On the young age of intraspecific herbaceous taxa

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Summary

- Dated phylogenies rarely include the divergence times of sister intraspecific taxa, and when they do little is said about this subject.
- We show that over 90% of the intraspecific plant taxa found in a literature search are estimated to be 5 million yr old or younger, with only 4% of taxa estimated to be over 10 million yr old or older.
- A Bayesian analysis of intraspecific taxon ages indicates that indeed these taxa are expected to be < 10 million yr old. This result for the young age of intraspecific taxa is consistent with the earlier observation that post-pollination reproductive barriers develop between 5 and 10 million yr after lineage splitting, thus leading to species formation.
- If lineages have not graduated to the species level of divergence by 10 million yr or so, they are likely to have gone extinct by that time as a result of narrow geographical distributions, narrow niche breadths, and relatively small numbers across populations.

Introduction

The tempo of post-pollination barrier evolution in plants can be judged using dated phylogenies in conjunction with crossing and fertility data from interspecific crosses. Fortunately, these data are now available for a large number of species pairs across a broad array of genera, spanning numerous and highly divergent angiosperm families. The ages of these intraspecific taxa suggest that in herbs substantial hybrid sterility, hybrid inviability, and cross-incompatibility usually develop no later than between 5 and 10 million yr after lineage splitting, through the accumulation of Dobzhansky–Muller (DM) incompatibilities (Levin, 2012, 2013). Sister taxa > 10 million yr old (Myo) probably would have strong reproductive barriers, and thus would be considered biological species rather than intraspecific entities, following the 'biological species concept' (Mayr, 1963).

The age of intraspecific taxa, as determined from molecular phylogenies, also provides a window into the rate at which subspecies or varieties accumulate genetic differences. For species identified by the genealogical species concept, that is, reciprocal monophyly, theory predicts that a sufficient number of neutral mutations should accumulate in subspecies that they should graduate to species after 4–12 N_e generations (Hudson & Coyne, 2002), where N_e is the historical effective population size; and the range comes from both stochasticity in mutation accumulation and different thresholds for identifying a species. This theoretical predication of a fairly narrow time until genealogical speciation – as measured in units of effective population size – is consistent with the observation that nearly all subspecies are < 10 Myo. Therefore, much of the deviation *c.* 10 Myo will be attributable to differences in N_e and/or selection pressures on speciation between taxa, for example, reinforcement.

The focal question here, then, is: are intraspecific taxa in herbaceous species usually less than 10 Myo as we might expect, and, if so, how much less? To date, there has been no comprehensive survey of intraspecific taxon age in plants. Indeed, although such ages occasionally appear in dated molecular phylogenies, very little attention is paid to them. In this paper, we collate information on the ages of 102 sister intraspecific taxa collected from dated molecular phylogenies in 47 herbaceous species from 30 genera and 20 families, as described in Supporting Information Table S1. Most of our taxa are dicots. Five sister pairs are in the Leguminosae/Fabaceae. Two taxon pairs are present in each of the following families: Gramineae, Caprifoliaceae, Balsaminaceae, Onagraceae, and Asteraceae. The remaining pairs are the only representatives of their families.

Our collection of taxa encompasses a large part of the world. Some sister pairs reside in North America, while others grow in Europe, eastern or southeastern Asia, South America, New Zealand, or East Africa. Some taxa are from Macaronesia, the Hawaiian Islands, or the Marquesa Islands. Whereas most taxa occur in mesic habitats, some occur in xeric habitats, and others reside in wet habitats. Some taxa grow above the tree line.

The information used in this study was garnered from a review of the journals *Molecular Phylogenetics and Evolution*, *Molecular Ecology*, and the *American Journal of Botany* since 2003. Keyword searches in Google Scholar also revealed several relevant publications in other journals. The subspecies is the intraspecific evolutionary unit that most often appears in chronograms, which explains why the following discourse is dominated by this taxon rather than by varieties, ecotypes or ecological races.

It is important to recognize that the ages of sister taxa presented in the literature and referred to later are very approximate estimates, because error terms in phylogenetic estimates of divergence

times may be substantial, and estimates may vary from one type of marker or method to another (Ho & Phillips, 2009; Schwartz & Mueller, 2010; Clarke *et al.*, 2011). Also, gene flow between diverging lineages may suggest more recent common ancestry than is actually the case. Yet these age estimates provide a temporal context for the persistence of intraspecific taxa heretofore lacking. These estimates are of the same quality as (and are no less valid than) those for the divergence times of species and genera that appear in the same chronograms from which intraspecific ages were extracted. Phylogenetic trees were anchored at or above the genus level in the genera referred to later.

Intraspecific taxa are described/diagnosed by specialists who have studied given species and the genera in which they reside, and who have evaluated the pattern and organization of phenotypic variation within them. Intraspecific taxa have distinctive morphologies (and sometimes phenologies) and distinctive ecogeographical ranges, which ostensibly are the products of selection by divergent physical and biological forces associated with range expansion or with local environmental change. We do not claim that all intraspecific taxon pairs within a species or among species are genetically or ecogeographically equivalent or divergent. Certainly, different pairs of congeneric sister species are not equivalent, nor are sister genera.

Materials and Methods

Using time-calibrated molecular phylogenies, we obtained the taxon (lineage) age for 102 subspecies. In total, we used 28 unique phylogenies, all of which were constructed at the family level or lower – family ($n = 4$), subfamily ($n = 6$), genus ($n = 13$), subgenus ($n = 2$), and species ($n = 3$) – using multiple molecular markers, and were time calibrated using multiple fossils ($n = 20$), the age of islands (Hawaiian $n = 2$, and Malaysian $n = 1$) or established mutation rates ($n = 4$). As discussed in greater detail later, we also performed a number of bootstrap analyses to determine whether our results were robust to differences in how the phylogenies were constructed and to the phylogenetic nonindependence of the data.

These 102 taxon ages allowed us to estimate the percentage of intraspecific taxa expected to be < 10 Myo. The standard approach for modelling lineage age is to assume that the observed distribution of ages is a balance between the rates of speciation and extinction. For such a model, the resulting distribution will be exponential with the rate parameter equal to 1 over the mean longevity of the taxa. To estimate the rate parameter of this distribution, we take a Bayesian approach. Because we use an exponential likelihood function, and desire an exponential posterior distribution, the most convenient prior is a gamma distribution. This distribution is conjugate to the exponential likelihood and, as a result, there is a simple analytic solution for the posterior distribution. Additionally, because the gamma distribution has two parameters, we can explore a broader range of prior distributions to better evaluate the sensitivity of our findings to prior specification.

Now that we have settled on the form of our prior distribution and likelihood, in principle, our task is straightforward. First, we select parameters for our gamma prior distribution and then solve for the posterior distribution using the observed subspecies ages and the following equation:

$$\Gamma\left(\alpha + n, \beta + \sum_{i=1}^{n} x_i\right)$$

(α, the shape parameter for the prior distribution, which is also a gamma distribution; n, the number of observations, that is, taxa; β, the rate parameter for the prior distribution; x, the age of each taxon in millions of years.)

We consider two prior distributions: the first is *uniform*, $\Gamma(\alpha = 0, \beta = 1)$, and the second is strongly peaked at *c.* 20 million yr, $\Gamma(\alpha = 10, \beta = 200)$. We refer to this second prior distribution as *skeptical*. Given that our hypothesis is that most sister intraspecific taxa are younger than 10 Myo, these two priors represent a compromise between letting the data speak freely and placing a strong prior against our hypothesis. We then consider three sampling strategies for our data. First, we include all 102 taxa (*all data*). Second, we construct 1000 data sets by selecting one taxon from each of the 27 publications in our data set (*publication sampling*). Finally, we construct 1000 data sets by selecting one taxon from each of the genera in our data set (*genus sampling*). These sampling strategies were selected to control for nonindependence resulting from phylogenetic relationship and researcher bias. We could not use traditional methods for controlling for phylogenetic nonindependence because a phylogeny uniting our 102 taxa is unavailable.

Results

All of the intraspecific herbaceous taxa uncovered in this survey are estimated to be *c.* 10 Myo or less, typically much less. Consider first the older taxa. Two subspecies of *Circaea canadensis* are *c.* 8 Myo (Xie *et al.*, 2009), *Platymiscium pubsecens* ssp. *pubescens* and ssp. *fragrans* are *c.* 6 Myo (Saslis-Lagoudakis *et al.*, 2008), and four subspecies of *Circaea alpina* (ssp. *alpina*, ssp. *imiacola*, ssp. *micrantha* and ssp. *pacifica*) are somewhat less than 5 Myo (Xie *et al.*, 2009). *Stachys rigida* ssp. *rigida* and ssp. *quercetorum* diverged *c.* 5 million yr ago (Ma) (Roy *et al.*, 2013).

Other subspecies are between 1 and 4 Myo (e.g. *Cyrtandra ootensis* ssp. *mollisima* and ssp. *ootensis*, 4 Myo, and *Cyrtandra kealiae* ssp. *kealiae* and ssp. *urceolata*, 2 Myo (Clark *et al.*, 2009); *Sarracenia rubra* ssp. *ruba* and ssp. *gulfensis*, 2 Myo, and *S. alabamensis* ssp. *alabamensis* and ssp. *wherryi*, 2 Myo (Ellison *et al.*, 2012); and *Lotus sessifolia* ssp. *sessifolia* and ssp. *villosissimus*, 1 Myo (Ojeda *et al.*, 2012)). Three subspecies of *Leptecophylla juniperina* are *c.* 2.5 Myo (Puente-Lelièvre *et al.*, 2013). *Bellis annua* ssp. *annua* and ssp. *minuta* diverged *c.* 2 Ma (Fiz-Palacio & Valcarcel, 2011). Four subspecies of *Portulaca oleracea* are *c.* 1 Myo (Ocampo & Columbus, 2012), as are *Impatiens meruensis* ssp. *meruensis* and ssp. *truciata* (Janssens *et al.*, 2009). *Pediomelum hypogaeum* var. *subulatum* and var. *scapusum* are *c.* 1 Myo, as are *Orbexilum pedicularum* var. *gracile* and var. *pedicularum* (Egan & Crandall, 2008). In *Chaetanthera*, *Chaetanthera linearis* ssp. *linearis*, ssp. *taltalensis* and ssp. *alba* are

c. 2 Myo, and *Chaetanthera chilensis* ssp. *chilensis* and ssp. *tenuifolia* are *c.* 1 Myo (Hershkovitz *et al.*, 2006).

Subspecies in different congeneric species may be of somewhat similar vintage, for example 2.5 Myo in *Mertensia oblongata* (four ssp.), *Mertensia viridus* (two ssp.), *Mertensia paniculata* (two ssp.) and *Mertensia arizonica* (two ssp.; Nazaire *et al.*, 2014). Conversely, subspecies within a genus may have very different ages, as in *Ipomopsis*, where *Ipomopsis aggregata* ssp. *aggregata* and ssp. *candida* are *c.* 3 Myo, and *Ipomopsis congesta* ssp. *frutescens* and ssp. *nevadensis* are *c.* 10 Myo (Porter *et al.*, 2010). In *Lilium*, two varieties within *Lilium bakerianum* and two within *Lilium japonicum* began diverging *c.* 3 Ma, two varieties of *Lilium leucanthum* and two varieties of *Lilium speciosum c.* 2 Ma, and two varieties of *Lilium xanthellum* and two of *Lilium primulinum c.* 1 Ma (Gao *et al.*, 2013). Sister subspecies of *Saintpaulia ionantha* have disparate ages, with one pair diverging 4 Ma, two pairs 3 Ma, one pair 2 Ma, three pairs 1 Ma, and three pairs 0.5 Ma (Dimitrov *et al.*, 2012). However, we ultimately excluded the study by Dimitrov *et al.* (2012) because they used only a single marker and geological events to construct their chronogram.

Some intraspecific taxa may be of relatively recent origin. For example, *Vigna angularis* var. *angularis* and var. *nipponensis* are *c.* 500 000 yr old, as are *Vigna reflexo-pilosa* var. *reflexo-pilosa* and var. *glabra* and *Vigna mungo* var. *mundo* and var. *silvestris* (Javadi *et al.*, 2011). Two subspecies of *Cyanthus flavus* are of the aforementioned vintage (Zhou *et al.*, 2013), as are three subspecies of *Cheirolophus intybus* (Vitales *et al.*, 2014). The two subspecies of *Oryza sativa* are *c.* 440 000 yr old (Garris *et al.*, 2005). *Zea mays* ssp. *mays*, ssp. *luxurians*, and ssp. *parviglumis* diverged from a common ancestor *c.* 150 000 yr ago (Ross-Ibarra *et al.*, 2009). North American and European subspecies of *Arabidopsis lyrata* split *c.* 300 000 yr ago (Pyhäjärvi *et al.*, 2012). In *Impatiens*, *Impatiens pallide-rosea* ssp. *pallide-rosea* and ssp. *lupangaensis* are *c.* 100 000 yr old (Janssens *et al.*, 2009). *Clarkia xantiana* ssp. *xantiana* and ssp. *parviflora* are *c.* 65 000 yr old (Pettengill & Moeller, 2012), and *Collinsia sparciflora* var. *sparciflora* and var. *collina* are *c.* 50 000 yr old (Baldwin *et al.*, 2011).

As we acknowledged earlier, the estimated dates of divergence may have considerable error associated with them. Most of the dated phylogenies used in these studies did not have error terms for their estimates, but a few did; and they do not change our interpretation that most intraspecific taxa are < 5 Myo. The estimates for intraspecific divergence in the two *Sarracenia* species (2 million yr in both cases; Ellison *et al.*, 2012) have 50% error bars, so divergence may be as recent as 1 Ma or as distant as 3 Ma. Taxon divergence estimates within *Impatiens meruensis* (Janssens *et al.*, 2009) and within *Orbexilum pedicularum* (Egan & Crandall, 2008) also have 50% error bars. Divergence times are estimated at 1 Ma. Larger errors (70%) are found in *Saintpaulia* (20 taxa), where most divergence times are estimated at < 4 Ma (Dimitrov *et al.*, 2012). Errors somewhat exceeding 100% are reported for the estimates in *Collinsia sparciflora* (Baldwin *et al.*, 2011), *Cyanthus flavus* (Zhou *et al.*, 2013), and *Cheirolophus intybus* (Vitales *et al.*, 2014), where intraspecific divergence is estimated at 0.5 Ma. The level of error (%) in intraspecific estimates is about the same as that for specific and generic estimates in the same studies. Accordingly, our interpretations of divergence times are no less reliable than those at higher levels of divergence.

It is noteworthy that some intraspecific taxa are not significantly younger than their parent species. This is evident in, for example, subspecies of two *Sarracenia* species (Ellison *et al.*, 2012), those of *Impatiens meruensis* (Janssens *et al.*, 2009) and those of *Orbexilum pedicularum* (Egan & Crandall, 2008). Ostensibly, the subspecies began diverging shortly after species formation. Conversely, subspecies of *Collinsia sparciflora* (Baldwin *et al.*, 2011), *Cyanthus flavus* (Zhou *et al.*, 2013), and *Cheirolophus intybus* (Vitales *et al.*, 2014) are significantly younger than the species in which they reside. Accordingly, subspecific divergence must have begun well after species formation.

Bayesian analysis of intraspecific ages

Table 1 presents the results for each prior distribution (table rows) and each sampling strategy (table columns). The values reported are the mean age for taxa and 95% credible intervals around those means. Table 2 reports the median age for taxa and the 95% confidence intervals around the median ages. Our results strongly support the view that the mean age of taxa is < 10 Myo. For the estimated mean ages and assuming the distribution of ages will be exponential – which is both an expected outcome for age distributions and a conservative assumption with respect to our hypothesis – 95% of all intraspecific taxa should be < 7.5 Myo if we use a uniform prior and genus sampling, and < 21 Myo if we use a skeptical prior and genus sampling. These values do not include uncertainty in the age estimates for the taxa and clearly do not come from an exhaustive or random sample of plants. We return to these issues in the Discussion.

Discussion

By compiling the ages of intraspecific taxa from published, dated phylogenies, we found that 94 intraspecific taxa of the 102 considered – representing 43 herbaceous species and 26 genera – are 5 Myo or less. Only four taxa are estimated to be older than 10 Myo (or < 4% of the data set). We did not observe any intraspecific taxa with estimated ages > 11 Myo. Notably, the majority of taxa (72%) are under 2.5 Myo. Our statistical analysis suggests that the median age of intraspecific taxa is < 10 Myo, which was robust to various specifications of the prior distribution, and phylogentic nonindependence. As a result, our analysis demonstrates that the paucity of older subspecies is very unlikely

Table 1 Posterior mean ages (million yr old) and their associated 95% credible intervals

	All data	Publication sampling	Genus sampling
Uniform prior	2.19 (1.82–2.69)	2.30 (1.63–3.48)	2.40 (1.72–3.60)
Skeptical prior	3.78 (3.16–4.58)	7.04 (5.22–9.99)	6.89 (5.15–9.69)

Table 2 Median ages (million yr old) and 95% confidence intervals

	All data	Publication sampling	Genus sampling
Uniform prior	1.52 (0.06–8.09)	1.59 (0.06–8.47)	1.67 (0.06–8.88)
Skeptical prior	2.62 (0.10–13.92)	4.88 (0.18–25.96)	4.77 (0.17–25.42)

The posterior means were used to calculate the median ages and associated uncertainties.

to be a statistical fluke or an artifact of sampling, which we will consider in detail later.

Graduation to the species level is probably governed – at least in part – by the accumulation of neutral mutations. Therefore, it is important to consider our findings in the context of the coalescent process. Using a coalescent model of the waiting time until genealogical speciation, Hudson & Coyne (2002) found a fairly narrow range of expected longevities for subspecies (measured in units of effective population size and generation time). Our finding that most intraspecific taxa are young is consistent with these theoretical predictions. However, because these predications were based on the accumulation of neutral mutations, or the appropriate correction to N_e, nonneutral evolutionary forces will affect the longevity of subspecies. As a result, we must also examine our results in a broader framework, which includes nonneutral processes governing taxon age.

There are two primary reasons why intraspecific taxa should have, compared with interspecific taxa, younger ages. The first is that their evolutionary duration is severely limited by their ascension to biological species status via the development of strong post- or prepollination barriers (Mayr, 1942, 1963). Graduation to the species level of divergence terminates the existence of sister intraspecific taxa, but not their lineages, which may persist for many millions of years. The second reason is taxon extinction, which will we consider in detail later.

Graduation to the species level of divergence may be an inevitable outcome of genomic divergence, which is expressed as post-pollination isolation. Hybrid sterility typically evolves c. 4–5 million yr after lineage splitting in herbaceous lineages (Levin, 2012). Cross-incompatibility is reached c. 7–10 million yr after lineage divergence, and hybrid inviability somewhat earlier than that (Levin, 2013). Hybrid sterility and lethality may build slowly through the gradual stochastic accumulation of many DM incompatibilities with small effects (Coyne & Orr, 2004). Conversely, genomic disharmony can arise through an association between genes conferring selective advantages and those responsible for incompatibilities (Agrawal *et al.*, 2011; Cutter, 2012; Crespi & Nosil, 2012; Corbett-Detig *et al.*, 2013; Seehausen *et al.*, 2014). One notable example of the latter involves a copper-tolerant population of *Mimulus guttatus*, where lethality in hybrids between copper-tolerant and intolerant populations is the result of close linkage between the gene conferring copper tolerance and that dictating lethality (Wright *et al.*, 2013).

Not only do crossing and fertility barriers arise among conspecific taxa, as very well demonstrated in *Gilia* (Grant, 1981) and in *Mimulus* (Vickery, 1978), but genomic incompatibility may

develop among different populations of the same two taxa (Levin, 1978; Martin & Willis, 2010; Scopece *et al.*, 2010; Pinheiro *et al.*, 2013). Genomic disharmony may even be expressed to various degrees within populations, as in *Mimulus guttatus* and *Mimulus nasutus* (Martin & Willis, 2010) and in other plants and animals (Cutter, 2012, Corbett-Detig *et al.*, 2013). Candidate genes contributing to variable disharmony have been described within populations (Rieseberg & Blackman, 2010; Aagaard *et al.*, 2013). In *Mimulus* species, DM incompatibilities evolve and spread at local (Martin & Willis, 2010; Grossenbacher *et al.*, 2014) or regional scales (Sweigart *et al.*, 2007; Sweigart & Willis, 2012).

Both sterility and incompatibility may arise much earlier than the aforementioned time intervals if lineages have experienced bottlenecks during their histories, as in *Arabidopsis* (Pyhäjärvi *et al.*, 2012) and *Draba* (Grundt *et al.*, 2006; Skrede *et al.*, 2008). A shift from outcrossing to selfing and the bottlenecks attendant to that have contributed to the evolution of *Capsella rubella* from *Capsella grandiflora* within the past 100 000 yr (Foxe *et al.*, 2009; Guo *et al.*, 2009). If species are prone to bottlenecks (weedy species), intraspecific taxa therein are apt to be relatively young, because they will ascend to species status sooner than intraspecific taxa with a more stable demographic. Consider that two pairs of *Arabidopsis lyrata* subspecies are c. 150 000 yr and 300 000 yr old, respectively (Pyhäjärvi *et al.*, 2012). The establishment of underdominant mutations by genetic drift, as promoted by small effective population size, and by cycles of localized extinction and recolonization (Lande, 1985; Gavrilets, 2004), ostensibly fostered the formation of cryptic species in *Draba* (Grundt *et al.*, 2006; Skrede *et al.*, 2008). Partial cross-incompatibility may evolve in a relatively short time when populations are subjected to multiple genetic bottlenecks, substantial inbreeding, and repeated episodes of intense directional selection, as occurs during domestication (Gross & Olsen, 2010).

Post-pollination isolation in herbs may take much longer to develop than prepollination isolation, as seen in many Hawaiian genera, wherein substantial adaptive radiation during the past 3–4 million yr has not been accompanied by strong post-pollination isolation (Baldwin & Sanderson, 1998; Price & Wagner, 2004; Keeley & Funk, 2011). This being the case, intraspecific taxa would graduate to species before strong post-pollination barriers were in place, and thus be younger on average than taxa waiting for such barriers. Relatively rapid prepollination isolation may accrue when flowering time, habitat preference, and floral attractants and architecture are acted upon directly and forcefully by natural selection (Levin, 2003; Givnish, 2010). Whereas environmental change may reverse some prepollination/ecological barriers, post-pollination barriers are irrevocable.

We do not contend that all sister intraspecific taxa will graduate to the species level as they age. Indeed, most probably will not. These taxa may fail to reach older ages because they go extinct. Intraspecific taxa are vulnerable to extinction because they often have narrow geographical distributions (Gaston & Fuller, 2009; Birand *et al.*, 2012), narrow niche breadths (Morin & Lechowicz, 2013; Slayter *et al.*, 2013), and relatively small numbers across populations (Dynesius & Jansson, 2014). Similar findings have also been demonstrated across a range of taxa, both

plant and nonplant, including island bird assemblages (Lasky *et al.*, 2016). The tendency of these entities to evolve in parts of species' range where environmental conditions are more extreme also contributes to their lower success rates (Botero *et al.*, 2014). Narrowly distributed peripheral isolates are especially prone to extinction, because their small sizes are associated with increased sensitivity to environmental and demographic stochasticity, heightened inbreeding, and reduced genetic diversity (Mayr, 1963; Anacker & Strauss, 2014). Not surprisingly, self-compatible plant lineages, which often evolve in geographically marginal populations and are inbred to various degrees, have higher extinction rates than related self-incompatible lineages (Schoen & Busch, 2008; Goldberg *et al.*, 2010).

Hybridization with a related and abundant taxon may further threaten the tenure of rare taxa. The production of hybrid seeds reduces the number of 'nonhybrid' seeds that individuals produce, which in turn negatively impacts population size and survival (Levin *et al.*, 1996). Hybridization also may lead to the absorption of a minor taxon by an abundant conspecific (Grant, 1963; Levin, 2005; Mallet, 2008; Seehausen *et al.*, 2008; Gilman & Behm, 2011).

Herbaceous taxa have been the focal point of this paper; and thus the expectation that intraspecific taxa rarely will reach 10 million yr. However, in trees, intraspecific taxa may reach much older ages than in herbs, because so much more time is required for post-pollination isolation. The latter is evident in the partially fertile hybrids obtained from crossing *Platanus occidentalis* and *Platanus orientalis* (Panetsos *et al.*, 1994), which have been separated for *c.* 50 million yr (Feng *et al.*, 2005). The extended waiting time for sterility and cross-incompatibility in trees is a consequence of their much longer generation time, and perhaps of their larger effective sizes as a result of less variable population sizes than herbs. This may explain why the speciation rates in the Saxifragales are about twice as high in herbaceous lineages as in woody lineages (Soltis *et al.*, 2013). The rate of molecular evolution in herbaceous plants is *c.* 2.5 times faster than that in woody plants based on a global phylogenetic analysis of angiosperms (Smith & Donoghue, 2008).

We have suggested that sister intraspecific taxa will inexorably march towards species status unless they go extinct. But may taxon divergence be arrested by hybridization? For this to happen, taxa would have to be within pollination or seed dispersal range in significant parts of their ranges. Most pairs of sister taxa are unlikely to meet these requirements, as they are usually ecologically and/or geographically isolated (Clausen, 1951; Grant, 1963, 1981). Even if widespread hybridization were possible, the requisite levels and character of gene flow and selection required for the stasis of DM incompatibilities are untenable (Pinho & Hey, 2010; Butlin & Ritchie, 2013; Feder *et al.*, 2013; Servedio *et al.*, 2013). Hybridization either will cause subspecies to fuse or will promote their divergence.

Conclusions

An extensive literature survey and Bayesian analysis indicate that sister intraspecific, herbaceous taxa typically are much less than 10 Myo. This finding is consistent with the view that strong post-pollination barriers arise roughly between 5 and 10 million yr after lineage splitting. Whereas intraspecific entities may terminate their existence below the species level by ascending to species status, one or both members of a taxon pair may go extinct before their reproductive isolation by virtue of their small geographical ranges, small collective population sizes, and narrow niches. Based on the distribution of taxon ages and on the factors that would terminate them as intraspecific entities, it seems unlikely that intraspecific herbaceous taxa would persist for tens of millions of years.

The proposition that intraspecific lineages are likely to be short-lived is compatible with the view that many more incipient species evolve than persist, and that their rates of extinction are high (Mayr, 1963; Stanley, 1978, 1985; Allmon, 1992; Rosenblum *et al.*, 2012). In birds, the rate of subspeciation is between 30 and 40 times higher than the rate of speciation (Martin & Tewksbury, 2008; Phillimore, 2010). The rate of subspeciation relative to speciation in plants has not been quantified. The fate of intraspecific taxa is similar to that of species whose lives may end when one species branches into two new species or when species go extinct (Gillespie & Ricklefs, 1979).

Even if intraspecific taxa fail to become species, they may still contribute to diversification in their genera. They may participate with other species in the formation of allopolyploids. The genomes of these transient novelties also might be preserved in autopolyploids. Finally, short-lived intraspecific entities might contribute genes to conspecifics, thus elevating their potential for divergent evolution at a later date.

Dynesius & Jansson (2014) consider the duration of divergent intraspecific lineages to be an important and underappreciated regulator of speciation rates. The longer the persistence time of intraspecific taxa the higher will be the speciation rate. Given that these taxa are especially vulnerable to extinction and that global climate change may be substantial and relatively rapid (Stanton *et al.*, 2014), it follows that the duration of extant intraspecific entities may be substantially shorter than they have been in the past several million years. Furthermore, these studies, coupled with our findings, support the emerging hypothesis that age-dependent speciation rates may be fairly constant (Hagen *et al.*, 2015). Accordingly, the proportion of sister taxa that survive long enough to develop post-pollination isolation, or prepollination isolation for that matter, may be much less than it has been over the past several million years.

Acknowledgements

Author contributions

The project was conceived by D.A.L., who garnered the ages of taxa, and their taxonomic and ecogeographical affinities from the literature. S.V.S. analysed the data and applied such to the models in the paper. D.A.L. wrote the evolutionary component of the

paper, and S.V.S. wrote the methods and an exposition of his analysis.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Table S1 The taxa, their ages and families used in this study

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