian vs. non-avian), **elevational distribution** (low vs. high [ $\geq 1000$  m]), and **arid/semi-arid habitat or microsite** (present vs. absent). To show *when* particular traits arose, ancestral state reconstructions were superimposed on the BEAST chronogram. To show *where* traits arose, the maximum-parsimony (MP) reconstruction of ancestral regions – very similar to those obtained via ML and S-DIVA (Givnish et al., 2011) – were also overlaid on the chronogram. Given the large differences in ecology between interior vs. coastal portions of the Brazilian Shield, and their invasion by different clades, here we separate the coding of the Atlantic Forest region (including the Serra do Mar and Serra da Mantiqueira) from the rest of the Brazilian Shield.

Data on habit, growth form, seeds, and habitat were drawn from Smith and Down (1974, 1977, 1979), Givnish et al. (1997), Schulte et al. (2009), and Zizka et al. (2009). Data on photosynthetic pathways were drawn from Crayn et al. (2004) (CAM for  $\delta^{13}C > -20\%$ , and  $C_3$  for  $\delta^{13}C < -20\%$ ), supplemented by  $\delta^{13}C$  measurements for *Puya mima* (R. Jabaily and T. Givnish) and *Pitcairnia carinata* and *P. felicianae* (J. A. C. Smith), and identification of *Tillandsia usneoides* (Spanish moss) as CAM by Kluge et al. (1973). For the few cases in which no  $\delta^{13}C$  value was available for a species, but all congeners studied have the same photosynthetic pathway, we coded remaining species as having that pathway. Data on pollination syndromes (avian, bat, insect) were drawn from Vogel (1954, 1969), Smith and Down (1974, 1977, 1979), Gardner (1986), Szazima et al. (1989, 1995a, 1995b, 1996, 1999), Galetto and Bernardello (1992), Till (1992), Smith and Till (1998), Benzing (2000), Kessler and Krömer (2000), Dziedziuch et al. (2003), Canela and Szazima (2005), Krömer et al. (2005, 2006, 2008), and Tschapka and von Helversen (2007). For species lacking direct observations of pollinators, pollination syndromes were deduced from floral traits such as corolla color, size, and shape, position of the anthers, and presence/absence of landing platforms (Vogel, 1954; Baker and Baker,

1990). Waser et al. (1996) has criticized this approach, but pollination syndromes have been shown to predict accurately hummingbird, bat, and hawkmoth pollination in several Neotropical plant groups (Cruden, 1997; Krömer et al., 2008). Data on elevational distributions were drawn from Smith and Down (1974, 1977, 1979) and an extensive literature search. Data on absorptive trichomes are too sparse and continuous in nature to be included in our analyses, but such trichomes are common in tillandsioids and tank-forming brocchinioids and bromelioids (Benzing et al., 1976, 1985; Givnish et al. 1984, 1997), while hydrophobic trichomes are common in other groups (Pierce et al., 2001).

We scored elevational distribution in three ways (low vs. high [ $>1000$  m]; low or infertile substrates [i.e., Guayana Shield sandstones and quartzites] vs. high and fertile [i.e., found in the Andes, Serra do Mar or similar mountains in the Brazilian Shield]; and low or infertile or dry [i.e., *Puya* and *Deuterocohnia* taxa above the cloud-trapping inversion layer on tropical mountains, ca. 3000 m on large massifs and much lower on smaller mountains] vs. high, fertile, and moist). Multiple scorings were needed because we hypothesized (see above) that fertile, moist conditions at higher elevations favor epiphytism and the tank habit, while fertile conditions at higher elevations (including those in cold, dry conditions above the inversion layer) favor ornithophily. Highly infertile conditions at any elevation should be inimical to epiphytism, the tank habit, and avian pollination. We also scored a composite eighth character, **epiphyte or arid/semi-arid habit** (present/absent), to test hypothesis 4 (see above).

### 2.4. Reconstruction of character-state evolution

We characterized evolutionary transitions of each of our focal characters in terms of the number, directionality, and timing of inferred shifts. We implemented maximum parsimony (MP) and Bayesian inference (BI) optimization of character evolution. MP reconstruction utilized the “trace character” option in MacClade (Maddison and Maddison, 2005) with the resolving option of “all most parsimonious states at each node”. The resulting ancestral-state reconstructions were visually displayed by color-coding the branches of the ML chronogram.

BI (MCMC – Pagel, 1999) reconstructions were implemented in BayesTraits v.1.0 (Pagel and Meade, 2007) using MultiState and a random set of 100 Bayesian prior probability trees. To reduce some of the uncertainty and arbitrariness of choosing priors under MCMC, we used the hyperprior approach (the *rjhp* command) as recommended (Pagel et al., 2004; Pagel and Meade, 2007). Combinations of hyperprior values (exponential or gamma, mean and variance) and rate parameter values were explored to find acceptance rates when running the Markov chains of between 20% and 40% (as recommended by Pagel and Meade, 2007). All subsequent analyses used the reversible-jump hyperprior command (*rjhp* gamma 0 30 0 10) that seeded the mean and variance of the gamma prior from uniform hyperpriors on the interval 0 to 10, and a rate parameter of 150 (rate parameters of 100 and 350 were used only for pollination and elevation, respectively). All Bayesian analyses used 25 million generations, with sampling every 1000 generations and a burn-in period of 20,000 generations. Ancestral reconstruction of character evolution under BI with the 100 randomly chosen PP trees was represented using pie charts to indicate state probabilities at each node in the bromeliad chronogram.

### 2.5. Tests of correlated evolution and directionality

We tested for correlated evolution between each pair of characters using BayesTraits (Pagel and Meade, 2008) under BI using the same methods and prior probability trees just described. We implemented the BayesDiscrete module, which investigates

correlated evolution between a pair of discrete binary traits by comparing the log likelihood of two models for independent vs. dependent evolution of binary traits. The first model assumes that the two states of two traits, such as **habitat** (terrestrial vs. epiphytic) and **photosynthetic pathway** ( $C_3$  vs. CAM), evolve independently on the tree. This creates two rate coefficients per trait, or four rate coefficients in all, that must be estimated. The second model allows the traits to evolve in a correlated fashion, such that the rate of change in one trait depends on the background state of the other. The dependent model has four states, one for each combination of the two binary traits, creating eight rate coefficients that must be estimated in all (see [Electronic appendix, Fig. A1](#)). To determine whether a character (e.g., habitat) shows correlated evolution with another trait (e.g., photosynthetic pathway), we compared the likelihood estimate of the independent model ( $L(I)$ ) to that for the dependent model ( $L(D)$ ). The pattern of correlated evolution is considered significant when  $-2[L(D) - L(I)]$  exceeds the critical value ( $P < 0.05$ ) for the  $\chi^2$  distribution with 4 d.f., based on a comparison of eight vs. four estimated rate coefficients in the dependent vs. independent model, respectively ([Pagel, 1999](#)). We also determined whether each of the eight transition parameters ( $q_{ij}$  in [Fig. A1](#)) in the dependent model is significantly greater than zero. Individual transition parameters were restricted to zero (e.g.,  $q_{12} = 0$ ) and the likelihood score of this seven-parameter dependent model was compared to the likelihood score of the full eight-parameter, dependent model using a  $\chi^2$  distribution with 1 d.f. Comparisons involving the equivalent of autocorrelation (e.g., habitats  $\geq 1000$  m elevation vs. fertile, moist habitats  $\geq 1000$  m elevation, or epiphytes vs. epiphyte or arid/semi-arid habitat) or associations between different environmental variables were excluded from analysis.

## 2.6. Tests of contingent evolution

We tested hypotheses of contingent evolution between each pair of characters (e.g., does CAM evolve equally frequently in terrestrial and epiphytic clades?) using BayesDiscrete. We tested specific hypotheses by restricting two rates to be equal (e.g., for  $q_{12} = q_{34}$ , where the former is the rate of evolution of CAM from  $C_3$  in a terrestrial clade, and the latter is the same rate in an epiphytic clade; [Fig. A1](#)). This seven-parameter model was then compared to the full eight-parameter model described above using a  $\chi^2$  test with 1 d.f. A significant outcome indicates that the state of the second character (terrestrial vs. epiphytic) influences the evolution of the first ([Pagel, 1994](#)). Critical  $\alpha$  values for  $\chi^2$  tests were adjusted using Bonferroni corrections for the four comparisons involved in each independent test ([Friedman and Barrett, 2008](#)).

## 2.7. Determinants of net rates of species diversification

We used phylogenetically unstructured and phylogenetically structured analyses to estimate rates of species diversification. We then related differences in diversification rate to variation among clades in age, habitat, growth form, pollination syndrome, photosynthetic pathway, mode of seed dispersal, and geographic distribution.

### 2.7.1. Phylogenetically unstructured analyses

We used phylogenetically unstructured analyses ( $t$ -tests and regressions) focused on non-overlapping lineages (subfamilies or subfamily subsets) ([Magallón and Castillo, 2009](#)), recognizing that the rapid divergence of most subfamilies from each other between 15 and 10 million years ago implies an almost star-shaped phylogeny relating those subfamilies to each other ([Givnish et al., 2011](#)). Species numbers per genus and subfamily ([Table A1](#)), or major clades of similar rank (i.e., the bromelioid tank-epiphyte clade sis-

ter to *Acanthostachys*, the Xeric clade (*Deuterocohnia*–*Dyckia*–*Encholirium*), the core tillandsioids (excluding *Catopsis*–*Glomeropitcairnia*); see [Schulte et al. 2009](#) and [Givnish et al. 2011](#)) were obtained from [Luther \(2008\)](#), with *Pepinia* sunk into *Pitcairnia* ([Robinson and Taylor, 1999](#)). We estimated the rate of net species diversification  $D$  for each subfamily and key subclade as  $D = (\ln N)/t$ , where  $N$  is the current number of species in a clade and  $t$  is its estimated stem age, based on a simple, birth-only model:  $N(t) = N(0) e^{Dt}$  ([Magallón and Sanderson, 2001](#); [Jansson and Davies, 2008](#)). Similar calculations were performed using crown ages. More complex, birth–death models to estimate  $D$  were used in phylogenetically structured analyses (see below).

We tested the hypotheses that species richness and net diversification rates should be greater in **younger vs. older lineages** ([Magallón and Sanderson, 2001](#); [Givnish et al., 2005, 2009](#); [Rabosky and Lovette, 2008](#); [Givnish, 2010](#)); in **epiphytic vs. terrestrial lineages** ([Gentry and Dodson, 1987](#); [Benzing, 1990, 2000](#)); in **hummingbird- vs. insect-pollinated lineages** ([Gentry, 1982](#); [Kay et al., 2005](#); [Schmidt-Lebuhn et al., 2007](#)); in **CAM vs.  $C_3$  lineages** ([Silvera et al., 2009](#)); in line ages with **entangling seeds vs. winged or unappendaged seeds** ([Givnish et al., 2007](#)); and in lineages occupying the **extensive, relatively fertile, topographically complex cordilleras of the Andes/Central America and Serra do Mar vs. other areas** ([Gentry, 1982](#); [Luteyn, 2002](#); [Hughes and Eastwood, 2006](#)) ([Fig. 1](#)). Given the one-sided nature of our predictions, we used one-tailed  $t$ -tests to evaluate the significance of differences in the average values of richness or net diversification of subfamilies (or groups of similar rank) characterized more or less entirely by one state of a given character vs. the other state. For comparisons of richness or net diversification as a function of lineage age, we used one-tailed  $t$ -tests to evaluate the significance of regressions of those variables against lineage age. Tests were conducted on both raw and log-transformed data.

### 2.7.2. Phylogenetically structured analyses

We employed two recently developed ML methods that incorporate nonrandom/incomplete sampling and extinction to infer significant shifts in diversification rates across a time-calibrated phylogeny (MEDUSA 3.0.0, [Alfaro et al., 2009](#)) and test for correlations between character states and diversification rates (BiSSE: [Maddison et al., 2007](#); [FitzJohn et al., 2009](#)). MEDUSA requires a time-calibrated phylogeny in which extant taxonomic diversity can be assigned to monophyletic terminal clades in order to avoid the problem of non-randomly sampled clades or unresolved clades. After removing outgroups while leaving Bromeliaceae rooted, we reduced the BEAST chronogram to 26 terminals ([Table A1](#)) to produce the most resolved tree representing bromeliad clades at the generic level or above, to which we could confidently assign essentially all members of the family. Due to the present lack of phylogenetic knowledge within the large core Bromelioideae and Tillandsioideae, several terminals within these groups are large (up to 868 spp.). Based on [Schulte et al. \(2009\)](#), we included *Orthophytum* with *Cryptanthus* as the sister to *Acanthostachys* + the tank-epiphyte clade of Bromelioideae. Based on [Barfuss et al. \(2005\)](#), we maintained the monophyly of both Tillandsiidae (*Guzmania*, *Mezobromelia*, *Racinaea*, *Tillandsia*) and Vrieseae (*Alcantarea*, *Vriesea*, *Werauhia*) in Tillandsioideae. *Steyerbromelia* was included in the *Navia/Brewcaria* clade. Only *Disteganthus* (2 spp.) and *Fernseea* (2 spp.) were not placed in the 26-terminal tree. We used the March 2013 version of MEDUSA embedded in GEIGER 1.99-3 in R version 3.0.0 ([R Core Team, 2012](#)) to estimate the best fit for rates of net species diversification ( $r = \text{birth} - \text{death}$ ) and relative extinction ( $\epsilon = \text{death/birth}$ ) among applications of both pure-birth and birth–death models to crown and stem ages. MEDUSA employs a stepwise process to evaluate the support for increasingly complex models of diversification based on the difference in sample-

size corrected AIC scores. We also calculated diversification rates in GEIGER for clades in which MEDUSA identified significantly acceleration of such rates (Magallón and Sanderson, 2001).

The BiSSE (Binary State Speciation and Extinction) model of Maddison et al. (2007), as implemented in Diversitree (FitzJohn et al., 2009) in R, was used to test the hypotheses that diversification rates should be greater in **epiphytic vs. terrestrial lineages**, in **hummingbird- vs. insect-pollinated lineages**, in **CAM vs. C<sub>3</sub>**, in line ages with **entangling seeds vs. winged or unappended seeds**, and in lineages occupying the **extensive, relatively fertile, topographically complex cordilleras of the Andes/Central America and Serra do Mar vs. other areas**. Proportions of taxa in each clade bearing each character-state were estimated from the literature (Table A2). BiSSE employs ML optimization to estimate absolute rates (vs. relative rates in MEDUSA) of asymmetric character change ( $q$ ), speciation ( $\lambda$ ), and/or extinction ( $\mu$ ) by maximizing the likelihood of these parameters on our 26-terminal chronogram. For each character, we compared three constrained models in BiSSE against the unconstrained model in which  $q$ ,  $\lambda$ , and  $\mu$  were allowed to vary. The three constrained models individually forced  $q_{01} = q_{10}$ ,  $\lambda_{01} = \lambda_{10}$ , and  $\mu_{01} = \mu_{10}$ , respectively. For example, if diversification rates are correlated with epiphytism, then the unconstrained model should be significantly favored over the constrained model with  $\lambda_{01} = \lambda_{10}$ . Because BiSSE often cannot complete computations involving unresolved tips with >100 species (R. FitzJohn, pers. comm.), we had to scale down the size of the terminals to a maximum of 90 species. This scaling roughly preserved relative clade size, although the smallest clades (always rounded up to 1.0 species) are larger relative to species-rich clades than in the unscaled data. Our rationale was that if BiSSE provided evidence for significant correlation of diversification rates with a character-state, despite the relative upscaling of the less diverse clades, then this would be a conservative and hence strong finding regarding the impact of that character-state on diversification.

### 2.8. Cumulative effects of multiple radiations

In addition to assessing whether particular traits accelerate net diversification within the clades bearing them, we calculated the fractions of the total number of present-day bromeliads added by the acquisition of particular traits or suites of traits (e.g., epiphytism, CAM in terrestrial species) strongly associated with later-divergent clades and the regions they invaded outside the ancestral Guayana Shield. Our aim was to estimate the augmentation of total bromeliad diversity due to the additive effects of broad-scale adaptive radiations, of the clades added and geographic areas invaded as a result of the morphological and physiological innovations, irrespective of any acceleration of diversification within particular clades or in association with particular traits.

## 3. Results

### 3.1. Phylogeny and time-line

The BEAST chronogram is nearly identical in topology to the ML tree of Givnish et al. (2011), but resolves *Puya* as monophyletic and places *Acanthostachys* as the non-tank, epiphytic sister to the bromelioid tank-epiphyte clade (Fig. 2). Nodal ages under BEAST are very similar to those derived using r8s ( $y = 1.107x - 0.683$ ,  $r^2 = 0.98$ ), with BEAST tending to produce slightly older dates for all but the shallowest and deepest events. The bromeliad stem is dated to 97.5 Mya; the bromeliad crown, to 22.7 Mya. The six subfamilies sister to Lindmanioideae, containing 98% of present-day taxa, arose within a relatively narrow window between 16.9 and 10.1 Mya.

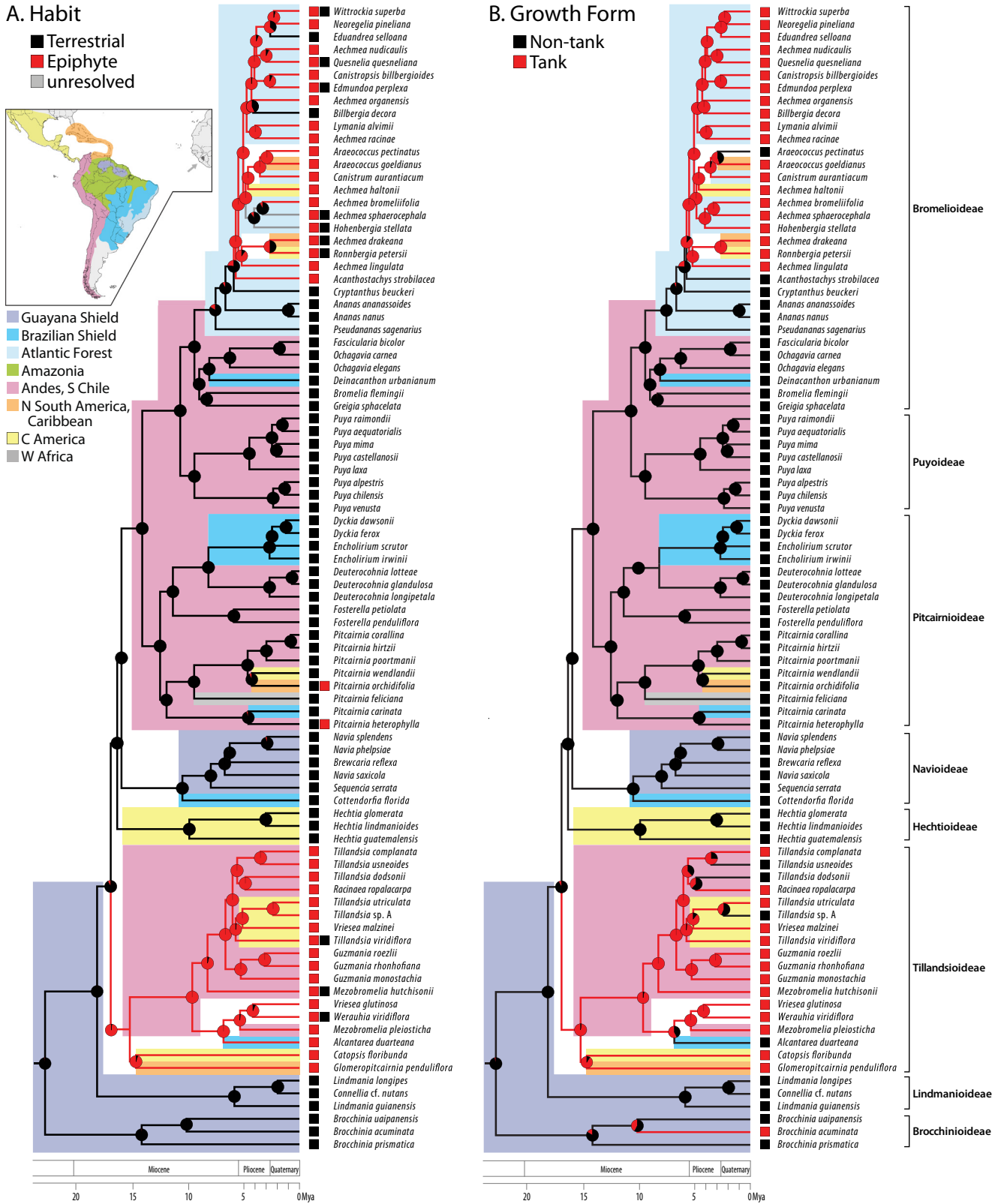
### 3.2. Reconstruction of character-state evolution

Ancestral bromeliads appear to have been terrestrial, non-tank-forming, and insect-pollinated, had winged seeds and C<sub>3</sub> photosynthesis, and grew on infertile, moist substrates >1000 m elevation (Figs. 2 and 3, A2–A4). Each focal character appears to have undergone at least two state transitions, and reconstructions based on MP and BI broadly agree. Almost all cases of **epiphytism** trace to two origins among the taxa surveyed (Fig. 2A). The first occurred at the base of Tillandsioideae ca. 16.9–15.2 Mya, with dispersal from the Guayana Shield into the Andes, Central America, and/or the northern littoral of South America or Caribbean. The second occurred ca. 5.9 Mya in the Atlantic Forest, in the clade subtended by and including *Acanthostachys*. Other scattered gains and losses are detailed in the Electronic appendix.

**Tanks** appear to have arisen three times: at the base of Tillandsioideae, coincident with the rise of epiphytism; ca. 10 Mya in *Brocchinia* within the Guayana Shield; and in Bromelioideae sister to *Acanthostachys* ca. 5.8 Mya in the Atlantic Forest region, soon after invasion from the Andes/central Chile via the Brazilian Shield (Fig. 2B). The bromelioid tank-epiphyte clade is sister to epiphytic but tankless *Acanthostachys*. Scattered losses occurred in five isolated taxa. **Entangling seeds** evolved without reversal from winged seeds twice, at the base of Tillandsioideae (see above), and at the base of Bromelioideae among terrestrial taxa ca. 10.1–9.4 Mya, in the Andes/central Chile (Fig. A2A). **CAM photosynthesis** arose from C<sub>3</sub> photosynthesis at least five times, at the base of Bromelioideae–Puyoideae ca. 10.7 Mya, in the Andes/central Chile; at the base of the Xeric Clade (*Deuterocohnia*–*Dyckia*–*Encholirium*) ca. 11.3–8.1 Mya, in the Andes and/or the Brazilian Shield; at the base of *Hechtia* ca. 16.2–9.9 Mya, in Central America; in *Tillandsia utriculata*-*T. sp. A* ca. 5.7 Mya, in Central America; and in widespread *Tillandsia usneoides* ca. 3.5 Mya (Fig. 3A). Other possible gains and losses of CAM are discussed in the Electronic appendix. CAM appears to be evolutionarily labile in *Puya* and *Tillandsia* – or reflect developmental plasticity – given that close relatives have  $\delta^{13}\text{C}$  values typical of C<sub>3</sub> and CAM photosynthesis.

**Avian pollination** – predominantly by hummingbirds – appears to have arisen 2–3 times, in each case from insect pollination (Fig. 3B). Ornithophily arose once in ancestral tillandsioids, or separately in *Glomeropitcairnia* 14.6 Mya (in the northern littoral of South America and the Caribbean) and in the core tillandsioids ca. 15.2 Mya (in the Andes/central Chile). Ornithophily also evolved in the ancestor of Pitcairnioideae–Puyoideae–Bromelioideae ca. 15.9–14.1 Mya, in the Andes/central Chile. Reversions to insect pollination from avian pollination appear to have occurred at least seven times in Bromelioideae during the last 6 Mya; once in *Fosterella* ca. 11.3 Mya, in the Andes; and four to five times in Tillandsioideae. Bat pollination appears to have arisen four times among the taxa surveyed – in *Alcantarea*, *Encholirium*, *Werauhia viridiflora*, and *Tillandsia viridiflora* – in each case from bird-pollinated ancestors.

**Elevations  $\geq 1000$  m above sea level** appear to have been invaded up to 13 times based on MP character-state reconstruction (Fig. A2B). Reconstructions based on Bayesian inference reveal a reasonable probability of six independent origins of high-elevation habitats, including the common ancestor of all bromeliads, and persistence in Navioideae and the bromeliad spine through one of the two basal lineages in Bromelioideae. Reversion to habitats <1000 m under BI appears to have occurred two to three times in tillandsioids, once in *Hechtia*, up to four times in Navioideae, three times in *Pitcairnia*, once in *Dyckia*–*Encholirium*, and once in Chilean *Puya* (see Appendix). The evolution of **moist habitats on fertile substrates  $\geq 1000$  m elevation** under MP largely parallel those for **moist habitats  $\geq 1000$  m**, and appear to involve 9–12 separate origins (Fig. A3A and B). **Arid or semi-arid habitats or microsites**



**Fig. 2.** Evolution of (A) epiphytic vs. terrestrial habit, and (B) tank vs. non-impounding growth form. Colors of branches reflect reconstruction of ancestral character-states using MP; pie-diagrams represent the probabilities of different states at each node under Bayesian inference. Colors of shaded boxes indicate the ancestral distribution of taxa under MP after Givnish et al. (2011); absence of color shows uncertainty of inferred ancestral region. The inset map shows the geographic arrangement of different ancestral regions. Branch lengths represent inferred times, keyed by the scales at the bottoms of the figures. Brackets at right delimit bromeliad subfamilies.

were invaded six times, by *Hechtia*, the Xeric Clade, and *Puya* plus Bromelioideae; by *Alcantarea* ca. 6.8 Mya in the Brazilian Shield; by *Ananas ananassoides* ca. 6.6–1.0 Mya in the Brazilian Shield,

Guayana Shield, or Amazon Basin; and by *Tillandsia* sp. A. ca. 2.4 Mya in Central America (Fig. A4A). There were no reversions to mesic habitats or microsites. Finally, **epiphytism or arid/semi-arid**

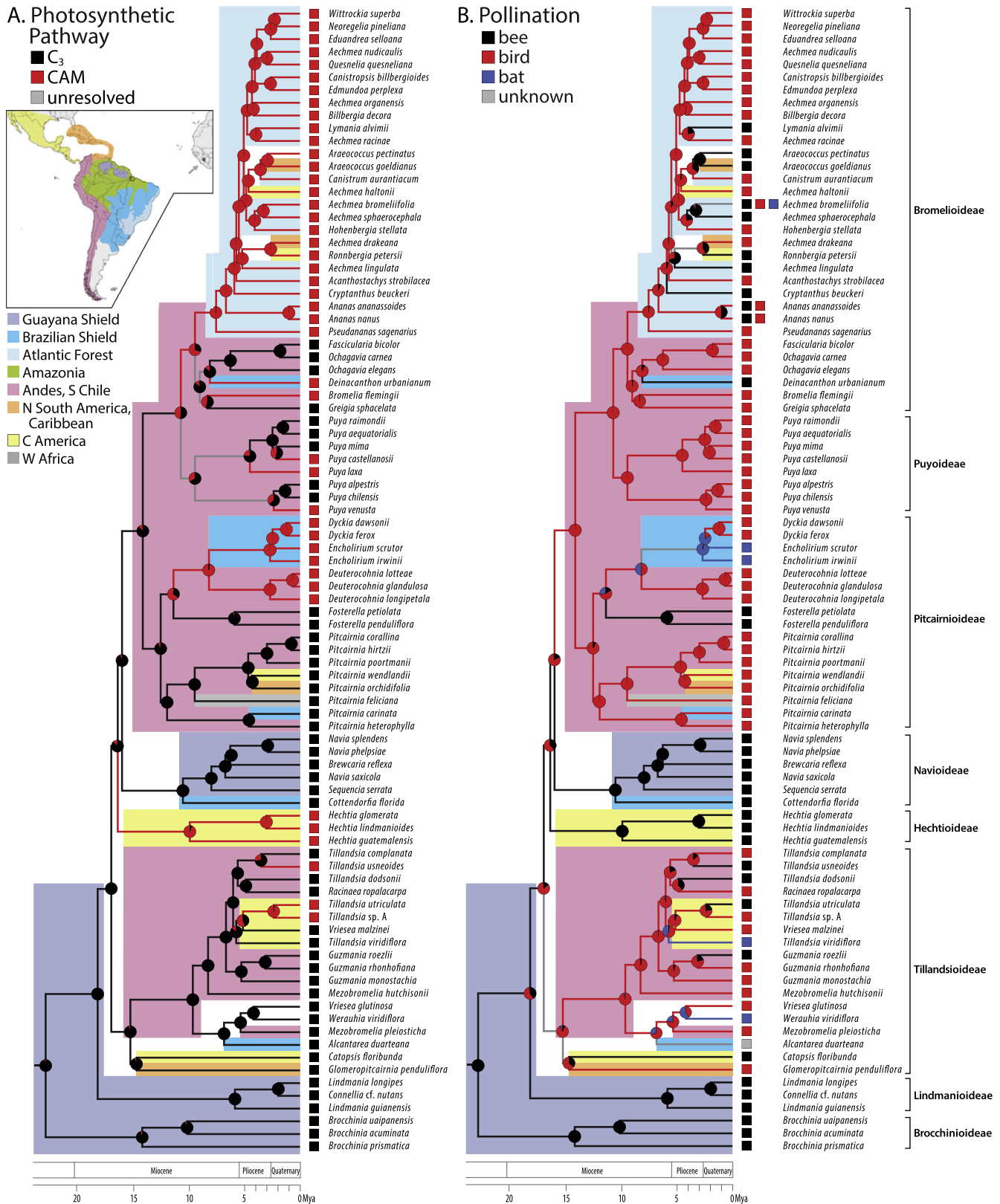


Fig. 3. Evolution of (A) C<sub>3</sub> vs. CAM photosynthesis, and (B) bee, bat, and bird pollination. See Fig. 2 legend for additional details.

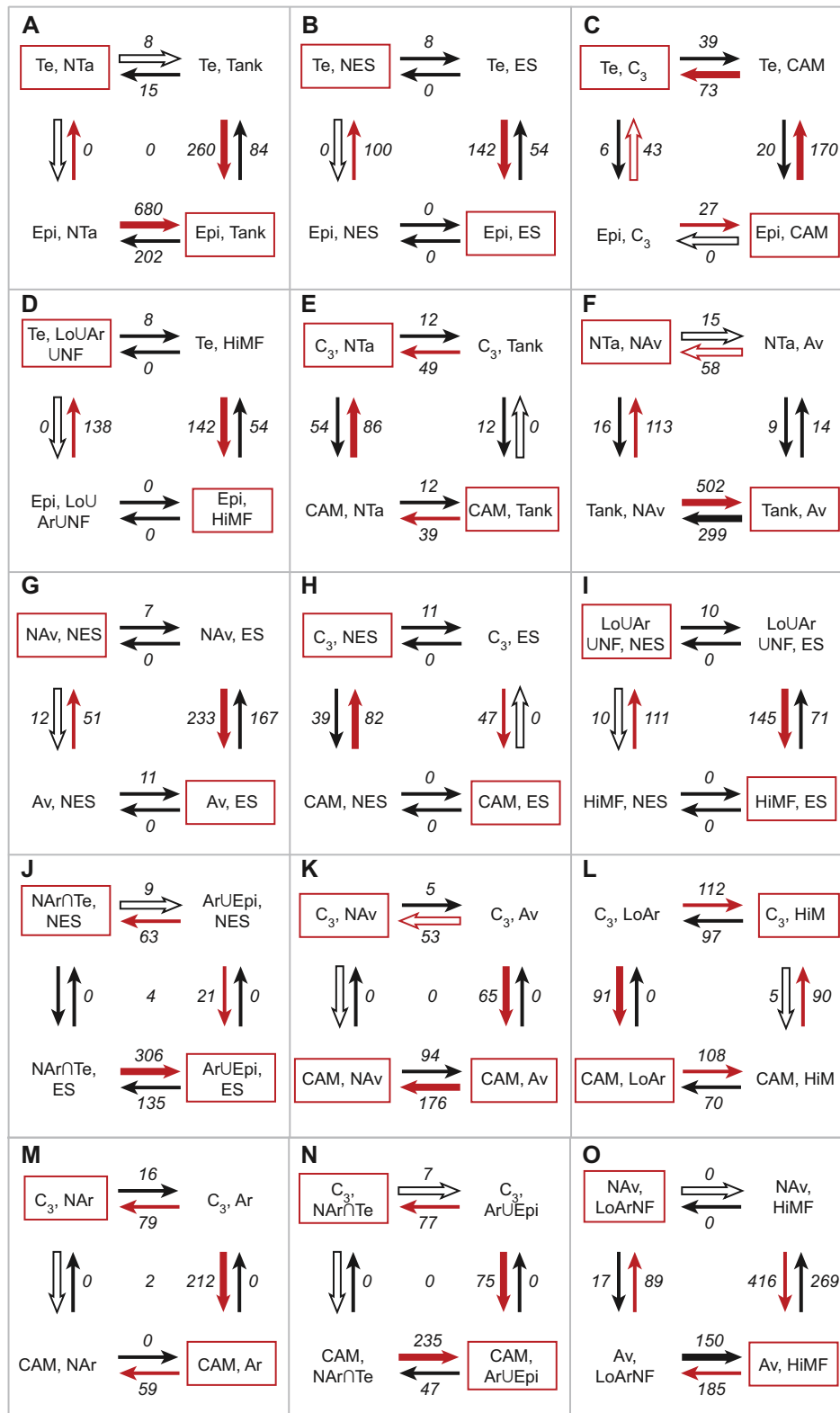
**habitats or microsites** evolved at least four times, at the bases of Tillandsioideae, *Hechtia*, the Xeric Clade, and *Puya* plus Bromelioideae (Fig. A4B). Reversions to terrestrial habit *and* mesic or wet sites appear to have occurred at least seven times.

### 3.3. Tests of correlated evolution

All nine associations between pairs of the focal plant traits, life in fertile, moist habitats  $\geq 1000$  m, and life in arid and semi-arid







**Fig. 4.** Contingent patterns of evolution among pairs of binary character-states. Rates corresponding to thick vs. hollow arrows differ significantly ( $P < 0.05$ ) in magnitude. Black arrows (red in the online color figure) highlight the net direction of transitions between adjacent pairs of character-states when the difference in rates exceeds 20. Boxes highlight pairs of character-states likely to account for a preponderance of taxa, given the ancestral condition in Bromeliaceae and pattern of transitions. Contingent patterns shown are for the evolution of **Terrestrial** vs. **Epiphytic** habit and (A) **Tank** vs. **Non-Tank** growth form, (B) **Entangling Seeds** vs. **Non-Entangling Seeds**, (C) **C<sub>3</sub>** or **CAM** photosynthetic pathway, and (D) **High, Moist, Fertile** conditions vs. **Low, Arid, or Non-Fertile** conditions; for the evolution of **Tank** vs. **Non-Tank** growth form and (E) **C<sub>3</sub>** and **CAM** photosynthesis, and (F) **Avian** and **Non-Avian** pollination; for the latter and (G) **Entangling Seeds** vs. **Non-Entangling Seeds**, (K) **C<sub>3</sub>** and **CAM** photosynthesis, and (O) **High** ( $\geq 1000$  m elevation), **Moist, Fertile** habitats vs. others; for **Entangling Seeds** vs. **Non-Entangling Seeds** and (I) **High** ( $\geq 1000$  m elevation), **Moist, Fertile** habitats vs. others, and (J) **Epiphytism** or **Arid** or semi-arid conditions vs. **Non-Arid** or semi-arid conditions; and for **C<sub>3</sub>** and **CAM** photosynthesis and (H) **Entangling Seeds** vs. **Non-Entangling Seeds**, (M) **Arid** or semi-arid conditions vs. **Mesic** conditions, (K) **C<sub>3</sub>** or **CAM** photosynthetic pathway vs. **Avian** or **Non-Avian** pollination, (L) **Low-elevation and Arid/semi-arid** habitats vs. **High-elevation, Mesic** conditions, and (N) **Epiphytism** or **Arid** or semi-arid conditions vs. **Non-Arid** or semi-arid conditions.

vary from 0.13 sp<sup>-1</sup> My<sup>-1</sup> (=0.13 My<sup>-1</sup>) in Brocchinioideae to 0.63 My<sup>-1</sup> in Bromelioideae. Crown rates range from 0.16 My<sup>-1</sup> in Brocchinioideae to 0.64 My<sup>-1</sup> in Bromelioideae (Table 2). Rates of net diversification are especially high in the bromelioid tank-epiphyte clade native to the Atlantic Forest region (1.11 and 1.05 My<sup>-1</sup> for stem and crown rates, respectively), Brazilian Shield-Atlantic Forest bromelioids (0.70 and 0.78 My<sup>-1</sup>), and the core tillandsioids (i.e., Tillandsioideae minus *Catopsis-Glomeropitcairnia*) (0.47 and 0.67 My<sup>-1</sup>).

Rates of net species diversification drop sharply with subfamily stem age ( $y = 2.17 e^{-0.122x}$ ,  $r^2 = 0.85$ ,  $P < 0.0006$  for 1-tailed  $t$ -test, 6 d.f.). This pattern is even stronger if the two most diverse subclades – the tank-epiphytic bromelioids and the core tillandsioids – are substituted for their respective subfamilies ( $y = 2.18 e^{-0.124x}$ ,  $r^2 = 0.94$ ,  $P < 0.0001$  for 1-tailed  $t$ -test, 6 d.f.). The increased explanatory power of the latter regression is driven largely by an outlier; when the tank-epiphytic bromelioids are excluded,  $r^2 = 0.88$ . There is no significant correlation of species number with subfamily age ( $r = -0.35$ ,  $P > 0.38$  for 6 d.f.).

Based on reconstruction of ancestral character-states, each subfamily or subfamilial subclade can be categorized by the sole/dominant character-states of habit, growth form, seeds, photosynthetic path way, pollination syndrome, and occurrence in extensive, moist, fertile cordilleras (Figs. 2 and 3, A2–A4). Based on this, net diversification rates based on stem ages are significantly higher in the two major epiphytic clades, Tillandsioideae and the bromelioid tank-epiphytes (mean  $D_{\text{stem}} = 0.77 \pm 0.49$  My<sup>-1</sup>), than in the remaining, almost entirely terrestrial subfamilies (mean  $D_{\text{stem}} = 0.31 \pm 0.14$  My<sup>-1</sup>) ( $P < 0.028$  for 1-tailed  $t$ -test with 6 d.f.). Weakly supported differences apply to tank- vs. non-tank lineages (mean  $D_{\text{stem}} = 0.77$  vs. 0.34,  $P < 0.047$ ), after Brocchinioideae is excluded due to its possessing large fractions of both tank and non-tank species. Similar conclusions apply to calculations based on  $\ln D$  rather than  $D$ , but with the difference between tank and non-tank lineages being marginally non-significant (Table 3).

Diversification rates are higher in the two subfamilies with entangling seeds than in the six without ( $D_{\text{stem}} = 0.57 \pm 0.15$  My<sup>-1</sup> vs.  $0.33 \pm 0.15$  My<sup>-1</sup>), but the difference is not significant for untransformed or log-transformed data (Table 3). Comparisons of diversification rates in CAM and C<sub>3</sub> lineages are more difficult, given the haphazard variation in reconstructed ancestral states within Puyoideae. Setting Puyoideae aside and splitting Pitcairnioideae into its largest, purely CAM and C<sub>3</sub> lineages, we found no significant difference in diversification rates between CAM lineages (Bromelioideae, *Dyckia-Encholirium-Deuterocohnia*, *Hechtia*) and

C<sub>3</sub> lineages (*Pitcairnia*, Navioideae, Tillandsioideae, Lindmanioideae, Brocchinioideae) ( $D_{\text{stem}} = 0.47 \pm 0.23$  My<sup>-1</sup> vs.  $0.31 \pm 0.14$  My<sup>-1</sup>) for arithmetic or log-transformed data (Table 3).

Net diversification rates based on stem ages are significantly higher for the two major clades pollinated primarily by hummingbirds, Tillandsioideae and Pitcairnioideae–Puyoideae–Bromelioideae (mean  $D_{\text{stem}} = 0.44 \pm 0.03$  My<sup>-1</sup>), than for the non-bird-pollinated subfamilies (mean  $D_{\text{stem}} = 0.22 \pm 0.07$  My<sup>-1</sup>) ( $P < 0.007$  for 1-tailed  $t$ -test with 4 d.f.). Mean diversification rates are thus more than 2.5 times higher in epiphytic clades than terrestrial clades, and 2.0 times higher in hummingbird-pollinated clades than in those not pollinated by birds and mainly by insects (Table 3).

Four lineages – the higher tillandsioids, pitcairnioids, puyoids, and tank-epiphytic bromelioids – are composed primarily of species native to the Andes and/or the Serra do Mar region of south eastern Brazil. Substrates in these two regions are also more fertile than the marine-derived Roraima sandstone of the tepuis in the Guayana Shield, and presumably more congenial to the evolution of tank bromeliads. The mean diversification rate of lineages in the Andes and Serra do Mar regions is  $0.43 \pm 0.23$  My<sup>-1</sup>, nearly twice that for lineages outside these regions ( $D_{\text{stem}} = 0.22 \pm 0.07$  My<sup>-1</sup>); when comparisons are made based on log-transformed data, this is the most highly significant difference observed in comparisons of subfamilies based on traits ( $P < 0.0017$  for 1-tailed  $t$ -test with 6 d.f.) (Table 3).

### 3.4.2. Determinants of net rates of species diversification – phylogenetically structured analyses

MEDUSA identified significant acceleration of net speciation rates at three points in the simplified 26-taxon tree, including (1) the crown group of the core tillandsioids, (2) the stem group of the Navioideae–Pitcairnioideae–Puyoideae–Bromelioideae clade, and (3) a further acceleration in the crown group of the tank-epiphytic bromelioids (Fig. 5). These accelerations were detected under a mixed birth–death model for (1) and (3), and a Yule birth-only model for (2). Net diversification rates were highest for the tank-epiphytic bromelioids ( $r = 0.815$ ) despite a high rate of extinction ( $\epsilon = 0.864$ ). The core tillandsioids had a somewhat slower diversification rate ( $r = 0.482$ ) but also had a high rate of extinction ( $\epsilon = 0.864$ ). A GEIGER analysis of crown diversification rates identified significant accelerated diversification at these same three nodes. GEIGER also identified a significant acceleration of net diversification (to  $r = 0.435$ ) in bromeliads other than Brocchinioideae and Lindmanioideae, and decelerations (to  $r = 0$ ) in

**Table 2**

Species richness, stem and crown ages, and net diversification rates ( $D_{\text{stem}}$  and  $D_{\text{crown}}$ ) for bromeliad subfamilies and key subclades.

Clade	# spp.	Stem age (My)	Crown age (My)	$D_{\text{stem}}$ (My <sup>-1</sup> )	$D_{\text{crown}}$ (My <sup>-1</sup> )
Brocchinioideae	20	22.7	14.1	0.13	0.16
Lindmanioideae	45	18.1	5.8	0.21	0.54
Tillandsioideae	1256	16.9	15.2	0.42	0.42
<i>Core tillandsioids</i>	1236	15.2	9.6	0.47	0.67
Hechtioideae	52	16.3	9.9	0.24	0.33
Navioideae	107	15.9	10.5	0.29	0.38
<i>Navia/Brewcaria</i>	99	7.9	6.7	0.58	0.58
Pitcairnioideae	587	14.1	11.9	0.45	0.48
<i>Deuterocohnia–Dyckia–Encholirium</i>	170	11.3		0.45	
<i>Pitcairnia</i>	387	12.5		0.48	
Puyoideae	217	10.7	9.4	0.50	0.50
Bromelioideae	856	10.7	9.4	0.63	0.64
<i>Brazilian Shield</i>	753	9.4	7.5	0.70	0.79
<i>Tank epiphytes</i>	629	5.8	5.5	1.11	1.05
Pu + Brom	1073	14.1		0.49	
Pit + Pu + Brom	1660	15.9		0.47	
Nav + Pit + Pu + Brom	1764	16.3		0.46	
Entire family	3140	97.5	22.7	0.08	0.32

**Table 3**  
Significance of differences between net diversification rates ( $D_{\text{stem}}$ ) associated with states of individual characters across bromeliad subfamilies and key subclades (see text).

Comparison	Result	Significance <sup>a</sup>	
Epiphytes vs. terrestrials	Higher in <b>Epi</b> ( $0.77 \pm 0.49 \text{ My}^{-1}$ ) than <b>Te</b> ( $0.31 \pm 0.14 \text{ My}^{-1}$ )	<0.028	<0.042
Tank vs. non-tank taxa	Higher in <b>Ta</b> ( $0.77 \pm 0.49 \text{ My}^{-1}$ ) than <b>NTa</b> ( $0.34 \pm 0.13 \text{ My}^{-1}$ )	<0.047	>0.052
Seeds entangling vs. not	Higher in <b>ES</b> ( $0.53 \pm 0.15 \text{ My}^{-1}$ ) than <b>NES</b> ( $0.31 \pm 0.14 \text{ My}^{-1}$ )	>0.055	>0.077
CAM vs. C <sub>3</sub>	Higher in <b>CAM</b> ( $0.47 \pm 0.23 \text{ My}^{-1}$ ) than <b>C<sub>3</sub></b> ( $0.31 \pm 0.14 \text{ My}^{-1}$ )	>0.13	>0.15
Avian vs. non-avian pollination	Higher in <b>Av</b> ( $0.44 \pm 0.03 \text{ My}^{-1}$ ) than <b>NAv</b> ( $0.224 \pm 0.07 \text{ My}^{-1}$ )	<0.007	<0.023
Moist, fertile cordilleras vs. not	Higher in <b>HiF</b> ( $0.43 \pm 0.31 \text{ My}^{-1}$ ) than not ( $0.22 \pm 0.07$ )	<0.029	<0.10

<sup>a</sup> First column gives *P* for untransformed data; the second, for log-transformed data.

**Table 4**  
Significant differences in rates of speciation and extinction associated with different character-states under BiSSE.

Comparison	Result	Significance
Epiphytes vs. terrestrials	Speciation higher in <b>Epi</b> ( $\lambda_1 = 1.176$ ) than <b>Te</b> ( $\lambda_0 = 0.221$ )	<0.015
Tank vs. non-tank taxa	Speciation higher in <b>Ta</b> ( $\lambda_1 = 0.870$ ) than <b>NTa</b> ( $\lambda_0 = 0.293$ )	<0.011
Avian vs. non-avian pollination	Speciation higher in <b>Av</b> ( $\lambda_1 = 0.870$ ) than <b>NAv</b> ( $\lambda_0 = 0.293$ )	<0.02
Moist, fertile cordilleras vs. not	Speciation higher in <b>HiMF</b> ( $\lambda_1 = 1.146$ ) than not ( $\lambda_0 = 0.207$ )	<0.0001
	Extinction higher in <b>HiMF</b> ( $\lambda_1 = 0.962$ ) than not ( $\lambda_0 = 0.091$ )	<0.006
CAM vs. C <sub>3</sub>	NS	>0.55
Seeds entangling vs. not	NS	>0.25

*Acanthostachys* (sister to the tank-epiphyte bromelioids), in *Deinacanthon*, and in *Cottendorfia*.

BiSSE analyses on the 26-terminal tree showed that tank formation, avian pollination, epiphytism, and especially life on moist, fertile cordilleras significantly accelerated speciation to progressively larger degrees, and that life on moist, fertile cordilleras also significantly accelerated the apparent rate of extinction (Table 4). CAM photosynthesis and entangling seeds had no significant effect on speciation or extinction rates (Table 4). Estimates of the incidence of various traits in all species in each clade (Table 2) were close to those implied by the traits of the 90 place-holder taxa, except that our 90-taxon sampling greatly underrepresented atmospheric non-tank *Tillandsia*, which appear to comprise 40% of Tillandsioideae.

### 3.5. Effects of broad-scale adaptive radiation on diversity

Evolution of epiphytism and associated traits is associated with the generation of some 1200 species of Tillandsioideae, mainly in the Andes and Central America, and some 600 species of the tank-epiphyte clade of Bromelioideae, mainly in the Atlantic Forest region (Table 5; graphic abstract). Subsequently, a limited number of species of both groups invaded almost all areas occupied by the family. Three major radiations of terrestrial bromeliads in arid and semi-arid regions appear to have been facilitated by the evolution of CAM photosynthesis, including (1) *Hechtia* (ca. 50 spp.) at low to mid elevations in Central America/Mexico; (2) *Deuterocohnia*–*Dyckia*–*Encholirium* (ca. 170 spp.) at mid to high elevations in the Andes, and then across the Brazilian Shield to the Horn of Brazil;

**Table 5**  
Summary of the six broad-scale adaptive radiations adding substantial diversity to Bromeliaceae.

Clades	Number of species	% Species in family
1. C <sub>3</sub> + CAM epiphytes (Tillandsioideae)	1256	40.0
2. CAM epiphytes (tank-epiphytic Bromelioideae)	629	20.0
3. CAM terrestrials ( <i>Hechtia</i> , Central America)	52	1.7
4. CAM terrestrials (Xeric clade, South America)	170	5.4
5. CAM terrestrials ( <i>Puya</i> , South America)	217	6.9
6. C <sub>3</sub> understory herbs ( <i>Pitcairnia</i> , South America)	387	12.3
Total radiations	2711	86.3
Total Bromeliaceae	3140	100.0

and (3) *Puya* (ca. 200 spp.) at high elevations in the Andes (Table 5). One additional radiation, not considered here in any detail, includes mostly broad-leaved *Pitcairnia* (ca. 390 spp.), a genus of exclusively C<sub>3</sub> species in rain- and cloud-forest understoreys. The three major clades – Brocchinioideae, Lindmanioideae, Navioideae – that did not (except for *Cottendorfia florida*) invade areas outside the ancestral region and habitats of the Guayana Shield contributed fewer than 200 species to the total of ca. 3140 species of present-day bromeliads.

## 4. Discussion

### 4.1. Origin and correlated evolution of key functional traits

Multiple, often closely associated origins of epiphytism, the tank habit, entangling seeds, CAM photosynthesis, and avian (mainly hummingbird) pollination in bromeliads occurred mostly during the mid to late Miocene (Figs. 2 and 3, A2–A4), and largely agree with our predictions (Fig. 1), with the timing of the orogenies of the Andes and of the Serra do Mar and nearby ranges, and with past global declines in moisture availability and atmospheric CO<sub>2</sub> concentrations (see below). Transitions to habitats >1000 m arose most frequently, at least 13 times, often in Atlantic Forest tank-epiphytic bromelioids (Figs. A3 and A4); transitions to the tank habit and epiphytic growth form arose least frequently, 2–4 times (Fig. 2A and B).

All nine predicted patterns of correlated evolution among these traits, life in moist, fertile habitats >1000 m elevation, and life in epiphytic or dry terrestrial microsites are phylogenetically significant (Table 1). Seventeen of the remaining 24 pairwise combinations of traits with each other or ecological conditions showed no significant pattern; seven did, however. Unexpected patterns include the rise of tanks with entangling seeds, avian pollination, and moist habitats  $\geq 1000$  m elevation; of entangling seeds with fertile, moist habitats  $\geq 1000$  m elevation and with epiphytism or arid/semi-arid conditions; of CAM with avian pollination; and of avian pollination with epiphytism or arid/semi-arid conditions (Table 1). With the exception of the tie between tanks and avian pollination, these patterns are probably best viewed as indirect results of the direct forces in our model, which tie together most of the key functional traits and environmental conditions studied in this paper. Below we discuss the factors favoring each predicted

pattern of correlated evolution, at the times and places where the associated character-states originated.

#### 4.1.1. Fertile, humid montane habitats favor epiphytes

Mid-elevation tropical habitats experience high rainfall and low evaporation, as well as a rich nutrient rain of detritus derived from leachate and shed parts from host trees, and possibly from animals or drop pings derived from nutrient-rich soils. The great abundance and diversity of epiphytes in mid-elevation cloud forests – and in areas of greater precipitation/fog at lower elevations (Kreft et al., 2004; Haeger and Dohrenbusch, 2011; Obregon et al., 2011) – are consistent with higher moisture availability resulting in greater epiphyte density and diversity. The mid-elevation maximum in epiphyte density often occurs at somewhat higher elevations than that for epiphyte species richness (Gentry and Dodson, 1987), but both (and especially that for species richness) appear to be better explained by gradients in moisture supply than by mid-domain sampling artifacts (Currie and Kerr, 2008; cf. Cardelus et al., 2006; Colwell and Rangel, 2010). High elevations above the inversion layer support very few epiphytic species or individuals (Gentry and Dodson, 1987). Experiments on 11 bromeliad species showed that water availability has a much stronger and consistent positive effect on epiphyte growth than nutrient or CO<sub>2</sub> supplies (Zotz et al., 2010).

Soil fertility appears to enhance epiphyte density and diversity. Our findings support this oft-debated proposition for bromeliads, given that the epiphytic habit only shows correlated evolution with fertile, moist habitats  $\geq 1000$  m elevation, and not with habitats  $\geq 1000$  m elevation, alone or in combination with substantial moisture supply (Table 1). On the rainy tepuis of the Guayana Shield, composed of highly leached sandstones and quartzites of marine origin, at most two epiphytic species have evolved in Brocchinioideae, none in Lindmanioideae, and perhaps one in Navioideae (Givnish et al., 1997, 2007; Holst, 1997). Outside South America, lowland kerangas vegetation on extremely infertile white sands on Borneo lack epiphytes except those fed by ants (Janzen, 1974a), and dipterocarp forests on infertile soils in southeast Asia often have very low epiphyte abundance except near roads where mineral input via dust is likely to be greater (Janzen, 1974b, 1977). Ground-level P fertilization of wet forests on 4.1 My-old soils on Kauai increased the abundance and diversity of epiphytic cyanolichens, chlorolichens, mosses, and ferns, whereas fertilization with N or with S, cations, and micronutrients had no significant effect (Benner and Vitousek, 2007). Natural occurrences of such epiphytes on several Hawaiian islands are significantly greater on trees with higher P content (Benner, 2011), suggesting that P limits epiphyte growth there. Depletion of <sup>15</sup>N and higher N:P ratios in response to N + P fertilization of the tank epiphyte *Werauhia* (formerly *Vriesea*) *sanguinolenta* in Panama indicate that its growth is often P-limited, with a breakpoint at a foliar N:P ratio of 10.4 (Wanek and Zotz, 2011). A strong correlation of foliar P content – but not N content – between epiphytes and their hosts along an extensive elevational gradient in Costa Rica also suggests a close link of epiphytes to hosts in terms of P (but not N) nutrition (Cardelus and Mack, 2010). Widespread natural depletion of <sup>15</sup>N of foliar tissue in epiphytes vs. hosts, as well as epiphytic foliar N:P ratios often greater than 12, strongly suggest that P limitation or co-limitation is widespread in bromeliads and other epiphytes (Cardelus and Mack, 2010; Wanek and Zotz, 2011). Tree litter in tropical rain forests exhibit the highest N:P ratios on Earth (McGroddy et al., 2004), and canopy soils – derived from litterfall, with both feeding rooted as well as tank epiphytes – have much higher N:P ratios than ordinary soils, in rain forests and especially cloud forests (Nadkarni and Solano, 2002; Cardelus et al., 2009; Wanek and Zotz, 2011). Levels of available soil P should be highest over young rocks and in areas of rapid uplift and erosion (Chadwick et al., 1999; Vitousek

et al., 2003; Porder et al., 2007). Such conditions prevail in the Andes, the mountains of Central America, and the Serra do Mar and nearby ranges in the Brazilian Shield. Factorial fertilization of three bromeliad species with three different levels of N and P pointed to P as the nutrient limiting growth (Zotz and Asshoff, 2010; see also Zotz and Richter, 2006).

The two main origins of epiphytism in bromeliads occurred in tillandsioids with the uplift of the northern Andes ca. 15 Mya (Hoorn et al., 1995, 2010; Potter, 1997; Givnish et al., 2011) and in the tank-epiphytic bromelioids with the accelerated uplift of the Serra do Mar and Serra da Mantiqueira in the Atlantic Forest region during the Pliocene–Pleistocene (Almeida, 1976; Amorim and Pires, 1996) (Fig. 2A). Origins of these radiations correspond reasonably well with the independently derived dates of origin of diving-beetle lineages endemic to bromeliad tanks ca. 12 Mya in northern South America and ca. 1.6–4.3 Mya in the Atlantic Forest region (Balke et al., 2008).

Uplift of the Serra do Mar coincided with the rise of the central Andean Altiplano toward the end of the Miocene (Garzzone et al., 2008), which should have triggered a cooler, rainier climate in the Atlantic forest region, with enhanced advection of moisture off the tropical south Atlantic as winds off the Pacific were blocked by the Altiplano (Ehlers and Poulsen, 2009). This effect, combined with the actual uplift of the Serra do Mar would have favored the onset of cooler, rainier, more humid conditions starting ca. 5.6 Mya (Vasconcelos et al., 1992; Grazziotin et al., 2006), the time of origin of the bromelioid tank-epiphyte clade (Fig. 2A). Today, the Atlantic Forest region – including remnant, highly diverse rain and cloud forests, sandy coastal restingas, mangroves, campos de altitude, and granitic outcrops of the Serra do Mar and Serra da Mantiqueira and adjacent coastal plains – is the wettest part of eastern South America, and the highlands, the coolest (Safford, 1999). Local bromeliad floras can be extremely rich, with up to 92 species in one 1° × 1° cell in Minas Gerais (Versieux and Wendt, 2007), and vary greatly geographically (Fontoura et al., 2012). The Serra do Mar and Serra da Mantiqueira form the elevated south east rim of the Brazilian Shield. Both experienced strong climatic fluctuations during the Pleistocene (Auler and Smart, 2001; Behling and Negrelle, 2001), as did the northern Andes (Gentry, 1982; van der Hammen, 1995).

#### 4.1.2. Epiphytism and fertile, moist montane habitats favor the tank habit

Two origins of the tank habit appear to coincide with the rise of epiphytism in tillandsioids in the northern Andes as they began their uplift ca. 15 Mya, and the rise of epiphytism in bromelioids as the Brazilian Highlands began their uplift ca. 5.6 Mya. The third origin of tanks, in *Brocchinia*, occurred ca. 9 Mya in mid- to high-elevation in the long-uplifted Guayana Shield (Fig. 2B), apparently as an adaptation to capture nutrients from falling debris, commensalants, or insect prey under exceedingly nutrient-poor and humid conditions atop tepuis (Givnish et al., 1997, 2007). Though not captured in our taxon sampling, at least one origin of epiphytism was associated with the acquisition of the tank habit in *Brocchinia*, in *B. tatei* and the unstudied *B. hitchcockii* (Givnish et al., 1997). The tank habit was lost at least five times. In three cases, this occurred in species with CAM photosynthesis, which have an additional means of conserving water. In two cases – Spanish moss, *Tillandsia usneoides*, and *T. sp. A* – there was a shift to the atmospheric habit.

Atmospheric species of *Tillandsia* are non-tank epiphytes that depend almost exclusively on absorbent leaf trichomes for water and nutrient uptake (Benzing, 1980, 2000). Abundant trichomes also make their dry leaves highly reflective, possibly reducing water loss and photoinhibition (cf. Pierce et al., 2001). Dense arrays of tillandsioid trichomes are highly efficient at capturing moisture

from fog when combined with narrow leaves that efficiently intercept fine droplets (Martorell and Ezcurra, 2007). Atmospherics tolerate desiccation better than tank species but have lower rates of photosynthesis per unit leaf mass (Benzing and Burt, 1970; Benzing and Renfrow, 1974; Reyes-Garcia et al., 2008), and almost all have CAM photosynthesis (Crayn et al., 2004). Many tank bromeliads exhibit developmental heterophylly, with juveniles starting as atmospherics (Adams and Martin, 1986; Benzing, 2000; Zotz et al., 2011) and then later forming tanks as body size increases. Krömer et al. (2006) found that large, tank-epiphyte bromeliads dominated the rainy, moist eastern slope of the Andes in Bolivia, while atmospheric *Tillandsia* taxa dominated the drier, more seasonal leeward slope. Atmospheric species of *Tillandsia* account for ca. 40% of the Tillandsieae (*Tillandsia*–*Racinaea*–*Guzmania*–*Mezobromelia*), and that that clade is nearly 2.4 times as species-rich as its sister, the Vrieseae, which is also nearly 100% epiphytic but lacks atmospherics.

#### 4.1.3. Epiphytism favors the evolution of entangling seeds, and vice versa

Such seeds characterize Tillandsioideae and Bromelioideae, which together contain almost all epiphytic bromeliads. Entangling seeds, epiphytism, tanks, and invasion of fertile, moist habitats  $\geq 1000$  m elevation evolved simultaneously in the northern Andes, Central America, or the northern littoral of South America in tillandsioids. In bromelioids, fleshy fruits evolved 1 My before invasion of the Brazilian Shield, and 4.4 My before epiphytism and the tank habit arose. Fleshy fruits frequently arise in forest understories, where wind dispersal is less effective, and the incidence of such fruits increases toward rainier habitats (Croat, 1978; Gentry, 1982; Givnish, 1998; Smith, 2001; Givnish et al., 2005; Sytsma et al., 2002). Life in forest and scrub understories is widespread in the basal bromelioid grade, including *Greigia*, *Ochagavia*, *Bromelia*, *Pseudananas*, *Ananas*, *Cryptanthus*, and *Acanthostachys*. Evolution of fleshy fruits under such conditions may be seen as a preadaptation for the later evolution of epiphytism in the Serra do Mar. An interesting case of apparent convergence involves the coma-like appendage in the epiphyte *Brocchinia tatei*, in which one end of the seed's bicaudate wing splits into several small processes; this is the only such dispersal apparatus in Brocchinioideae (Givnish et al., 1997).

#### 4.1.4. Dry conditions favor CAM

CAM dominates three terrestrial lineages from arid sites (*Dyckia*–*Deuterocohnia*–*Encholirium*, *Puya*, *Hechtia*) as well as some epiphytic lineages (especially bromelioids from humid Atlantic forests), with a high incidence of CAM in atmospheric *Tillandsia* species in dry, seasonal areas (Krömer et al., 2006). As predicted, CAM photosynthesis shows a significant pattern of correlated evolution with epiphytism or terrestrial growth in arid or semi-arid microsites (Fig. 3A). Correlations with dry sites alone are also significant, but not those with epiphytism (Table 1). CAM is more common in epiphytes from several families in warmer, drier, lower-elevation tropical forests than elsewhere (Earnshaw et al., 1987; Zotz and Ziegler, 1997; Silvera et al., 2009), and in bromeliads of the upper canopy vs. the lower canopy or understory (Griffiths and Smith, 1983; Zotz and Ziegler, 1997; Zotz, 2004).

The three origins of CAM on terrestrial sites all occurred 16.2–8.1 Mya, at a time of increasing aridification, warm but dropping temperatures, and declining atmospheric concentrations of CO<sub>2</sub> (Zachos et al., 2001; Crayn et al., 2004; Sage, 2004; Kürschner et al., 2008; Tripathi et al., 2009). Selection should have favored the water-conserving and CO<sub>2</sub>-concentrating mechanism of CAM photosynthesis at that time, in much the same way as it apparently favored multiple origins of C<sub>4</sub> photosynthesis in terrestrial plants during the same period (Ehleringer et al., 1991; Sage, 2004; Ed-

wards et al., 2010; Christin et al., 2011; Sage et al., 2011). Arakaki et al. (2011) have made the same argument for other groups, and observed that several succulent lineages with CAM photosynthesis (higher cacti, Agavaceae, Aizoaceae) began to diversify extensively about 15–10 Mya. Most likely, the drop in global CO<sub>2</sub> levels from 500 to 300 ppm in mid-Miocene reflected increased carbon burial in the titanic sediment train from the newly uplifting Himalayas (France-Lanord and Derry, 1997), increased productivity of the Pacific Ocean (Vincent and Berger, 1985), or the global formation of large brown-coal deposits (Holdgate and Clarke, 2000).

Near closure of the Isthmus of Panama by the Middle Miocene (Farris et al., 2011; Montes et al., 2012) would have made dispersal by CAM-bearing *Hechtia* to arid and semi-arid sites in Central America easier than envisioned by Givnish et al. (2011), who assumed a much later closure (see Kirby et al., 2008). Uplift of the northern Andes beginning in the mid-Miocene (Hoorn, 1994; Hoorn et al., 1995, 2010) helped to create dry habitats in rain shadows in northwestern and southeastern South America, and at high elevations above the inversion layer along the length of the Andes. The latter were invaded independently by *Puya* and early-divergent members of the Xeric clade (*Deuterocohnia*, several *Dyckia*) (Fig. 3A; see also Givnish et al., 2007). The basal bromelioid grade – consisting of seven small, terrestrial genera – colonized dry, rocky microhabitats or open, relatively dry forests in many cases. Of the taxa involved, all but the three small Chilean genera exhibit CAM. The occurrence of C<sub>3</sub> photosynthesis in these is likely related to their occurrence in deciduous forest understories (*Greigia*, *Ochagavia carnea*) and/or cool microsites immediately next to the coast (*Fascicularia* on the mainland, *O. elegans* on Robinson Crusoe Island in the Juan Fernández archipelago) (see habitat descriptions by Zizka et al. (2009)). *Dyckia*–*Encholirium* secondarily invaded dry, rocky sites through the interior of the Brazilian Shield to the Horn of Brazil (Givnish et al., 2007, 2011). *Hechtia* invaded arid and semi-arid areas near 30°N in Central America. These and similar areas in the Caribbean, as well as dry areas in the lee of the Andes, were colonized by the fourth bromeliad CAM clade, composed of epiphytes in subfamily Tillandsioideae (e.g., *Tillandsia utriculata*, *T. sp. A*).

Our data support five origins of CAM in Bromeliaceae, compared with the three recognized by Crayn et al. (2004). Our more extensive data allowed us to recognize additional origins of CAM in the Xeric clade of Pitcairnioideae and within *Tillandsia*, as captured in *T. usneoides*, a placeholder for the large number of CAM atmospherics in that genus. C<sub>3</sub> photosynthesis characterizes the basal grade of pitcairnioids, consisting of broad-leaved *Pitcairnia* (native to rain- and cloud-forest understories, especially along the Andes) and soft-leaved *Fosterella* (native to open, mesic habitats at mid-elevations in the Andes). The mesic terrestrial sites inhabited by all navioideae and basal pitcairnioids clearly implies that CAM arose in the Xeric clade after a shift from mesic conditions (Figs. 2A and 3A).

Crayn et al. (2004) surveyed  $\delta^{13}\text{C}$  values for 1837 species stratified across all but three bromeliad genera; of these, 44% possessed CAM, almost all of which can be assigned to the five lineages shown in Fig. 3A. Only three genera – *Acanthostachys*, *Puya*, *Tillandsia* – have photosynthetic pathways that differ among species; the four species of *Vriesea* known to possess CAM will likely be re-assigned to *Tillandsia* (Grant, 1993). More research on *Puya* and *Tillandsia* is needed to exclude the possibility that variation in  $\delta^{13}\text{C}$  within these genera reflects developmental plasticity related to moisture supply. An MP overlay (not shown) of CAM vs. C<sub>3</sub> photosynthesis on the Bayesian phylogeny of *Tillandsia* (Barfuss et al., 2005) suggests that CAM may have evolved three times in that genus (in Barfuss' clades N and O, and the common ancestor of all *Tillandsia* excluding clades H, I, and J). The latter origins are recent and may reflect adaptation to drying cycles during the Pliocene–Pleistocene.

Paradoxically, CAM occurs in several epiphytic bromelioids and tillandsioids in wet, often shaded microsites, where  $C_3$  photosynthesis should be favored. Under frequently rainy conditions, CAM can permit the recycling of respiratory  $CO_2$  through CAM idling when leaf gas exchange is blocked by dense arrays of wet leaf trichomes (Pierce et al., 2002; Freschi et al., 2010). The high diversity of CAM epiphytic bromelioids in the Atlantic Forest region may primarily reflect this advantage of CAM. Other factors that may help account for the presence of CAM epiphytes in shaded, rainy microsites – despite the relatively small additional energetic cost of CAM vs.  $C_3$  photosynthesis (Winter and Smith, 1996a,b) – include (1) efficient use of sunflecks for carbon gain during Phase III when intercellular  $CO_2$  is high (Skillman and Winter, 1997), and (2) greater allocation to light-absorbing foliage and less to roots, at least in the CAM terrestrial *Aechmea magdalenae* vs. sympatric  $C_3$  species (Skillman et al., 1999).

#### 4.1.5. Epiphytism favors absorptive leaf trichomes and vice versa

We lack enough data on absorptive trichomes across Bromeliaceae to overlay them on our phylogeny and rigorously test predictions regarding their evolution. However, such trichomes are known throughout tillandsioids, in many species of the bromelioid tank-epiphyte clade, and in tank-forming *Brocchinia* (Benzing et al., 1976, 1985; Givnish et al., 1984, 1997; Benzing, 2000; Pierce et al., 2001). Absorptive trichomes appear to exhibit the same pattern of evolution as tanks, and would – based only on current data – seem likely to exhibit significant patterns of correlated evolution with epiphytism and fertile, moist habitats  $\geq 1000$  m elevation. Within *Brocchinia*, absorptive trichomes evolved to acquire nutrients in the extremely rainy and infertile habitats on tepuis and adjacent sandplains (Givnish et al., 1997). Brocchinoid trichomes retain live cap cells (Givnish et al., 1984; Benzing et al., 1985; Owen et al., 1988), and thus do not provide the one-way valves for water and nutrient uptake – and thus for life in somewhat drier circumstances – that tillandsioid trichomes provide. This may have greatly limited the brocchinoid radiation.

#### 4.1.6. Fertile, humid montane habitats favor avian pollination

Avian (mainly hummingbird) pollination showed significant correlated evolution with fertile, moist habitats  $\geq 1000$  m elevation. Ornithophilous flowers, adapted primarily to hummingbirds, include an estimated 60% of all bromeliad species in the Bolivian Andes (Kessler and Krömer, 2000) and 85% of those in Atlantic Forest fragments (Piacentini and Varassin, 2007). Such flowers have arisen at least twice, in the tillandsioid ancestor ca. 15.4 Mya, associated with the Andes/central Chile, Central America, or the Caribbean and northern littoral of South America, and in the common ancestor of pitcairnioids, puyoids, and bromelioids ca. 14.4 Mya, associated with the Andes/central Chile (Fig. 3B). These origins occurred at about the same time as the uplift of the northern Andes and the initial origin of two main Andean lineages of hummingbirds (Bleiweiss, 1998), although McGuire et al. (2007) recently argued suggested that these clades represent one invasion of montane sites. No comparably large lineages of hummingbirds evolved in the Serra do Mar or the Guayana Shield (Bleiweiss, 1998). Hummingbirds in these areas appear to represent eclectic and not especially diverse mixes of taxa with various geographic affinities (R. Bleiweiss, pers. comm.).

Kessler and Krömer (2000) and Krömer et al. (2006) found that birds pollinate an increasing fraction of bromeliads at higher elevations and heavier rainfalls in the Bolivian Andes, as expected. Bat pollination is most common in the humid lowlands, and insect pollination, in drier low-elevation sites. The dearth of insect pollination in cooler/wetter sites accords with the expectation that thermoregulating pollinators should dominate such sites (Cruden, 1972; Mabberley, 1975; Feinsinger, 1983; Bawa, 1990; Givnish

et al., 2009). The shift from bat to hummingbird pollination toward higher elevations is harder to explain. The high absolute caloric requirement of nectarivorous bats – based on their larger body mass ( $10.2 \pm 2.5$  g [Patterson et al., 1996]) than Andean hummingbirds (ca. 6 g excluding *Patagonia gigas* [Altschuler et al., 2004]) – may make bat pollination, with its large amounts of associated nectar (nearly ten times that of hummingbird-pollinated flowers in two Atlantic forest remnants [Sazima et al., 1996, 1999]) too costly for plants in nutrient-poor, relatively unproductive cloud forests. High elevations may also not be favorable for bats given their large heat and water losses from naked flight membranes at low air temperatures relative to well-feathered hummingbirds. Shifts from bird to bat pollination in bromeliads (Fig. 3B) accord with studies on other families (Kay, 2003; Perrett et al., 2007; Knox et al., 2008; Martén-Rodríguez, 2008), and may also reflect the greater efficiency of pollen transfer by bats (Muchhala and Thomson, 2010) as well as the context-specific advantages just discussed.

#### 4.1.7. The tank habit favors ornithophily

This relationship was *not* predicted by our original model, but receives support from observed patterns of correlated evolution (Table 1), and marginal support from observed patterns of contingent evolution (Fig. 4E). In retrospect, it also appears to be explicable in terms of bromeliad biology. Water-filled tanks are likely to lure and/or support large numbers of small insects, which may be attractive prey to hummingbirds. In addition, once an inflorescence adapted to avian pollination opens, a water-filled tank can help provide the fluid required to secrete the large amounts of nectar required to attract hummingbirds.

#### 4.2. Contingent evolution of key functional traits

Nine of the 16 significant patterns of contingent evolution involving pairs of traits, or of traits and environmental conditions, mirror expectations from our model or are consistent with them. One additional pattern – life in moist, fertile habitats  $\geq 1000$  m elevation evolving more frequently in entangling-seed backgrounds – might have arisen indirectly from the close association of epiphytism with such habitats and such seeds. Another – non-avian (i.e., insect) pollination evolving more from a CAM background – might have arisen in similar fashion from the close association of insect pollination and CAM with arid/semi-arid conditions (see above). The same may be true for avian pollination evolving 20 times more frequently in an entangling-seed background, given the correlation of both with tanks (Table 1). Yet another significant pattern – avian pollination evolving more frequently in tank backgrounds – may reflect the potential availability of insect prey for hummingbirds at or near tanks, and the ability to secrete large nectar volumes with access to tank fluid (see above). The remaining four significant patterns remain puzzling, and join the 120 cases that did not show significant patterns of contingent evolution *and* were not expected to do so. The four anomalous cases thus represent, in some sense, an error rate of  $4/124 = 3.2\%$ , below the 5% level of error expected from chance alone.

#### 4.3. Determinants of net rates of species diversification

The sharp drop in the rate of net species diversification with subfamily stem age could reflect a slowing of speciation as adaptive radiations fill ecological space (Givnish et al., 2005, 2009; Rabosky and Lovette, 2008), or a statistical artifact of regressing  $D = (\ln N)/t$  (or its more complicated analogue for birth–death processes) against  $t$  (Givnish, 2010). The decline in net diversification with stem age across angiosperm families (Magallón and Castillo, 2009) and adaptive radiations generally might reflect either

process, or both. Across bromeliad subfamilies,  $D$  declines at  $t < -1$ , suggesting that at least part of the pattern reflects a slowing of speciation in older bromeliad lineages, possibly via ecological saturation.

Based on phylogenetically unstructured comparisons among subfamilies, significantly higher rates of net diversification occur in lineages that occupy moist, fertile, extensive cordilleras, are pollinated by hummingbirds, are epiphytic, possess tanks, or bear entangling seeds (Table 3). Claims by Quezada and Gianoli (2011) that CAM is associated with higher diversification rates in bromeliads are based on their incorrect identification of four of five sister-group comparisons they employed.

Although our comparisons are based on non-overlapping clades defined by particular character-states, the comparisons themselves are not independent of each other. Six character-states are broadly associated with epiphytic lineages – tanks, entangling seeds, avian (usually hummingbird) pollination, CAM photosynthesis, absorptive trichomes, and occupation of extensive, moist, fertile montane regions – and a contrasting suite of states is associated with terrestrial lineages (Figs. 2 and 3, A2–A4). We lack enough degrees of freedom to dissect the relative contributions of each trait to net diversification. But, based on the magnitude of effects of individual character-states, epiphytism appears to accelerate diversification to the greatest extent, by a factor of 2.4, while life in fertile, extensive cordilleras and hummingbird pollination have the greatest effects in terms of statistical significance.

Phylogenetically structured analyses similarly identify tank formation, avian pollination, epiphytism, and especially life on moist, fertile cordilleras as accelerating speciation with progressively greater support, and that the latter also significantly accelerated the apparent rate of extinction (Table 4). MEDUSA identified significant accelerations of net diversification in the core tillandsioids and the common ancestor of Navioideae–Pitcairnioideae–Puyoideae–Bromelioideae, and a further, nested acceleration in the bromelioid tank-epiphytic clade (Fig. 5). The inclusion of Navioideae in an accelerated clade is not predicted by our model, but may reflect high rates of local speciation in *Navia-Brewcaria* associated with a complete loss of long-distance seed dispersal (naked, unappendaged seeds), combined with it being sister to a large clade (Pitcairnioideae–Puyoideae–Bromelioideae) strongly associated with moist, fertile, extensive cordilleras and hummingbird pollination. The general concordance of results based on phylogenetically unstructured and structured analyses of the relationship of net diversification rate to lineages and individual plant character-states is itself notable, and most likely reflects the nearly star-like divergence of most subfamilies from each other during the so-called “bromeliad revolution”.

Among vascular epiphytes, 80% of all species are concentrated in just four families: Orchidaceae, Bromeliaceae, Polypodiaceae, and Araceae (Gentry and Dodson, 1987; Zotz, 2013). Gentry and Dodson (1987) and Benzing (2000) proposed that, for these families, the evanescent nature of epiphytic substrates, of unoccupied twigs and branches, select for short-generation species that are likely to speciate rapidly. However, Ibsch (1996) showed that epiphytic *Tillandsia adpressa* takes 6–8 years to flower, about 10 years after the twigs first formed, making even such epiphytic pioneers among bromeliads more similar to slow-growing forest herbs than to rapidly speciating desert annuals (Givnish, 2005, 2010).

We propose that epiphytism is associated with high rates of diversification in bromeliads mainly as a result of (1) the extensive area and dynamism of habitat available for colonization and speciation; (2) the recent invasion of a new adaptive zone; (3) coevolution with a rapidly diversifying clade of pollinators, the hummingbirds; (4) partitioning habitats by elevation and exposure in montane regions that favor epiphytes; and – most importantly – (5) acceleration of speciation via invasion of the fertile, geographic

ally extensive, topographically dissected, edaphically and climatically complex Andes and Serra do Mar.

#### 4.3.1. Extensive area and dynamism of the epiphytic biotope

Gentry and Dodson (1987) and Benzing (2000) noted the potential importance for diversification of frequent shifts in the location of optimal microsites for epiphytes in mountainous terrain, due to geological and climatic dynamism and their impacts on the concentration of mist in a few favorable microsites (e.g., narrow wet ridges). Temporal shifts in the location of such microsites could plausibly lead to frequent founder events and rapid speciation even in plants with long generation times, as could divergence in elevation and seasonal time of reproduction. The surface area available for epiphyte to colonize is also generally much bigger than the ground below, which might also act to increase epiphyte diversification.

#### 4.3.2. Recent invasion of a new adaptive zone, key innovations, and key landscapes

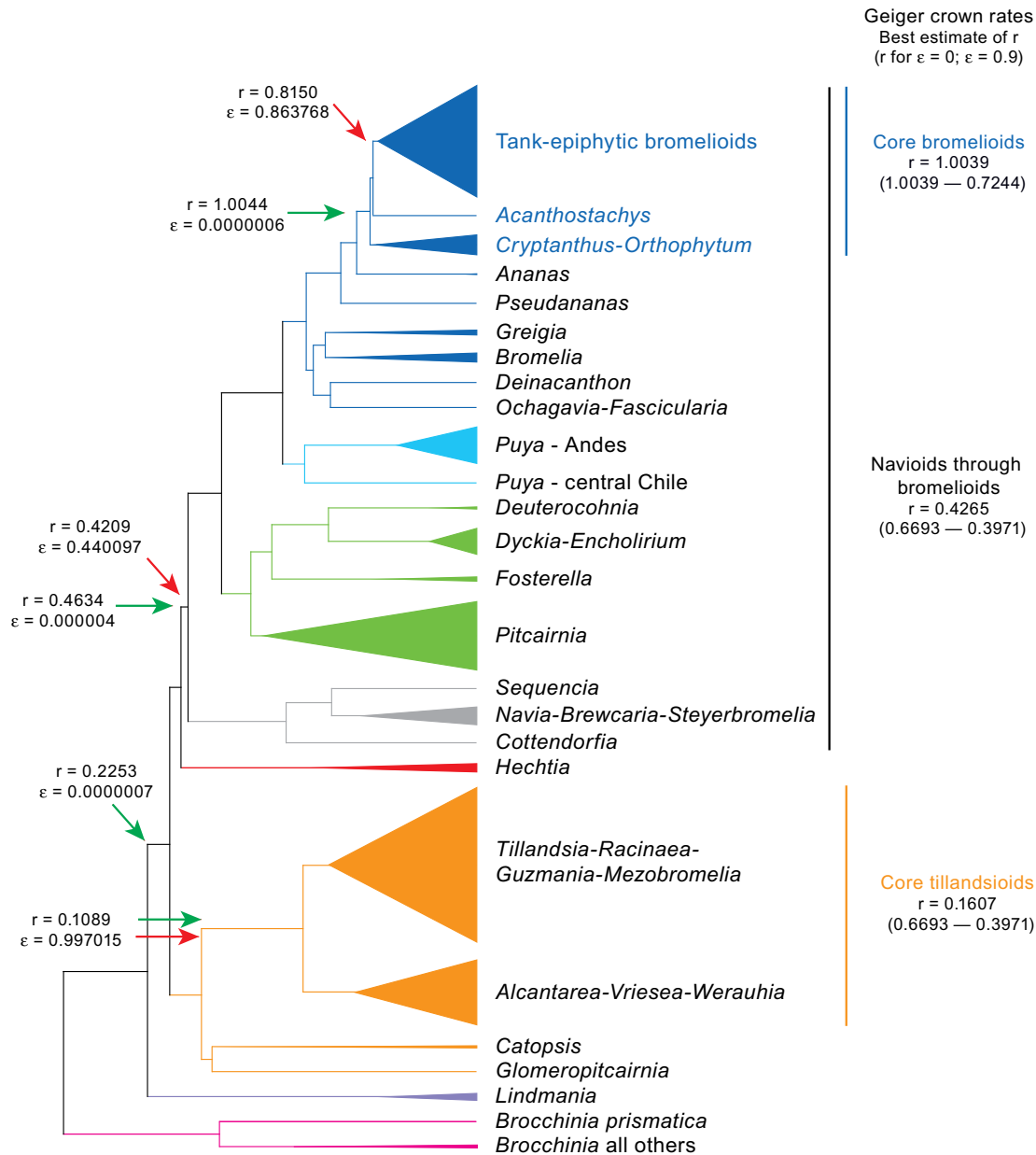
Key innovations that open access to new adaptive zones (Simpson, 1944), such as epiphytism and associated traits, are likely to be associated with high net rates of diversification only if they have arisen recently (Linder, 2008) and are likely to arise only in the “key landscapes” that favor their evolution (e.g., canopies of tropical rain and cloud forests: Givnish, 1997). Epiphytism arose in both tillandsioids and the tank-epiphyte bromelioids at just about the times that the northern Andes and the Serra do Mar – two key areas occupied by these clades – began their major uplifts in the Middle and Late Miocene, respectively. Access to volcanically active Central America after the Isthmus of Panama narrowed by the Middle Miocene (Farris et al., 2011; Montes et al., 2012) as well as continued uplift of the Andes 3–5 Mya (Steinmann et al., 1999; Coltorti and Ollier, 2000; Gregory-Wodzicki, 2000) continued to provide a diversifying influence for tillandsioids. Uplift of the Serra do Mar during the Pliocene apparently triggered a radiation of epiphytic bromelioids there. While the newly uplifted northern Andes and Serra do Mar would have provided unoccupied montane regions likely to trigger adaptive radiations in epiphytic groups, we must recognize that any such radiation in bromeliads would have had to compete at least with the epiphytic epidendroid orchids, which began diversifying 50 Mya (Ramirez et al., 2007).

Two unique features of bromeliads may have expanded their adaptive zone beyond that of other epiphytes: (1) the **tillandsioid trichome** and the **atmospheric habit** that it makes possible (Benzing, 2000), and (2) **augmentation of nutrient inputs** to some tank bromeliads by **resident ants** (Benzing, 1970, 1990; Huxley, 1980; Givnish et al., 1997) and by **predators** (e.g., spiders, damselfly larvae, frogs and tadpoles) that consume aerial prey (Romero et al., 2006), **submersed detritivores** (Ngai and Srivastava, 2006) or **fruits and vegetable debris** (da Silva and Britto-Pereira, 2006), and thereby add or retain nutrients in the tank ecosystem, with microbes living in tanks capable of rapidly mineralizing many forms of added nitrogenous compounds (Inselbacher et al., 2007). Modern data – often using  $\delta^{15}\text{N}$  to trace the contribution of animals to a plant’s nitrogen supply – are beginning to support Picado’s (1913) proposal that many tank-epiphytic bromeliads depend on animals, at least indirectly, for much of their nutrient supply.

#### 4.3.3. Coevolution with rapidly diversifying hummingbirds

Acquisition of hummingbird pollination in cool montane habitats would open another adaptive zone for bromeliads: a range of new pollinators with different bill lengths and shapes to be partitioned. In bromeliads, bird-pollinated lineages do have significantly higher rates of net diversification, roughly twice that of lineages pollinated by other animals, primarily insects. In five of six cases reviewed by Schmidt-Leubuh et al. (2007),





**Fig. 5.** MEDUSA 26-taxon tree, with grey arrows (green in the online color figure) highlighting nodes at which there was a significant acceleration of speciation in the Yule model, and black arrows (red in the online color figure) highlighting nodes at which there was a significant acceleration of speciation in the birth–death model.

hummingbird-pollinated lineages had a higher net diversification rate than sister groups pollinated by other animals, including hummingbird-pollinated *Tillandsia* subg. *Tillandsia* (227 spp.) having three times as many species as its sister clade, insect-pollinated *Tillandsia* subg. *Phytarrhiza* and *Racinaea* (77 spp.). To these, we add our finding that mostly hummingbird-pollinated Pitcairnioideae-Puyoideae–Bromelioideae (1306 spp.) has 13 times as many species as its sister, insect-pollinated Navioideae (96 spp.). The reason for higher speciation rates in hummingbird-pollinated lineages is not clear (Castellanos et al., 2003; Schmidt-Lebuhn et al., 2007), but association with continued uplift of the northern Andes and climatic oscillations during the Pliocene–Pleistocene and coevolution there with >300 recently derived hummingbird species may have played a role (Gentry, 1982; Graham, 1997; Berry et al., 2004; Kay et al., 2005). We propose that hummingbird pollination may also stimulate speciation by favoring the rise of gullet-shaped flowers from ancestral cup-shaped blossoms. Once such exclusionary

flowers are present, their length and shape can quickly evolve to attract different hummingbird species, leading to pre-mating barriers for the plants. Coevolution with rapidly radiating hummingbirds cannot account, however, for rapid diversification of tank-epiphyte bromelioids centered in the Serra do Mar. Indeed, the reliance of large numbers of Atlantic bromelioids on just a few hummingbird species, or strongly overlapping sets of species, begs the question as to how such bromelioids are reproductively isolated (Piacentini and Varassin, 2007; Wendt et al., 2008).

#### 4.3.4. Epiphyte partitioning of habitats by elevation and exposure in montane regions

Gentry and Dodson (1987) argued that one factor promoting high diversity in epiphytes should be partitioning of habitats by elevation and exposure/rainfall. The data of Krömer et al. (2006) show substantial turnover in the composition of epiphytic bromeliads along one wet elevational transect in the Bolivian Andes, as do

the data of Kessler and Krömer (2000) for Bolivia generally. Kessler (2001) and Kreft et al. (2004) document large shifts in the total number of epiphyte species with rainfall in Bolivia and Ecuador. It remains to be seen whether epiphytes show greater compositional turnover with a given change in elevation, rainfall, or exposure than other kinds of plants, but their strong association with montane regions creates the possibility of substantial shifts in composition with total changes of elevation and precipitation.

#### 4.3.5. Invasion of extensive, fertile, topographically, climatically, and edaphically complex montane regions

In general, limited dispersal should elevate speciation rate, by decreasing the scale at which genetic differentiation occurs within species and increasing the likelihood that such differences would become large enough to lead to partial mating barriers and, ultimately, to speciation and endemism at small spatial scales (Mayr, 1970; Diamond et al., 1976; Givnish et al., 1995, 2009). This prediction is in accord with the relative high rate of net species diversification seen in *Navia-Brewcaria* ( $D = 0.55 \text{ My}^{-1}$ ), associated with no apparent means of long-distance seed dispersal (Table 1), and with a general tendency for parallel, species-rich adaptive radiations to occur in poorly dispersing groups, from fossorial rodents, brooding sea anemones, and heavy seeded monocots, to fleshy-fruited plants dispersed by sedentary forest-interior birds, to philopatric, mouth-breeding cichlids of the African Rift Lakes (Givnish, 1998, 1999a,b, 2010).

The capacity for occasional medium- to long-range dispersal can, however, also lead to rapid speciation if it permits invasion of an extensive, topographically dissected region, but does not allow the frequent crossing of habitat barriers within such a region. The rise of epiphytism in tillandsioids and bromelioids is likely to have accelerated speciation in this way by increasing seed dispersal ability and consequent ability to colonize different sites and differentiate populations in parallel along the lengths of the Andes and the Serra do Mar. Across 172 bromeliad species in Bolivia, Kessler (2002a) found that range size is greater in (a) species with fleshy fruits (bromelioids) or plumose seeds (tillandsioids) vs. those with winged seeds; (b) epiphytic vs. terrestrial taxa; and (c) species at lower vs. higher elevations. The first pattern supports our assumption that entangling, plumose seeds and fleshy fruits adapted for epiphytism also have greater dispersal ability than winged seeds. The second follows immediately from the first, given that almost all epiphytic taxa are tillandsioids and bromelioids. In bromelioids, dispersal of fleshy fruits over longer distances may be more likely in epiphytic than terrestrial taxa, given that canopy birds are more mobile than those in the understory (Diamond et al., 1976; Burney and Brumfield, 2009). Many bromelioid tank epiphytes, however, occur in the understory of the Atlantic forests (Leme and Marigo, 1993; Siqueira Filho and Leme, 2007), raising the possibility for differentiation and, ultimately, speciation and endemism at small spatial scales within such groups. The third pattern almost surely results from epiphytism being favored in cloud forests and the increasing spatial discontinuity of bands of such vegetation at higher elevations.

Given the greater dissection of higher-elevation habitats by drier valleys, it is not surprising that range size decreases with elevation (Kessler, 2002a, 2002b), or that closely related species at mid elevations often have peripatric ranges that abut deep Andean valleys (see Berry, 1982, 1989; Norman, 2000; Andersson, 2006; Smith and Baum, 2006; Antonelli et al., 2009). The ability of a lineage to invade an elongate geographic area with a wide range of elevations to partition and many natural barriers to dispersal – especially in the latitudinally extensive, topographically and edaphically complex Andes and Serra do Mar (Luteyn, 2002; Young et al., 2002) – coupled with a tendency to speciate at small spatial scales at mid elevations, should lead to high levels of species

diversity at continental scales. As previously argued, richer substrates are likely to favor epiphytes even more within such regions; the much greater diversity of (mainly epiphytic) Ericaceae in the Andes (586 spp.) vs. the Guayana Highlands (71 spp.) (Luteyn, 2002) is consistent with this argument. Furthermore, if such montane regions were newly formed, ecologically empty slates, we would expect several lineages to diversify rapidly within them, irrespective of life form (Linder, 2008).

The above ideas are confirmed by the association of the Andean and Serra do Mar orogenies – marked by newly formed montane habitats, numerous natural barriers to gene flow, and highly dynamic climates and landscapes during the Plio-Pleistocene (Gentry, 1982; Berry, 1989; Vasconcelos et al., 1992; van der Hammen, 1995; Gregory-Wodzicki, 2000; Grazziotin et al., 2006; Garzone et al., 2008; Antonelli and Sanmartin, 2011) – with several highly diverse plant groups that are widely distributed within each region (e.g., *Calceolaria*, *Centropogon-Burmeistera*, *Epidendrum*, *Espeletia*, *Fuchsia*, *Lepanthes*, and *Pleurothallis* in the Andes; and Asteraceae [*Lychnophora*], Bromeliaceae-Bromelioideae, Eriocaulaceae [*Leiothrix*, *Paepalanthus*], Gentianaceae, Lentibulariaceae, Myrtaceae, and Velloziaceae in the Serra do Mar) (Gentry, 1982; Peixoto and Gentry, 1990; Luteyn, 2002; Young et al., 2002; Knox et al., 2008; Alves and Kolbek, 2009). The northern Andes are a hotspot for diversity of angiosperm families, especially herbaceous ones (Hawkins et al., 2011). Several clades with the highest rates of net diversification known in plants occur wholly or partly in the Andes, including Andean *Lupinus* ( $2.49\text{--}3.79 \text{ My}^{-1}$  [Hughes and Eastwood, 2006]), Andean *Valeriana* ( $1.71\text{--}3.2 \text{ My}^{-1}$  [Bell and Donoghue, 2005]), Neotropical *Costus* ( $0.6\text{--}2.6 \text{ My}^{-1}$  [Kay et al., 2005]), and Andean *Astragalus* ( $2.01\text{--}2.07 \text{ My}^{-1}$  [Scherson et al., 2008]). Many of these and other plant and animal clades from the Andes have origins around or after the uplift of the northern cordilleras ca. 15 Mya (Hooen et al., 2010). To this roster we now add the largely Andean, largely epiphytic core tillandsioids ( $0.67 \text{ My}^{-1}$ ) and, especially, bromelioid tank epiphytes from the Atlantic Forest region ( $1.05 \text{ My}^{-1}$ ).

Diversification rates for the fastest diversifying bromeliad clades are comparable to those for the fastest adaptive radiations of plant lineages on islands, including the Hawaiian silversword alliance ( $0.56 \text{ My}^{-1}$  [Baldwin and Sanderson, 1998]), Macaronesian *Sideritis* and *Echium* ( $0.79$  and  $0.60 \text{ My}^{-1}$  [Kim et al., 2008]), and Hawaiian *Cyanea* (maximum of  $1.36\text{--}2.09 \text{ My}^{-1}$  [Givnish et al., 2009]). They are, however, substantially less than those for South African ice plants ( $1.75 \text{ My}^{-1}$  [Klak et al., 2004]), European *Dianthus* ( $2.2 \text{ My}^{-1}$  [Valente et al., 2010]) and certain groups of African rift-lake cichlids ( $2.93 \text{ My}^{-1}$  for Bermin *Tilapia*,  $6.1 \text{ My}^{-1}$  for Malawi *Astatotilapia*, and  $178.8 \text{ My}^{-1}$  for Natron *Oreochromis* [based on data compiled by Seehausen, 2006; see also McCune, 1997]).

The isolation of many bromeliad taxa on isolated peaks or inselbergs (especially in the Serra do Mar) may select for reduced dispersal and thereby trigger additional pulses of local speciation, as Moyle et al. (2009) have argued for the “great speciator” lineage of Asian and Pacific white-eyes (*Zosterops*). Our explanations for rapid speciation in epiphytic tillandsioids and bromelioids differ from those of Qian and Ricklefs (2000), Schluter (2000) and Linder (2008) in incorporating the effect of specific biological features of epiphytes on the ability to infiltrate, speciate, and diversify across extensive montane regions.

#### 4.4. Bromeliad diversity in relation to regional patterns and broad-scale adaptive radiation

Our findings confirm the widespread pattern for many Neotropical plant groups to have diversified mostly since the Middle Miocene, associated with uplift of the northern Andes and the Serra do Mar and nearby ranges in southeastern Brazil (Givnish et al., 2004,

2007, 2011; Hughes and Eastwood, 2006; Antonelli et al., 2009; Antonelli and Sanmartin, 2011; Arakaki et al., 2011; Hoorn et al., 2010; Nagalingum et al., 2011; Drew and Sytsma, 2013; Perret et al., 2013; Roncal et al., 2013; cf. Rull, 2008; Lohmann et al., 2013). Bromeliads differ from most of these groups, however, in containing the only major lineages of epiphytes studied to date, and in having an ancient stem age (97.5 Mya) but a recent crown age (22.7 Mya). Although bromeliads arose about when continental drift split South America from Africa, they show no trace of ancient colonization of the Paleotropics (Givnish et al., 2011). While diversification of several Neotropical plant groups appears related to edaphic diversity or rain shadows created by northern Andean uplift, our results indicate that bromeliad diversity is tied more to epiphytism and associated traits arising on moist, fertile, montane conditions in the northern Andes and southeastern Brazil, to the occupancy of extensive and heterogeneous cordilleras, and to coevolution with hummingbird pollinators whose own diversity is centered on the Andes.

The two regions worldwide with the highest average rates of net species diversification in previously studied plant groups are the Andes and the Atlantic forests (Jansson and Davies, 2008) – the two areas where we have documented the highest rates of diversification in bromeliads. The tropical Andes are the world's leading hotspot for plant biodiversity, with ca. 15% of all angiosperms worldwide (Gentry, 1982; Myers et al., 2000). The Andes and the Brazilian coastal forests and mountains rank first and third, respectively, in terms of the number of species endemic to individual regions (Jansson and Davies, 2008). Lineages within Bromeliaceae parallel these global patterns of diversification, species richness, and richness of endemic species at the family level, and detailed studies of factors in each that promote genetic differentiation, ecological specialization, and regional colonization could thus provide a model for future studies of plant diversity and diversification. Elevational heterogeneity is a major driver of plant species richness worldwide (Kreft and Jetz, 2007). Our thesis is that, for different reasons, elevational heterogeneity and life on extensive, fertile cordilleras are also major drivers of epiphytic plant diversity.

On a global scale, Jansson and Davies (2008) found that differences in species richness between sister families of angiosperms are most strongly correlated with differences in the areas of their geographic ranges. This pattern also appears to hold, at least qualitatively, across bromeliad subfamilies, with the four having the smallest ranges – Brocchinioideae, Lindmanioideae, Navioideae, Hechtioideae – having the fewest species (20–107), while the two with the largest ranges (Tillandsioideae, Bromelioideae) have the greatest number of species (1256 and 856 species, respectively).

Previous attempts to explain differences among lineages in diversity based on differences in the spatial extent of regions invaded, or the diversity of adaptive zones occupied (e.g., Ricklefs and Renner, 1994; Davies et al., 2004), have foundered on the question of whether broad-scale adaptive radiation or geographic spread caused extensive speciation, or extensive speciation permitted adaptive differences and geographic differences in distribution to accumulate (Dodd et al., 1999; Givnish, 2010). We have attempted to cut this Gordian knot by coupling specific traits (or suites of traits) to individual bromeliad clades and to the particular regions and environmental conditions they were able to invade by evolving those traits, tracing the causal arrow as flying from functional diversification to geographic diversification to species diversification. This does not remove the problem entirely. But invasion of geographic regions and ecological zones by particular lineages facilitated by particular traits, with speciation ensuing as those lineages spread, makes it hard to argue that speciation drives the accumulation, through some random process, of adaptive and

geographic/functional diversity within a lineage, rather than functional divergence, then geographic spread driving speciation in a straightforward fashion. Further, we argue that causes of bromeliad diversity should be sought not only in the rise of traits that accelerate the net rate of diversification, but also in the cumulative effect of broad-scale radiations on the total range of adaptive zones and geographic areas added, and their associated complements of clades and species.

Specifically, the subfamilies Brocchinioideae, Lindmanioideae, and Navioideae – which continue to be limited to the nutrient-poor, extremely rainy habitats of the Guayana Shield where the family arose – comprise 172 species or 5.4% of present-day bromeliad species. Evolution of epiphytism and a suite of related traits added 1256 species of tillandsioids, mainly in the Andes, but spreading throughout Central and South America, the Caribbean, and southeastern North America, as well as 629 species of bromelioid tank epiphytes, mainly in the Serra do Mar and nearby areas (Table 5). Epiphytism could thus be said to have increased the number of bromeliad species 11-fold, and the geographic area occupied by at least 30-fold and to account for 60% of current species richness. Evolution of CAM in terrestrial species in arid habitats and microsites permitted the radiation of (1) *Hechtia* at low to mid elevations in Central America, adding 52 species; (2) *Deuterocohnia–Dyckia–Encholirium* at low to high elevations in the Andes and drier parts of the Brazilian Shield, adding 170 species; and (3) *Puya* at high elevations in the Andes, adding 217 species (Table 5). CAM in terrestrial plants thus appears responsible for adding ca. 430 species, or 13.6% of current bromeliad diversity. The final major radiation in bromeliads outside the Guayana Shield was that of *Pitcairnia* (387 spp., 12.3% of all bromeliads), many bearing large, broad leaves and adapted to rain- and cloud-forest understories. Two radiations based on epiphytism, three based on terrestrial CAM plants, and one based on tropical forest understories thus underlie, in some sense, 86% of all current bromeliad species. This is not to say that divergence in pollinators, elevation, rainfall, exposure, or frugivores, or the acquisition of mutualists like ants, were unimportant, or that they did not, in fact, contribute other axes and specific shares of biodiversity to the six radiations just listed. But we can now see that these six large-scale radiations account, directly or indirectly, for more than six-sevenths of total present-day bromeliad diversity, partly through the acceleration of net species diversification in epiphytic lineages inhabiting the Andes and the Atlantic Forest region, and partly through additions to the total range of physiological capabilities in bromeliads and thus, to the geographic regions occupied by different bromeliad clades in aggregate (see **graphical abstract**).

This study is the first to relate determinants of net diversification within a major group to *a priori* predictions that particular key innovations would lead their bearers to invade specific ecological zones and geographic areas (including “key landscapes”) and diversify at different rates. Such predictions, when combined with differences among clades in dispersalability and thus the tendency to speciate, can help explain the overall diversity of innovations, species, ecological zones, and geographic areas invaded, summed across radiations. Moore and Donoghue (2007) and Drummond et al. (2012b) addressed similar questions involving two families of Dipsacales and for *Lupinus*. Both studies identified invasion of extensive cordilleras as a major determinant of diversification, but failed to recognize the cumulative contribution of different radiations to overall diversity even when diversification showed no acceleration in any particular radiation, failed to identify key innovations that might underlie the invasion of different regions and ecological zones, and failed to recognize the importance of shared key landscapes (e.g., recently uplifted, extensive cordilleras) that could themselves trigger multiple radiations (Givnish, 1997). The assertion by Drummond et al. (2012b) that perenniality is

the key innovation driving high rates of diversification in *Lupinus* is not plausible: most montane lineages are composed of perennials but none have as high a diversification rate as *Lupinus*.

We believe that an approach similar to ours might help revolutionize the study of diversification, biogeography, and adaptive radiation in many other groups. It provides a direct means for testing *a priori* hypotheses about the relationships among geographic spread, phenotypic evolution, and net species diversification, and thus for making historical biogeography a hypothesis-driven enterprise (Crisp et al., 2011). Just as importantly, the results of our study show that – while phylogenetic niche conservatism, or the tendency for closely related species to have similar ecologies and traits, may be a broad rule in many plant groups (Donoghue, 2008; Wiens et al., 2010) – in bromeliads, at least, it is precisely when adaptive radiation and the invasion of new geographic areas jump the tracks of phylogenetic niche conservatism that lineages can spawn large amounts of new species diversity.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympcv.2013.10.010>.

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