

EVOLUTIONARY FLEXIBILITY AND FLOWERING PLANT FAMILIAL DIVERSITY:
A COMMENT ON DODD, SILVERTOWN, AND CHASE

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Ricklefs and Renner (1994) analyzed the relationship between number of species in families of flowering plants and four classification variables: geographical distribution, growth form, pollination mode, and dispersal mode. They found that families with more than one state for any of these four variables had more species than did families exhibiting a single “character” state, and they proposed that evolutionary flexibility with respect to the classification variables promoted diversification. Dodd et al. (1999) reanalyzed these data in a phylogenetic context using sister-taxon comparisons and independent contrasts. Dodd et al. conducted a further test of the “flexibility hypothesis” involving analyses of proportions of sister taxon pairs with neither, either, or both being variable with respect to growth form, pollination mode, and dispersal mode. Based on this test, they rejected the idea that character variability results in high net speciation rate. Here we comment on two issues raised by Dodd et al.’s analysis. The first is the relative performance of phylogenetic and nonphylogenetic analyses of comparative data. We cannot detect substantial differences in the results of these two approaches. The second concerns difficulties in assessing evolutionary flexibility. Tests that involve analyses of the distribution of character variation among pairs of sister taxa are complicated by taxon size. We also examine plant radiation in the Hawaiian Islands to determine whether the probability that a colonizing lineage proliferates is related to character trait variability in the family to which it belongs, and we find no effect.

PHYLOGENETIC AND NONPHYLOGENETIC COMPARISONS

Dodd et al. (1999) performed a series of phylogenetic comparisons to test the statistical effects of various character traits on the species richness of families of flowering plants. The hypotheses tested were based on results of previous nonphylogenetic comparative analyses of correlations between family species richness and growth form, pollination mode, and dispersal mode (Herrera 1989; Eriksson and Bremer 1992; Ricklefs and Renner 1994; Tiffney and Mazer 1995): (1) pollination: biotic > abiotic; (2a) dispersal: biotic > abiotic; (2b) dispersal: biotic < abiotic (herbs only; see Tiffney and Mazer 1995); (2c) dispersal: biotic > abiotic (woody plants only); (3) growth form: herbs > no herbs. Dodd et al. also

tested hypotheses relating diversity in families to the presence of more than one character state; (4a) pollination: two modes > biotic; (4b) dispersal: two modes > biotic; (4c) growth form: two forms > herbs only. The results of these comparisons are summarized in Table 1, with the corresponding results of Ricklefs and Renner (1994). Only in test 2c do the results of nonphylogenetic analyses contradict the results of analyses conducted within a phylogenetic context. The three analytical approaches are fully consistent with respect to tests 1, 2a, 3, and 4b, and they are consistent in the direction of observed effects, but not level of statistical confidence, with respect to tests 2b, 4a, and 4c. For test 2c, the two phylogenetically informed tests differed from each other in the direction of the effect, and neither was significant. Nonphylogenetic analyses showed stronger effects, particularly with respect to the comparisons of two modes versus one in the cases of dispersal and life form.

Although phylogenetically informed analyses are preferable to nonphylogenetic analyses in principle owing to the statistical independence of comparisons and the possibility of sister-taxon analyses, other studies have revealed few differences in results from these two approaches (e.g., Ricklefs and Starck 1996). This is to be expected when traits are sufficiently labile for character states to be independently derived in most of the monophyletic groups being compared, which appears to be the case for traits considered here at the family level in flowering plants. Dodd et al. (1999) placed 299 families in their phylogenetic reconstruction of the angiosperms (see their fig. 1). From their table 2, the number of independent character state changes varied between eight and 55 for each of the eight tests, with an average of 30.9. From their table 1, the number of sister families with contrasting states for the different traits varied from three to 20, with an average of 12.4, about 40% of the total character state changes. This indicates that a large proportion of character state changes occur close to the taxonomic level of the comparisons, or at a lower level, providing a reasonable degree of independence of families with respect to character state. Considering that most of the effects observed by Ricklefs and Renner (1994) exhibited statistical confidence of $P < 0.0001$, their results would have been robust even to a high level of non-independence in the data.

A problem in any phylogenetically informed analysis is

TABLE 1. Comparison of tests of hypotheses relating family species richness to character states. Numbers in parentheses are ratios of average species richness across families associated with each character state, for example, biotic/abiotic in test 1.

Test	Trait	Hypothesis	Sister-taxon comparisons ^a	Phylogenetic contrasts ^b	Ricklefs and Renner (1994) ^c
1	Pollination	biotic > abiotic	Yes (1.19)	Yes (2.36)	Yes (1.97)
2a	Dispersal	biotic > abiotic	No (0.32)	No (0.98)	No (0.91)
2b	Dispersal	biotic < abiotic (herb)	Yes (0.08)	No (0.39)	Yes (0.39)
2c	Dispersal	biotic > abiotic (woody)	No (0.64)	No (1.40)	Yes (3.55)
3	Growth form	herbs > no herbs	Yes (4.15)	Yes (1.65)	Yes (2.50)
4a	Pollination	two modes > biotic	Yes (1.69)	No (1.36)	No (1.41)
4b	Dispersal	two modes > biotic	Yes (2.58)	Yes (2.07)	Yes (13.56)
4c	Life form	two forms > herbs	Marg. (1.00)	Marg. (1.48)	Yes (5.70)

^a Dodd et al. (1999, table 1); ^b Dodd et al. (1999, table 2); ^c Ricklefs and Renner (1994, table 5, except tests 2b and 2c from Figure 4). Marg. (marginal) refers to statistical significance close to 0.05.

the accuracy of the phylogenetic hypothesis. Support for particular relationships varies widely and phylogenetic trees change, sometimes dramatically, as new taxa and data are added. For example, 13 (33%) of the 39 pairs of sister families identified by Barraclough et al. (1996) on the angiosperm phylogeny of Chase et al. (1993) were no longer sister taxa on the tree used by Dodd et al. (1999). The more recent phylogeny includes over half of the angiosperm families, but parts of the tree are affected by incomplete sampling or are poorly supported. For instance, of the sister family pairs used by Dodd et al. (1999), Calycanthaceae and Hernandiaceae appear as sister groups and Penaeaceae as sister to Lythraceae only as long as Laurales and Myrtales, respectively, are insufficiently sampled; Amborellaceae is sister to Nymphaeaceae only in a poorly supported part of the *rbcL* tree. Sister taxon relationships among angiosperm families are not perfectly known, and including uncertain sister-group pairs adds noise to comparisons, which partly offsets the advantage of a phylogenetic approach to comparative analysis.

CHARACTER FLEXIBILITY

The presence of multiple character states in dispersal mode, growth form, and (not assessed by Dodd et al. 1999) geographic distribution is associated with high familial diversity. The underlying cause of these relationships is less clear. Dodd et al. (1999) concluded that "more species-rich families tend to have two modes of dispersal due to a sampling effect." Ricklefs and Renner (1994) argued against a sampling artifact from the large proportion of species-rich families with single modes of dispersal or growth forms. A fundamental aspect of this issue is whether character flexibility is conservative within clades. That is, do clades vary with

respect to "evolutionary flexibility"? To answer this question, Dodd et al. (1999) proposed a sister-taxon test for the existence of evolutionary flexibility (test 5). If flexibility were not a clade-specific trait, then it would not make sense to ask whether more flexible families are more diverse. Their test evaluated the proportions of sister family pairs in which (1) both families possessed two states for a particular trait; (2) only one family was variable for that trait; and (3) neither family was variable for the trait. The results indicated that multiple character states were homogeneously distributed among the sister family pairs found on the tree. That is, the proportion of sister pairs in which both, one, and neither had two character states did not differ from random. A potential problem with this approach is that the probability that two or more character states appear in a monophyletic group depends on the number of species in the group.

Consider a null model that assumes a single probability of character state change along each branch within a monophyletic group. This is equivalent to a punctuated model of character evolution. The number of branches (n) within a monophyletic group is equal to $2(s - 1)$, where s is the number of terminal taxa. When the probability of a character state change along a single branch is p , the probability that no change in a trait occurs within a group (hence the character is uniform) is $P(\text{uniform}) = (1 - p)^n$ (ignoring reversals), and the probability that change will occur, yielding multiple character states, is $P(\text{various}) = 1 - (1 - p)^n$. Clearly, $P(\text{uniform})$ depends on the size of the monophyletic group and thus the expected proportions of uniform and mixed sister-taxon pairs depends on the sizes of the groups used in the comparison. We shall return to this point below.

APPARENT CHARACTER FLEXIBILITY (p)

To assess character state flexibility in a nonphylogenetic context, we may ask whether a single value of p can account for observed proportions of groups with only one or with both character states. Alternatively, if species proliferation rate depended on the value of p , then p would increase with the species richness of groups. When the number of branches per group is n , we can estimate p from the proportion of groups that are uniform with respect to a character by $p = 1 - \exp(\ln P[\text{uniform}]/n)$. In Table 2, we have estimated p for transitions among biotic and abiotic dispersal states for families falling into five size range classes to determine

TABLE 2. Probability of character state change per branch (p) within a family estimated from the proportion (P) of families with only one character state and the number of terminal taxa (species, s).

Family size (s , range)	Geometric mean size (s)	Number of families	P (uniform)	p (estimated)
10–39	19.7	56	0.911	0.00249
40–99	68.0	41	0.902	0.00077
100–399	238.8	52	0.654	0.00089
400–999	670.9	51	0.510	0.00050
1000–3999	2136.4	46	0.522	0.00015

TABLE 3. Probability of apparent character state change per branch (p) within a monophyletic group estimated from the proportion (P) of groups with only one character state and the number of terminal taxa (species, s), when rate of character state change is heterogeneous among groups.

s	P (uniform)		Proportion $p = 0.0025$	Average	Estimated p	Proportion $p = 0.0025$	Average	Estimated p
	$p = 0.0025$	$p = 0.0001$						
20	0.909	0.991	0.50	0.953	0.00127	0.20	0.979	0.00057
65	0.726	0.987	0.50	0.857	0.00121	0.30	0.909	0.00075
200	0.369	0.961	0.50	0.65	0.00102	0.40	0.724	0.00081
650	0.039	0.878	0.50	0.459	0.00060	0.50	0.459	0.00060
2000	0.000	0.670	0.50	0.335	0.00027	0.60	0.268	0.00033

whether p increases with family size. With respect to dispersal mode, the estimated probability of evolutionary transition per branch appears to decrease, by more than an order of magnitude, from the smallest to the largest category of family size (or species richness). This result would appear to reject the hypothesis of Ricklefs and Renner (1994) that diversity is associated with flexibility (rate of character state change). The inverse relationship of p to s was unchanged when the analysis was based on total branch length, that is, $n/\ln(s)$ rather than n , and when the analysis was applied to growth form (herb vs. woody).

Taken at face value, these results suggest that high diversity may be associated with fixation of a single dispersal mode within a lineage, that is, with specialization, and that the high diversity of families with varied modes may be a statistical artifact, as suggested by Dodd et al. (1999). However, these results are confounded by the assumption that monophyletic groups of the same size have the same probability of character state change per branch. To visualize the effect of heterogeneity in character state change, suppose that monophyletic groups exhibited either rapid change ($p = 0.0025$) or slow change ($p = 0.0001$). These values are similar to the maximum and minimum homogeneous values of p in Table 2. A 1:1 mix of such groups would result in an apparent decrease in p as a function of increasing number of taxa, as shown in Table 3. Moreover, if the proportion of groups with rapid character change increased with increasing group species richness, as would be the case if character flexibility promoted proliferation, the apparent decrease in p would be less marked, and estimated p may even increase, as shown in the right-hand columns of Table 3. Thus, the estimates of p in Table 2 based on homogeneous rates of character change in each lineage are not inconsistent with marked heterogeneity in rate of character change among groups. Nor are they inconsistent with an increase in the proportion of rapidly evolving groups as group size increases.

HETEROGENEITY IN CHARACTER STATE CHANGE AND DODD ET AL.'S TEST FOR FLEXIBILITY

We assume that the ancestor of two sister families exhibits a single character state, and that the probability of a character change in the stem branch of a family is small. Accordingly, any character change within a family (that is, beyond its basal node) will result in a family that is variable for the trait. Dodd et al. (1999) reasoned that if the ancestor of two sister families possessed a "flexibility" trait, both descendants should exhibit multiple states more frequently than by

chance. The null model states that the probability of finding variable traits within sister pairs of families is determined by chance. We define P as the probability that no character state change occurs within a lineage; $Q = 1 - P$. As we have seen, P depends on the number of branches (n) and the probability of change per branch (p). For ancestral state A, pairs of sister taxa could be (A,A), (A/B,A), or (A/B,A/B). The probabilities of these types of sister-taxon pairs under the null model are P^2 , $2PQ$, and Q^2 . For example, with $n = 100$ and $p = 0.01$, the probabilities of the three types of sister taxon relationships under the null model are 0.402, 0.464, and 0.134.

Heterogeneity in p among lineages, that is, variation in flexibility, creates a deficit in the proportion of (A/B,A) combinations. For example, when half of a sample of sister-taxon pairs have $p = 0.002$ (one-fifth of the homogeneous rate) and half have $p = 0.05$ (five times the homogeneous rate), the expected proportions of the three types of sister taxon relationships are 0.511, 0.155, and 0.335. These probabilities vary with n in the same way when familial species richness varies. For example, for $p = 0.01$ and equal numbers of families with 10, 100, and 1000 internal branches, the expected proportions are 0.470, 0.212, and 0.318. When sister-family pairs are heterogeneous for both n and p , the expected proportions are 0.335, 0.177, and 0.488.

Dodd et al. (1999) accepted the null model for dispersal mode and marginally rejected it for growth form. However, the null model is inappropriate for samples of sister-taxon pairs with variable familial diversity and heterogeneous probabilities of character state change. Nonetheless, if "flexibility" were correlated among sister-taxa, heterogeneity in size and rate of character state change would cause the proportions of sister-taxon pairs with zero, one, and two variable taxa to deviate even further from the proportions P^2 , $2PQ$, and Q^2 calculated from the overall proportion of variable taxa. Thus the "flexibility" test of Dodd et al. (1999) appears to be conservative. Clearly, patterns of character state distribution produced by phylogenetic models with variable rates of character state change and diversification should be explored in more detail.

At this point, evidence from flowering plant families is ambivalent concerning the idea that diversification is promoted by enhanced evolutionary flexibility. The significant results in tests 4a–4c could be explained as sampling artifacts under a model of uniform rate of character state change, but this model requires that the rate of character state change decreases with increasing species richness within families,

as shown in Table 2. However, the apparent decline in p caused by sampling could mask an increase in average p that would result from an association of higher diversity within clades with higher p , as originally proposed by Ricklefs and Renner (1994).

EVOLUTIONARY RADIATION IN THE HAWAIIAN FLORA

Suppose that evolutionary flexibility is a family-level character indicated by frequent character state change and the resulting occurrence of various character states within a family, and further that evolutionary flexibility promotes diversification. If this were true, then individual lineages from evolutionarily flexible families should show a greater tendency to proliferate than lineages from uniform families when placed in a common ecological/geographical setting. We tested this prediction by examining whether colonists to Hawaii from families with varied character states tended to proliferate more than colonists from families with uniform character states.

The Hawaiian Islands have 203 genera of flowering plants belonging to 82 families (Imada et al. 1989). Some nonendemic genera are believed to have colonized the islands more than once (e.g., *Ipomoea* [Convolvulaceae], *Carex* [Cyperaceae], *Cyrtandra* [Gesneriaceae], *Hibiscus* [Malvaceae], and *Peperomia* [Piperaceae]) and some endemic genera are thought to have originated from a single colonizing lineage (e.g., *Clermontia/Cyanea/Delissea/Rollandia* [Campanulaceae], *Haplostachys/Phyllostegia/Stenogyne* [Lamiaceae], *Argyroxiphium/Dubautia/Wilkesia* [Asteraceae]) (Sakai et al. 1995). According to Sakai et al. (1995), the angiosperm flora of Hawaii developed from 265 colonization events, not including introductions or doubtfully native taxa. The number of species per colonist in the Hawaiian Islands varies from one to 91. The number of colonizing lineages per family varies from one to 37. Here we ask whether the propensity of a colonizing lineage to diversify is correlated with the global species richness or variation in character states of the family to which it belongs. The logarithm of the number of species per Hawaiian lineage was unrelated to the logarithm of the global species richness of its family ($F_{1,263} = 1.29$, $P = 0.26$). It was also unrelated to familial character states associated with the following traits: distribution (tropical, temperate, cosmopolitan, temperate-high altitude tropical), pollination (abiotic, biotic, both), dispersal (abiotic, biotic, both), and growth form (herbaceous, woody, both), whether global species richness was included as a covariate ($F_{10,254} = 1.90$, $P = 0.045$) or not ($F_{9,253} = 1.86$, $P = 0.045$). The only significant relationship in the analysis ($F_{2,262} = 5.55$, $P = 0.0043$, $R^2 = 0.041$) was a tendency for lineages from families with biotic pollination to have produced more species on Hawaii than those from families with abiotic pollination ($1.5 \times$), which is consistent with a comparison of diversity in such families overall ($1.97 \times$, Table 1). On the whole, this analysis suggests that propensity for adaptive radiation of lineages within the Hawaiian Islands is generally unrelated to the relative success of a family globally or to character traits possessed by the larger monophyletic group to which colonists belong. In particular, the occurrence of two or more states of a character within a family is not as-

sociated with species proliferation within the Hawaiian archipelago.

DETERMINANTS OF THE SPECIES RICHNESS OF FAMILIES

What of the main effects identified in the analyses of Ricklefs and Renner (1994) and Dodd et al. (1999)? The clearest results are that biotic pollination and herbaceous growth form are associated with higher diversity. However, the effects, amounting to a factor of approximately two, are small compared to the range in familial diversity, which extends over four orders of magnitude. It is safe to say that if one is interested in variation in familial diversity, one must consider other factors than pollination, dispersal, and growth form.

A clear advantage of phylogenetic analysis is its ability to identify gains and losses of characters over evolutionary time. Dodd et al. (1999; table 3) found that most transitions in pollination involve loss of biotic pollination. With respect to dispersal, gains and losses of animal seed transport are evenly balanced, and in growth form they mostly represent losses of arborescent growth. Comparison of the common descendant character state with the species richness of lineages suggests that not all transitions stimulate diversification. That is, morphological/ecological transitions do not necessarily result in the greater success of a lineage measured as species proliferation. Such transitions may often enable a lineage to occupy an unexploited, but restrictive ecological niche. For instance, whereas herbaceous growth form is associated with higher diversity, abiotic pollination in the angiosperms is associated with lower diversity. Furthermore, the direction of evolutionary transitions also does not predict the frequency of character states over families as a whole. For example, in spite of the predominance of losses of biotic pollination, only 57 of 365 families in Ricklefs and Renner's (1994) summary are exclusively abiotically pollinated. This reinforces the idea that loss of biotic pollination arises only infrequently in special ecological circumstances and may be a dead end in terms of diversity (many of these 57 families are temperate). The predominance of gains of herbaceous growth forms over losses also is not associated with an especially high proportion of families (122 exclusively herbaceous families). As in the case of abiotic pollination, herbaceous life forms may be associated with more recently appearing (and often temperate) dry habitats that are difficult to escape evolutionarily. This suggests that herbaceous growth form often arises under special circumstances that also favor high diversity. Further analyses of these data with respect to aspects of ecology, including geographic distribution, would be useful.

COVARIANCE IN FAMILIAL SPECIES RICHNESS AMONG SISTER-TAXON PAIRS

The key question raised by Dodd et al. (1999) is, "Do evolutionary lineages possess traits that promote diversification?" Dodd et al. attempted to answer this question by comparing diversity in sister families with contrasting states of particular character traits (table 1). We can go beyond their analysis by asking whether sister-family pairs share high or low rates of diversification regardless of traits they possess. We presume that many traits potentially could affect rate of diversification. If any of these traits are shared between sister

lineages then species richness should exhibit a significant covariance among lineages. We compiled 62 sister-family pairs from the list in Barraclough et al. (1996), which we updated, and from the list in Dodd et al. (1999). Number of species in each family was obtained from Mabberley (1987). We could find no significant association of log-transformed species richness within sister-family pairs when the data were analyzed by one-way analysis of variance ($F_{1,122} = 1.38$, $P = 0.11$) or by a nonparametric Kruskal-Wallis test ($\chi^2 = 73.2$, $df = 60$, $P = 0.12$). Either many of these sister-family pairs have different contrasting characters that affect diversity in different ways, or the number of species in a phylogenetic lineage is essentially haphazard. In the latter case, species richness may be affected by so many different factors in addition to intrinsic character states that one has little hope of identifying key innovations or key environmental conditions in a comparative analysis.

What of the hypothesis that evolutionary flexibility promotes diversification? The analyses of Dodd et al. (1999) and additional analyses described here provide little support for the idea and moreover indicate that the result of Ricklefs and Renner (1994), showing that family species richness is associated with multiple character state traits, is likely an artifact of sampling. Dodd et al.'s sister-taxon test of the hypothesis that evolutionary flexibility is a family level trait also was negative. However, considerable variation evidently exists in rate of character state change among lineages, although the implications of this variation for diversification are unknown.

Studies of phylogenetic tree balance indicate great variation among lineages in rates of speciation (Heard 1996), although it is unclear which attributes of lineages, if any, are responsible for this variation (Barraclough et al. 1998). Evolutionary flexibility is especially difficult to recognize as a lineage-specific trait (Heard and Hauser 1995, Mooers and Heard 1997). Flexibility itself can be measured unequivocally only by estimating the rate of character state transition per branch or unit of branch length in detailed phylogenetic studies of individual monophyletic groups. Barraclough et al. (1996) characterized families of flowering plants by the rate of nucleotide substitution in the chloroplast *rbcL* gene and found this rate to be weakly correlated with species richness in sister-family comparisons. It remains to be seen whether similar measures of evolutionary flexibility for phenotypic traits are associated with enhanced proliferation.

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