PHYLOGENETIC SIGNAL IN POLLINATION NETWORKS VARIES IN STRENGTH WITH POLLINATOR TYPE AND COMMUNITY PLANT SPECIES RICHNESS

by

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ABSTRACT

Phylogenetic constraints have been hypothesized to influence the complex network structure found in plant-pollinator communities. Here, I develop and test a conceptual model of factors that might modulate any signal of phylogenetic clustering of plants visited by individual pollinator species. Across 29 communities, pollinators visited weakly phylogenetically clustered plant species. Plant relatedness was positively correlated with community plant richness; and plants visited by versatile pollinators were phylogenetically random in small communities but became clustered as richness increased. However, these patterns were not explained by a simple dichotomous scoring of plants as restrictive or unrestrictive to unversatile pollinators. Collectively, these results suggest that constraints imposed by plant phylogeny on pollination networks are moderated by current ecological processes such as community assembly and pollinator foraging behaviour, but mechanisms are unclear. Future research should consider the opportunity for bidirectional interplay between ecological and phylogenetic effects.

Keywords: plant-pollinator network; phylogenetic relatedness; phylogenetic signal; community structure; species richness; floral traits.

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1: INTRODUCTION

1.1 Overview: community ecology of pollination

The mutualistic interactions between plants and their animal pollinators are critical to the maintenance of terrestrial ecosystems. At the scale of an ecological community, the pairwise interactions between individual pollinator species and the plant species that they visit collectively form complex networks, which can be visualized and analysed in a similar manner to food webs (Memmott 1999; see Figure 1a). Learning the structural properties of these networks can shed light on how communities function and help us to predict how communities will respond to ecological perturbation or species loss (see e.g., Memmott & Waser 2002, Memmott *et al.* 2004, Jordano *et al.* 2006).

Research performed over the past two decades has yielded substantial insight into the structural properties that are common to most pollination networks. These universal properties include nestedness (e.g., Vázquez & Aizen 2006; see Figure 1b), asymmetric specialization (Vázquez & Aizen 2004, Jordano *et al.* 2006; Figure 1c), compartmentalization (Dicks *et al.* 2002, Prado & Lewinsohn 2004, Olesen *et al.* 2007; Figure 1d), weak connectance (Jordano 1987; Figure 1e), and right-skewed distribution of degree (Vázquez 2005; Figure 1f).

More recently, research has shifted from describing the structural properties of pollination networks to evaluating the mechanisms from which they may arise: through sampling artefacts (see e.g., Ollerton & Crammer 2002, Devoto *et al.* 2005, Vázquez & Aizen 2006, Blüthgen *et al.* 2008); neutral processes (i.e., patterns driven by relative species abundances; e.g., see Ollerton *et al.* 2003, Stang *et al.* 2006, Vázquez *et al.* 2007); and trait-based processes described by complementarity models (i.e., complementarity between the traits of a flower and the trait preferences of a pollinator, such as bees' preference for blue flowers; see e.g., Santamaría & Rodríguez-Gironés 2007, Krishna *et al.* 2008), barrier models (i.e., the traits of some flowers, such as nectar tubes, restricting access to nectar or pollen rewards to only certain pollinators; e.g., see Stang *et al.* 2006 & 2009), and phylogenetic constraints (phylogenetically conserved traits constrain which species interact; see e.g., Rezende *et al.* 2007a, Vázquez *et al.* 2009a).

1.2 Phylogenetic constraints in pollination networks

Because phylogenetic relatedness is assumed to often be correlated with phenotypic similarity (i.e., closely-related species are more similar in their traits than distantly-related species, see Prinzing *et al.* 2001), phylogenetic signal can be used as a proxy to study the contribution of trait-based mechanisms towards community structure. This can be a useful approach because it allows for the evaluation of macroecological hypotheses that would normally be difficult or intractable to test (discussed in Rezende *et al.* 2007b and Vázquez *et al.* 2009b): pollination-related traits are often unknown, hard to measure, many in number, may be correlated with each other, and the importance of any single trait likely varies with local ecological conditions. Furthermore, several authors have shown how network properties such as nestedness (Rezende *et al.* 2007b) and compartmentalization (Lewinsohn *et al.* 2006, Olesen *et al.* 2007) might be explained by phylogenetic constraints, which suggests that evolutionary processes may be important mechanisms in generating pollination network structure. Pollination networks are subject to potential constraints from the phylogenetic relationships of both plants and pollinators. However, in this thesis I will focus specifically on constraints arising from plant phylogenies.

Two studies have previously looked for a phylogenetic signal in pollination networks. Rezende *et al.* (2007a) found that phylogenetic relatedness correlated with similarity in the identity of interaction partners in approximately half of the 36 pollination networks they tested, although this relationship was much less common for plants than for animals (significant association in 25.0% and 60.8% of datasets, respectively). Rezende *et al.* (2007a) suggest that this difference between animals and plants could arise from differences in their evolvability or mobility, and note that variation between communities in the strength of phylogenetic signal is due in part to the taxonomic diversity of plant lineages, but not to that of pollinators. Vázquez *et al.* (2009a) found that phylogenetic relatedness of plants contributed very weakly to network structure in the single community that they examined, and that relatedness of pollinators did not contribute at all. In a recent review paper, Vázquez *et al.* (2009b) concluded from these two studies that "although the phylogenetic signal was detectable in some cases, the influence of phylogeny on network attributes such as degree or species strength was rather low, suggesting that the influence of phylogenetic effects on network structure is weak compared with current ecological processes" (Vázquez *et al.* 2009b).

1.3 Effect of point-of-view on detection of phylogenetic constraints

Are these results sufficient to abandon the idea of a substantial influence of plant phylogeny on pollination network structure? Vázquez *et al.* (2009a) examined a single community, so one cannot generalize from their result. Rezende *et al.* (2007a) tested for phylogenetic constraints across a large number of communities. Their methodology approached the question of whether the phylogenetic relatedness of plants influences network structure from the point-of-view of the plants (i.e., do closely related plants tend to share pollinators more often than do distantly related plants), using a Mantel test to detect significant community-wide correlation between the pairwise phylogenetic distances and pairwise ecological distances between plants (where ecological distance is the difference between the memberships of the pollinator assemblages that visited those plants, calculated as 1-*S* where *S* is the Jaccard index of similarity). However, a completely different result is possible if the question is asked from the pollinators' point-of-view; that is, do the sets of plants visited by individual pollinator species in a community usually consist of closely related species? These two points-of-view correspond to independent proximate questions, although both address the ultimate question of whether pollination network structure is constrained by phylogenetic relationships among plants. As illustrated in Figure 2, a pollination network may appear to be subject to phylogenetic constraints when assessed from one point-of-view but not from the other, because, for instance, phylogenetic signal in floral traits need not be uniformly present across the entire network. Because networks are typically nested (Vázquez & Aizen 2006) and have a rapidly decaying degree distribution (Vázquez 2005), a small minority of the plants are responsible for hosting visits from most of the pollinators, and a small number of pollinators are responsible for the visits received by most plants. From the pollinator point-of-view, highly connected plants (those that interact with a large number of pollinator species) will make a stronger contribution to the overall community-level result than will the majority of plants, those that interact with only a few pollinators each. Conversely, from the point-of-view of the plants, the community-level result will be driven by the majority of plants – those that host visits from few pollinators – and most of these visits will be made by the same few high-degree pollinators in the community. Because the two points-of-view weight plants differently depending on their degree, any correlation between the degree of a plant and the amount of phenotypic resemblance it bears to its close relatives would cause the two points-of-view to yield different results. Such a correlation is ecologically plausible because a plant's local abundance may be correlated with its degree (Stang *et al.* 2006) and also with its competitive ability. The theory of limiting similarity predicts that competitive interactions prevent the co-occurrence of species that are too similar (Abrams 1983), which in turn suggests that those closely related plant species of high degree that co-occur in a community are less likely to share traits (including pollination traits) than lower degree plants

(Webb 2000, Kraft *et al.* 2007; Figure 2b). Simultaneously, among low-abundance (and low-degree) plant species in a community, pollination facilitation may favour the persistence of those that co-occur with phenotypically similar close relatives via increased pollinator visits and resultant mitigation of Allee effects (Schemske 1981, Moeller 2004; Figure 2b). Facilitation can also operate between high density plant species that share pollinators but differ in phenology, by ensuring that pollinators are continuously provided with resources (Waser & Real 1979). This latter type of facilitation might favour high visitation to phenotypically similar closely related plants and would create the opposite expectation, that closely related plants of high degree that co-occur are *more* likely to share traits and pollinators (Figure 2a). Because research on the relative importance of competition and different types of facilitation between plants is currently inconclusive, my intent in the above discussion is not to predict which pattern is more likely, but instead to emphasize that it is plausible that a plant's degree may be correlated (positively or negatively) with the strength of phenotypic similarity it bears to its close relatives within a community. Hence, the failure to detect a strong effect of plant phylogeny on pollination network structure from the plants' point-of-view does not preclude such an effect from being present from the pollinators' point-of-view.

In this thesis, I test whether constraints of plant phylogeny are generally present in pollination networks when evaluated from the pollinators' point of view: that is, whether the assemblages of plants visited by individual pollinator species tend to comprise closely-related species. Additionally, I test whether the answer to this question depends upon the between- and within-community ecological factors of plant species richness and pollinator versatility, as discussed below.

1.4 Between community variation in phylogenetic constraints

Phylogenetic constraints in some community-scale ecological phenomena, such as plant community assembly and invasive species establishment, are known to vary with ecological context, including successional stage (Verdú *et al.* 2009), and spatial and taxonomic scales of assessment (Cadotte *et al.* 2009, Swenson *et al.* 2006, Kress *et al.* 2009). These relationships have been interpreted as being driven by changes in the strength of competition or facilitation across different spatial scales, successional stages, and degrees of phylogenetic relatedness via the mechanisms of limiting similarity and environmental filtering acting on traits that carry a phylogenetic signal (e.g., Swenson *et al.* 2006). Limiting similarity, which should inhibit the co-occurrence of close relatives through competitive exclusion, operates most strongly at small spatial scales, in successional stages with high competition, and at fine-scale taxonomic relatedness (Slingsby & Verboom 2006, Swenson *et al.* 2006, Verdú *et al.* 2009). Environmental filtering, which should promote the co-occurrence of close relatives, operates most strongly at larger spatial scales, in successional stages with lower competition, and at coarser taxonomic scales (Swenson *et al.* 2006, Verdú *et al.* 2009).

The finding that the strength and direction of phylogenetic effects on community assembly vary with ecological context motivated me to consider whether phylogenetic effects on pollination networks might also be context-dependent. Some of the structural properties of pollination networks vary with community-level ecological factors, most notably species richness. For example, compartmentalization was present in all communities with over 150 plants species but none with less than 50 species among those tested by Olesen *et al.* (2007); and connectance, strength of nestedness, and truncation of degree distribution vary with community species richness (reviewed in Vázquez *et al.* 2009b). Both neutral and mechanistic trait-driven ecological processes have been invoked to explain the relationship between network structure and richness, but the possibility of a relationship between species richness and phylogenetic patterns in pollination networks has not yet been explored.

Plant community assembly processes determine the relatedness of the plants present in a community, and hence the relatedness of the plants available to pollinators. As I will discuss in more detail in Section 1.6, the result of assembly processes may determine whether the plants present in a community are sufficiently closely related to retain a phylogenetic signal for pollination traits.

Ecological context could also affect the strength of phylogenetic structure in pollination networks through mechanisms such as the foraging behaviour of pollinators. Pollinator responses to floral traits are not absolute, but are instead modulated by local abiotic and biotic conditions (e.g., see Possigham 1992, Rodríguez-Gironés & Santamaría 2006, Fontaine *et al.* 2008, Sargent & Ackerly 2008). For example, where plant assemblages are species-poor, pollinators may be less specialized on particular plants. This could be due to the form of the assemblages, or to changing interactions within them. The lower floral diversity of species-poor plant communities may make more pollinators unable to establish there due to a lack plants that they can access (see discussion in Sargent & Ackerly 2008); this effect may be stronger for pollinators who are less versatile in their foraging behaviour (e.g., pollinators who are unable to access plants with selective barriers such as the nectar contained at the base of a tubular flower). In addition, communities with few plant species usually also have few pollinator species, which might result in relaxed competition between pollinators for plants. Optimal foraging theory predicts that when competition is less acute, niche breadth of individual pollinator species should increase, encompassing a broader trait-space, but when competition is high pollinators should restrict their foraging to a narrower range of flower morphologies (Possingham 1992, Rodríguez-Gironés & Santamaría 2006); there is some experimental evidence to support this (e.g., Inouye 1978). If habitats poor in plant species are more likely to favour greater generalization by pollinators, then in these habitats neutral processes may increase in importance relative to trait-based processes. Consequently, phenotypic similarly between closely related plants might impose weaker effects on pollination networks in species-poor communities.

In section 1.6, I will expand on these ideas to develop specific predictions about the effects of community assembly and pollinator behaviour on phylogenetic constraints on pollination networks.

1.5 Within-community variation in phylogenetic constraints

As discussed in Section 1.3, phylogenetic signal in pollination networks may be concentrated around some pollinators or plants more than others. Within communities, plant species are differently subject to competition and facilitation, which theoretically affects the likelihood of phenotypic resemblance between closely related plant species (Kraft *et al.* 2007). Additionally, as discussed in section 1.4, pollinators within a community vary in the extent to which their interactions are influenced or limited by floral trait complementarity or floral barriers. Pollinators that are relatively unconstrained by barriers (e.g., long-tongued pollinators that can access nectar tubes but may also visit "open" flowers) or complementarity of traits (e.g., pollinators with the behavioural flexibility to adjust their preferences to include plants with lower complementarity depending on local conditions) have a larger fundamental niche with respect to the phenotype of the flowers that they can access ("versatile pollinators" hereafter). The realized niche of versatile pollinators may vary from fewer to more species depending on ecological conditions, but overall, should be less strongly constrained by floral traits than the niche of less versatile pollinators (e.g., those with short tongues or less behavioural flexibility, termed “unversatile pollinators” hereafter). Because the existence of phylogenetic correlation of floral traits in the local plant assemblage must underlie the finding of phylogenetic constraints in pollination networks, unversatile pollinators, if more strongly constrained by traits, are more likely to display phylogenetic signal in the plants that they visit. The question of whether phylogenetic constraints vary in strength *within* pollination networks, such that certain types of pollinators or plants are more subject to constraints on their interactions than others, has not, to my knowledge, been previously explored. I develop specific predictions about the relationship between pollinator versatility and phylogenetic clustering amongst their visited plants in section 1.6, and discuss how this relationship may change between communities with different plant species richnesses, as I have alluded to above in section 1.4.

1.6 Conceptual model

In this section I expand on expected neutral, historical, and trait-based processes that determine phylogenetic constraints in pollination network structure to develop specific hypotheses about relationships between plant species richness, pollinator versatility, and phylogenetic effects on pollination networks.

The basic condition that must be met in order that the plant species visited by a given pollinator are phylogenetically clustered is that the community's plant phylogeny must possess an evolutionary signal for those traits that substantially influence whether that pollinator will visit the plant. In order for this to be the case, a number of sub-conditions must collectively be met. Whether these conditions are met is potentially subject to the outcome of both neutral and deterministic processes.

First, there must be a phylogenetic signal present for relevant phenotypic traits over the evolutionary history of angiosperms (Figure 3a). Traits may differ between sister species under a number of evolutionary processes (Revell *et al.* 2008), so although floral traits may determine the identity of visiting pollinators, these traits need not be phylogenetically correlated. Notably, character displacement in sympatry can simultaneously favour divergent evolution between close relatives and convergent evolution between distantly related species (see Sargent & Ackerly 2008 and references therein). Nonetheless, at least some floral traits, such as basic floral symmetry, are obviously correlated with phylogeny to some extent (Judd *et al.* 2007), so this condition can be assumed to be met.

Second, the plant species that are present in the community must be sufficiently closely related that the "global" phylogenetic signal of floral traits is retained among the plants locally present (Figure 3b). In order that a pollinator may visit phylogenetically clustered plants, closely related plants that resemble each other must physically co-occur with each other. If community assembly is a neutral process (i.e., the probability of a plant species being present in a community is solely a function of random recruitment from the global species pool without any effect of traits or historical processes), then a phylogeny of the plant species present in the community will be, in essence, a randomly "pruned" version of the global angiosperm phylogeny. When more species are randomly pruned from a phylogeny (i.e., in communities with lower species richness), mean phylogeny node depth increases and the average relatedness of species decreases (Figure 3b, lower two phylogenies). Therefore, under random assembly, the fewer plant species there are in the community, the more distantly related these species will tend to be, the weaker will be the phylogenetic signal for floral traits within the community cladogram, and the less likely it will be that pollinators will visit phylogenetically clustered plants.

However, as introduced on page 5 in the context of plant versus pollinator "point-of-view", community assembly may not be neutral. Historical biogeography, ecological filtering, and interspecific interactions (e.g., competition and facilitation) also affect community phylogenetic structure during community assembly. Biogeographic processes operating over evolutionary timescales should create phylogenetic correlation between species ranges. Species' current ranges result from descendent species dispersing from a common ancestor's historical geographic range and diverging from the common ancestor's climatic niche, both of which are time-dependent processes (Wiens & Donoghue 2004). Thus, regional species pools should comprise species that are more closely related than a random sample from the phylogeny of all angiosperms. Ecological filtering will tend to create additional phylogenetic clustering in community membership: local abiotic and biotic conditions favour some traits over others, and phylogenetic correlation of these traits will produce local assemblages whose members are more closely related than a random sample from the regional species pool (Swenson *et al.* 2006). As discussed on page 6, facilitation between phenotypically similar plant species can also increase phylogenetic clustering. On the other hand, limiting similarity and competitive exclusion of close relatives during community assembly will operate in the opposite direction, and limit the co-occurrence of close relatives. In sum, the phylogenetic distance between species in a community will reflect the local net balance between neutral "pruning" and competitive exclusion of similar species on the one hand, and phylogenetic correlation of species ranges, interspecific facilitation, and ecological filtering on the other.

The factors discussed above will influence the average amount of phylogenetic signal in floral traits that exists in the overall community and should tend to affect all pollinators in the same qualitative ways. However, other factors are superimposed on this plant template that will operate at the scale of individual pollinators instead of the whole community and will create within-community variation in the strength of phylogenetic effects on plant-pollinator interactions. As discussed above in Sections 1.4 and 1.5, I expect that pollinators that are more versatile with respect to the floral traits of the plant species that they visit will be less strongly influenced by particular floral traits than unversatile pollinators. In order that a floral trait that retains phylogenetic signal within the community phylogeny significantly affect the probability of visitation by a particular pollinator, <u>the pollinator species must be strongly enough affected by that plant trait (Figure 3c).</u> The more strongly that traits with phylogenetic signal act on a pollinator, the more likely it is that the plants visited by that pollinator will be phylogenetically clustered. The degree to which a pollinator is influenced by floral traits, manifest as its realized niche, is a function of its fundamental niche combined with ecological factors that determine its realized niche in the particular ecological context. All else being equal, I expect that versatile pollinators are less influenced by traits *in general* because they have a broader fundamental niche; and also that their realized niche may be more strongly subject to ecological context, such as the effects of plant species richness. I predict that as less floral variety is available, such as in communities with lower plant species richness, floral traits will tend to become less important, especially for versatile pollinators.

In sum, this model predicts that phylogenetic constraints on community structure are modulated such that:

- Phylogenetic constraints will be stronger in communities with higher plant species richness, stronger ecological filtering, and facilitation between similar species; and weaker where competition between similar plants (i.e., limiting similarity) is stronger (because these factors affect expected node depth and phylogenetic signal of floral traits).
- Phylogenetic constraints will be stronger for less versatile pollinators.
- Ecological context and pollinator versatility will interact so that versatile pollinators will show stronger phylogenetic clustering in the composition of their visitation partners in communities that favour a narrower realized niche (e.g., species-rich communities), whereas unversatile pollinators will be less affected.

Some elements of my conceptual model are beyond the scope of this thesis to test, but may be tested at a later date. This model gives rise to the following specific predictions that I test below using 29 previously published plant-pollinator networks:

1. ***Overall, the plants visited by pollinator species tend to be phylogenetically clustered relative to the plants available in the community.*** This question complements previous studies that have tested for an influence of plant phylogeny on pollination network structure (Rezende *et al.* 2007a, Vázquez *et al.*, 2009a), but asks the question from the pollinators' point-of-view. This prediction does not follow directly from my conceptual model, but is preliminary to the subsequent questions.
2. ***The average relatedness of the plants present in a community (inverse of mean phylogeny node depth) is proportional to community plant species richness.*** Relatedness is a function of the number of species that remain after "pruning" of the phylogeny of all angiosperms during regional sampling and community assembly, but it is still possible that this relationship is obscured by the effects of range correlations, ecological filtering, and facilitation between similar species (Figure 3b). I test whether species richness is negatively correlated with node depth in order to determine whether phylogenetic signal in community phylogenies, and hence phylogenetic constraints on pollination network structure should likewise be expected to vary with richness.
3. ***The strength of phylogenetic signal of floral traits is proportional to community plant species richness***. The relatedness of plants in a community (i.e., the inverse of mean

node depth) may increase with species richness, but in order for this to translate into an effect on network structure, it must act through the mechanism of increased floral trait signal. To test whether this may occur, I test for phylogenetic signal of floral restrictiveness, coded as a binary character (restrictive vs. unrestrictive, defined on page 25). In reality, a large number of traits collectively influence visitation by pollinators. I chose this single trait for demonstration purposes because its value could be relatively easily assigned to all species across a large number of communities, which allows me to test whether richness can impact floral trait signal in the manner I predict.

4. ***The plants visited by unversatile pollinators are more strongly phylogenetically clustered than those visited by versatile pollinators, and the difference between these pollinator types increases as plant species richness decreases.*** I predict that versatile pollinators will be more weakly constrained by floral traits (Figure 3c), and that this effect will be enhanced by ecological conditions that favour a larger realized pollination niche. To test this prediction, I coded pollinators as versatile or unversatile according to a simple classification scheme described below, assessed whether the two types differ in the phylogenetic clustering of their visited plants, and whether the difference decreases with increasing plant species richness. I chose to assess the effect of species

richness because it is an ecological factor that was known for all the datasets to which I had access and is expected to affect pollinator niche breadth (in species-poor community with more limited choice optimal foraging may favour exploitation of a broader set of resources).

5. ***Versatile pollinators visit a higher proportion of restrictive flowers than unversatile pollinators and this difference increases with community species richness.*** The relationship described in prediction four invokes variation in niche breadth between pollinator types and with species richness. To supplement the results of question four, I directly test for changes in floral visitation niche (proportion of restrictive flowers visited) between pollinator types (versatile vs. unversatile) in communities of different species richness.

Support for my predictions would strengthen the assertion that shared evolutionary history of plants can commonly influence pollination network structure, and would endorse my conceptual model of factors that affect phylogenetic constraints in pollination networks at the scale of communities and individual pollinator species.

2: METHODS

2.1 Datasets

I conducted a literature search to find community plant-pollinator interaction datasets. Datasets were used if they attempted to record all pollinator taxa visiting at least the dominant plants present in a defined community at the morphospecies or species level, resulting in 29 usable datasets (see Table 1).

An initial search for datasets was performed in Web of Science (http://isiwebofknowledge.com/products_tools/multidisciplinary/webofscience/) using the search terms ((pollinat* OR ((plant* OR flower* OR floral) AND (insect* OR visitor* or animal*)) AND (network* OR web* OR interact* OR communit*)), and by consulting the NCEAS Interaction Web Database (www.nceas.ucsb.edu/interactionweb/), a repository of interaction matrices hosted by National Center for Ecological Analysis and Synthesis, at the University of California, Santa Barbara, U.S.A. A further search was made of the references within the initial papers found.

Frequency data were discarded if present, so that all data matrices comprised binary interaction data. Plant names were verified and updated where nomenclature changes have occurred, so that assignation of species to genera would reflect recent changes, following International Legume Database & Information Service (2009), the Integrated Taxonomic Information System (ITIS) (http://www.itis.gov), the Flora of China and the Flora of Nepal in eFloras (2008), and Tropicos.org (www.tropicos.org). Plants that were present in the community but not visited by any pollinators were removed from the few datasets where these were listed. Some datasets contained some pollinator groups that were not identified to species level, but pooled together as a single "visiting species" (e.g., Acari); these were also removed prior to using the datasets.

2.2 Phylogenies

I used the Phylomatic tool (Webb & Donoghue 2005) in the software package Phylocom (Webb *et al.* 2008a) to construct cladograms of the plants present in each community. Phylomatic constructs a cladogram for a list of plant species input by the user by grafting these species onto a backbone tree, and then removing all higher taxa from the tree that are not represented on the list; for the tree backbone I used the Angiosperm Phylogeny Group (APG) supertree R20090303.new (Stevens 2001 and onward), further resolved using other published sources.

The default APG supertree used by Phylomatic is resolved only to the family level across most of the tree. I used other sources to resolve taxa within those families that were represented among my datasets by at least five genera, provided that these genera spanned more than one taxon below the level of family (e.g., belonged to more than one subfamily) and that phylogenetic relationships within the family had at least 80% support as defined by the source. Following these criteria, the following families were considered for higher resolution using sources other than the APG tree:

- *Fabaceae*: The APG tree was resolved to the level of genus for many genera; genera occurring in datasets but not included in APG tree were assigned to the lowest possible taxon in the backbone tree between the family and generic level using LegumeWeb (International Legume Database & Information Service 2009) and The Pea Key (Australian Pea-Flowered Legume Research Group 2009).
- *Rosaceae, Malvaceae, Ericaceae, Papaveraceae, Ranunculaceae* and *Orchidaceae*: Phylogenetic relationships within the family Rosaceae were taken from the APG website (Stevens 2001 and onwards; accessed June 10-11, 2009) and species were assigned to taxa according to the Germplasm Research Information Network (GRIN) website (USDA 2009, accessed June 10-11, 2009).
- *Lamiaceae* and *Scrophulariacaeae*: Phylogenetic relations within these families are currently too poorly resolved to allow resolution of the tree below the family level (Stevens 2001 and onwards).
- *Asteraceae*: Phylogenetic relationships to the level of tribe were taken from Funk *et al.* 2005. Species in my datasets were assigned to tribes using the NCBI taxonomy browser (National Center for Biotechnology Information, U.S. National Library of Medicine 2009; retrieved June 11, 2009).
- *Polygonaceae* and *Myrtaceae*: according to the GRIN website (USDA 2009, accessed June 11, 2009), all genera within these families that occurred within my datasets were within a single subfamily and no resolution was available below the level of subfamily from the APG website (Stevens 2001 and onwards).

All remaining taxa were left as polytomies. I created an initial master phylogeny of all plant species present across all datasets combined (Appendix A) based on this modified APG supertree.

I then used BLADJ package of Phylocom (Webb *et al.* 2008a) to assign branch lengths on the master phylogeny based on the angiosperm supertree dated by Wikström *et al.* (2001), which used nonparametric rate smoothing to assign ages to most nodes on the tree above the level of family. The BLADJ package adjusts the remaining undated nodes at equal intervals between the dated nodes (Webb *et al.* 2008b). Finally, I created individual community phylogenies (Appendix B) by "pruning" the dated master phylogeny of all species not present in each dataset.

2.3 Null model test of phylogenetic clustering of visited plants

In order to determine the degree to which the plants visited by each pollinator were more or less closely related than expected by chance, I used a null model that assumes random visitation with respect to species identity, but maintains the other aspects of community structure, i.e., the total number of visits made by each pollinator species and the total number of visits received by each plant species in the original dataset (Gotelli 2000). Randomization was performed using the Independent Swap method (Gotelli & Entsminger 2003), using 100000 swaps per run and 1000 runs per community.

All pollinators were included in the null model randomizations, but some pollinators were excluded from subsequent analyses. Pollinators who visited a single plant species were excluded, while pollinators who visited at least two plant species were retained. This is the minimum number of plant taxa for which phylogenetic dispersion is relevant and can be calculated. Some previous studies of pollinator specialization (e.g., see Vázquez & Aizen 2004) have chosen to exclude pollinators which visit fewer than five plant taxa under the rationale that a smaller number of taxa provides an insufficient sample from which to infer a measure for the pollinator; however, this exclusion also means that a large proportion of pollinators, biased towards those that are locally rare and/or specialized, are excluded from consideration. I have included all pollinators that visited two or more taxa in the present study to avoid this bias, and with the hope that although more noise is introduced into the statistical analysis, the large number of pollinators that visit few species or are rarely observed will allow more power to detect an overall difference in their mean dispersion.

2.4 Metric of phylogenetic clustering of visited plants

I used the comstruct function in the software package Phylocom (Webb *et al.* 2008a), which assesses whether the species present in a sample are phylogenetically random with respect to species available in a set; here, the plant species visited by a pollinator comprise a sample of the set of all plant species in the community.

The Net-Relatedness Index (NRI) that Phylocom computes for each sample can be biased, because it assumes a normal distribution of mean phylogenetic distances (MPD) between members of the sample under the null model. However, this distribution is expected to be right-skewed, which biases NRI towards underdispersion. MPD distributions derived from repeated randomizations of the community should tend to be right-skewed for two reasons: first, the distribution is bounded at zero (i.e., there is no such thing as a negative phylogenetic distance); and secondly, any amount of tree imbalance will tend to increase the relative proportion of smaller phylogenetic distances. Therefore, the median MPD from a series of randomizations (representing the midpoint of the probability distribution) will tend be to the right of the mean, so that NRI is biased towards finding phylogenetic clustering. The use of standard deviation in calculating NRI produces further problems with the interpretation of this index.

To address these problem I used a nonparametric metric calculated from the phylocom output, Rank-based Net-Relatedness Index (RNRI), which eliminates this problem of bias because it is based on the actual distribution of MPDrnd values.

The original NRI is calculated as (MPDobs-MPDrnd)/SD(MPDrnd), where MPDobs is the mean pairwise phylogenetic distance between all species present in the observed sample from the dataset, MPDrnd is the mean of the MPD values calculated for corresponding samples generated under the null-model randomizations of the dataset, and SD(MPDrnd) is the standard deviation of these randomly generated MPD values (Webb *et al.* 2008b). The calculation of RNRI that I prefer is the proportion of the randomly generated MPD values that lie between the observed value and the median of the randomly generated MPD values, multiplied by two, and with sign assigned such that RNRI is positive when MPDobs < median(MPDrnd) and negative when MPDobs > median(MPDrnd). RNRI ranges from -1 (maximally phylogenetically overdispersed) to +1 (maximally phylogenetically clustered), with 0 corresponding to no phylogenetic signal. In order to calculate RNRI, I used the rank information output by Phylocom (MPD.rankLow and MPD.rankHi). RNRI is equal to ((MPD.rankLow/runs) – (MPD.rankHi/runs)), where MPD.rankLow is the number of runs where MPDobs is lower than or equal to the MPD from the randomization run; and MPD.rankHi is the number of runs where MPDobs is higher than or equal to the MPD from the randomization run.

2.5 Classification of floral morphology and pollinator type

As an extension of Faegri & van der Pijl's (1979, Chapters 10 and 11) description of floral morphologies and floral syndromes, I categorized plants dichotomously as "restrictive" or "unrestrictive" based on whether they possessed a morphological barrier that prevents some pollinators from accessing their floral rewards. Flowers that are gullet-shaped, flag-shaped, urn-shaped, tubular, or spurred and other flowers with obvious restrictions on accessing rewards were classified as restrictive. Flowers with readily accessible rewards not requiring specialized morphology to access, generally encompassing dish-, bowl-, bell- and funnel-shaped flowers, were classified as unrestrictive. Where flowers had combined morphologies, I used the morphological feature that corresponded to reward access (e.g., a flower that is funnel-shaped overall, but with nectar located within a tubular base would be classified as restrictive). I used many different sources for classification, including descriptions and illustrations in floras, and photographs.

Pollinators were classified as "versatile" or "unversatile" based on the general tendency within the group to have the ability to access restricted floral rewards. Bees, moths and butterflies were classified as versatile, whereas wasps, flies, beetles, bugs, and miscellaneous other pollinators (e.g. neuropterans) were classified as unversatile.

This classification of flower and pollinator types follows Faegri & van der Pijl's (1979, Chapters 10 and 11) paradigm of "mess and soil" vs. highly adapted pollinators, and their assignment of flower morphologies to these pollinator groups. Although this classification scheme is extremely simplistic, previous studies have been able to detect significant evolutionary and ecological patterns related to pollination using a simple classification of flowers as possessing radial vs. bilateral symmetry (e.g., Sargent 2004, Gong & Huang 2009).

2.6 Mean node depth of community phylogenies

I calculated mean node depth for all community phylogenies as the mean of the log-transformed ages of all nodes present in the phylogeny. Where polytomies were present in the phylogeny, the node was counted towards the whole-tree average multiple times (i.e., x-1 times where x is the number of dependent branches). This procedure produces a bias towards a greater mean node depth, but this bias should not increase Type I error (see Discussion).

2.7 Phylogenetic signal

To determine whether phylogenetic signal in floral restrictiveness is a plausible basis for phylogenetic clustering to plants visited by pollinators, I evaluated whether phylogenetic signal is generally present in this trait. Although floral restrictiveness will clearly show some degree of phylogenetic signal overall, I could not assume that signal would be retained in the "pruned" phylogenies that contain only those plants present in a community. Therefore, I examined whether a statistically significant phylogenetic signal was present within the communities at all, and whether the strength of signal depended on plant species richness. I used the D statistic as a measure of phylogenetic signal of flower type (restrictive versus unrestrictive), which was calculated with the phylo.d function in the CAIC package of R (Orme 2009). D is based on a Brownian motion model of continuous trait evolution combined with a threshold function that allows the resulting distribution to be converted to a dichotomous trait, with the threshold chosen to yield the observed frequencies of the two states. D is therefore independent of the number of terminal taxa and trait prevalence. D scales such that a value of one indicates no phylogenetic signal, and a value of zero indicates that phylogenetic signal is the same as under a Brownian model of trait evolution, with negative values indicating greater extremes of signal and positive values above one indicating overdispersion (Fritz & Purvis 2009). D handles polytomies well, with polytomies having little effect on D of trees with at least 70% resolution (Fritz & Purvis 2009).

2.8 Statistical analysis

All statistical analyses except for those described above were performed in JMP for Mac version 7.0.2 (SAS Institute Inc. 2007). Whenever parametric tests were used, I tested that residuals were normally distributed using the Shapiro-Wilk test with alpha=0.05 and, where applicable, I tested that residuals were homoscedastic by visually examining residual plots.

2.8.1 Overall presence of phylogenetic clustering

Under the null hypothesis, RNRI values should be uniformly distributed with a mean of zero. If, instead, pollinators tend to visit plants that are more closely related than expected by chance, then an excess of positive RNRI values will result. Because pollinators occurring in the same dataset (community) cannot be considered independent data points, and because RNRI scores within datasets were not consistently normally distributed, I tested for whether RNRI values tended towards positive values based on the community-level pooled medians (i.e., the median of all pollinators within a community). I used a 2-tailed t-test to determine whether the mean community-level median RNRI differed from zero.

2.8.2 Relationship between plant species richness and phylogenetic signal of flower type

I used Spearman's rank correlation to test whether phylogenetic signal varies with community plant species richness. Parametric tests were not appropriate due to extreme heteroscedasticity.

2.8.3 Relationship between plant species richness and mean phylogeny node depth

I tested for a relationship between these two variables using a regression of mean node depth versus log-transformed plant species richness.

2.8.4 Difference in phylogenetic clustering between pollinator types versus community plant species richness

Because pollinator types are paired within communities, I calculated the difference between median RNRI scores for each set of versatile and non-versatile pollinators, and performed a regression of this value against 1/(community plant species richness). Preliminary visual analysis suggested that a better fit would be achieved by applying a reciprocal transformation to the X axis, which I believe can be reasonably biologically justified on the grounds that there may be diminishing returns of an increase in richness on a pollinators' lack of choosiness (i.e., when richness is very low, a versatile pollinator may be extremely indiscriminate and visit all plants that it is able to, but after a certain level of plant species richness is available, saturation will occur).

2.8.5 Difference in pollinator preference for floral morphology versus community plant species richness

For each pollinator, I calculated the proportion of the plant species that it visited that have restrictive morphology. I then calculated the difference between the median proportions for each of the two pollinator types within each community and performed a regression of this value against community plant species richness.

3: RESULTS

Amongst all the datasets, there were 4313 pollinator species, including those that visited only one plant species (where a single species appears in multiple datasets it is counted as multiple species in this number). RNRI values were calculated for 1687 pollinator records, those that visited more than one plant species. Birds that visited more than 1 plant species were excluded (8 records), leaving 1679 pollinators included in the analysis.

908 (54.08%) of the pollinators had positive RNRI values, and 770 (45.86%) had negative values (Figure 4). The median RNRI value pooled over all pollinators in all communities was 0.120 (mean = 0.11525), suggesting weak phylogenetic clustering.

Nineteen of 29 datasets (66%) had positive median RNRI scores. The estimated mean of community median RNRI ± SE is +0.12397 ± 0.03973, again indicating weak but significant phylogenetic clustering overall (2-tailed P = 0.004, t=3.1206, df=28; Figure 5). RNRI was not correlated with community plant species richness (regression of community median RNRI vs. ln(species richness); F=1.5792; P=0.2196; df=28; R-square=0.06).

Phylogenetic signal for flower type was demonstrably absent in only one community (community BA; nominally significant departure from Brownian expectation but not from the expectation under absence of signal; Figure 6, Table 2). Although 8 communities failed to reject the null hypothesis of absence of signal, these also failed to reject the hypothesis of Brownian evolution (uncorrected alpha = 0.5; Table 2). There was, however no relationship between phylogenetic signal (estimated D) and community plant species richness (Spearman's rho=0.0474, P=0.8073; Figure 6).

Mean phylogeny node depth was strongly negatively correlated with community plant species richness. (F= 38.5352; P<0.0001; df=28; R-square=0.59, Figure 7). This was not due to the presence of polytomies pushing nodes deeper in smaller trees, as larger trees were less resolved than smaller ones (slope of number of nodes in a community tree vs. community size = 0.69, significantly less than the null 1:1 line, s.e. of slope = 0.02).

There was an interaction effect between pollinator type and community plant species richness on RNRI (F= 5.1864; P=0.0309; df=28; R-square=0.161; Figure 8), indicating that as community richness decreases, the degree of phylogenetic clustering among plants visited by unversatile vs. versatile pollinators diverge. Median community RNRI of unversatile pollinators indicates mild phylogenetic clustering and shows no relationship with species richness. In contrast, clustering of plants visited by versatile pollinators increases with community richness, being completely absent in the smaller communities, and similar to that of unversatile pollinators in the larger communities.

Finally, as expected, versatile pollinators include a higher proportion of restrictive flowered species among those that they visit than do unversatile pollinators; the dataset median proportion for versatile and unversatile pollinators were 0.294 and 0.131 respectively (Wilcoxon test of paired median proportions, z=105.5, p<0.0001). However, this difference between pollinator types did not change with community plant species richness (F=0.0013, P=0.9712, df=28, R-square<0.01; Figure 9).

4: DISCUSSION

4.1 Summary of results

I first summarize the results with reference to my five predictions and then discuss them in turn: three (1, 2, and 4) received support, while two (3 and 5) did not. I found that pollinator species tend to visit phylogenetically clustered plants in a community, but this effect is weak overall (1). Plant species richness was strongly negatively correlated with mean node depth of the community phylogeny (2), but, contrary to my prediction, increases in richness were accompanied by a decrease in the variance but did not affect the magnitude of phylogenetic signal of floral restrictiveness (3). The plants visited by unversatile pollinators were weakly phylogenetically clustered at all levels of plant richness, whereas those visited by versatile pollinators were random with respect to phylogeny in small communities but became moderately clustered as plant richness increased (4). Versatile pollinators visit a higher proportion of restrictive flowers than do unversatile pollinators, but, contrary to my prediction, this difference is unaffected by the species richness of the plant community (5).

4.2 Overall presence of phylogenetic clustering (question 1)

I found that, overall, the plants visited by pollinators were more closely related to each other than expected by chance, and that the median RNRI for pollinators was positive (indicating phylogenetic clustering) in 19 of the 29 datasets I examined. Rezende *et al.* (2007a) found that phylogenetic similarity of plants correlates significantly with similarity in pollinator identity in only a minority of their datasets, but if their data is reconsidered globally, 24 of 33 had a positive correlation coefficient between phylogenetic relatedness of plants and similarity in the identities of the pollinators that visited them ($P<0.01$, binomial test; 72% vs. 66% of datasets in my results). Therefore, despite using different datasets, evaluating the question from a different "point-of-view" (my research considers the pollinators' perspective, whereas Rezende *et al.* (2007a) consider the plants' perspective), and using different methods of assessing phylogenetic signal, my results are qualitatively similar to those of Rezende *et al.* (2007a). This lends further support to the idea that phylogenetic constraints contribute, but weakly, to the structure of pollination networks. Higher resolution increases power to detect phylogenetic constraints. Notably, I did not find a strong effect of phylogeny despite my phylogenies being more highly resolved than those used by Rezende *et al.* (2007a). Rezende *et al.* (2007a) constructed their phylogeny using the basic APG supertree, whereas I incorporated taxonomic information from other sources to improve resolution below the level of family. Several studies have shown that phylogenetic resolution and taxonomic scale can influence the results of this type of study (Cavender-Bares *et al.* 2004, Swenson *et al.* 2006, Kress *et al.* 2009).

Why are phylogenetic constraints weak in pollination networks? As I discussed in the introduction, closely related species are often assumed to be phenotypically similar, and hence ecologically similar; however, many mechanisms exist which can reduce phylogenetic constraints, some of which I have discussed above. These include lack of phenotypic resemblance between closely related species under various evolutionary processes (Revell *et al.* 2008); overdispersed phylogenetic community structure and/or low trait signal in community plant phylogeny due to neutral or deterministic community assembly processes (Section 1.6, Figure 3b); and pollinator foraging behaviour (Section 1.6, Figure 3c). The rest of my results provide some insight into which of these mechanisms may be more important, so I will return to this question in the following discussion.

4.3 Effect of plant species richness on mean node depth (question 2)

Based on my conceptual model, I expected that communities with higher plant species richness would be composed of plants that are more closely related to each other (i.e., their phylogenies would have shallower mean node depth). I found strong support for this prediction: mean phylogenetic node depth was very strongly negatively correlated with richness (R-square=0.59).

Although node depth under neutral community assembly is expected to decrease with richness, ecological and historical processes (e.g., environmental filtering, competition and facilitation, and geographic range correlation) operating during community assembly could obscure such a relationship. The very strong correlation that I found between species richness and mean node depth is consistent with neutral processes in community assembly having a substantial influence on the relatedness of plant species in a community. My result is, in fact, biased to underestimate the correlation between richness and node depth because the phylogenies of my larger datasets were less well resolved than those of the smaller ones; polytomies produce a bias towards deeper nodes, so this would tend to reduce the slope of the regression line between richness and node depth and reduce the R-square value.

The overall relatedness of plants in the community is important because under some models of trait evolution (e.g., Brownian motion), phenotypic similarity between species is expected to be proportional to the amount of shared history: species that are less closely related have less shared history and hence would be expected to bear less resemblance to each other (Revell *et al.* 2008). Therefore, the correlation between richness and mean relatedness introduces an caveat into interpreting the result of question 1 (above) and also the results of Rezende *et al.* (2007a). Previous authors (e.g., Vázquez *et al.* 2009b) have concluded that phylogenetic constraints are generally weak in pollination networks, but this conclusion is based on testing for phylogenetic constraints in relatively few pollination networks (Rezende *et al.* 2007a, Vázquez *et al.* 2009a; also this study). Although these communities encompass diverse geographic locations and habitats, they are too few in number to be globally representative. Most importantly, because constructing comprehensive community pollination networks is extremely labour intensive, the datasets available may be biased towards communities that contain relatively few species. This would produce a bias towards communities with relatively distantly related plants, where phylogenetic constraints may be less likely to be found. Therefore, the impression that phylogenetic constraints on pollination networks are "typically" weak may be due in part to undersampling of species-rich datasets, and in many real communities the true strength of phylogenetic constraints could be greater.

4.4 Effect of plant species richness on phylogenetic signal of floral restrictiveness (question 3)

I found no support for my prediction that a negative correlation between species richness and phylogeny mean node depth would result in richer communities retaining a stronger phylogenetic signal for floral traits. Phylogenetic signal (D) of floral restrictiveness decreased in variance with richness but showed no trend in its mean magnitude. Phylogenetic signal for floral restrictiveness was present in all but one dataset (dataset BA). Although in eight communities it was not possible to reject the null hypothesis of absence of signal, these communities also failed to reject the hypothesis of Brownian evolution. Additionally, these were also all communities with fewer than 25 species; Fritz & Purvis (2009) note that power to detect phylogenetic signal is low for trees with fewer than 25 tips.

Species-poor communities had high variance in D, ranging from extremely weak to extremely strong signal, but variance in D decreased abruptly when plant richness exceeded 25 species, possibly converging on the approximate value of D in the global phylogeny. This suggests that phylogenetic signal in the trait that I evaluated, floral restrictiveness, is consistently retained in communities that contain enough species that the D test of phylogenetic signal gives meaningful results.

The lack of correlation between species richness and and signal strength underscores that the correlation between species richness and mean phylogenetic node depth may not have a carry-on effect on the likelihood of related species in a community resembling each other in restrictiveness, or that such an effect may be weak and idiosyncratic. This, in turn, would imply that richness might be a poor predictor of the presence of phylogenetic constraints on pollination network structure.

What does this mean for other floral traits? Floral phenotype as perceived by pollinators is a complex of many interacting traits, each of which is subject to different evolutionary processes. It is likely that at least some of these traits will be subject to a more rapid phylogenetic decay in similarity than is floral restrictiveness. I chose floral restrictiveness as a sample trait to map onto the community phylogenies that I tested because it was an easily quantified trait that I expected to be ecologically relevant within all the communities that I assessed. However, this trait may be less likely to show variation in signal with node depth than some other traits because across much of the angiosperm phylogeny it is conserved relatively deeply, often at the level of family. Although some families (e.g., Ericaceae) contained variation for this trait in my master phylogeny, many globally well-represented families such as Rosaceae, Asteraceae and Lamiaceae contained little or no intrafamily variation. Other traits that are known to be important to pollinators, especially continuous traits such as the size of the floral nectar holder (e.g., Stang *et al.* 2006), may be more likely to experience a decay in phylogenetic correlation much closer to the tips of the phylogeny. Phylogenetic signal for such traits might be more sensitive to differences in mean phylogeny node depth, as driven by species richness. Therefore, although my result does not support a positive relationship between species richness and phylogenetic signal for floral restrictiveness, such a relationship may exist for other important traits that I did not assess here.

4.5 Effect of pollinator type and community plant species richness on phylogenetic clustering of visited plants (question 4)

My conceptual model predicted that versatile pollinators would relax their floral trait specificity in communities with low plant richness, causing them to visit plants that are less phylogenetically clustered; while unversatile pollinators would be more strongly constrained by floral traits, and, thus, relatively weakly affected by community richness. Consistent with my predictions, I found that community richness and pollinator type (versatile vs. unversatile) interacted to affect the phylogenetic clustering of plants visited by pollinators. Unversatile pollinators displayed moderate phylogenetic clustering of the plants that they visit, the strength of which was unaffected by community species richness. On the other hand, versatile pollinators visited plants that were phylogenetically random in communities with the lowest plant species richness, but visited increasingly clustered plants as species richness increased.

What are the implications of this result? Firstly, this result demonstrates that phylogenetic constraints in pollination networks do, in fact, vary with plant species richness, at least for some pollinators. This, in turn, suggests which mechanisms may be important towards generating a relationship between community plant species richness and strength of phylogenetic constraints on network structure. Because not all pollinators responded to community richness in the same manner, it is unlikely that the relationship between richness and phylogenetic clustering is solely driven by community assembly effects on the mean relatedness of plant species; differences between the behaviour of pollinators among communities likely contributed to this result. That my results support behavioural mechanisms points to a complex relationship between phylogeny and pollination network structure. In the pollination network literature, constraints on interactions arising from evolutionary history have often, to date, been theoretically conceptualized as being uniform within and between communities. Modulation of the effects of phylogeny through such local ecological factors as behavioural flexibility in pollinators, may be equally important, but has rarely been discussed.

Secondly, the effect of plant species richness on the relatedness of plants visited by versatile pollinators reinforces my concern that the strength of phylogenetic constraints measured within a pollination network can depend on plant species richness, and that a bias in the literature towards species poor communities may result in underestimation of the global importance of phylogeny.

Lastly, the difference between pollinator types demonstrates that phylogenetic constraints are not uniform across the whole pollination network, but instead can be predictably driven by some species types more than others.

Few studies have previously examined whether pollinator types differ in how they contribute to pollination network structure, but Olesen *et al.* (2007) found that flies and beetles and small bees commonly act as "connectors" between compartments in modular pollination networks, whereas social bees and large solitary bees act as "hubs" within compartments. Together, these results suggest that examining the roles of different pollinator functional groups towards generating network structure may be an interesting avenue of future research.

4.6 Effect of plant species richness and pollinator type on proportion of restrictive flowers visited (question 5)

If the relationship between phylogenetic clustering of visited plants, community plant species richness, and pollinator type is driven by the optimal foraging paradigm described in Sections 1.5 and 1.6, I predicted that (1) in species-rich communities the plants visited by versatile pollinators would comprise a high proportion of restrictive flowers relative to unversatile pollinators; but (2) in species-poor communities this proportion would be more similar between the pollinator types as versatile pollinators relax their floral trait specificity. Floral restrictiveness retains a phylogenetic signal in most of my datasets and, thus, versatile pollinators relaxing their response to this trait could result in lower phylogenetic clustering in these communities. However, my results show that although versatile pollinators tend to visit a higher proportion of restrictive plants than do unversatile pollinators, the magnitude of the difference does not change with species richness (Figure 9). As with the result found for phylogenetic signal in floral type (question 3), this result fails to increase support for my model but it does not contradict it. As mentioned above, pollinators are influenced simultaneously by a large number of traits, and floral restrictiveness, as defined here, may have simply been a trait that is not biologically relevant. Several studies have shown that size matching between pollinators and flowers can be an important determinant of pollination interactions (Stang *et al.* 2006, 2009, Santamaría and Rodríguez-Gironés 2007, Krishna *et al.* 2008,); this would have been a stronger candidate trait to test, but it was not feasible to collect this type of information for the large number of species present among my datasets. It is also possible, as mentioned above, that pollinators respond more strongly to the multidimensional phenotype than to any individual trait, and that phylogenetic signal in the whole phenotype may behave differently than the signal for individual traits (Rezende *et al.* 2007b).

5: CONCLUSION

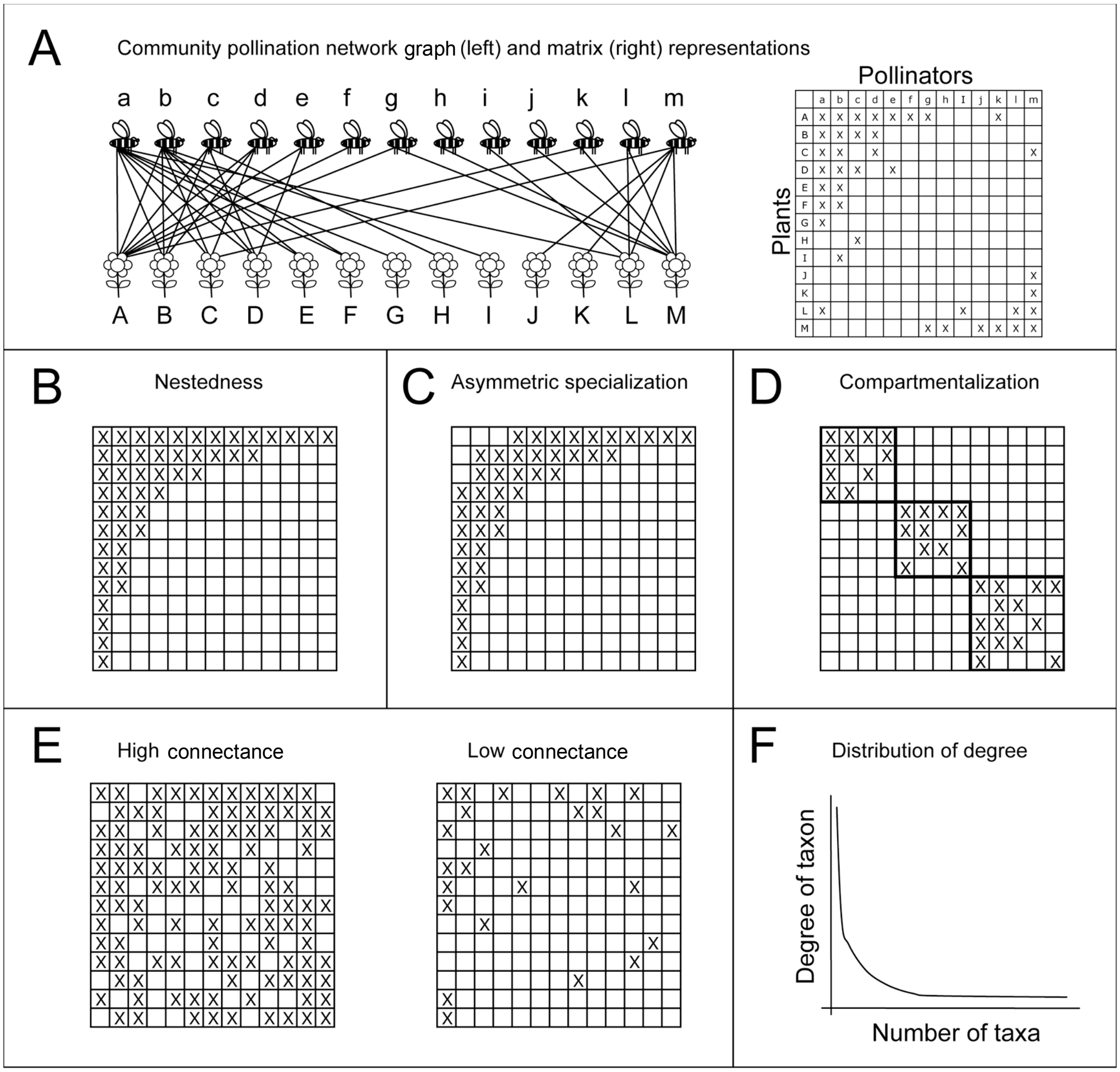
Phylogenetic relatedness of the plants present in a community commonly imposes weak constraints on pollination network structure whether this question is addressed from the point-of-view of plants or pollinators. Phylogenetic constraints can be weak or absent due to lack of phenotypic resemblance between closely related species (Revell *et al.* 2008), and overdispersed phylogenetic structure and/or low trait signal in community plant phylogenies due to neutral or deterministic community assembly processes. I found that in species-poor communities plants are more distantly related, display higher variance in the strength of phylogenetic signal for floral morphology, and plants visited by versatile pollinators within such communities are random with respect to phylogeny. Collectively, these results suggest that plant phylogenetic relatedness more consistently imposes constraints on pollination network structure in species-rich communities, and that a bias towards studying relatively species-poor communities may result in an underestimation of the "typical" strength of phylogenetic constraints

Consistent with my conceptual model, the relationship between species richness and the strength of the phylogenetic clustering of plants visited by pollinators differed between versatile and unversatile pollinators. This shows that phylogenetic constraints vary among species within networks, and suggests that the relationship between richness and strength of phylogenetic constraints may be driven in part by pollinator behaviour (in addition to community assembly effects on the mean relatedness of plant species).

Although I found that richness and pollinator type predicted phylogenetic clustering in the manner I had predicted, my tests of the mechanistic basis of these relationships did not produce informative results. However, these tests were based on the single dichotomous trait of floral restrictiveness, and my negative results cannot be extended to other traits. Unfortunately, this was the only trait that seemed tractable to assess in the context of this thesis.

Overall, my results strongly suggest that the strength of plant phylogeny constraints on pollination networks can be moderated by current ecological factors such as community species richness and pollinator behaviour. Therefore, future research should consider the opportunity for bidirectional interplay between ecological and phylogenetic effects.

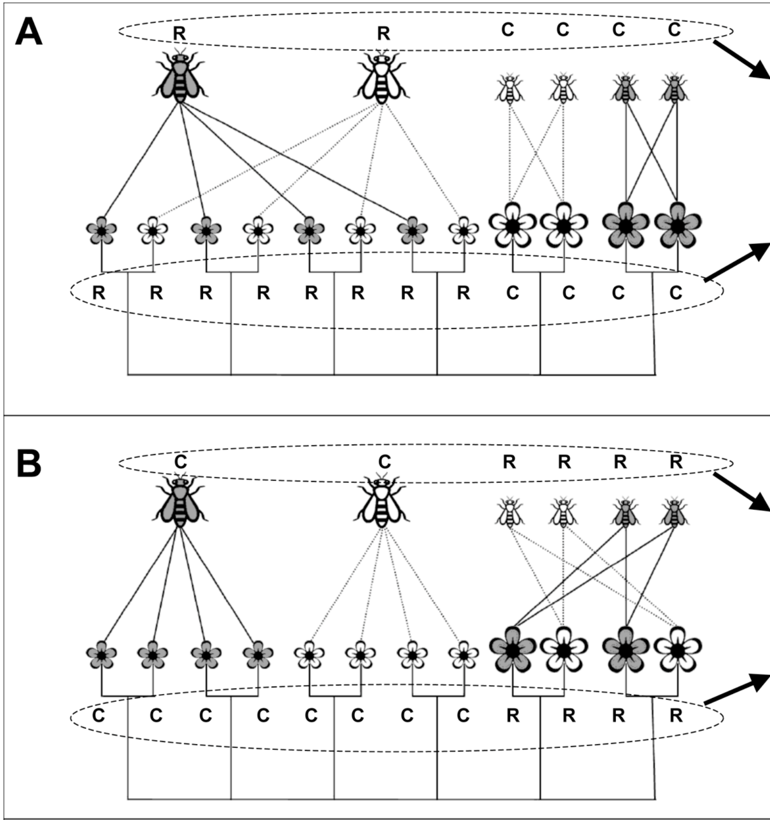
FIGURES



	a	b	c	d	e	f	g	h	I	j	k	l	m
A	X	X	X	X	X	X	X				X		
B	X	X	X	X									
C	X	X		X									X
D	X	X	X		X								
E	X	X											
F	X	X											
G	X												
H			X										
I		X											
J													X
K													X
L	X								X			X	X
M							X	X		X	X	X	X

Figure 1: Overview of pollination network structure.

(A) Pollination networks can be visualized in several ways, including as network graphs (left; interacting plants and pollinators are connected by a line) and matrices (right; rows and columns correspond to plant and pollinator species respectively; each cell contains a value that represents whether the corresponding species interact with each other). Pollination networks tend to possess the following properties. (B) *Nestedness*. Pollinators that are poorly connected (i.e., visit few plant species) visit a nested set of those plants visited by well-connected pollinators. (C) *Asymmetric specialization*. Well connected species and poorly connected species interact with each other more often than expected based on their frequencies alone. Poorly connected species are *not* usually reciprocally specialized with other poorly connected species. (D) *Compartmentalization*. Large communities contain modules of species that are well connected to each other, but poorly connected to the rest of the network. Note that communities that are compartmentalized can show nestedness within compartments (Lewinsohn *et al.* 2006). (E) *Low connectance*. Relatively few of the potential pairwise interactions are observed to actually occur. (F) *Degree distribution* is right-skewed: Communities are composed of a small number of high-degree species (i.e., those that interact with a large number of species) and many low-degree species. See main text for citations.



Pollinator point-of-view:
- 2/3 of pollinators show phylogenetic constraints of visited plant (C)
- 1/3 visit plants that are phylogenetically random (R)
- **Community shows phylogenetic constraints**

Plant point-of-view:
- 1/3 of plants share pollinators with their close relatives through phylogenetic constraints (C)
- 2/3 are random as to whether they share pollinators with closely related plant species (R)
- **Community is phylogenetically random**

Pollinator point-of-view:
- 1/3 of pollinators show phylogenetic constraints of visited plant (C)
- 2/3 visit plants that are phylogenetically random (R)
- **Community is phylogenetically random**

Plant point-of-view:
- 2/3 of plants share pollinators with their close relatives through phylogenetic constraints (C)
- 1/3 are random as to whether they share pollinators with closely related plant species (R)
- **Community shows phylogenetic constraints**

Size of plants and pollinators indicates number of species it interacts with. Their colour indicates a trait that is complementary between plants and pollinations such that dark plant are visited by dark pollinators and light plants are visited by light pollinators.

Figure 2: Pollinator vs. plant perspectives can give different results for tests of phylogenetic constraints in pollination networks.

Here we assume that the majority of pollinators visit high-degree plants (i.e., plants that interact with a relatively large number of pollinator species), but the majority of plants are of low degree (Jordano *et al.* 2006); and that low-degree species tend to preferentially interact with high degree species and *vice versa* (Vázquez & Aizen 2004). (A) If closely related plant species of high-degree tend to share trait values (and hence pollinators) *more* often than do closely related plant species of low-degree, then most pollinators tend to visit plants that are phylogenetically clustered, but most highly related plants do NOT tend to share pollinators. (B) If closely related plant species of high-degree tend to share trait values (and hence pollinators) *less* often than do closely related plant species of low-degree, then most pollinators tend to visit plants that are unrelated, but closely related plants tend to share pollinators.

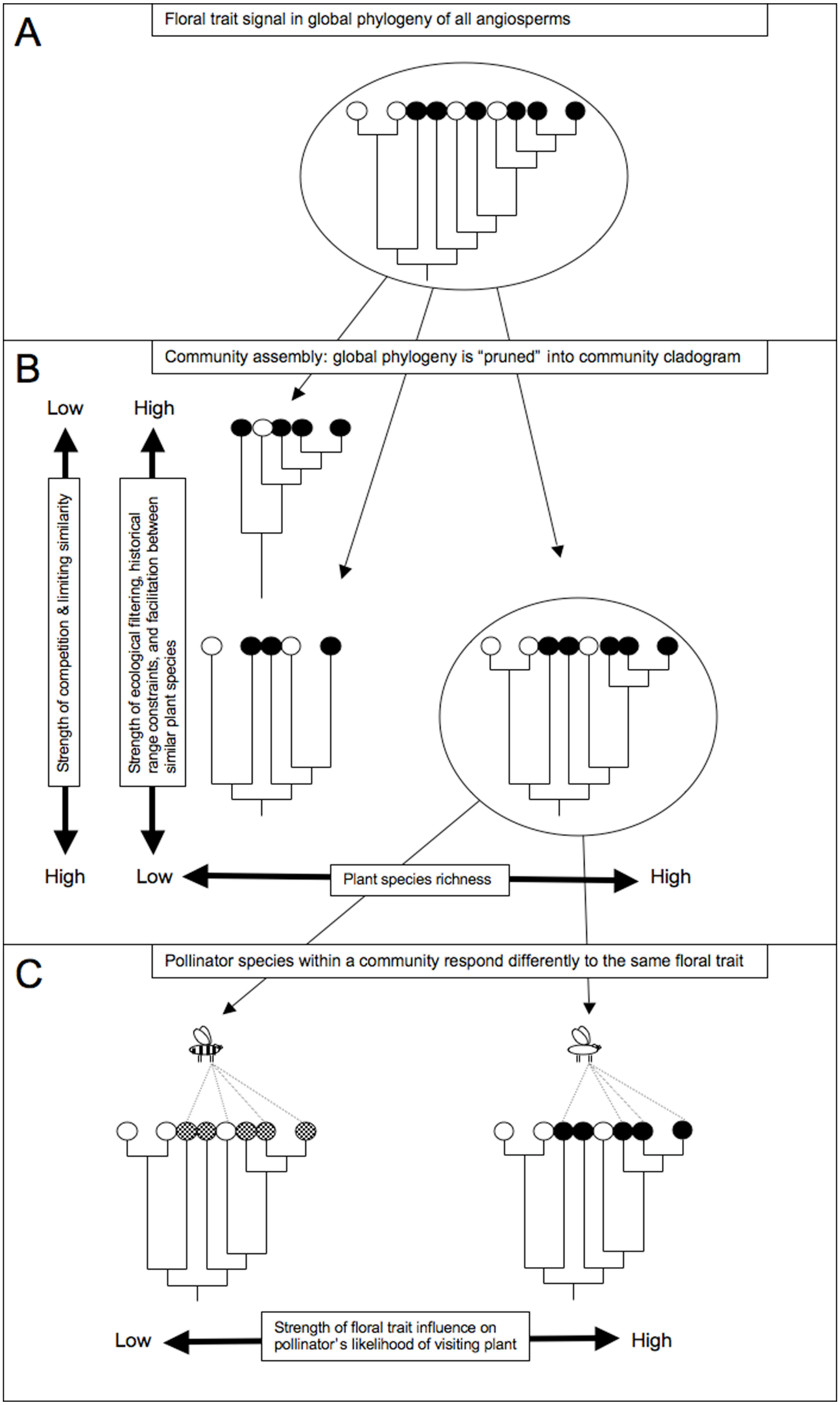

A
Floral trait signal in global phylogeny of all angiosperms
B
Community assembly: global phylogeny is “pruned” into community cladogram
Low
High
Strength of competition & limiting similarity
High
Strength of ecological filtering, historical range constraints, and facilitation between similar plant species
Low
High
Low
Plant species richness
High
C
Pollinator species within a community respond differently to the same floral trait
Low
Strength of floral trait influence on pollinator's likelihood of visiting plant
High

Figure 3: Conceptual model of mechanisms underlying the strength of phylogenetic constraints on pollination networks.

A) Phylogenetic signal for some floral traits exists in the global phylogeny of angiosperms. Open and closed circles represent the two possible states of a hypothetical binary floral trait. Close relatives are more likely to have the same trait state. (B) Community assembly "prunes" the global phylogeny into a community cladogram. Neutral, historical, and deterministic processes collectively determine the average relatedness of plants in the community cladogram, and how much phylogenetic signal of the trait will be retained. (C) Traits can vary in the strength of their effect between pollinators. In this example, all pollinators favour the trait state indicated by the darker circle. The left-hand side pollinator perceives the effect more weakly than does the pollinator on the right; therefore, the latter will experience a stronger effect of plant phylogeny. See Section 1.6 of main text for further details.

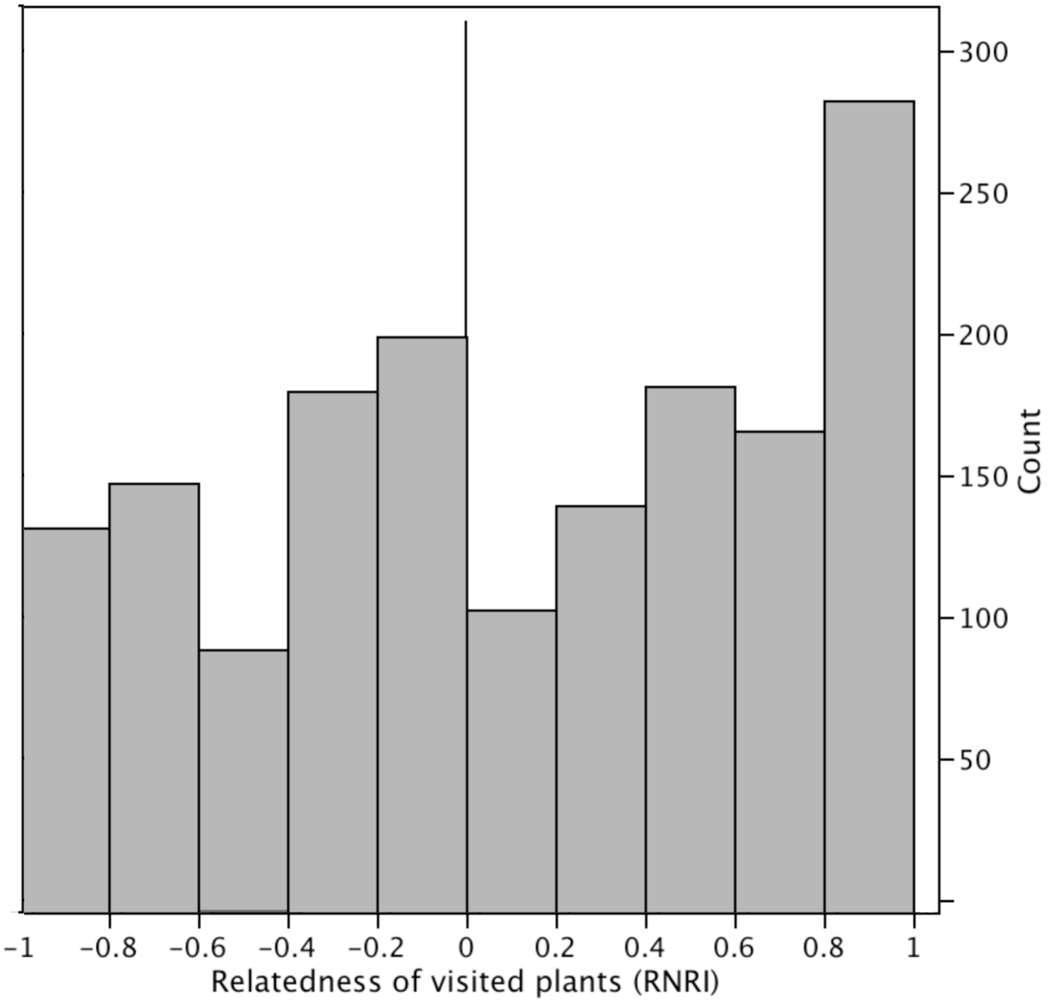


Figure 4: Histogram of individual pollinator RNRI scores pooled across all datasets

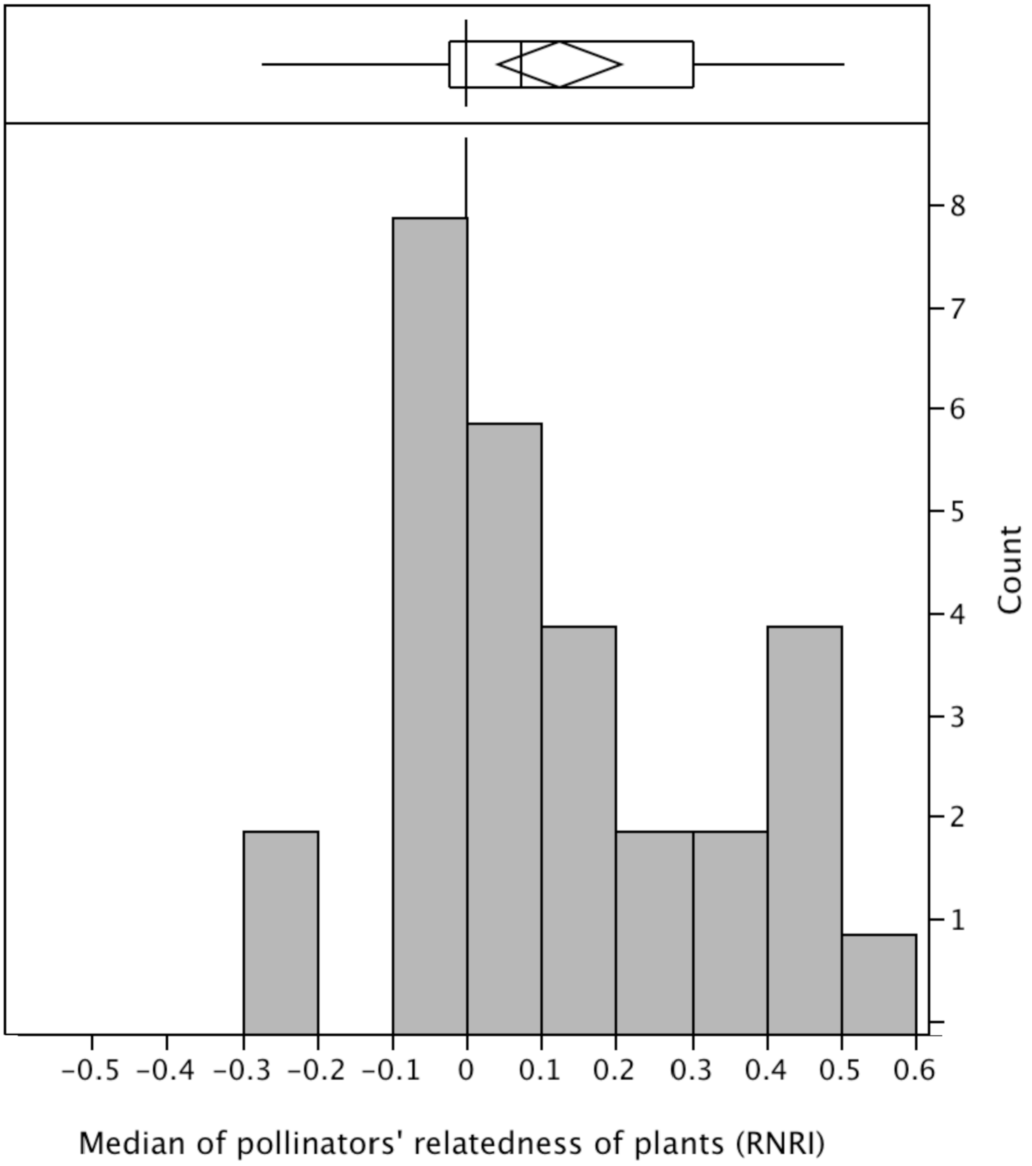


Figure 5: Histogram of community-level median RNRI scores. Diamond represents 95% CI of the mean. Mean ± SE = +0.12397 ± 0.03973, indicating slight phylogenetic clustering overall (2-tailed t-test, P = 0.004, t=3.1206, df=28).

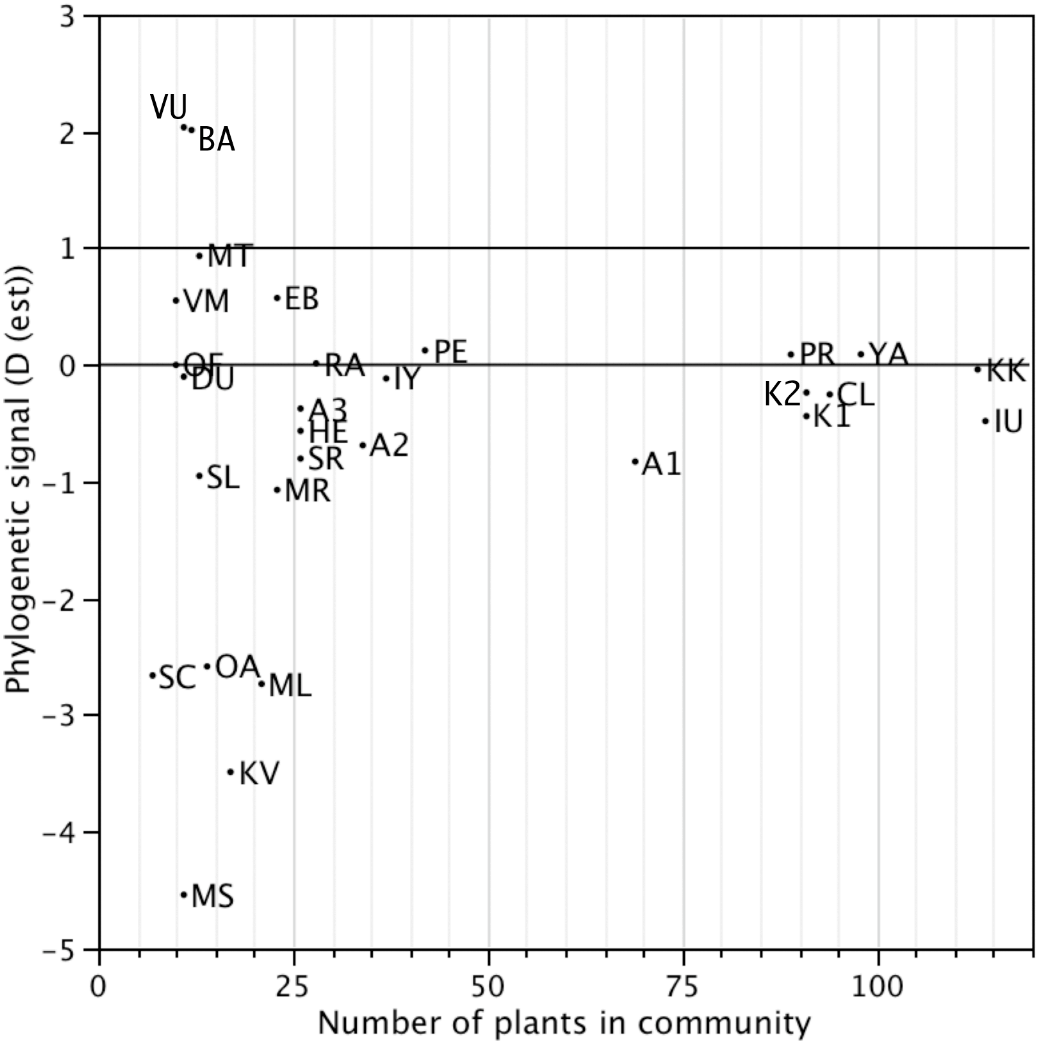


Figure 6: Phylogenetic signal of flower type (restrictive or unrestrictive) in community plant phylogenies.

Zero corresponds to the expectation of phylogenetic signal under Brownian trait evolution, and one corresponds to no phylogenetic signal. Only one community phylogeny departs (uncorrected alpha < 0.05) from the Brownian expectation (BA), and 8 community phylogenies fail to reject the null hypothesis of no phylogenetic signal (BA, DU, EB, MT, OF, SC, VM, VU); all these datasets have a low numbers of plants, so type 2 error rates are expected to be high.

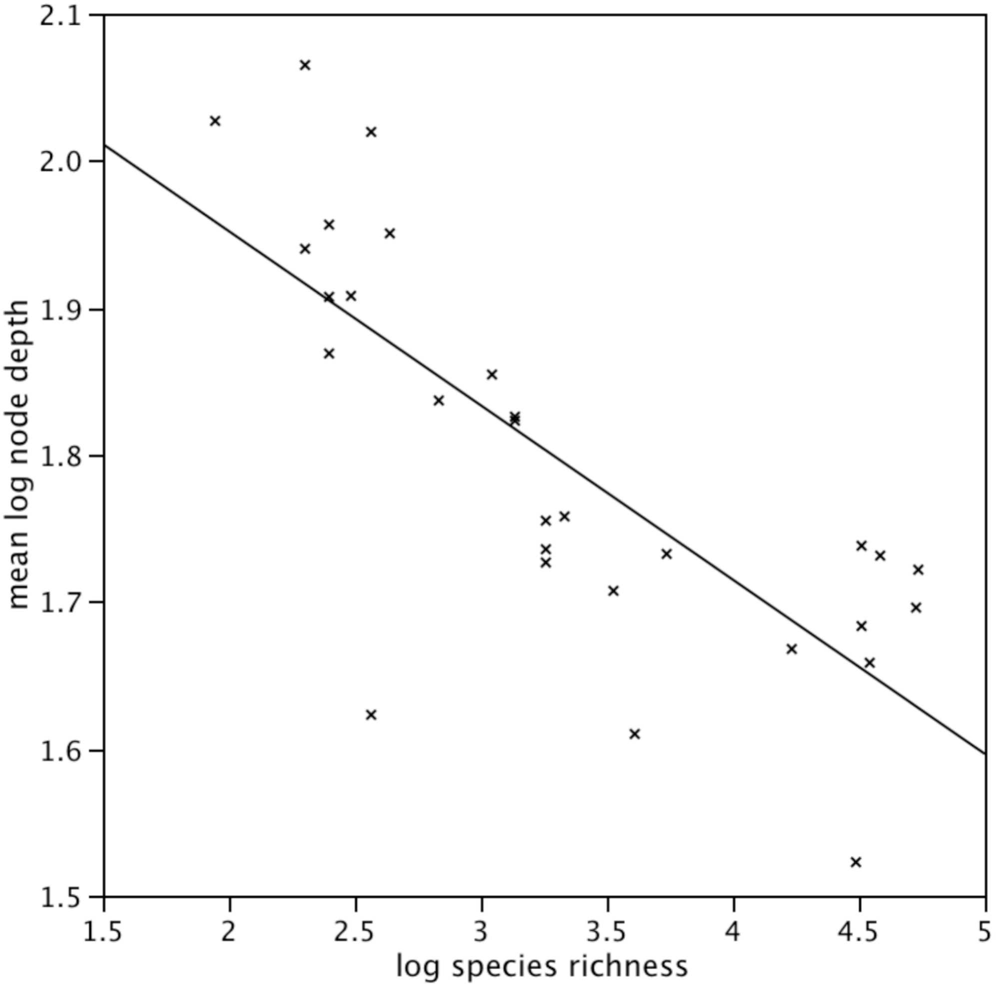


Figure 7: Relationship between species richness and mean phylogeny node depth (F= 38.5352; P<0.0001; df=28; R-square=0.59). As community plant species richness increases, the mean phylogenetic distance between plants decreases.

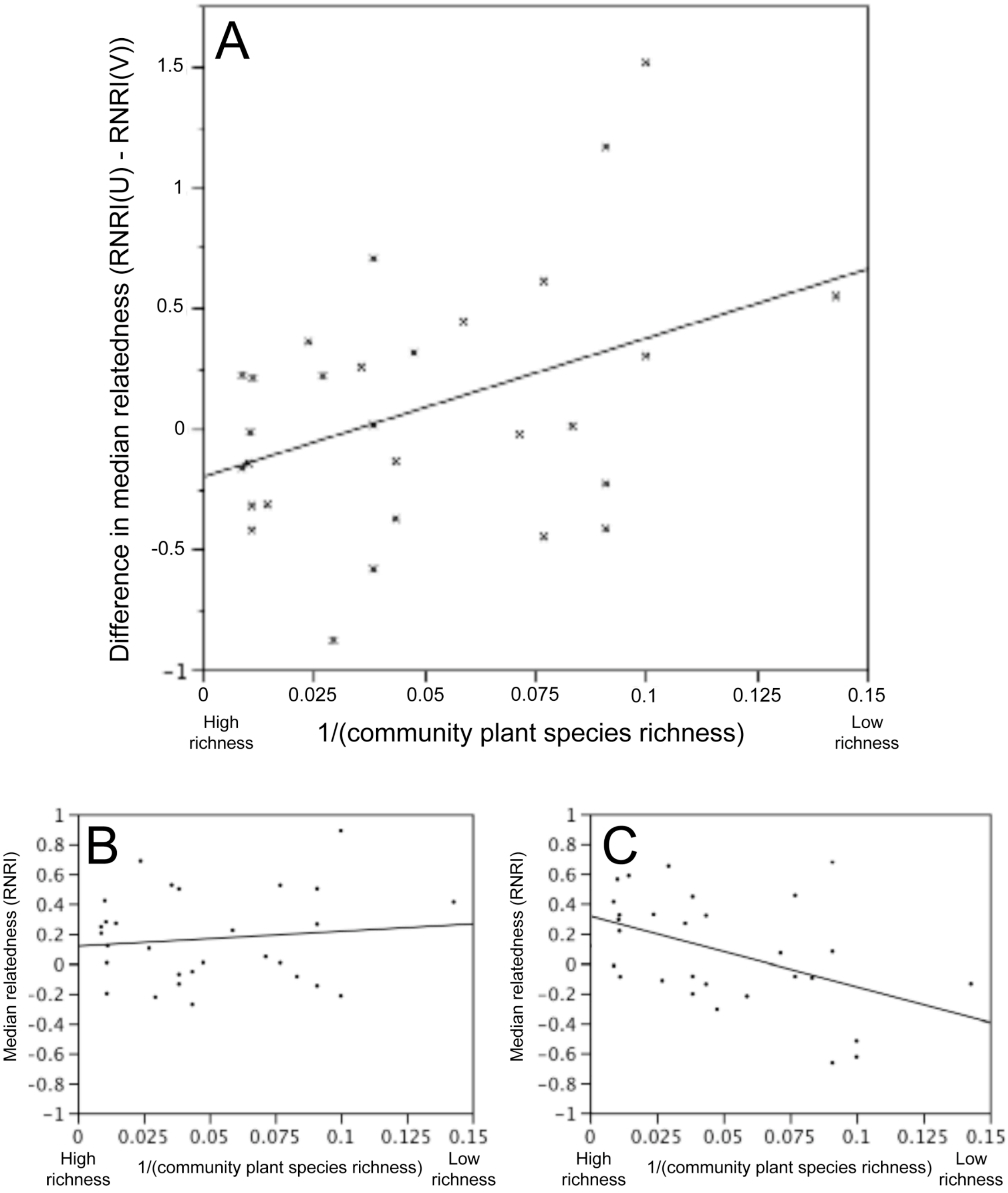


Figure 8: Interaction effect between pollinator type and community species richness on median RNRI (regression of difference within each community of median RNRI(unversatile; U) and median RNRI(versatile; V) versus reciprocal-transformed richness; F= 5.1864; P=0.0309; df=28; R-square=0.161). (A) As community richness decreases, the relatedness of plants visited by unversatile vs. versatile pollinators diverge such that the former are more closely related than the latter. Lower graphs show relationship between plant richness and community median RNRI scores for unversatile (B) and versatile (C) pollinators separately, and their best-fit line.

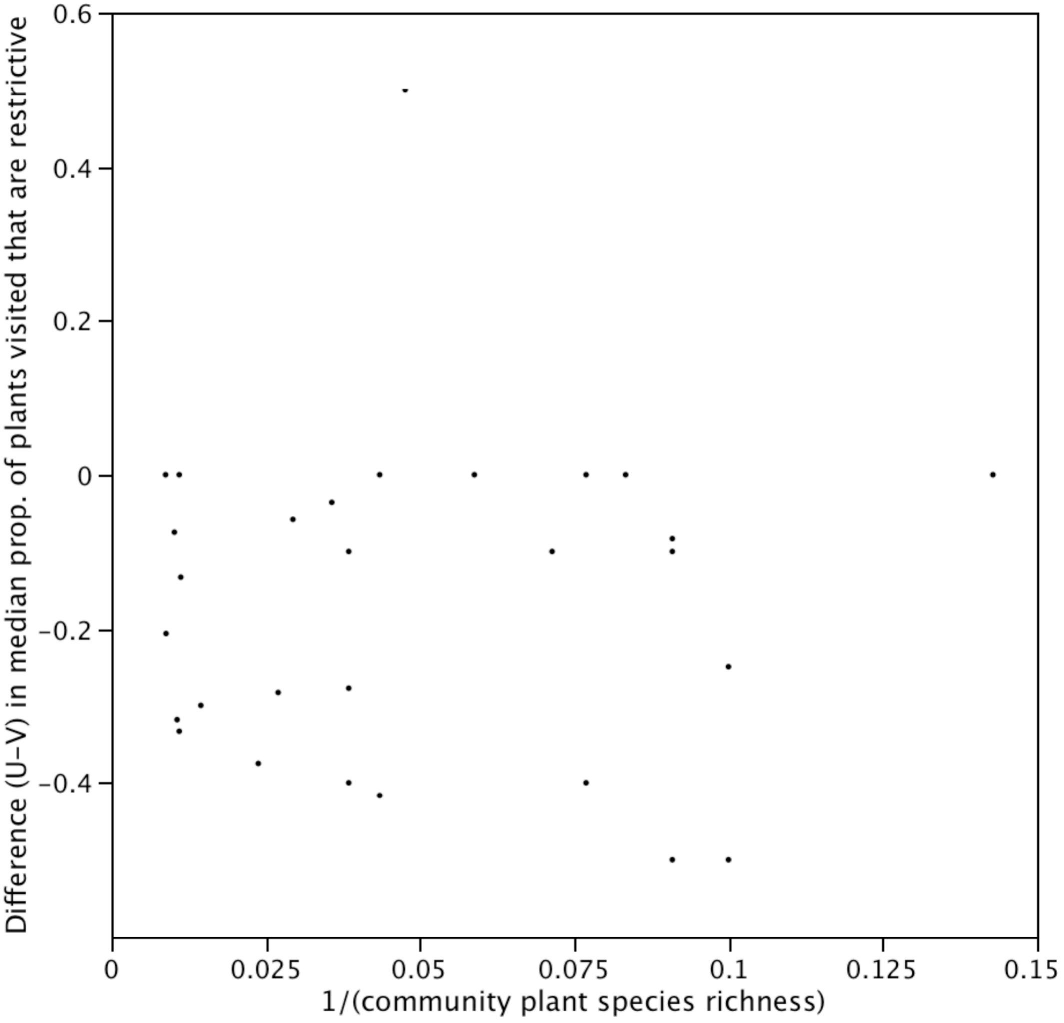


Figure 9: Comparison of flower type preference (community medians of proportion that are restrictive) between unversatile (U) and versatile (V) pollinators, versus reciprocal-transformed species richness of plant community. Versatile pollinators visit a higher proportion of restrictive flowers than do unversatile pollinators, but species richness has no effect on the relationship (full model P=0.9712, F=0.0013, df=28, R-square<0.01).

TABLES

Table 1: Datasets used and their attributes

Dataset code	Reference of dataset source	Latitude	Plant richness	Median RNRI	Mean log(node depth)
A1	Arroyo *et al.* 1982 (subandean scrub)	33º17'S	69	0.412	1.66780
A2	Arroyo *et al.* 1982 (cushion zone)	33º17'S	34	0.0365	1.70737
A3	Arroyo *et al.* 1982 (subniveal tussock)	33º17'S	26	0.1555	1.75508
BA	Barrett & Helenurm 1987	46º33'N	12	-0.09	1.90802
CL	Clements & Long 1923	38º50'N	94	0.281	1.65842
DU	Dupont *et al.* 2003	28º13'N	11	-0.085	1.90731
EB	Elberling & Olesen 1999	68º21'N	23	-0.2735	1.82579
HE	Herrera 1988	37º01'N	26	-0.071	1.72661
IU	Inoue *et al.* 1990	35º10'N	114	0.3195	1.72174
IY	Inouye & Pyke 1988	36º25'S	37	0.087	1.61000
K1	Kato *et al.* 1990	35º20'N	91	-0.0395	1.73800
K2	Kato *et al.* 1993	35º35'N	91	0.013	1.68340
KK	Kakutani *et al.* 1990	35º02'N	113	0.155	1.69594
KV	Kevan 1970	81º49'N	17	0.0135	1.83683
ML	Medan *et al.* 2002 (Laguna Diamante)	34º10'S	21	-0.005	1.85451
MR	Medan *et al.* 2002 (Rio Blanco)	33º00'S	23	-0.0335	1.82303
MS	Mosquin & Martin 1967	75º00'N	11	-0.016	1.86882
MT	Motten 1982	36º00'N	13	-0.016	2.01953
OA	Olesen *et al.* 2002 (Isle d'Aigrettes)	20º25'S	14	0.071	1.95054
OF	Olesen *et al.* 2002 (Flores Island)	39º20'N	10	0.469	1.94004
PE	Percival 1974	17º55'N	42	0.3845	1.73245
PR	Primack 1983	43º00'S	89	0.024	1.52279
RA	Ramirez & Brito 1992	8º56'N	28	0.504	1.75793
SC	Schemske *et al.* 1978	40º09'N	7	0.172	2.02705
SL	Small 1976	45º24'N	13	0.255	1.62304
SR	Smith-Ramirez *et al.* 2005	42º30'S	26	0.19	1.73563
VM	Vázquez & Simberloff 2002 (Mascardi – No Cows)	41º00'S	10	-0.225	2.06506
VU	Vázquez & Simberloff 2002 (Quetrihue – Cows)	41º00'S	11	0.4405	1.95648
YA	Yamazaki & Kato 2003	33º24'N	98	0.4665	1.73128

Table 2: Phylogenetic signal (D) of floral restrictiveness in community phylogenies, and P-values corresponding to the null hypotheses of no phylogenetic signal and Brownian structure. See text for details.

Dataset code	D (estimate) of floral restrictiveness	P (no signal) (uncorrected)	P (Brownian structure) (uncorrected)
A1	-0.8295423	0	0.985
A2	-0.6902146	0	0.881
A3	-0.3754871	0.006	0.713
BA	2.010538	0.808	0.044
CL	-0.2540678	0	0.772
DU	-0.1021077	0.178	0.594
EB	0.5721124	0.239	0.318
HE	-0.5663248	0.006	0.811
IU	-0.4822334	0	0.899
IY	-0.1176149	0.007	0.591
K1	-0.4399114	0	0.867
K2	-0.2381469	0	0.738
KK	-0.0406498	0	0.567
KV	-3.488294	0.01	0.904
ML	-2.734245	0.001	0.992
MR	-1.071553	0.004	0.862
MS	-4.540462	0.019	0.894
MT	0.9328936	0.416	0.334
OA	-2.584246	0.018	0.903
OF	-0.0017479	0.26	0.464
PE	0.1230291	0.01	0.421
PR	0.08752266	0	0.445
RA	0.01226239	0.02	0.498
SC	-2.661392	0.05	0.818
SL	-0.951709	0.006	0.836
SR	-0.8037963	0.001	0.879
VM	0.5498262	0.41	0.431
VU	2.034475	0.689	0.11
YA	0.08949033	0	0.448

APPENDICES

Appendix A: Backbone phylogeny (Newick format)

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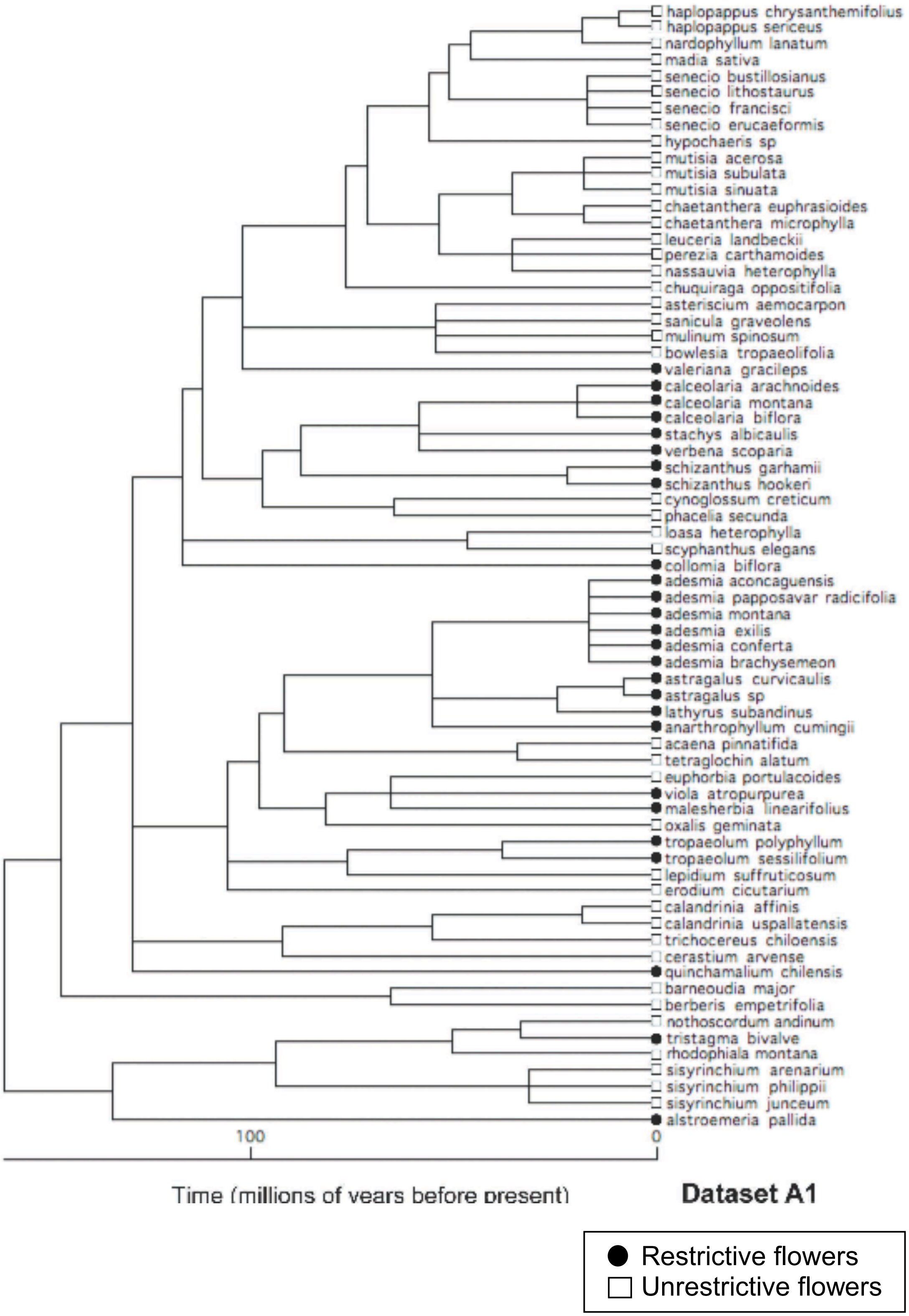
Appendix B: Dataset phylogenies and floral morphology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senecio erucaeformis
hypochaeris sp
mutisia acerosa
mutisia subulata
mutisia sinuata
chaetanthera euphrasioides
chaetanthera microphylla
leuceria landbeckii
perezia carthamoides
nassauvia heterophylla
chuquiraga oppositifolia
asteriscium aemocarpon
sanicula graveolens
mulinum spinosum
bowlesia tropaeolifolia
valeriana gracileps
calceolaria arachnoides
calceolaria montana
calceolaria biflora
stachys albicaulis
verbena scoparia
schizanthus garhamii
schizanthus hookeri
cynoglossum creticum
phacelia secunda
loasa heterophylla
scyphanthus elegans
collomia biflora
adesmia aconcaguensis
adesmia papposavar radicifolia
adesmia montana
adesmia exilis
adesmia conferta
adesmia brachysemeon
astragalus curvicaulis
astragalus sp
lathyrus subandinus
anarthrophyllum cumingii
acaena pinnatifida
tetraglochin alatum
euphorbia portulacoides
viola atropurpurea
malesherbia linearifolius
oxalis geminata
tropaeolum polyphyllum
tropaeolum sessilifolium
lepidium suffruticosum
erodium cicutarium
calandrinia affinis
calandrinia uspallatensis
trichocereus chiloensis
cerastium arvense
quinchamalium chilensis
barneoudia major
berberis empetrifolia
nothoscordum andinum
tristagma bivalve
rhodophiala montana
sisyrinchium arenarium
sisyrinchium philippii
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alstroemeria pallida
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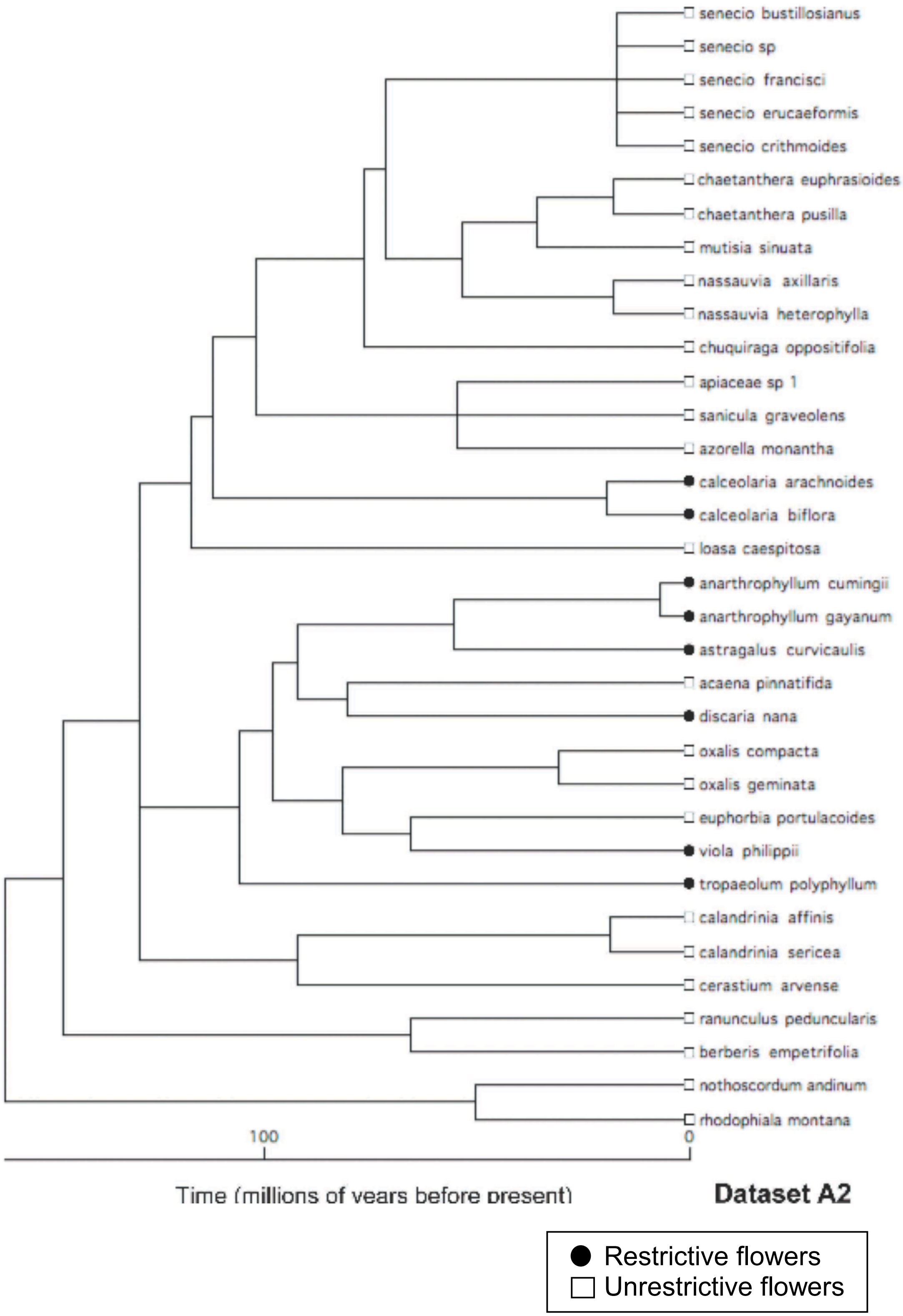
Time (millions of years before present)
Dataset A1
● Restrictive flowers
☐ Unrestrictive flowers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mutisia sinuata
nassauvia axillaris
nassauvia heterophylla
chuquiraga oppositifolia
apiaceae sp 1
sanicula graveolens
azorella monantha
calceolaria arachnoides
calceolaria biflora
loasa caespitosa
anarthrophyllum cumingii
anarthrophyllum gayanum
astragalus curvicaulis
acaena pinnatifida
discaria nana
oxalis compacta
oxalis geminata
euphorbia portulacoides
viola philippii
tropaeolum polyphyllum
calandrinia affinis
calandrinia sericea
cerastium arvense
ranunculus peduncularis
berberis empetrifolia
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rhodophiala montana
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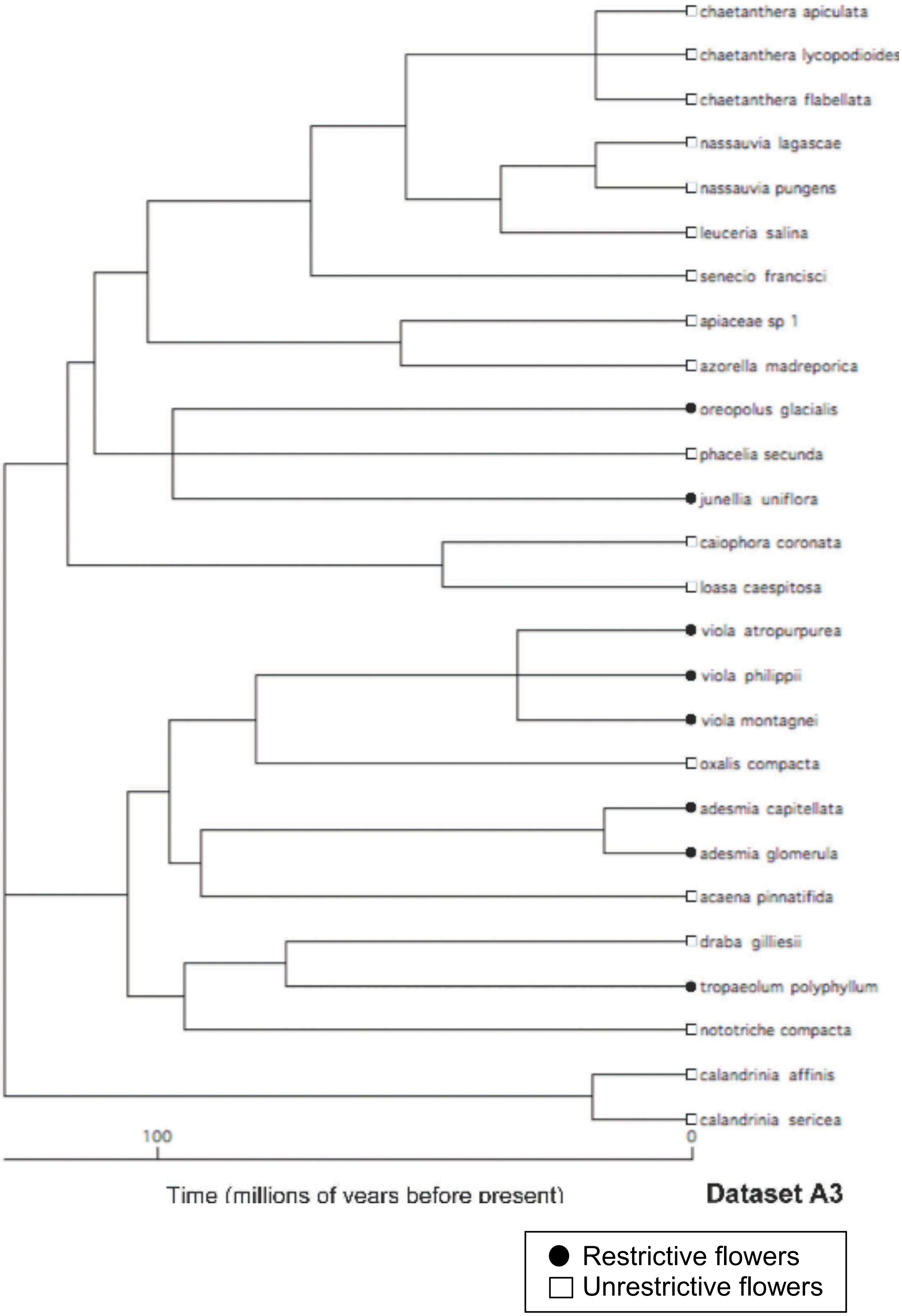
Time (millions of years before present)
Dataset A2
● Restrictive flowers
☐ Unrestrictive flowers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leuceria salina
senecio francisci
apiaceae sp 1
azorella madreporica
oreopolus glacialis
phacelia secunda
junellia uniflora
caiophora coronata
loasa caespitosa
viola atropurpurea
viola philippii
viola montagnei
oxalis compacta
adesmia capitellata
adesmia glomerula
acaena pinnatifida
draba gilliesii
tropaeolum polyphyllum
nototriche compacta
calandrinia affinis
calandrinia sericea
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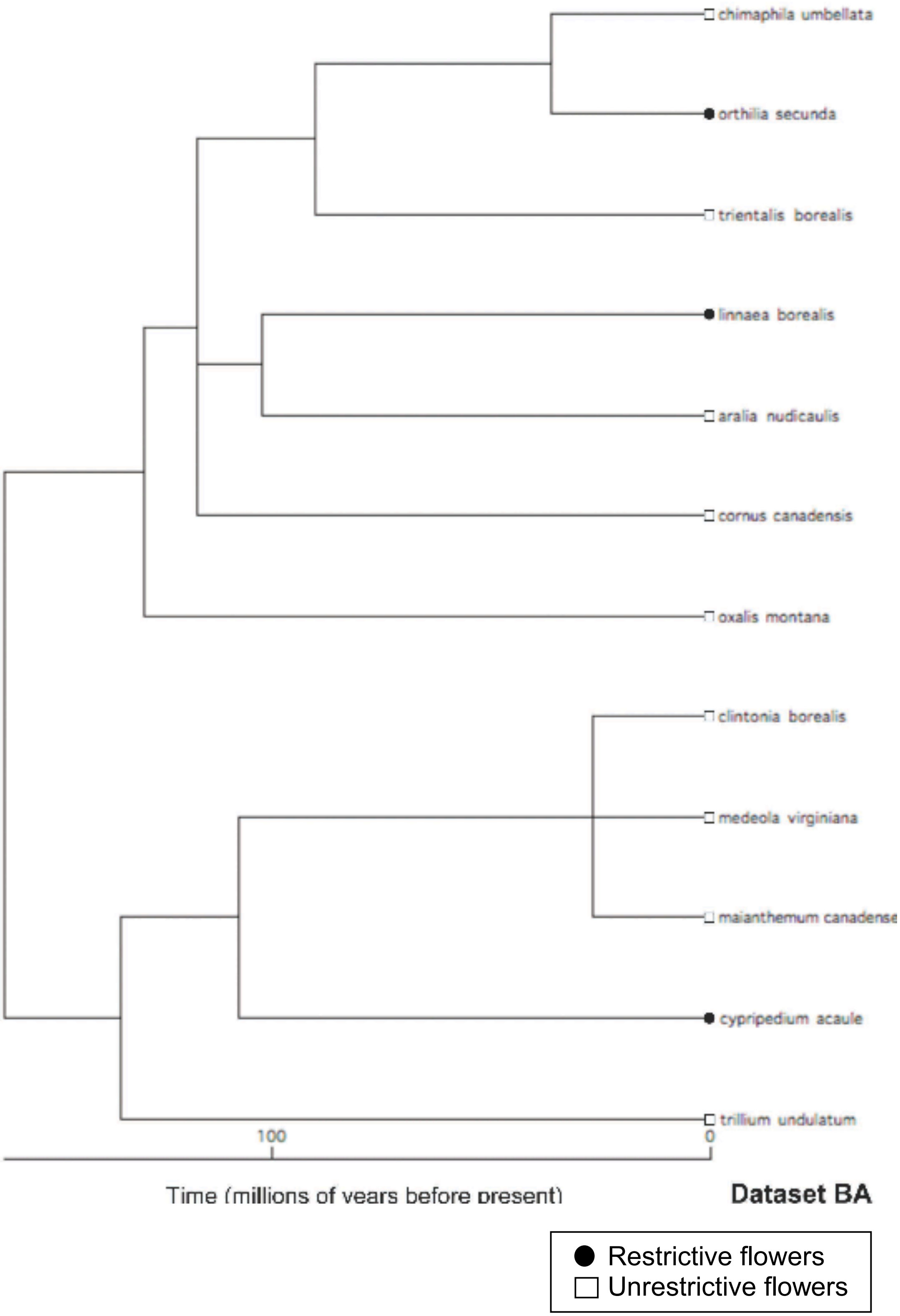
Time (millions of years before present)
● Restrictive flowers
□ Unrestrictive flowers

Dataset A3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aralia nudicaulis
cornus canadensis
oxalis montana
clintonia borealis
medeola virginiana
maianthemum canadense
cypripedium acaule
trillium undulatum
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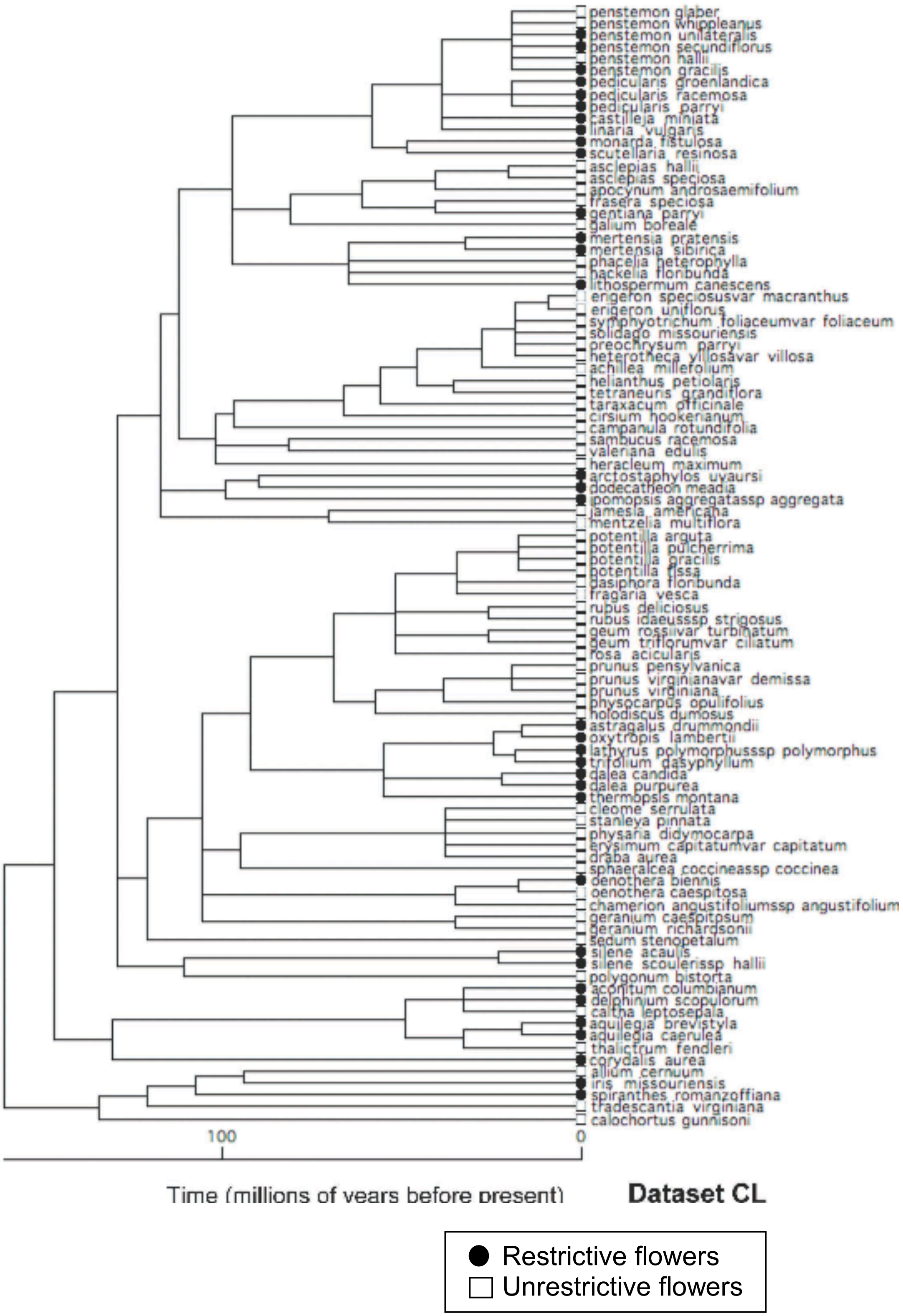
Time (millions of years before present)
Dataset BA
● Restrictive flowers
□ Unrestrictive flowers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penstemon whippleanus
penstemon unilateralis
penstemon secundiflorus
penstemon hallii
penstemon gracilis
pedicularis groenlandica
pedicularis racemosa
pedicularis parryi
castilleja miniata
linaria vulgaris
monarda fistulosa
scutellaria resinosa
asclepias hallii
asclepias speciosa
apocynum androsaemifolium
frasera speciosa
gentiana parryi
galium boreale
mertensia pratensis
mertensia sibirica
phacelia heterophylla
hackelia floribunda
lithospermum canescens
erigeron speciosusvar macranthus
erigeron uniflorus
symphyotrichum foliaceumvar foliaceum
solidago missouriensis
oreochrysum parryi
heterotheca villosavar villosa
achillea millefolium
helianthus petiolaris
tetraneuris grandiflora
taraxacum officinale
cirsium hookerianum
campanula rotundifolia
sambucus racemosa
valeriana edulis
heracleum maximum
arctostaphylos uvaursi
dodecatheon meadia
ipomopsis aggregatassp aggregata
jamesia americana
mentzelia multiflora
potentilla arguta
potentilla pulcherrima
potentilla gracilis
potentilla fissa
dasiphora floribunda
fragaria vesca
rubus deliciosus
rubus idaeusssp strigosus
geum rossiivar turbinatum
geum triflorumvar ciliatum
rosa acicularis
prunus pensylvanica
prunus virginianavar demissa
prunus virginiana
physocarpus opulifolius
holodiscus dumosus
astragalus drummondii
oxytropis lambertii
lathyrus polymorphusssp polymorphus
trifolium dasyphyllum
dalea candida
dalea purpurea
thermopsis montana
cleome serrulata
stanleya pinnata
physaria didymocarpa
erysimum capitatumvar capitatum
draba aurea
sphaeralcea coccineassp coccinea
oenothera biennis
oenothera caespitosa
chamerion angustifoliumssp angustifolium
geranium caespitosum
geranium richardsonii
sedum stenopetalum
silene acaulis
silene scoulerissp hallii
polygonum bistorta
aconitum columbianum
delphinium scopulorum
caltha leptosepala
aquilegia brevistyla
aquilegia caerulea
thalictrum fendleri
corydalis aurea
allium cernuum
iris missouriensis
spiranthes romanzoffiana
tradescantia virginiana
calochortus gunnisoni
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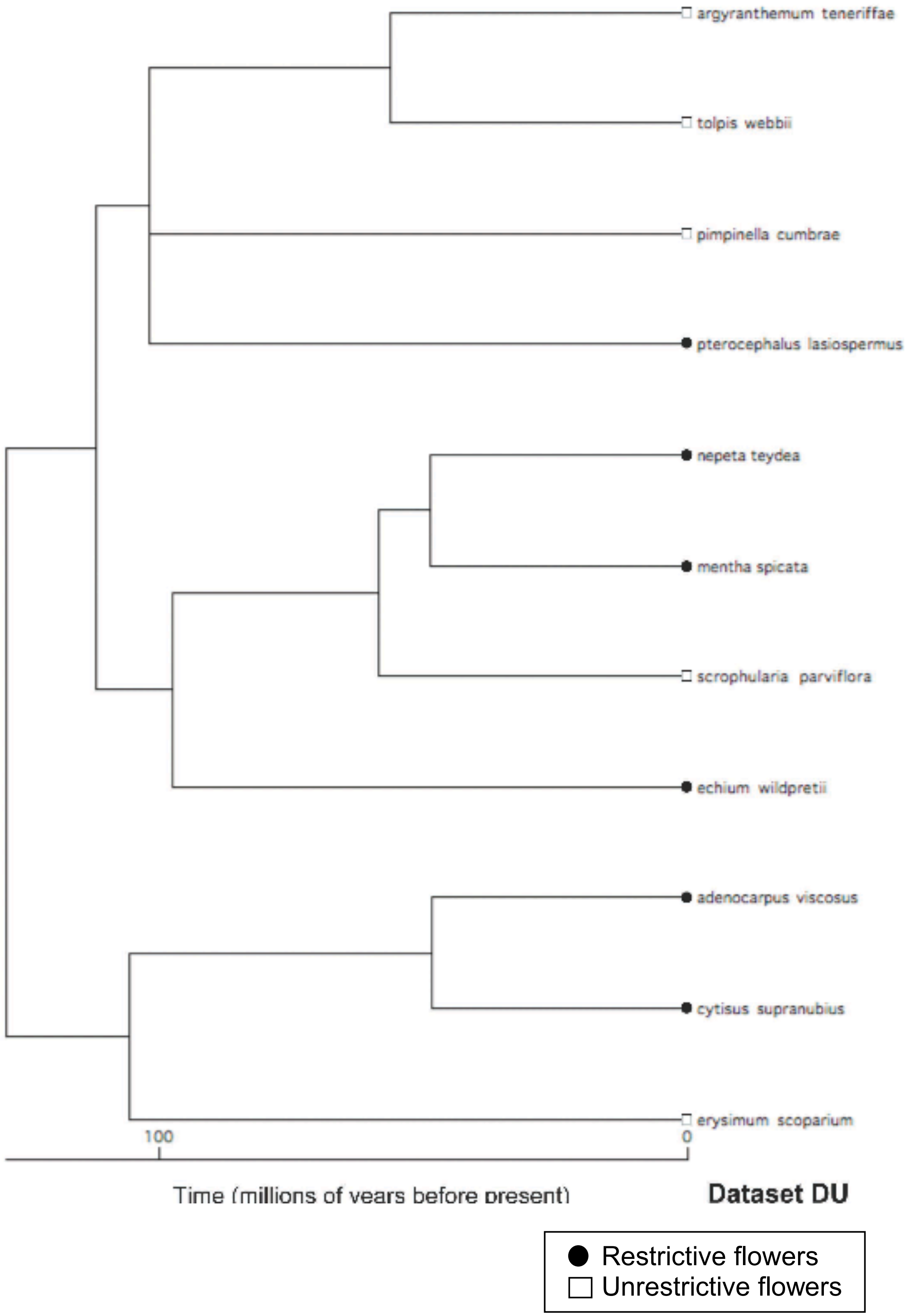
Time (millions of years before present)
Dataset CL
● Restrictive flowers
□ Unrestrictive flowers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pimpinella cumbrae
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mentha spicata
scrophularia parviflora
echium wildpretii
adenocarpus viscosus
cytisus supranubius
erysimum scoparium
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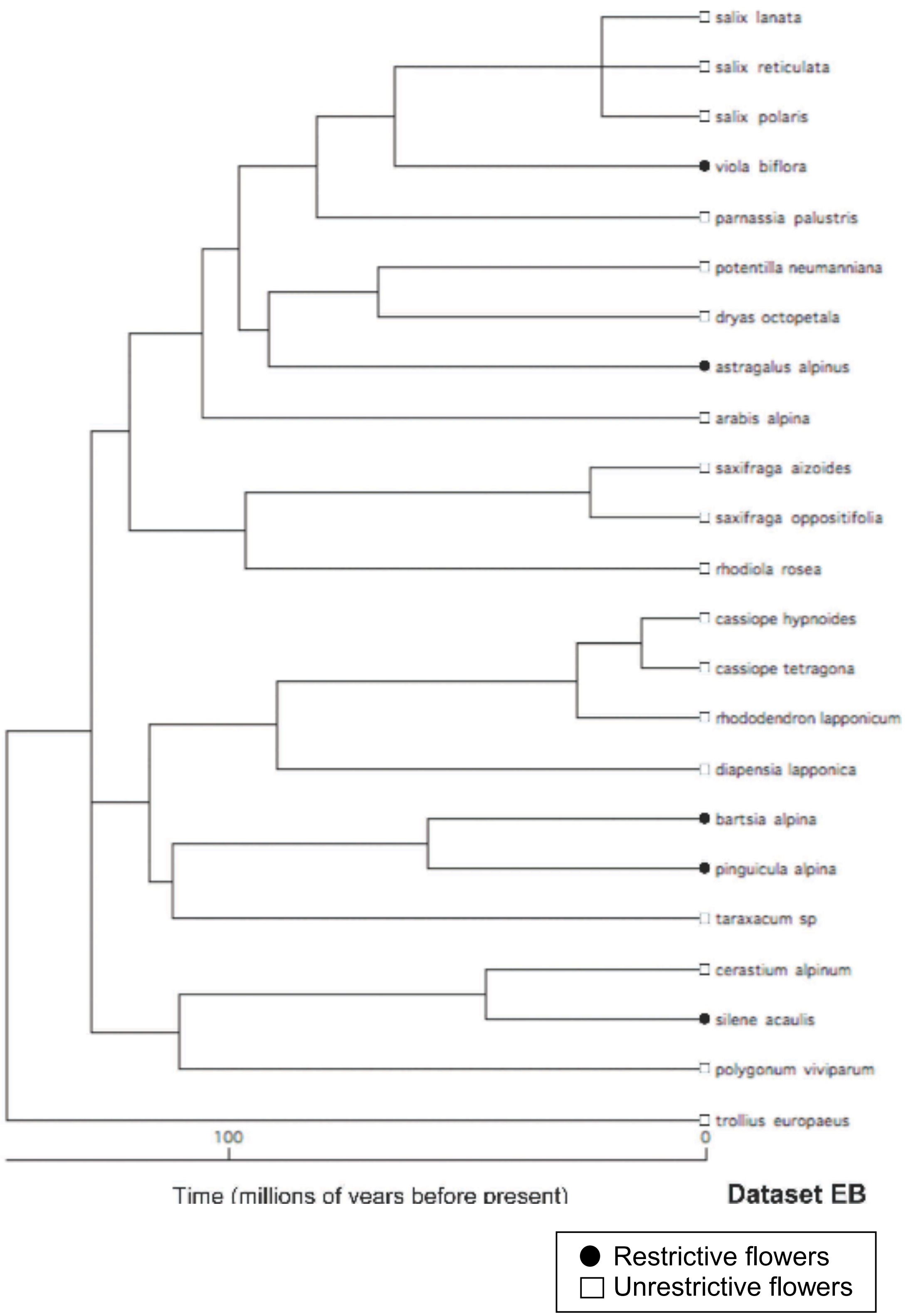
Time (millions of years before present)
Dataset DU
● Restrictive flowers
☐ Unrestrictive flowers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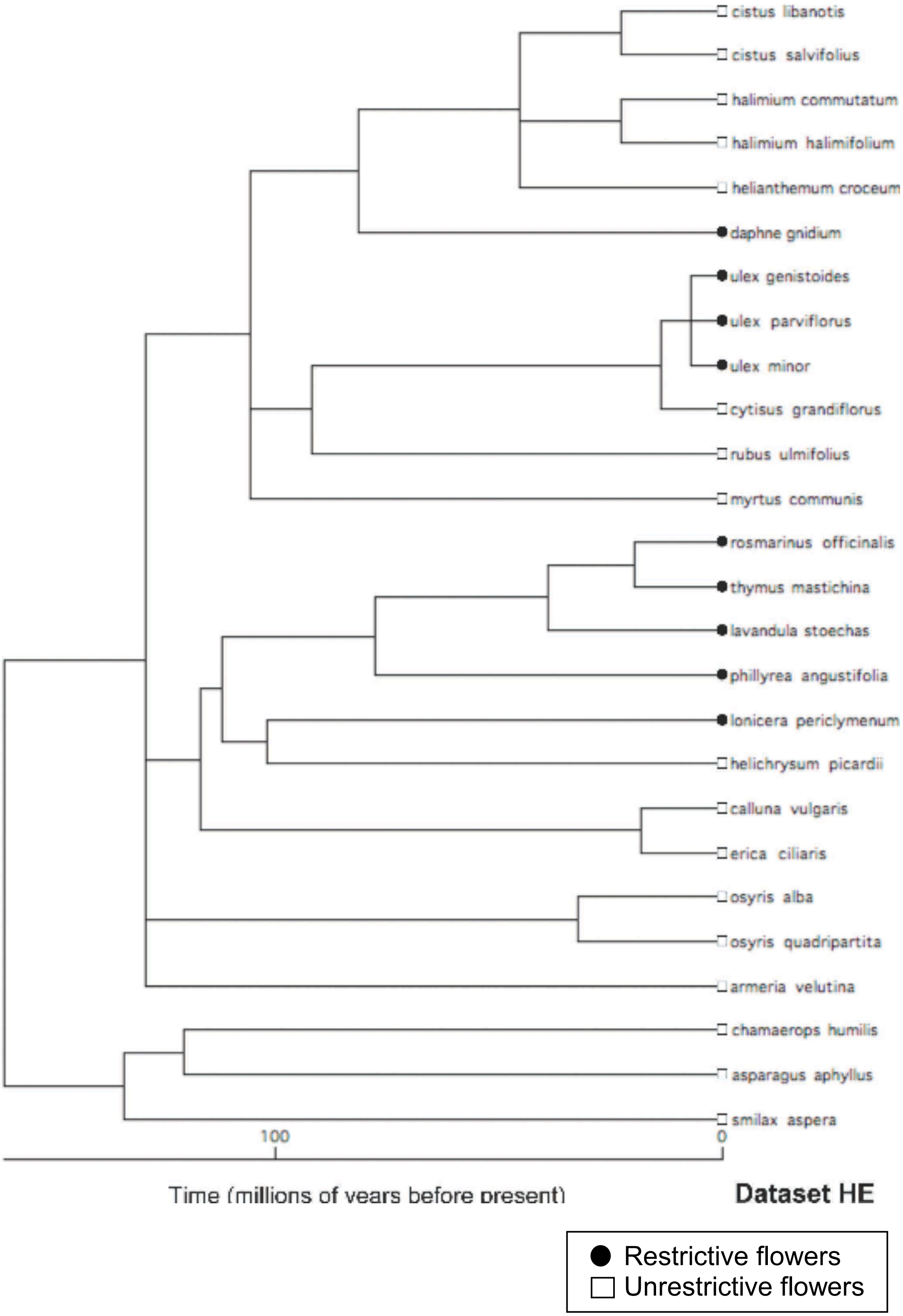
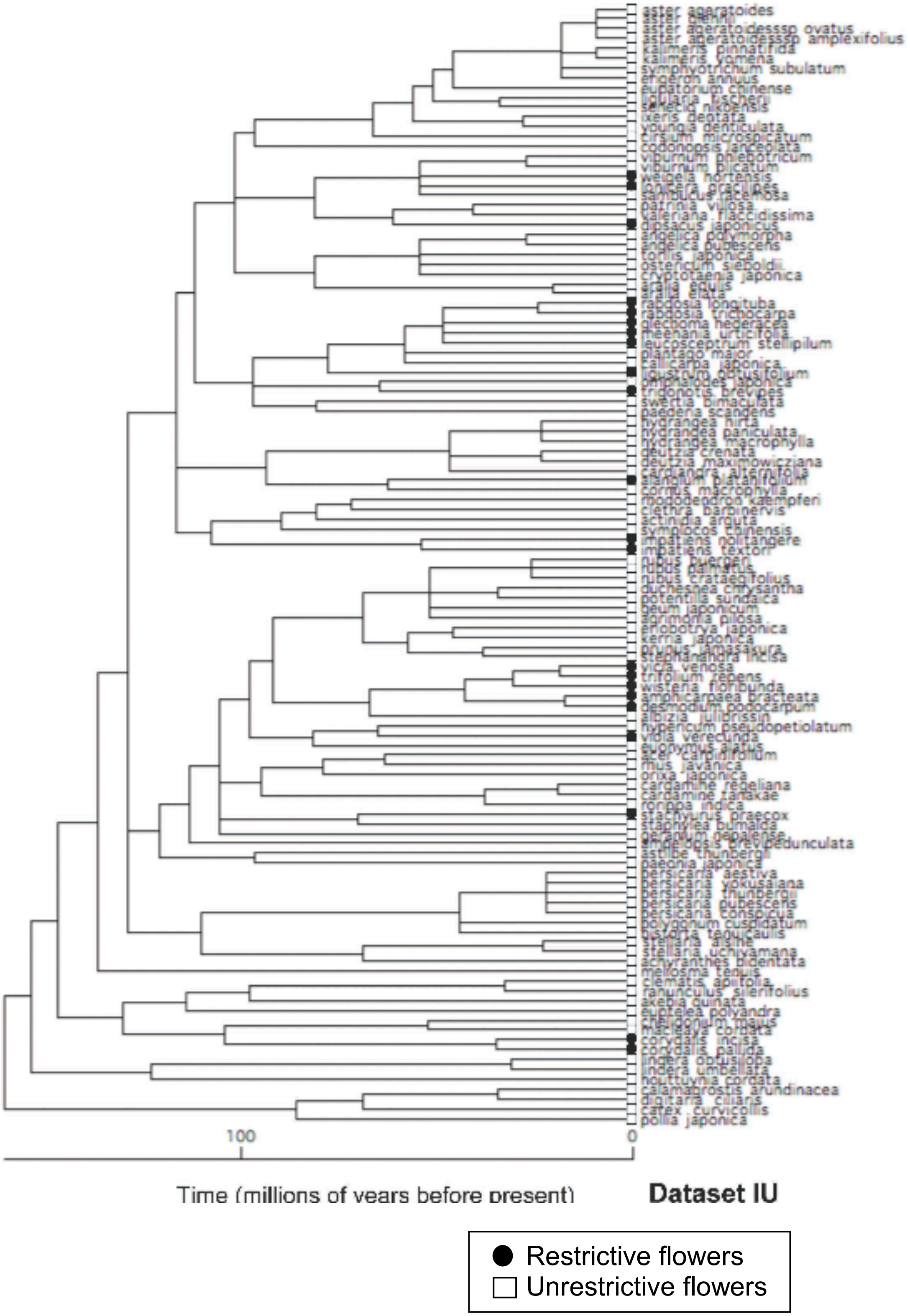
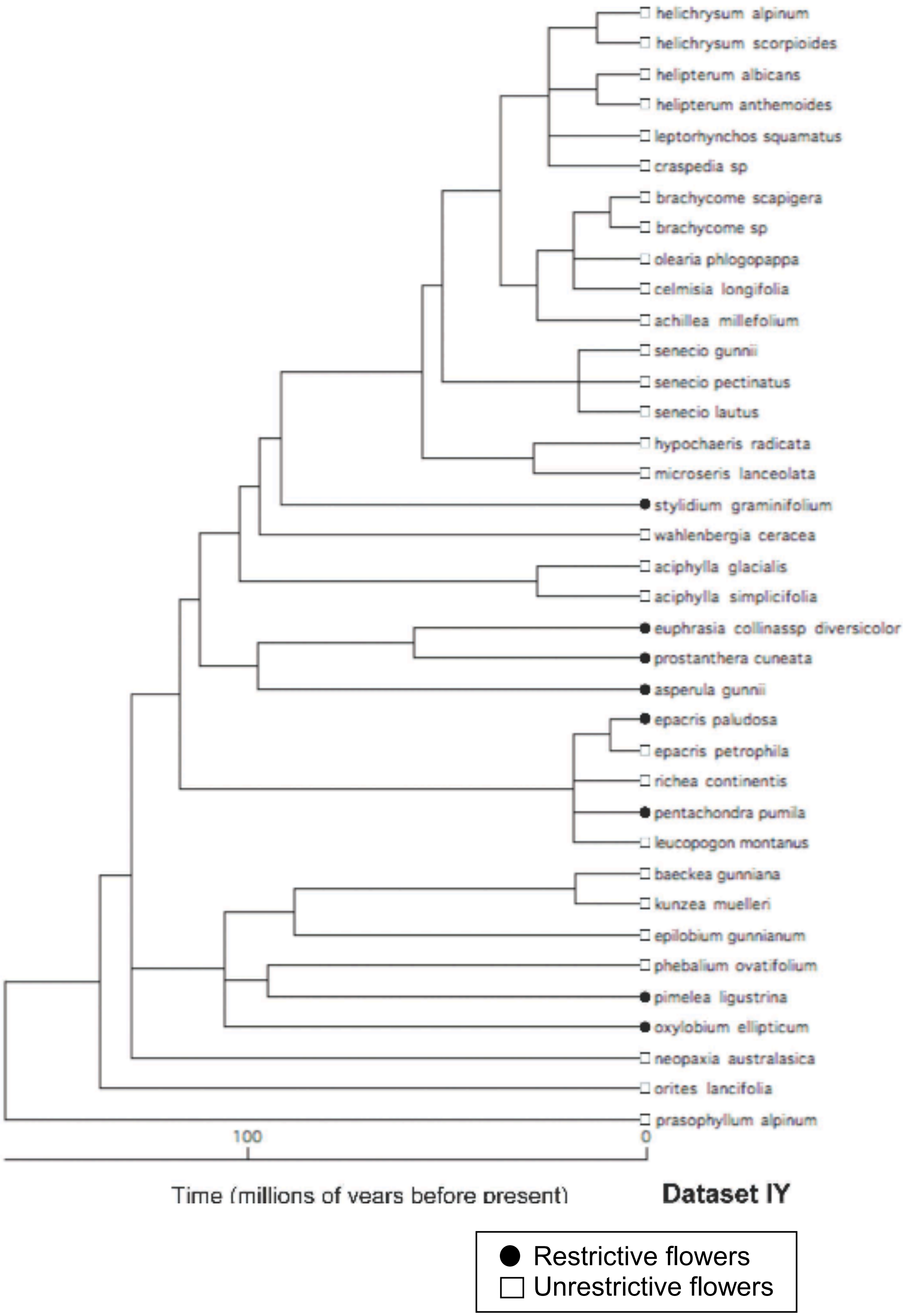
astragalus alpinus
arabis alpina
saxifraga aizoides
saxifraga oppositifolia
rhodiola rosea
cassiope hypnoides
cassiope tetragona
rhododendron lapponicum
diapensia lapponica
bartsia alpina
pinguicula alpina
taraxacum sp
cerastium alpinum
silene acaulis
polygonum viviparum
trollius europaeus
100
0
Time (millions of years before present)
Dataset EB
● Restrictive flowers
☐ Unrestrictive flowers


☐ cistus libanotis
☐ cistus salvifolius
☐ halimium commutatum
☐ halimium halimifolium
☐ helianthemum croceum
● daphne gnidium
● ulex genistoides
● ulex parviflorus
● ulex minor
☐ cytisus grandiflorus
☐ rubus ulmifolius
☐ myrtus communis
● rosmarinus officinalis
● thymus mastichina
● lavandula stoechas
● phillyrea angustifolia
● lonicera periclymenum
☐ helichrysum picardii
☐ calluna vulgaris
☐ erica ciliaris
☐ osyris alba
☐ osyris quadripartita
☐ armeria velutina
☐ chamaerops humilis
☐ asparagus aphyllus
☐ smilax aspera
100
0
Time (millions of years before present)
● Restrictive flowers
☐ Unrestrictive flowers

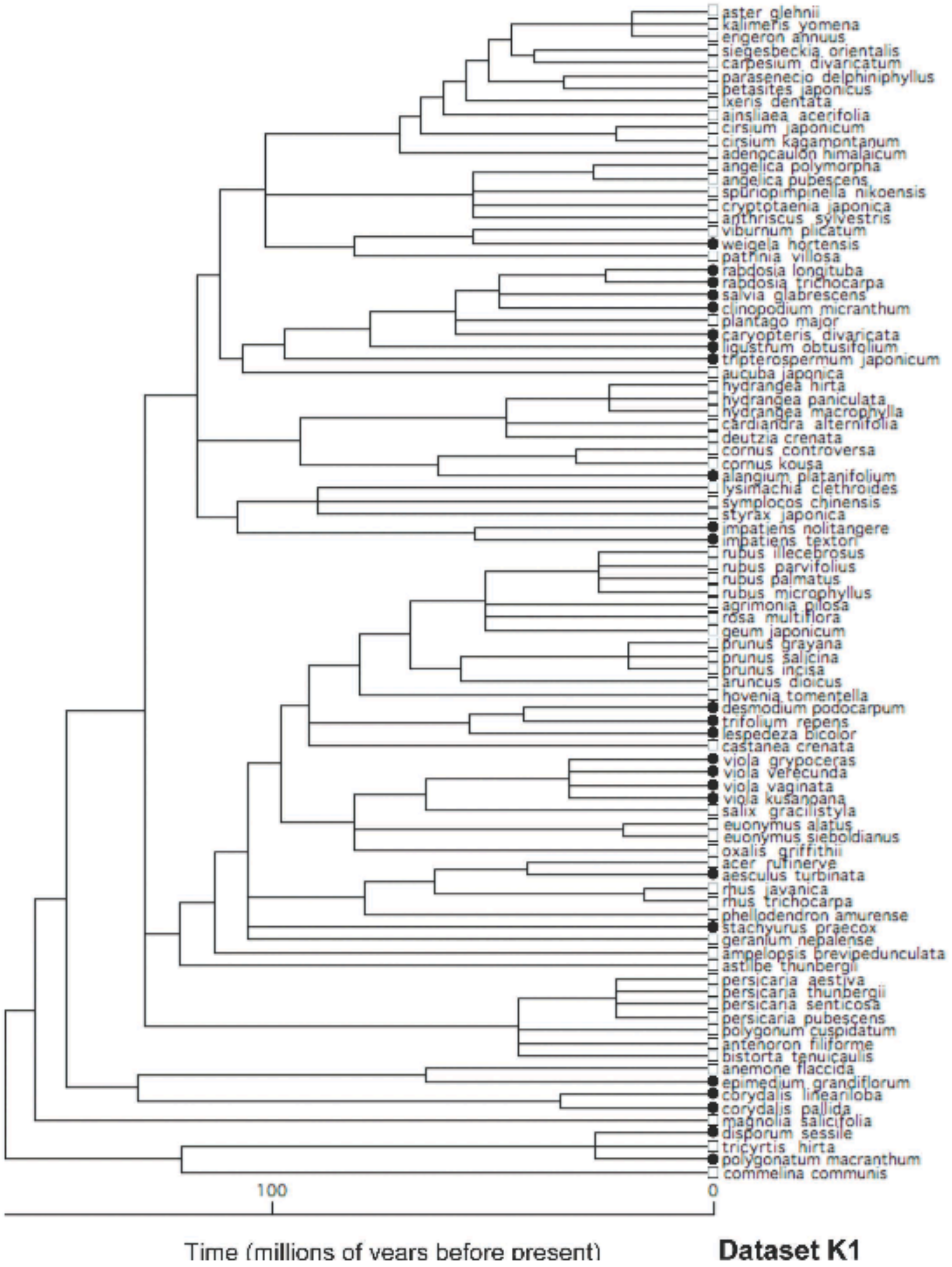
Dataset HE


aster ageratoides
aster glehnii
aster ageratoidesssp ovatus
aster ageratoidesssp amplexifolius
kalimeris pinnatifida
kalimeris yomena
symphyotrichum subulatum
erigeron annuus
eupatorium chinense
ligularia fischeri
senecio nikoensis
ixeris dentata
youngia denticulata
cirsium microspicatum
codonopsis lanceolata
viburnum phlebotricum
viburnum plicatum
weigela hortensis
lonicera gracilipes
sambucus racemosa
patrinia villosa
valeriana flaccidissima
dipsacus japonicus
angelica polymorpha
angelica pubescens
torilis japonica
ostericum sieboldii
cryptotaenia japonica
aralia equlis
aralia elata
rabdosia longituba
rabdosia trichocarpa
glechoma hederacea
meehania urticifolia
leucosceptrum stellipilum
plantago major
callicarpa japonica
ligustrum obtusifolium
omphalodes japonica
trigonotis brevipes
swertia bimaculata
paederia scandens
hydrangea hirta
hydrangea paniculata
hydrangea macrophylla
deutzia crenata
deutzia maximowicziana
cardiandra alternifolia
alangium platanifolium
cornus macrophylla
rhododendron kaempferi
clethra barbinervis
actinidia arguta
symplocos chinensis
impatiens nolitangere
impatiens textori
rubus buergeri
rubus palmatus
rubus crataegifolius
duchesnea chrysantha
potentilla sundaica
geum japonicum
agrimonia pilosa
eriobotrya japonica
kerria japonica
prunus jamasakura
stephanandra incisa
vicia venosa
trifolium repens
wisteria floribunda
amphicarpaea bracteata
desmodium podocarpum
albizia julibrissin
hypericum pseudopetiolatum
viola verecunda
euonymus alatus
acer carpinifolium
rhus javanica
orixa japonica
cardamine regeliana
cardamine tanakae
rorippa indica
stachyurus praecox
staphylea bumalda
geranium nepalense
ampelopsis brevipedunculata
astilbe thunbergii
paeonia japonica
persicaria aestiva
persicaria yokusaiana
persicaria thunbergii
persicaria pubescens
persicaria conspicua
polygonum cuspidatum
bistorta tenuicaulis
stellaria alsine
stellaria uchiyamana
achyranthes bidentata
meliosma tenuis
clematis apiifolia
ranunculus silerifolius
akebia quinata
euptelea polyandra
chelidonium majus
macleaya cordata
corydalis incisa
corydalis pallida
lindera obtusiloba
lindera umbellata
houttuynia cordata
calamagrostis arundinacea
digitaria ciliaris
carex curvicollis
pollia japonica
100
0
Time (millions of years before present)
● Restrictive flowers
☐ Unrestrictive flowers

Dataset IU

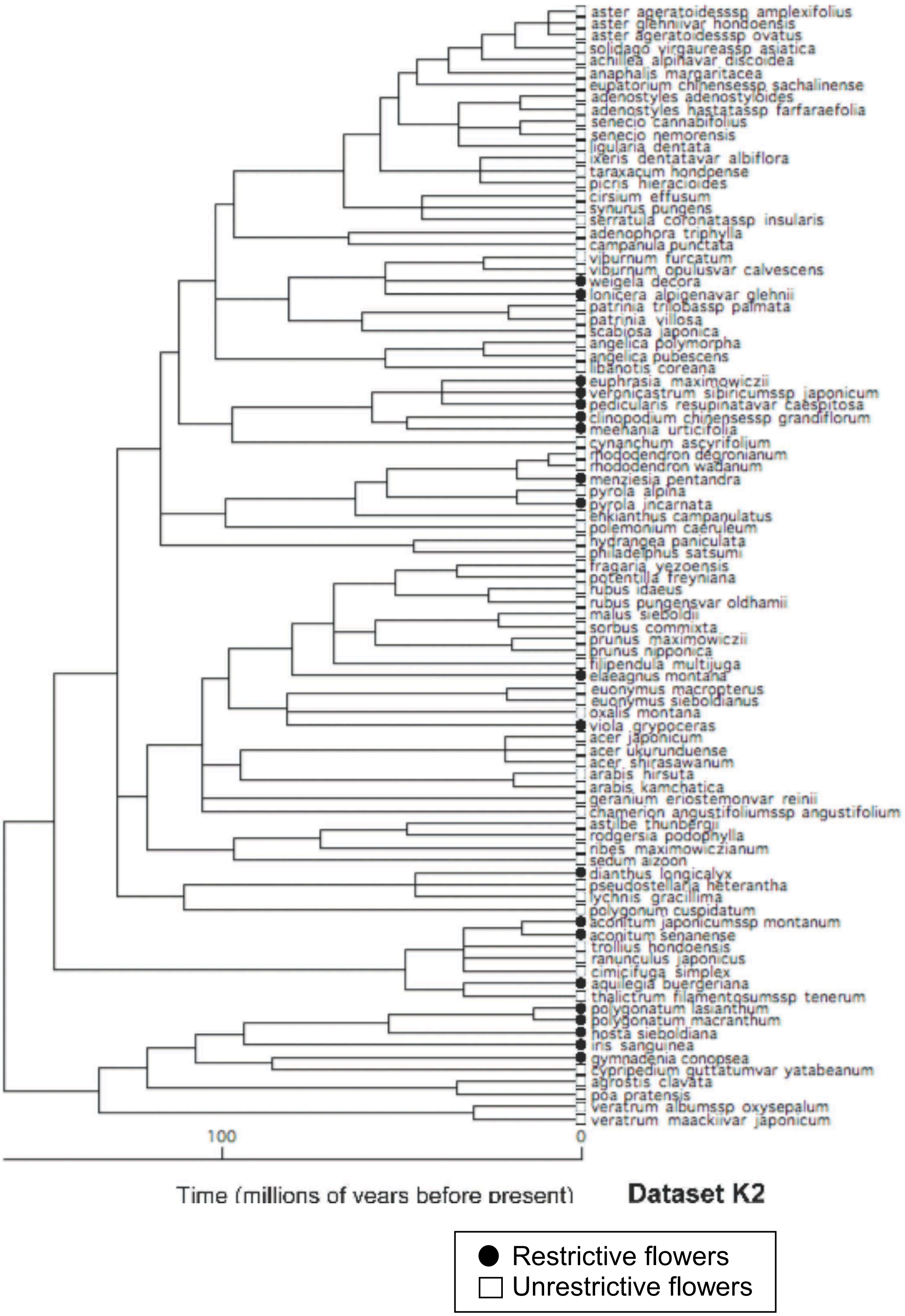

☐ helichrysum alpinum
☐ helichrysum scorpioides
☐ helipterum albicans
☐ helipterum anthemoides
☐ leptorhynchos squamatus
☐ craspedia sp
☐ brachycome scapigera
☐ brachycome sp
☐ olearia phlogopappa
☐ celmisia longifolia
☐ achillea millefolium
☐ senecio gunnii
☐ senecio pectinatus
☐ senecio lautus
☐ hypochaeris radicata
☐ microseris lanceolata
● stylidium graminifolium
☐ wahlenbergia ceracea
☐ aciphylla glacialis
☐ aciphylla simplicifolia
● euphrasia collinassp diversicolor
● prostanthera cuneata
● asperula gunnii
● epacris paludosa
☐ epacris petrophila
☐ richea continentis
● pentachondra pumila
☐ leucopogon montanus
☐ baeckea gunniana
☐ kunzea muelleri
☐ epilobium gunnianum
☐ phebalium ovatifolium
● pimelea ligustrina
● oxylobium ellipticum
☐ neopaxia australasica
☐ orites lancifolia
☐ prasophyllum alpinum
100
0
Time (millions of years before present)
● Restrictive flowers
☐ Unrestrictive flowers

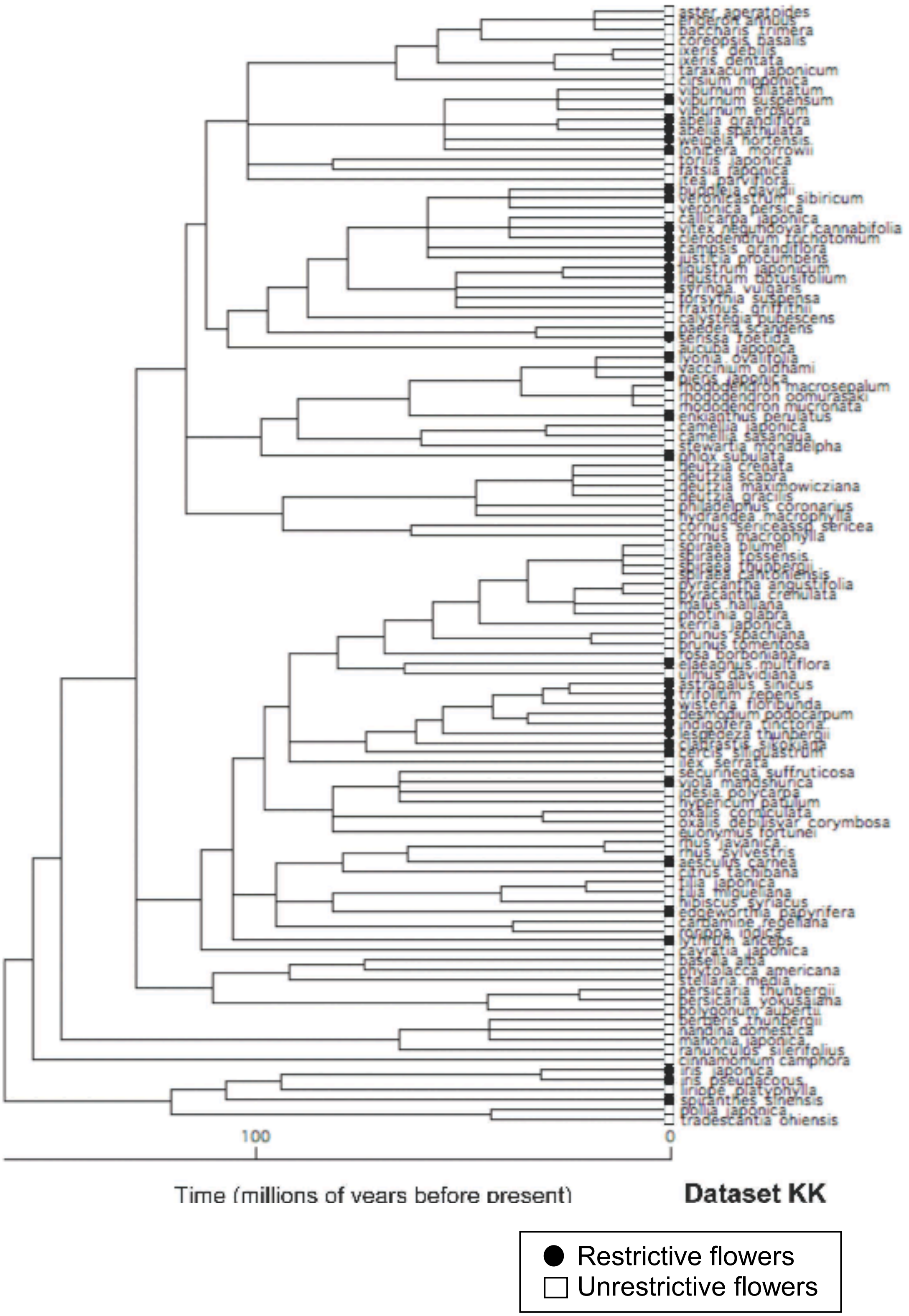
Dataset IY

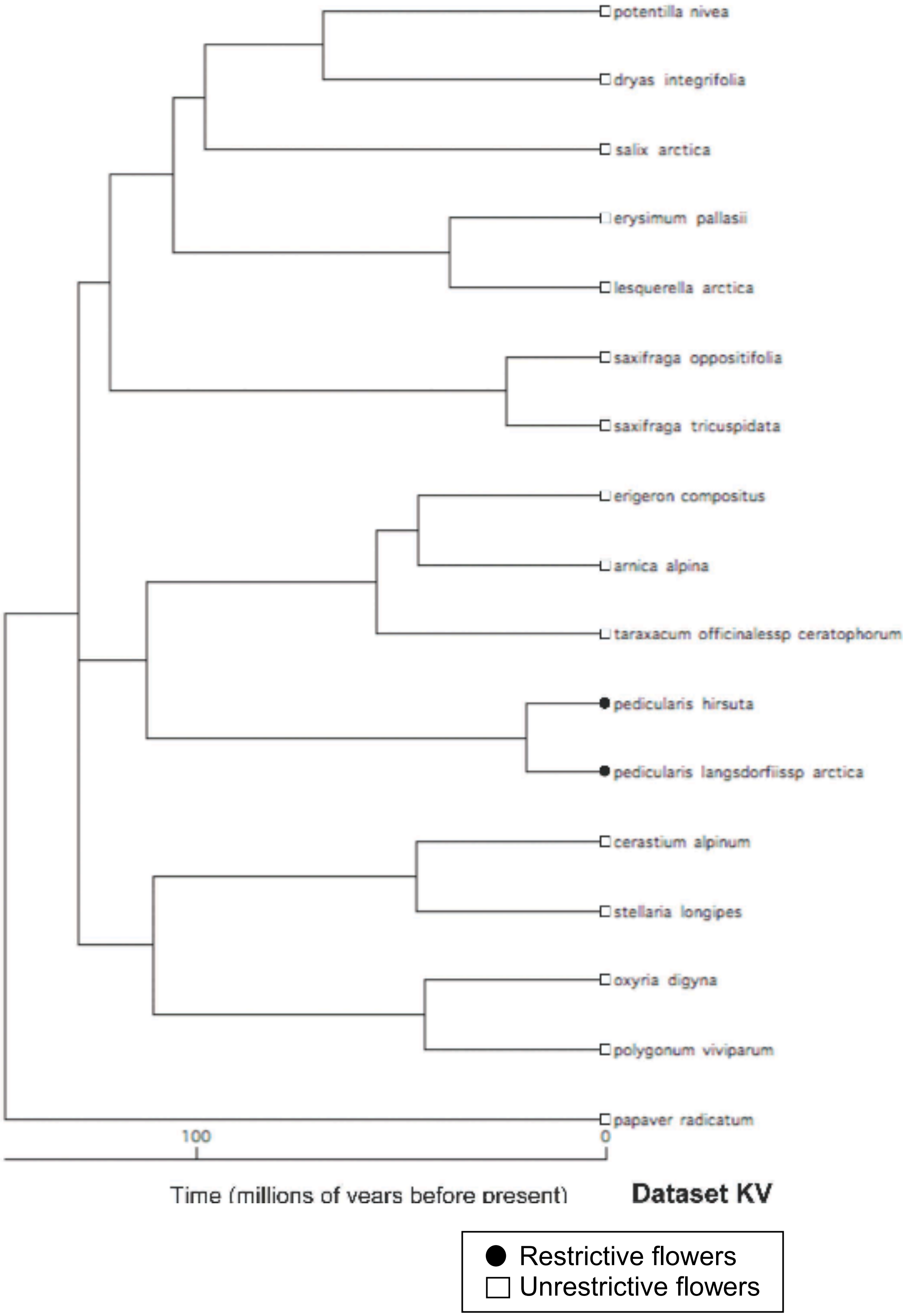


Dataset K1

● Restrictive flowers
☐ Unrestrictive flowers

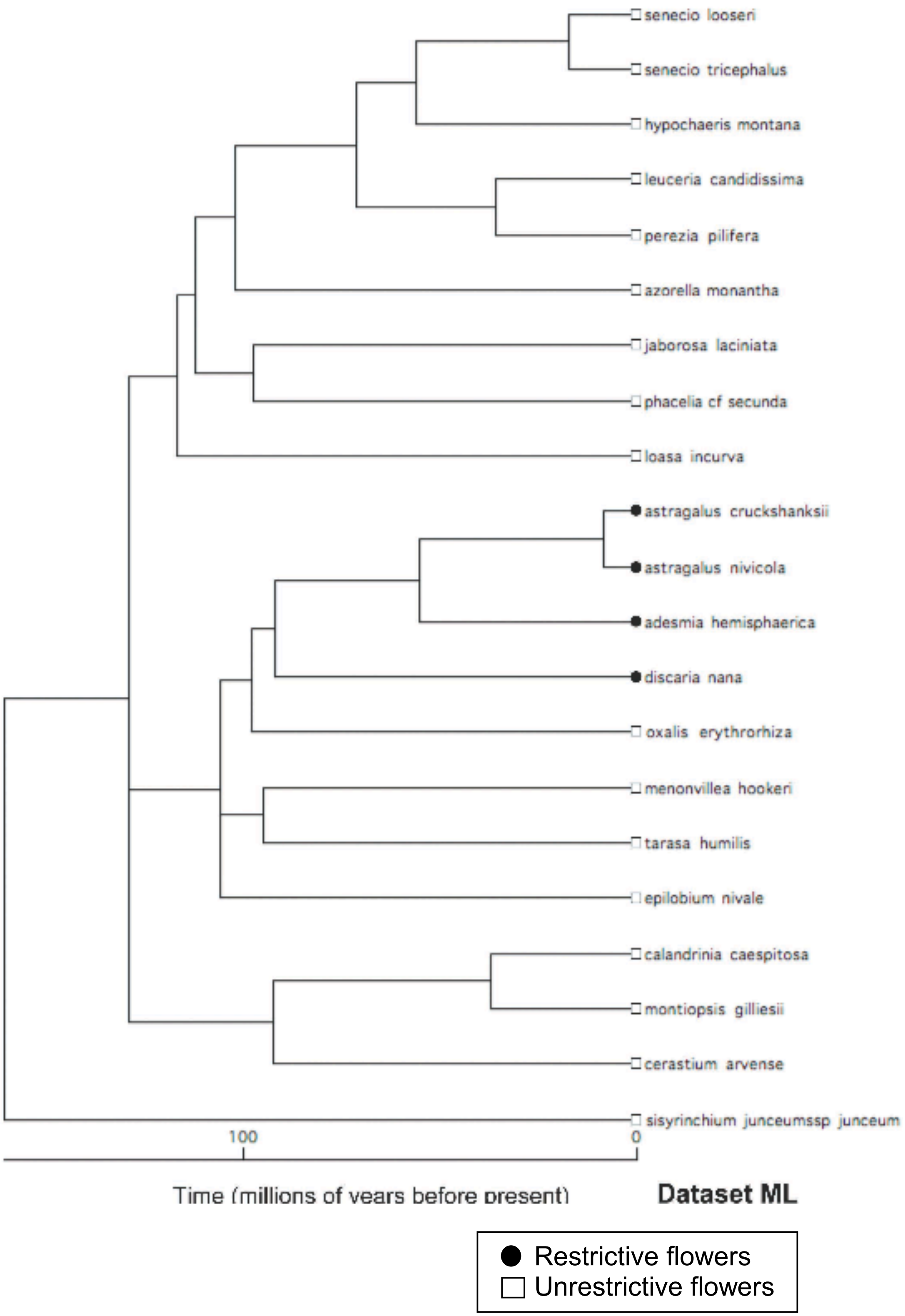

aster ageratoidesssp amplexifolius
aster glehniivar hondoensis
aster ageratoidesssp ovatus
solidago virgaureassp asiatica
achillea alpinavar discoidea
anaphalis margaritacea
eupatorium chinensessp sachalinense
adenostyles adenostyloides
adenostyles hastatassp farfaraefolia
senecio cannabifolius
senecio nemorensis
ligularia dentata
ixeris dentatavar albiflora
taraxacum hondoense
picris hieracioides
cirsium effusum
synurus pungens
serratula coronatassp insularis
adenophora triphylla
campanula punctata
viburnum furcatum
viburnum opulusvar calvescens
weigela decora
lonicera alpigenavar glehnii
patrinia trilobassp palmata
patrinia villosa
scabiosa japonica
angelica polymorpha
angelica pubescens
libanotis coreana
euphrasia maximowiczii
veronicastrum sibiricumssp japonicum
pedicularis resupinatavar caespitosa
clinopodium chinensessp grandiflorum
meehania urticifolia
cynanchum ascyrifolium
rhododendron degronianum
rhododendron wadanum
menziesia pentandra
pyrola alpina
pyrola incarnata
enkianthus campanulatus
polemonium caeruleum
hydrangea paniculata
philadelphus satsumi
fragaria yezoensis
potentilla freyniana
rubus idaeus
rubus pungensvar oldhamii
malus sieboldii
sorbus commixta
prunus maximowiczii
prunus nipponica
filipendula multijuga
elaeagnus montana
euonymus macropterus
euonymus sieboldianus
oxalis montana
viola grypoceras
acer japonicum
acer ukurunduense
acer shirasawanum
arabis hirsuta
arabis kamchatica
geranium eriostemonvar reinii
chamerion angustifoliumssp angustifolium
astilbe thunbergii
rodgersia podophylla
ribes maximowiczianum
sedum aizoon
dianthus longicalyx
pseudostellaria heterantha
lychnis gracillima
polygonum cuspidatum
aconitum japonicumssp montanum
aconitum senanense
trollius hondoensis
ranunculus japonicus
cimicifuga simplex
aquilegia buergeriana
thalictrum filamentosumssp tenerum
polygonatum lasianthum
polygonatum macranthum
hosta sieboldiana
iris sanguinea
gymnadenia conopsea
cypripedium guttatumvar yatabeanum
agrostis clavata
poa pratensis
veratrum albumssp oxysepalum
veratrum maackiivar japonicum
100
0
Time (millions of years before present)
Dataset K2
● Restrictive flowers
☐ Unrestrictive flowers

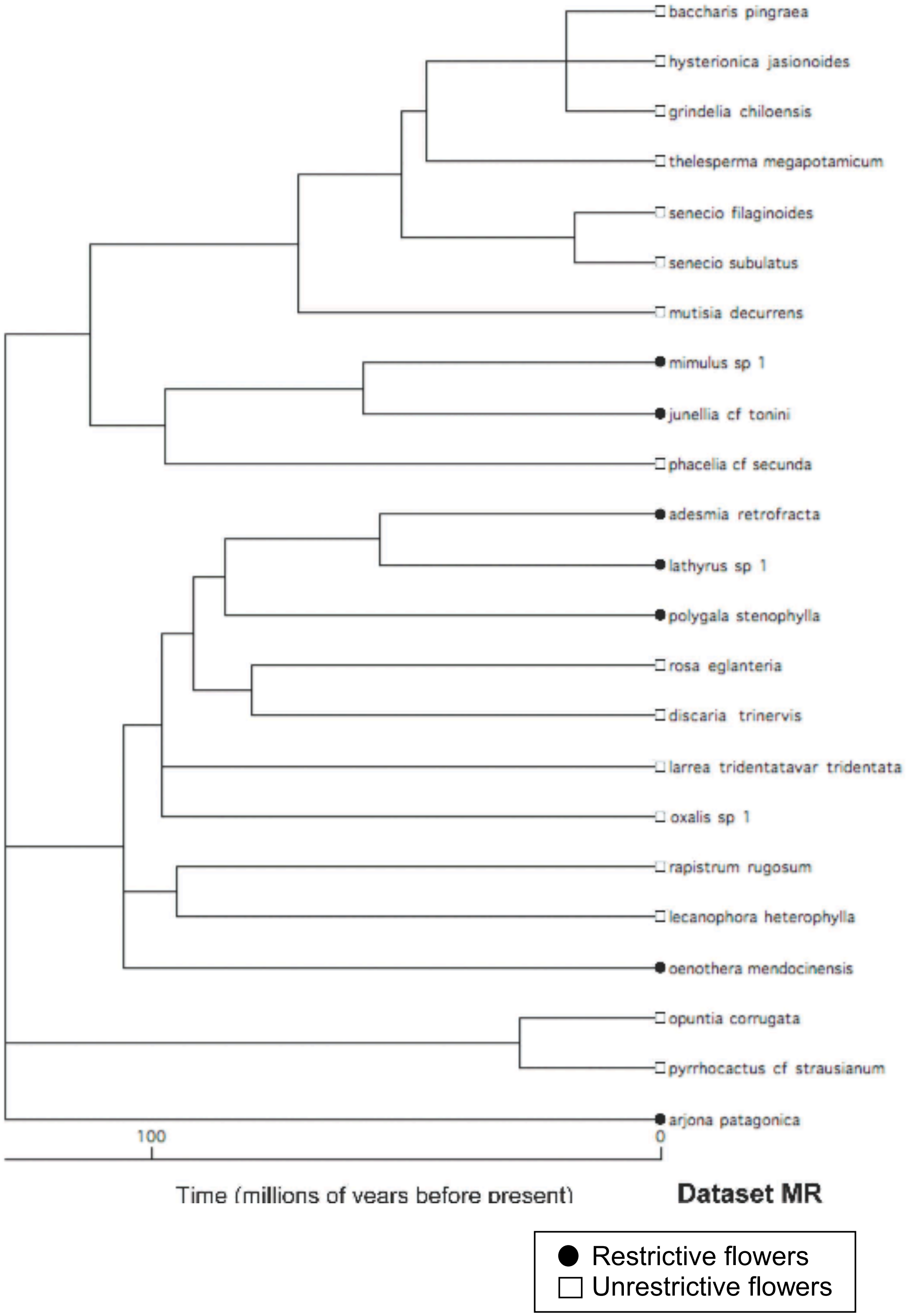

aster ageratoides
erigeron annuus
baccharis trimera
coreopsis basalis
ixeris debilis
ixeris dentata
taraxacum japonicum
cirsium nipponica
viburnum dilatatum
viburnum suspensum
viburnum erosum
abelia grandiflora
abelia spathulata
weigela hortensis
lonicera morrowii
torilis japonica
fatsia japonica
itea parviflora
buddleja davidii
veronicastrum sibiricum
veronica persica
callicarpa japonica
vitex negundovar cannabifolia
clerodendrum trichotomum
campsis grandiflora
justicia procumbens
ligustrum japonicum
ligustrum obtusifolium
syringa vulgaris
forsythia suspensa
fraxinus griffithii
calystegia pubescens
paederia scandens
serissa foetida
aucuba japonica
lyonia ovalifolia
vaccinium oldhami
pieris japonica
rhododendron macrosepalum
rhododendron oomurasaki
rhododendron mucronata
enkianthus perulatus
camellia japonica
camellia sasanqua
stewartia monadelpha
phlox subulata
deutzia crenata
deutzia scabra
deutzia maximowicziana
deutzia gracilis
philadelphus coronarius
hydrangea macrophylla
cornus sericeassp sericea
cornus macrophylla
spiraea blumei
spiraea tosaensis
spiraea thunbergii
spiraea cantoniensis
pyracantha angustifolia
pyracantha crenulata
malus halliana
photinia glabra
kerria japonica
prunus spachiana
prunus tomentosa
rosa borboniana
elaeagnus multiflora
ulmus davidiana
astragalus sinicus
trifolium repens
wisteria floribunda
desmodium podocarpum
indigofera tinctoria
lespedeza thunbergii
cladrastis sikokiana
cercis siliquastrum
ilex serrata
securinega suffruticosa
viola mandshurica
idesia polycarpa
hypericum patulum
oxalis corniculata
oxalis debilisvar corymbosa
euonymus fortunei
rhus javanica
rhus sylvestris
aesculus carnea
citrus tachibana
tilia japonica
tilia miqueliana
hibiscus syriacus
edgeworthia papyrifera
cardamine regeliana
rorippa indica
lythrum anceps
cayratia japonica
basella alba
phytolacca americana
stellaria media
persicaria thunbergii
persicaria yokusaiana
polygonum aubertii
berberis thunbergii
nandina domestica
mahonia japonica
ranunculus silerifolius
cinnamomum camphora
iris japonica
iris pseudacorus
liriope platyphylla
spiranthes sinensis
pollia japonica
tradescantia ohiensis
100
0
Time (millions of years before present)
Dataset KK
● Restrictive flowers
☐ Unrestrictive flowers

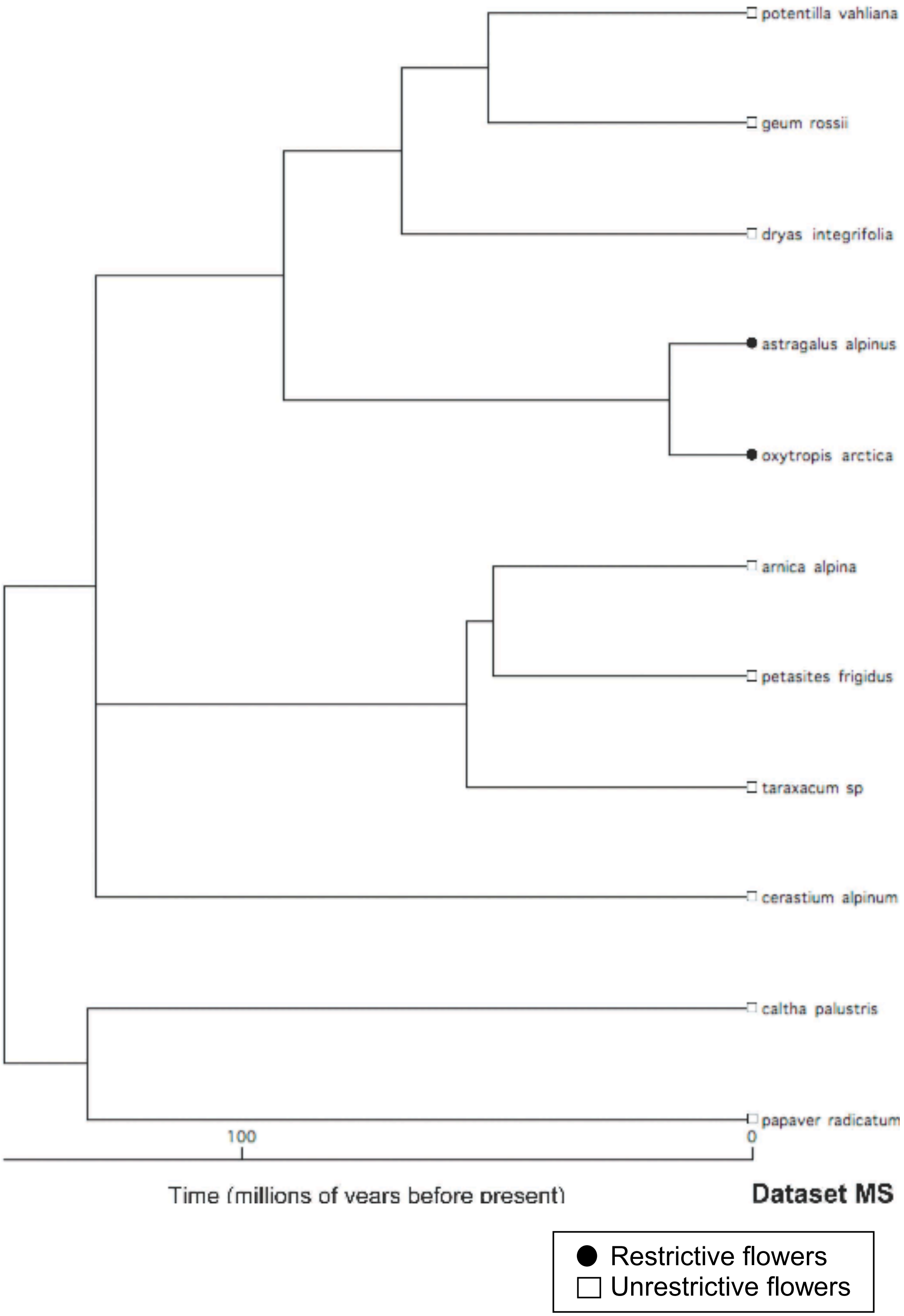


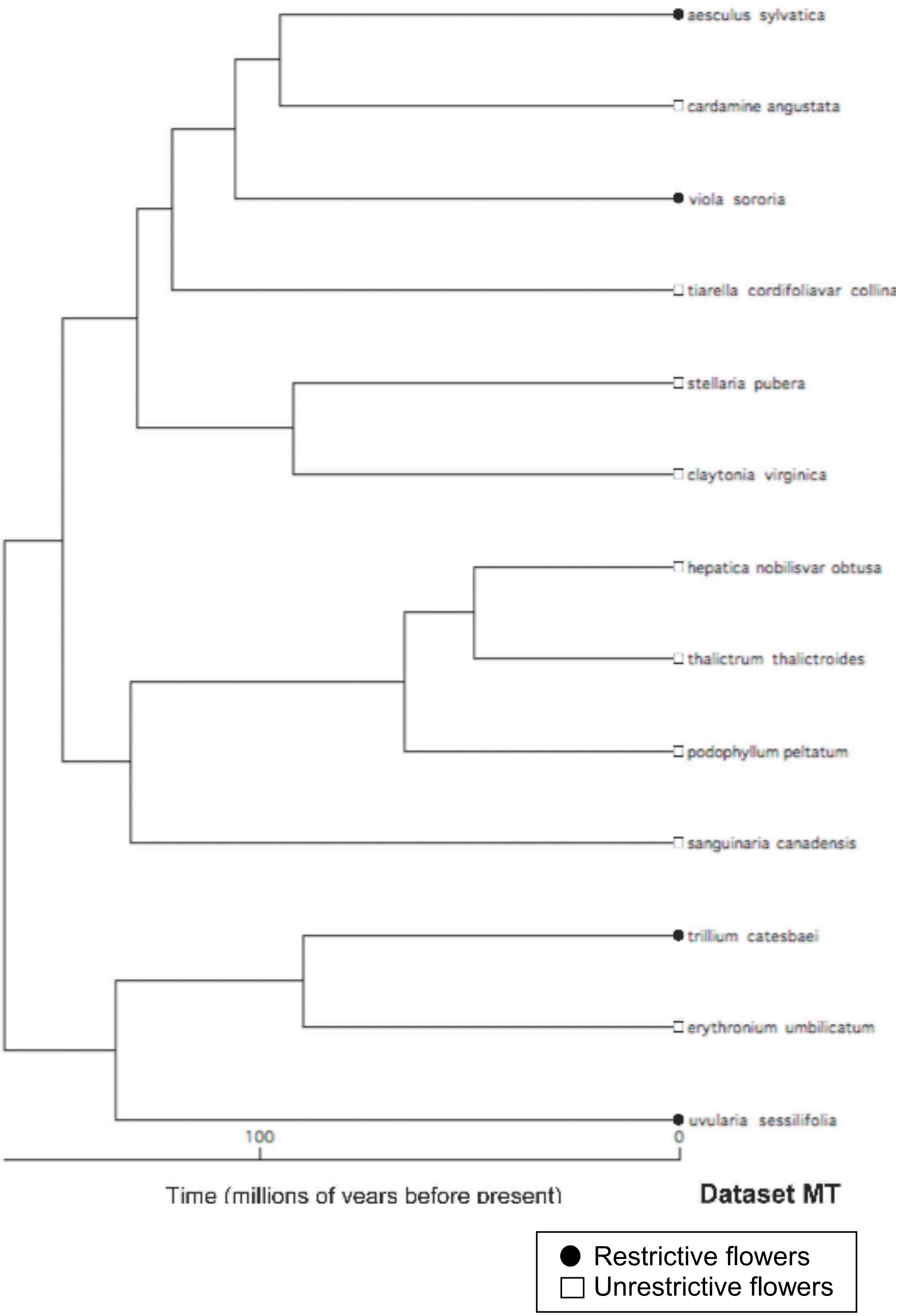
Dataset KV

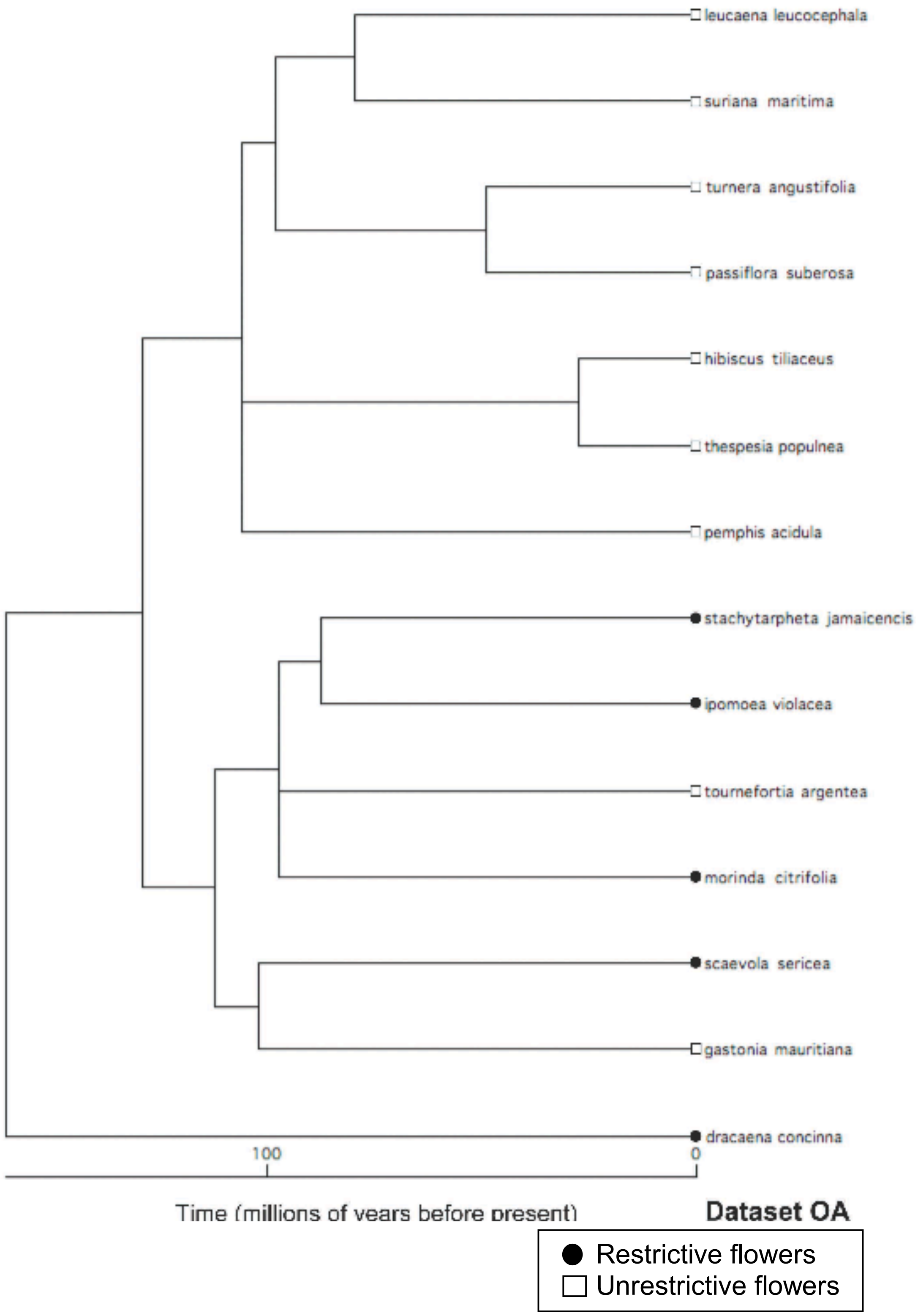
potentilla nivea
dryas integrifolia
salix arctica
erysimum pallasii
lesquerella arctica
saxifraga oppositifolia
saxifraga tricuspidata
erigeron compositus
arnica alpina
taraxacum officinalessp ceratophorum
pedicularis hirsuta
pedicularis langsdorfiissp arctica
cerastium alpinum
stellaria longipes
oxyria digyna
polygonum viviparum
papaver radicatum
100
0
Time (millions of years before present)
● Restrictive flowers
☐ Unrestrictive flowers

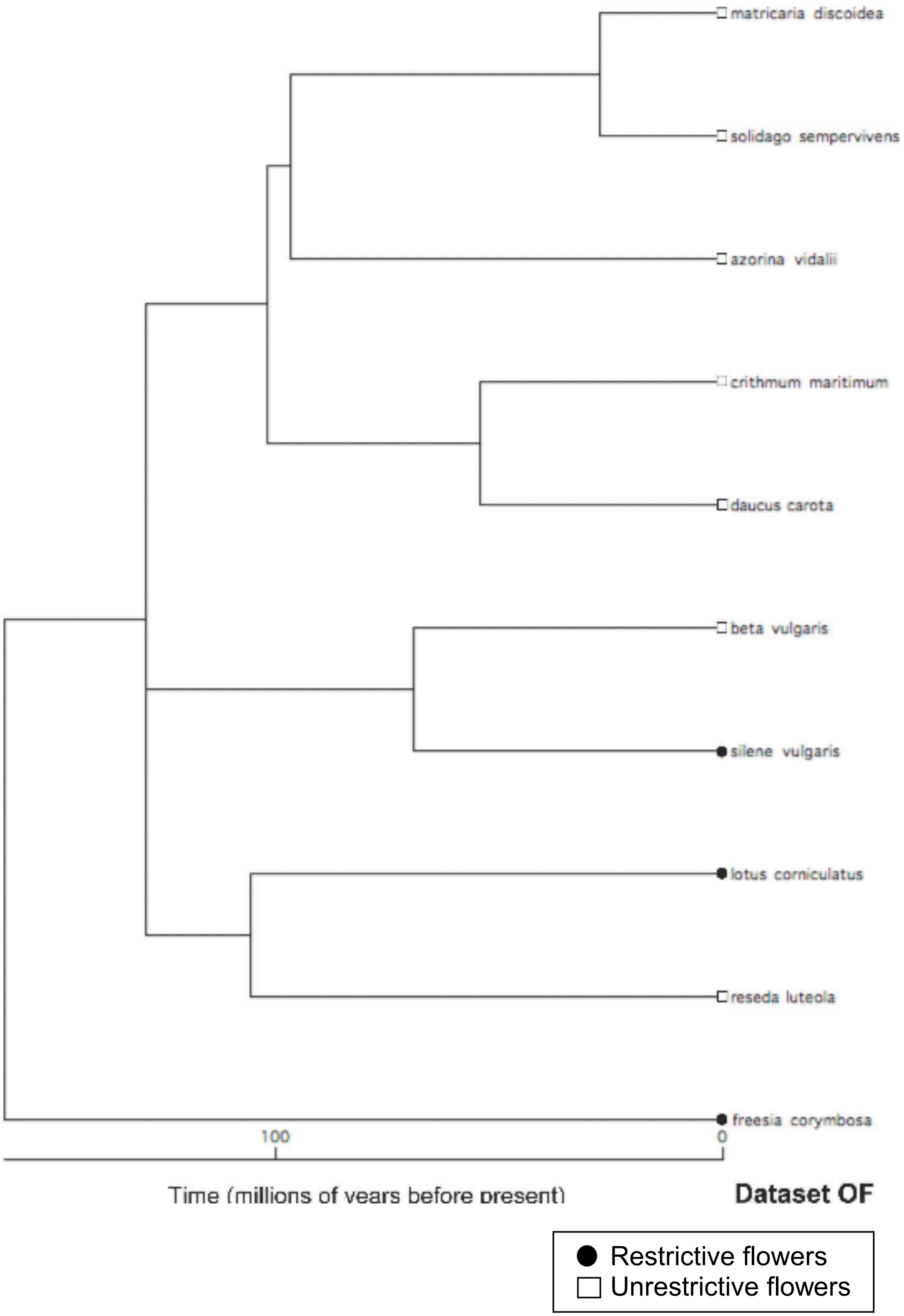

senecio looseri
senecio tricephalus
hypochaeris montana
leuceria candidissima
perezia pilifera
azorella monantha
jaborosa laciniata
phacelia cf secunda
loasa incurva
astragalus cruckshanksii
astragalus nivicola
adesmia hemisphaerica
discaria nana
oxalis erythrorhiza
menonvillea hookeri
tarasa humilis
epilobium nivale
calandrinia caespitosa
montiopsis gilliesii
cerastium arvense
sisyrinchium junceumssp junceum
100
0
Time (millions of years before present)
Dataset ML
● Restrictive flowers
☐ Unrestrictive flowers

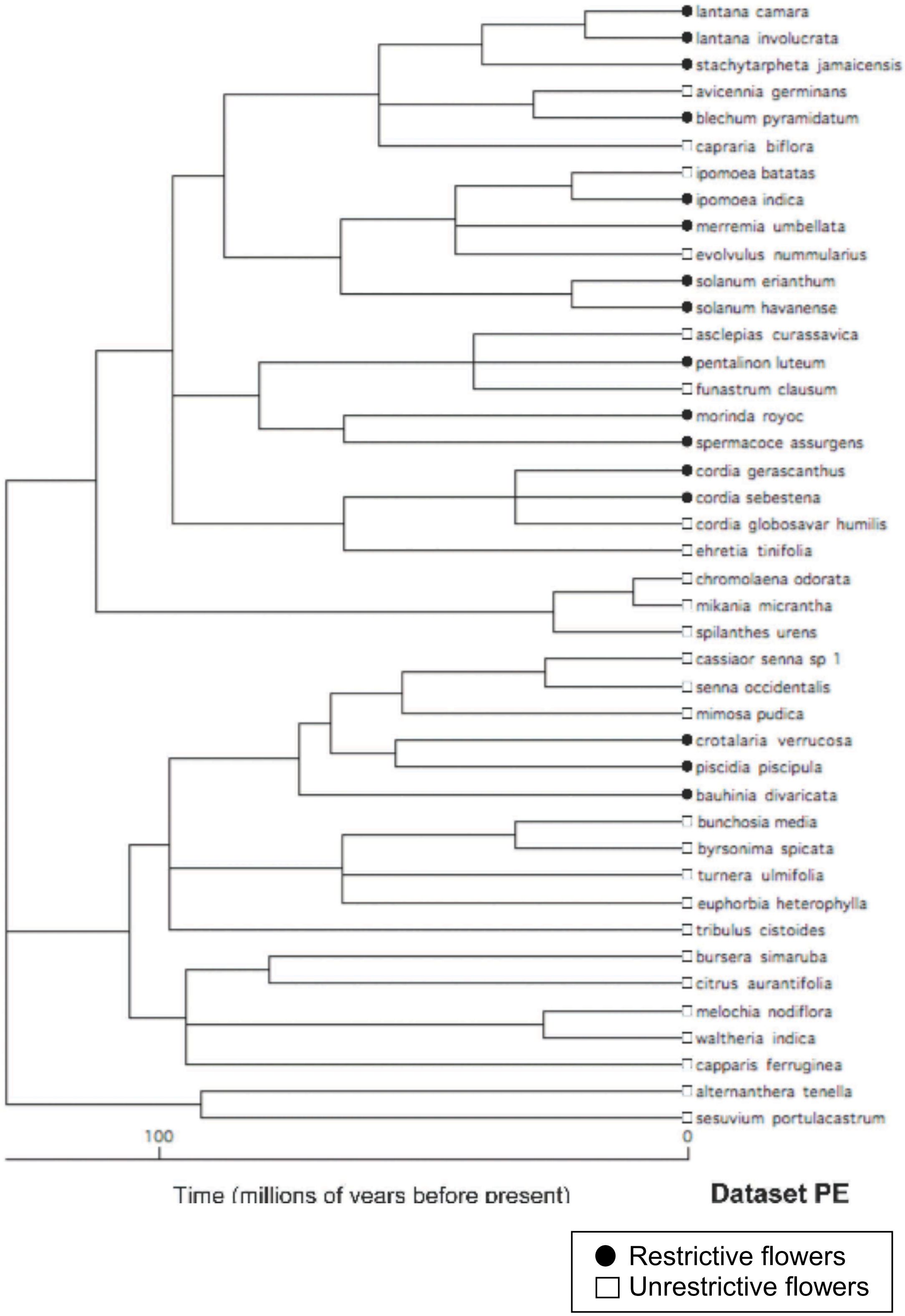

baccharis pingraea
hysterionica jasionoides
grindelia chiloensis
thelesperma megapotamicum
senecio filaginoides
senecio subulatus
mutisia decurrens
mimulus sp 1
junellia cf tonini
phacelia cf secunda
adesmia retrofracta
lathyrus sp 1
polygala stenophylla
rosa eglanteria
discaria trinervis
larrea tridentatavar tridentata
oxalis sp 1
rapistrum rugosum
lecanophora heterophylla
oenothera mendocinensis
opuntia corrugata
pyrrhocactus cf strausianum
arjona patagonica
100
0
Time (millions of years before present)
Dataset MR
● Restrictive flowers
☐ Unrestrictive flowers

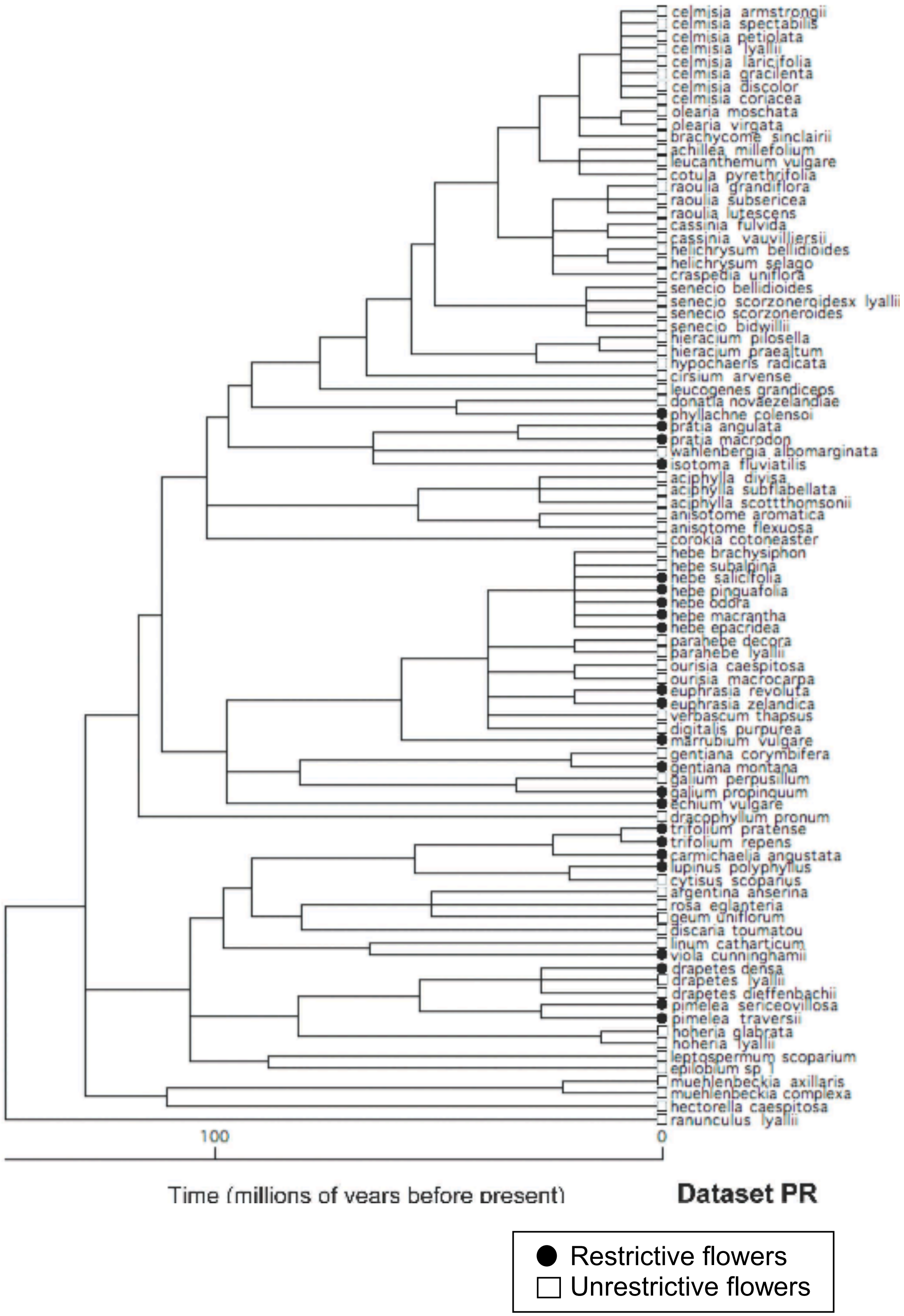

potentilla vahliana
geum rossii
dryas integrifolia
astragalus alpinus
oxytropis arctica
arnica alpina
petasites frigidus
taraxacum sp
cerastium alpinum
caltha palustris
papaver radicatum
100
0
Time (millions of years before present)
Dataset MS
● Restrictive flowers
□ Unrestrictive flowers

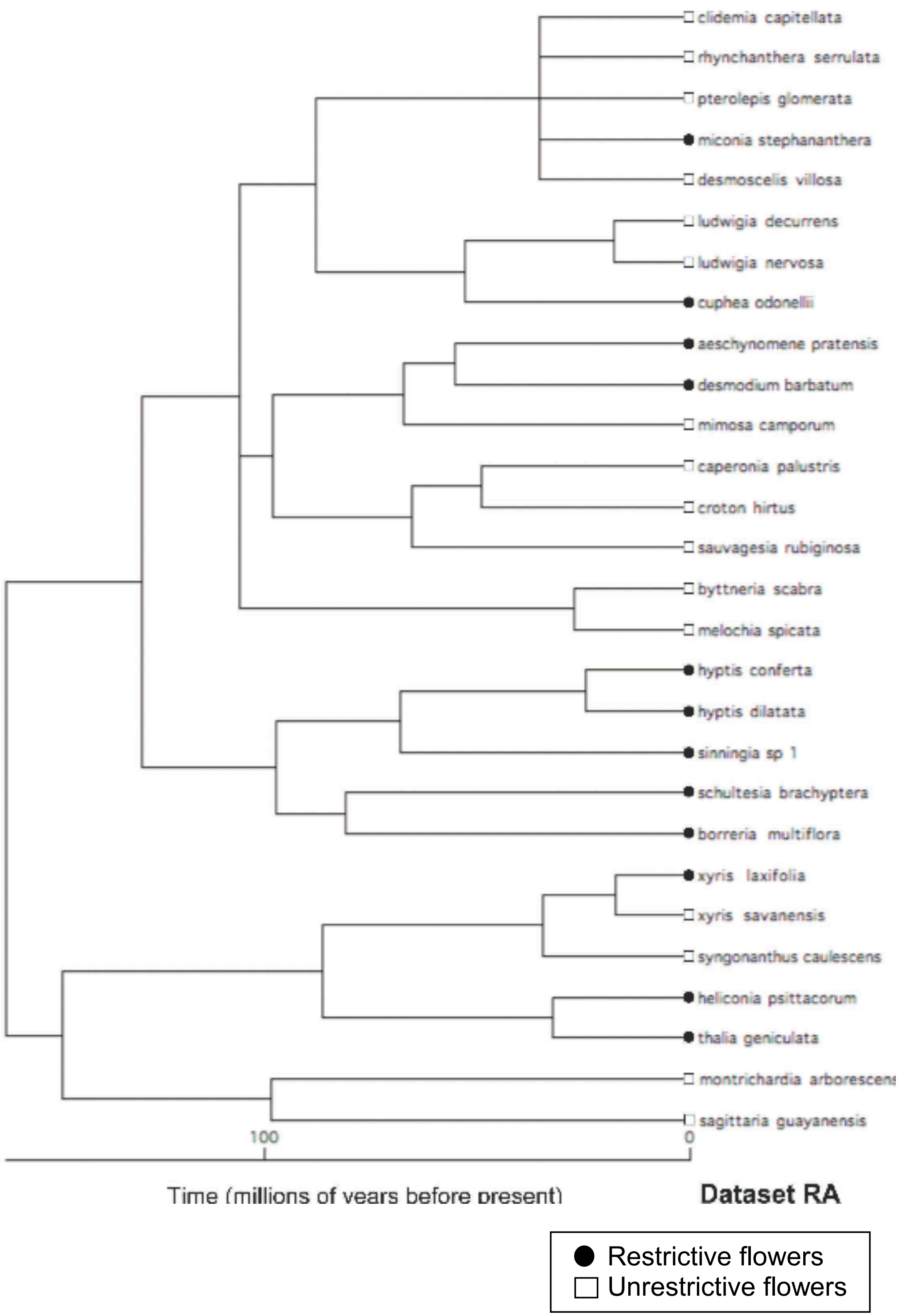

aesculus sylvatica
cardamine angustata
viola sororia
tiarella cordifoliavar collina
stellaria pubera
claytonia virginica
hepatica nobilisvar obtusa
thalictrum thalictroides
podophyllum peltatum
sanguinaria canadensis
trillium catesbaei
erythronium umbilicatum
uvularia sessilifolia
100
0
Time (millions of years before present)
Dataset MT
● Restrictive flowers
□ Unrestrictive flowers


leucaena leucocephala
suriana maritima
turnera angustifolia
passiflora suberosa
hibiscus tiliaceus
thespesia populnea
pemphis acidula
stachytarpheta jamaicencis
ipomoea violacea
tournefortia argentea
morinda citrifolia
scaevola sericea
gastonia mauritiana
dracaena concinna
100
0
Time (millions of years before present)
Dataset OA
● Restrictive flowers
☐ Unrestrictive flowers

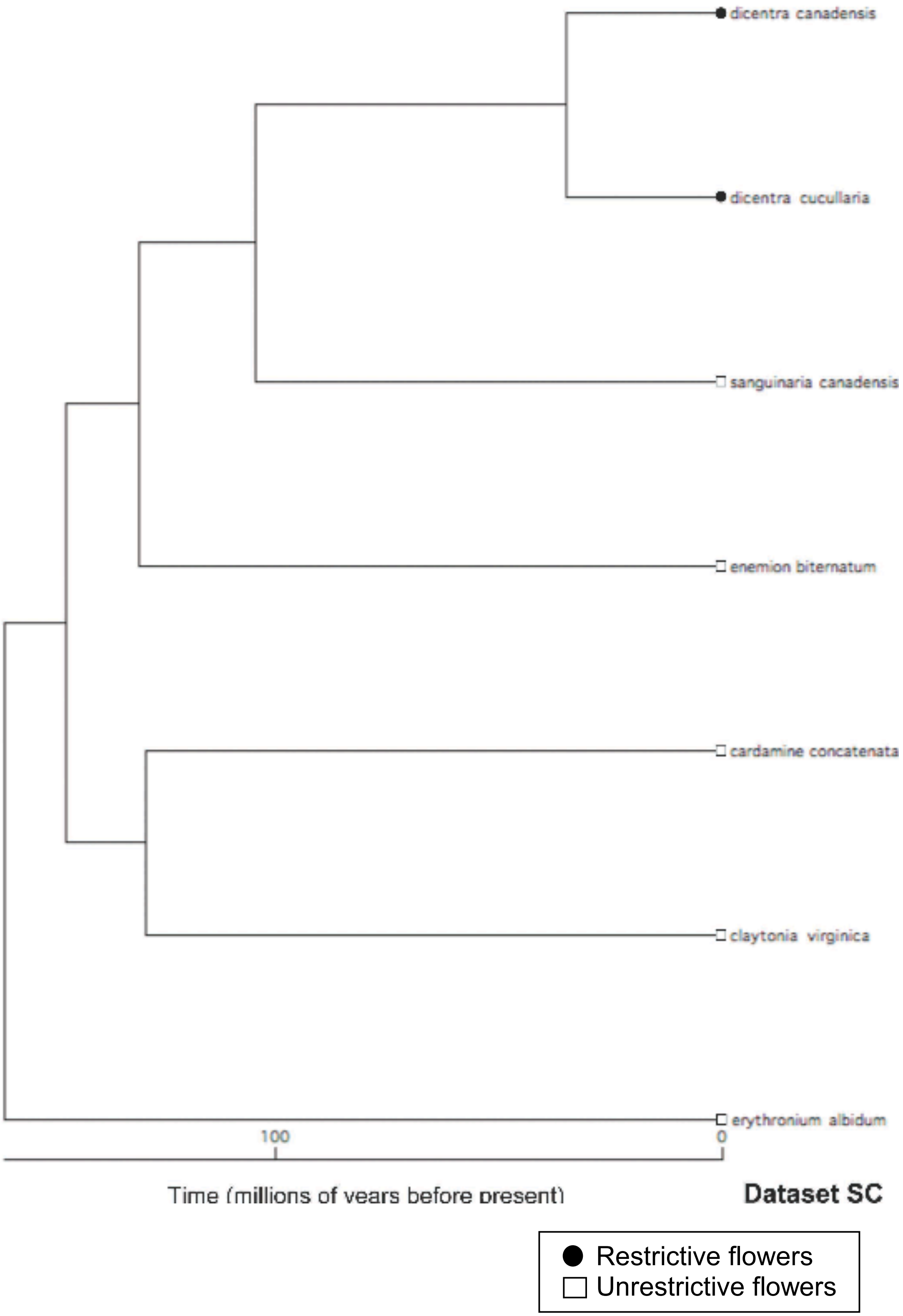

matricaria discoidea
solidago sempervivens
azorina vidalii
crithmum maritimum
daucus carota
beta vulgaris
silene vulgaris
lotus corniculatus
reseda luteola
freesia corymbosa
100
0
Time (millions of years before present)
Dataset OF
● Restrictive flowers
☐ Unrestrictive flowers

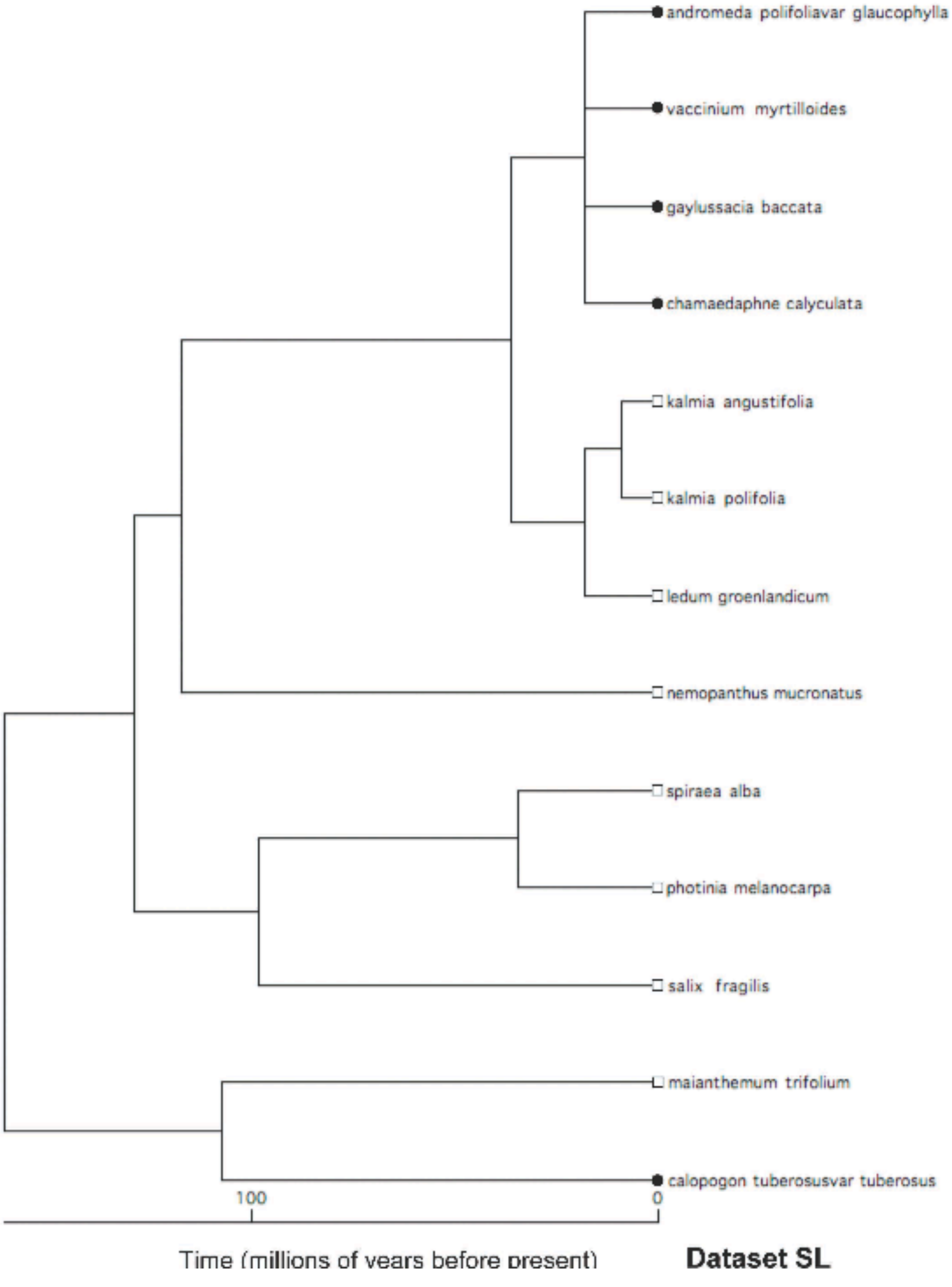

lantana camara
lantana involucrata
stachytarpheta jamaicensis
avicennia germinans
blechum pyramidatum
capraria biflora
ipomoea batatas
ipomoea indica
merremia umbellata
evolvulus nummularius
solanum erianthum
solanum havanense
asclepias curassavica
pentalinon luteum
funastrum clausum
morinda royoc
spermacoce assurgens
cordia gerascanthus
cordia sebestena
cordia globosavar humilis
ehretia tinifolia
chromolaena odorata
mikania micrantha
spilanthes urens
cassiaor senna sp 1
senna occidentalis
mimosa pudica
crotalaria verrucosa
piscidia piscipula
bauhinia divaricata
bunchosia media
byrsonima spicata
turnera ulmifolia
euphorbia heterophylla
tribulus cistoides
bursera simaruba
citrus aurantifolia
melochia nodiflora
waltheria indica
capparis ferruginea
alternanthera tenella
sesuvium portulacastrum
100
0
Time (millions of years before present)
Dataset PE
● Restrictive flowers
☐ Unrestrictive flowers


celmisia armstrongii
celmisia spectabilis
celmisia petiolata
celmisia lyallii
celmisia laricifolia
celmisia gracilenta
celmisia discolor
celmisia coriacea
olearia moschata
olearia virgata
brachycome sinclairii
achillea millefolium
leucanthemum vulgare
cotula pyrethrifolia
raoulia grandiflora
raoulia subsericea
raoulia lutescens
cassinia fulvida
cassinia vauvilliersii
helichrysum bellidioides
helichrysum selago
craspedia uniflora
senecio bellidioides
senecio scorzoneroidesx lyallii
senecio scorzoneroides
senecio bidwillii
hieracium pilosella
hieracium praealtum
hypochaeris radicata
cirsium arvense
leucogenes grandiceps
donatia novaezelandiae
phyllachne colensoi
pratia angulata
pratia macrodon
wahlenbergia albomarginata
isotoma fluviatilis
aciphylla divisa
aciphylla subflabellata
aciphylla scottthomsonii
anisotome aromatica
anisotome flexuosa
corokia cotoneaster
hebe brachysiphon
hebe subalpina
hebe salicifolia
hebe pinguafolia
hebe odora
hebe macrantha
hebe epacridea
parahebe decora
parahebe lyallii
ourisia caespitosa
ourisia macrocarpa
euphrasia revoluta
euphrasia zelandica
verbascum thapsus
digitalis purpurea
marrubium vulgare
gentiana corymbifera
gentiana montana
galium perpusillum
galium propinquum
echium vulgare
dracophyllum pronum
trifolium pratense
trifolium repens
carmichaelia angustata
lupinus polyphyllus
cytisus scoparius
argentina anserina
rosa eglanteria
geum uniflorum
discaria toumatou
linum catharticum
viola cunninghamii
drapetes densa
drapetes lyallii
drapetes dieffenbachii
pimelea sericeovillosa
pimelea traversii
hoheria glabrata
hoheria lyallii
leptospermum scoparium
epilobium sp 1
muehlenbeckia axillaris
muehlenbeckia complexa
hectorella caespitosa
ranunculus lyallii
100
0
Time (millions of years before present)
Dataset PR
● Restrictive flowers
☐ Unrestrictive flowers



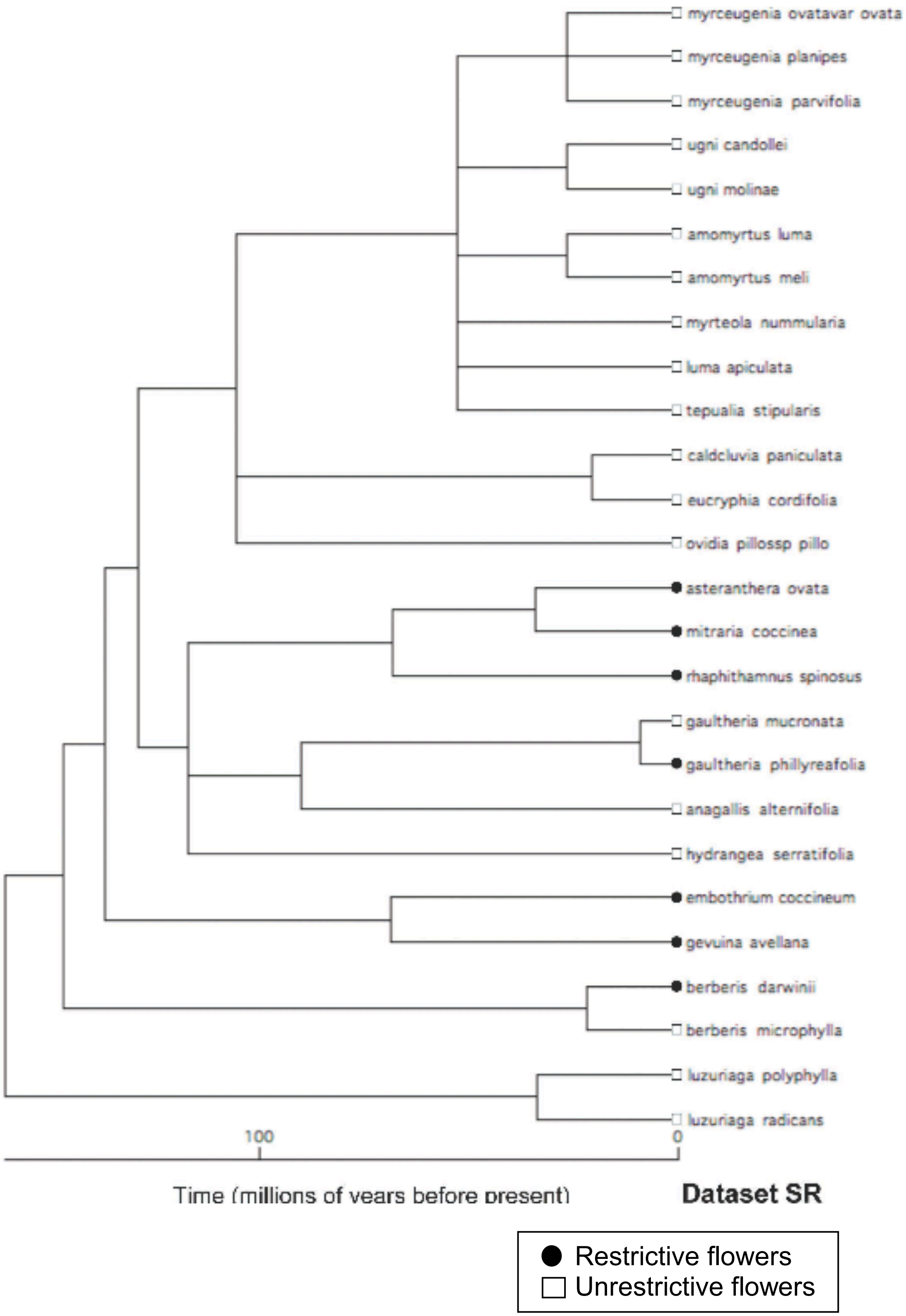
clidemia capitellata
rhynchanthera serrulata
pterolepis glomerata
miconia stephananthera
desmoscelis villosa
ludwigia decurrens
ludwigia nervosa
cuphea odonellii
aeschynomene pratensis
desmodium barbatum
mimosa camporum
caperonia palustris
croton hirtus
sauvagesia rubiginosa
byttneria scabra
melochia spicata
hyptis conferta
hyptis dilatata
sinningia sp 1
schultesia brachyptera
borreria multiflora
xyris laxifolia
xyris savanensis
syngonanthus caulescens
heliconia psittacorum
thalia geniculata
montrichardia arborescens
sagittaria guayanensis
100
0
Time (millions of years before present)
Dataset RA
● Restrictive flowers
☐ Unrestrictive flowers

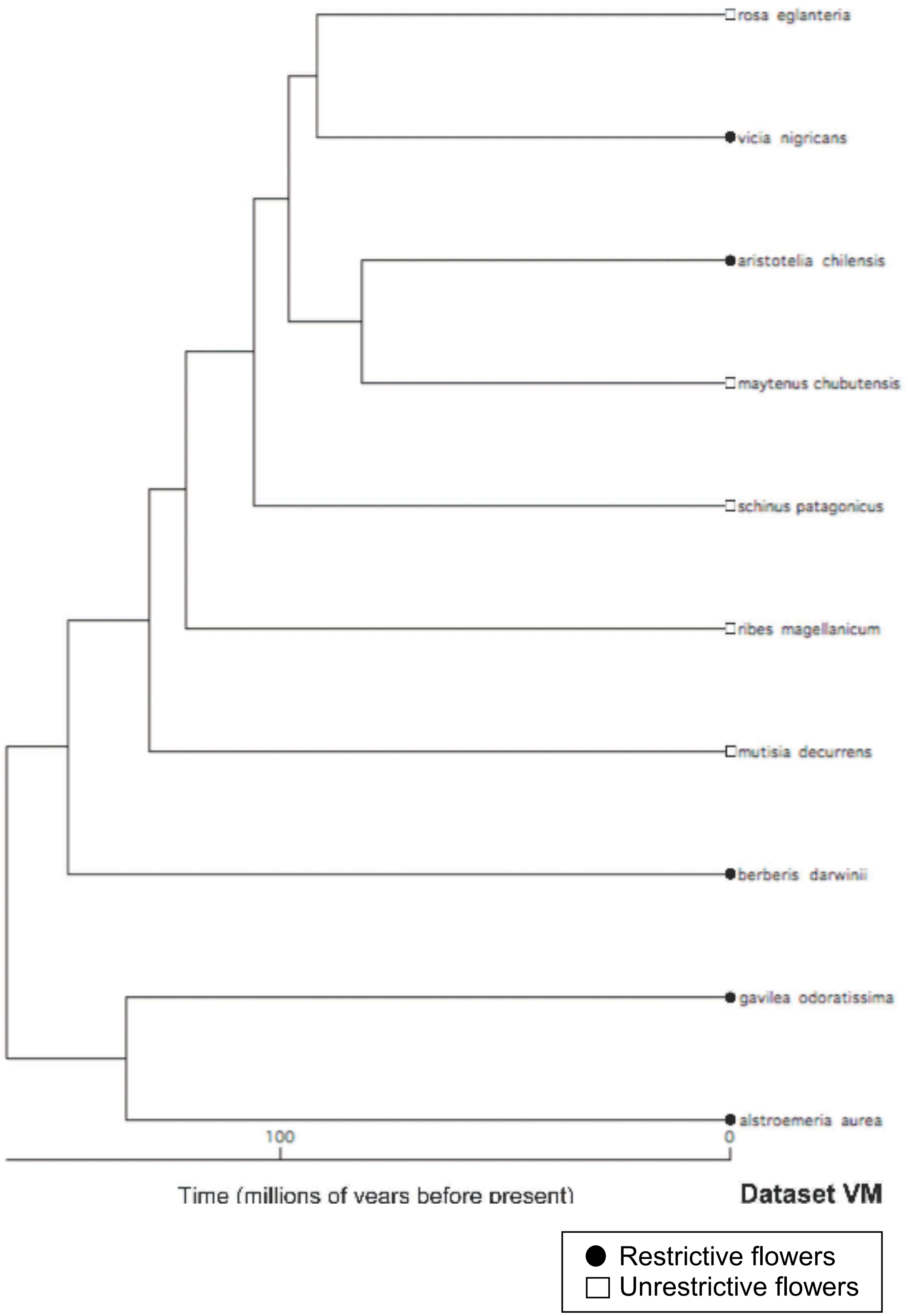

dicentra canadensis
dicentra cucullaria
sanguinaria canadensis
enemion biternatum
cardamine concatenata
claytonia virginica
erythronium albidum
100
0
Time (millions of years before present)
Dataset SC
● Restrictive flowers
□ Unrestrictive flowers

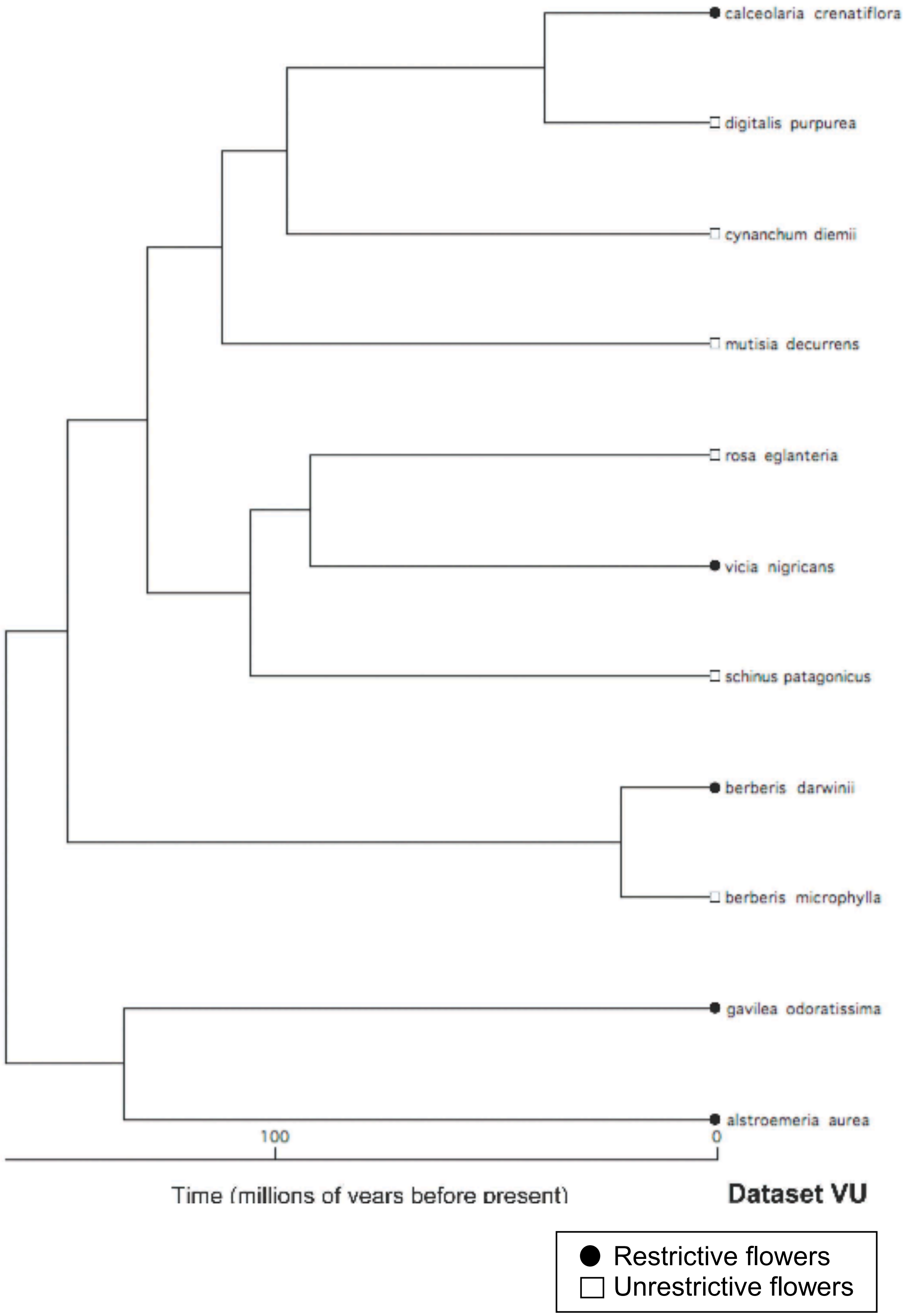


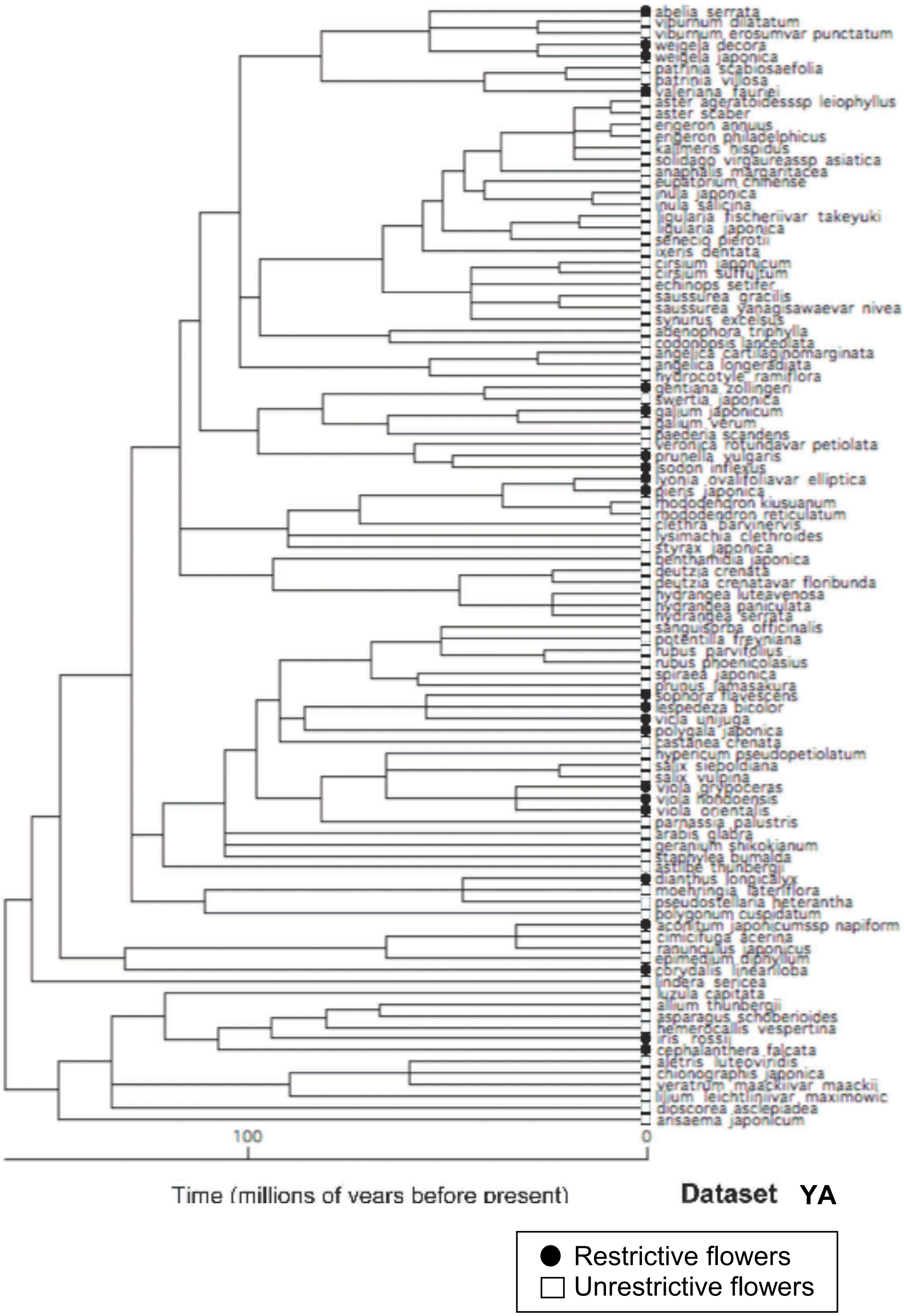
Dataset SL

● Restrictive flowers
☐ Unrestrictive flowers


myrceugenia ovatavar ovata
myrceugenia planipes
myrceugenia parvifolia
ugni candollei
ugni molinae
amomyrtus luma
amomyrtus meli
myrteola nummularia
luma apiculata
tepualia stipularis
caldcluvia paniculata
eucryphia cordifolia
ovidia pillossp pillo
asteranthera ovata
mitraria coccinea
rhaphithamnus spinosus
gaultheria mucronata
gaultheria phillyreafolia
anagallis alternifolia
hydrangea serratifolia
embothrium coccineum
gevuina avellana
berberis darwinii
berberis microphylla
luzuriaga polyphylla
luzuriaga radicans
100
0
Time (millions of years before present)
Dataset SR
● Restrictive flowers
☐ Unrestrictive flowers


☐ rosa eglanteria
● vicia nigricans
● aristotelia chilensis
☐ maytenus chubutensis
☐ schinus patagonicus
☐ ribes magellanicum
☐ mutisia decurrens
● berberis darwinii
● gavilea odoratissima
● alstroemeria aurea
100
0
Time (millions of years before present)
Dataset VM
● Restrictive flowers
☐ Unrestrictive flowers


calceolaria crenatiflora
digitalis purpurea
cynanchum diemii
mutisia decurrens
rosa eglanteria
vicia nigricans
schinus patagonicus
berberis darwinii
berberis microphylla
gavilea odoratissima
alstroemeria aurea
100
0
Time (millions of years before present)
Dataset VU
● Restrictive flowers
☐ Unrestrictive flowers


abelia serrata
viburnum dilatatum
viburnum erosumvar punctatum
weigela decora
weigela japonica
patrinia scabiosaefolia
patrinia villosa
valeriana fauriei
aster ageratoidesssp leiophyllus
aster scaber
erigeron annuus
erigeron philadelphicus
kalimeris hispidus
solidago virgaureassp asiatica
anaphalis margaritacea
eupatorium chinense
inula japonica
inula salicina
ligularia fischeriivar takeyuki
ligularia japonica
senecio pierotii
ixeris dentata
cirsium japonicum
cirsium suffultum
echinops setifer
saussurea gracilis
saussurea yanagisawaevar nivea
synurus excelsus
adenophora triphylla
codonopsis lanceolata
angelica cartilaginomarginata
angelica longeradiata
hydrocotyle ramiflora
gentiana zollingeri
swertia japonica
galium japonicum
galium verum
paederia scandens
veronica rotundavar petiolata
prunella vulgaris
isodon inflexus
lyonia ovalifoliavar elliptica
pieris japonica
rhododendron kiusianum
rhododendron reticulatum
clethra barvinervis
lysimachia clethroides
styrax japonica
benthamidia japonica
deutzia crenata
deutzia crenatavar floribunda
hydrangea luteavenosa
hydrangea paniculata
hydrangea serrata
sanguisorba officinalis
potentilla freyniana
rubus parvifolius
rubus phoenicolasius
spiraea japonica
prunus jamasakura
sophora flavescens
lespedeza bicolor
vicia unijuga
polygala japonica
castanea crenata
hypericum pseudopetiolatum
salix sieboldiana
salix vulpina
viola grypoceras
viola hondoensis
viola orientalis
parnassia palustris
arabis glabra
geranium shikokianum
staphylea bumalda
astilbe thunbergii
dianthus longicalyx
moehringia lateriflora
pseudostellaria heterantha
polygonum cuspidatum
aconitum japonicumssp napiform
cimicifuga acerina
ranunculus japonicus
epimedium diphyllum
corydalis lineariloba
lindera sericea
luzula capitata
allium thunbergii
asparagus schoberioides
hemerocallis vespertina
iris rossii
cephalanthera falcata
aletris luteoviridis
chionographis japonica
veratrum maackiivar maackii
lilium leichtliniivar maximowic
dioscorea asclepiadea
arisaema japonicum
100
0
Time (millions of years before present)
Dataset YA
● Restrictive flowers
□ Unrestrictive flowers

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