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The evolutionary reality of species and higher taxa in plants: a survey of post-modern opinion and evidence

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Summary

Species are normally considered to be the fundamental unit for understanding the evolution of biodiversity. Yet, in a survey of botanists in 1940, twice as many felt that plant genera were more natural units than plant species. Revisiting the survey, we found more people now regarded species as a more evolutionarily real unit, but a sizeable number still felt that genera were more evolutionarily real than species. Definitions of 'evolutionarily real' split into those based on shared evolutionary history and those based on shared evolutionary fate via ongoing evolutionary processes. We discuss recent work testing for shared evolutionary fate at the species and higher levels and present preliminary evidence for evolutionarily significant higher taxa in plants.

I. Introduction

Species are a fundamental unit for studies of biodiversity and evolution. Genetic theories of natural selection focus on populations as units, but populations evolve along similar trajectories if there is gene flow among them. Species instead reflect separate arenas for selection, drift and gene flow that evolve independently (Fisher, 1930) – often defined based on reproductive isolation in sexual organisms (Coyne & Orr, 2004). Species are frequently ecologically divergent as well, either as a consequence of independent evolution or because adaptation to distinct habitats or niches drives their divergence (Nosil, 2012). The cohesive effects of drift, selection and gene flow maintain genetic and phenotypic similarity within species (Templeton, 1989), while independence allows

divergence between species, leading to genetic and phenotypic 'gaps' between species (Fig. 1b). Consequently, research into the origins of diversity focuses on which mechanisms drive species divergence and on how species richness accumulates in different clades and geographic regions. Indeed, the level of species separates evolutionary biology into distinct approaches: population genetic studies of microevolution within species versus phylogenetic studies of macroevolution above species (although ideas are regularly shared between these fields; Barraclough & Nee, 2001).

But is life so simple? Is there really a single level in the hierarchy of life that can be used to explain evolutionary processes? Perhaps populations are just as important for understanding the evolution of diversity? And what about levels above the species? In the past, higher taxa were afforded similar status to species. For example,

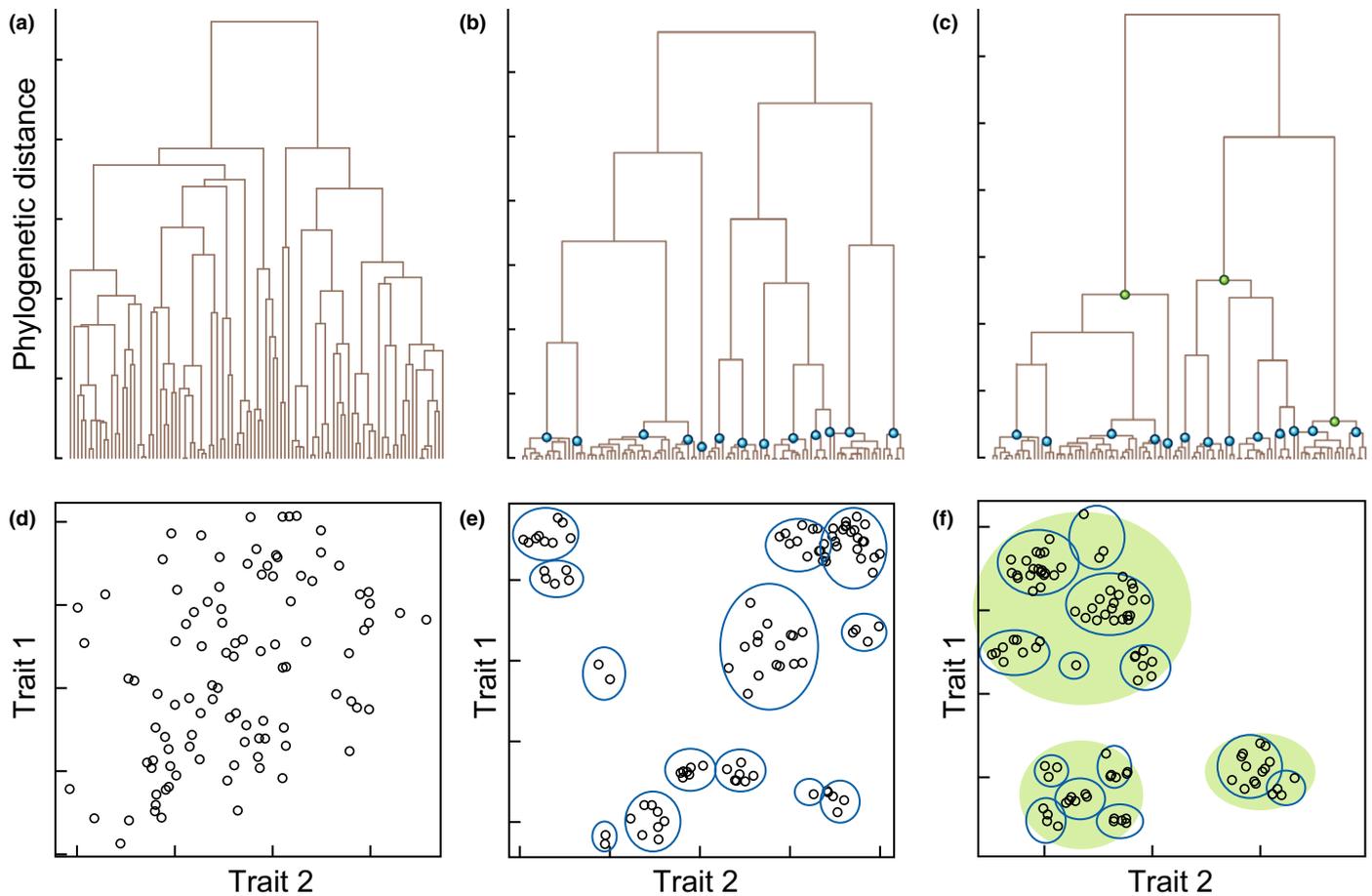


Fig. 1 Three theoretical models for the structure of diversity that make different predictions about the structure of genetic and phenotypic variation within clades. (a, d) Individuals within a wider clade form a continuous hierarchy. No processes are operating that create independently evolving subunits within the clade. (b, e) The clade has diversified into independently evolving species (blue dots and ellipses). Cohesive processes within species lead to genetic clustering, resulting in long stem branches subtending groups of closely related individuals, and phenotypic clusters. (c, f) Additional processes operate to create cohesion and clustering within subclades (green dots and shading) above the level of species. As described in Barraclough (2010) and the main text, and simulated in Humphreys & Barraclough (2014), this could arise through shared ecological limits and ongoing species turnover independently within each subclade. The predicted outcome is again discrete clustering, evident in genetic data as long stem branches leading to each subclade and in trait variation as phenotypic clusters. The data shown are hypothetical. In all three cases, taxonomists might have named ranks, such as genera or families, at other nodes within the clade. Alternatively, either by coincidence or because their eye was drawn by discrete trait variation, they might have named distinct units caused by evolutionary processes as a particular rank. Adopting this approach for defining higher taxa incorporates more phylogenetic information into the taxonomic process, by including phylogenetic branch lengths to identify discrete clades, compared with using topology alone to define monophyletic groups.

Linnaeus regarded both species and genera as ‘natural’, meaning a true feature of the natural world, whereas families and orders were ‘art’, meaning human constructs of classification (Linnaeus, 1751). Similarly, Simpson developed theories of higher taxa as discrete units and processes behind their formation and cohesion (i.e. adaptive radiation into new adaptive zones (Simpson, 1953; see also Stebbins, 1974)). Paradigm shifts in the 20th Century culminating in the cladistics revolution, however, led to higher taxa declining in fortune (Humphreys & Linder, 2009). They are still used for classification, but from a cladistic view, even if monophyletic, higher taxa are simply one arbitrary level within the cladistic hierarchy (Hennig, 1966; Fig. 1a). The only ‘reality’ of higher clades is shared evolutionary history. Members share phenotypic characteristics because they diverged relatively recently, but there are no cohesive mechanisms that cause shared evolutionary fate as in species (Coyne & Orr, 2004).

Seventy-five years ago the botanist Edgar Anderson asked 50 colleagues whether species or genera represent the most natural unit and whether the same processes are involved in the formation of species and genera (Anderson, 1940). Since then, our theoretical understanding of species and higher taxa has grown immensely and a range of new data are available for testing the nature of species and higher taxa, including genomes, phylogenies and trait data sets. To gain an overview of how these advances have changed perceptions of the evolutionary reality of plant taxa, we conducted a short survey revisiting Edgar Anderson’s original questions. Although there has been a shift in opinions, it is clear that opinions still hold sway and vary widely. We then describe concrete theories and evidence for the evolutionary reality of species and higher taxa. In the near future, these questions should be a matter of empirical fact over opinion.

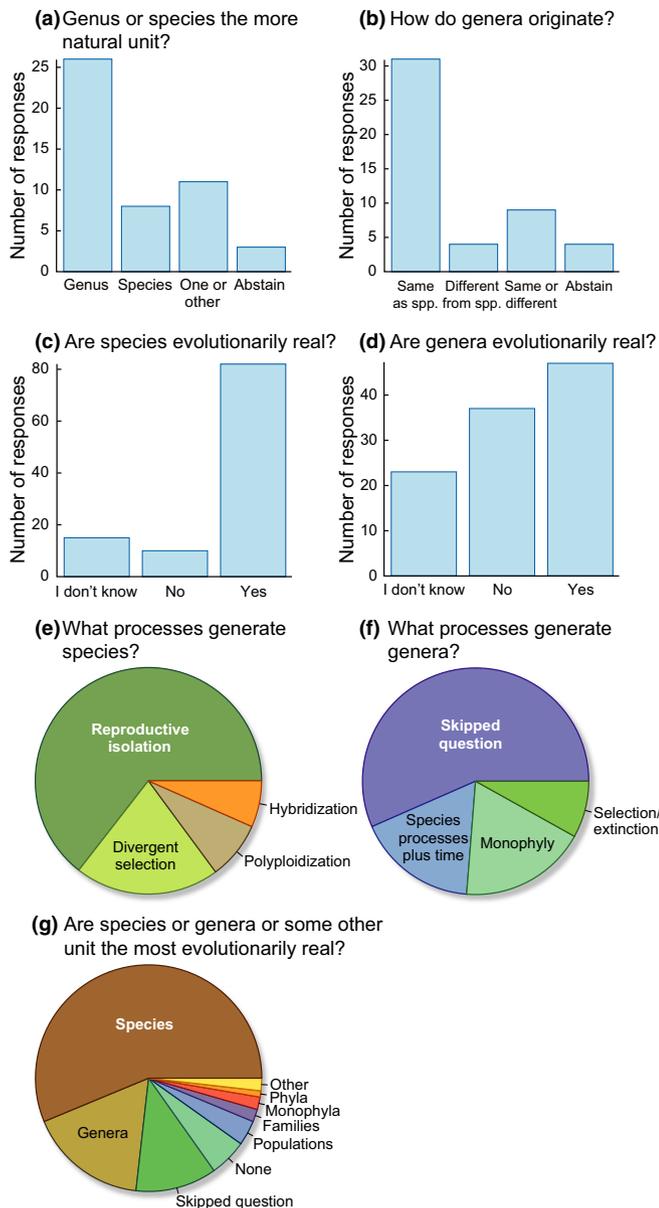


Fig. 2 Summary of responses (a, b) to the original Edgar Anderson (1940) survey and (c–g) to our June 2014 survey. In (a) ‘one or other’ refers to respondents who felt that sometimes genera and sometimes species were the more natural unit. In (g) ‘monophyla’ includes the view that monophyletic groups are real – rank is irrelevant – and the view that ‘only lineages’ are real. ‘Other’ includes ‘all taxa are equally real’ and ‘I don’t know’. A few respondents said more than one rank, for example ‘species and genera’ or ‘species and populations’. These have been scored in both mentioned categories.

II. A survey of post-modern opinion

The results of the original Anderson survey might look surprising to 21st Century readers, especially to card-carrying evolutionary biologists working on reproductive isolation and speciation. Twice as many respondents felt that plant genera were more natural units than thought that species were more natural (Fig. 2a). Most respondents also felt that genera originated by the same processes as species (Fig. 2b).

We expanded the original survey to ask for separate perceptions on species and genera and which processes cause each unit to form (Supporting Information Table S1). Replies came from 107 researchers working in universities, museums and botanical gardens (Tables S2, S3). Respondents were biased towards institutions attending the Evolutionary Plant Radiations symposium in Zurich, Switzerland 12–15 June 2014; <http://www.systbot.uzh.ch/static/congresses/radiations/>. Over half the respondents were under 40 yr old and around a third were plant taxonomists. Contrary to the original survey, taxonomic experience and age had little bearing on responses. There was widespread agreement that plant species are real evolutionary groups and reproductive isolation was most commonly cited for their formation, followed by divergent selection, polyploidy and hybridization (Fig. 2c,e). There was less agreement on genera, however (Fig. 2d,f). Around half of respondents thought they were real and offered a range of explanations for their formation. Genera either formed by the same processes as species but over longer timeframes, or were monophyletic groups and hence real (i.e. shared evolutionary history) or resulted from patterns of selection and/or extinction leading to gaps and phenotypic discreteness. Many respondents said that genera were not real or they did not know.

Compared with the original survey, there has been a switch towards a majority view that species are the more natural evolutionary unit in plants, although many respondents still consider genera more natural than species. A few respondents felt that populations, families or phyla were more evolutionarily real (Fig. 2g). Many had no opinion. The responses revealed a range of interpretations of what constitutes a real, evolutionary group. Some respondents equated different levels, stating there is ‘no fundamental distinction between microevolution and macroevolution’. Others regarded shared evolutionary history as the only meaningful definition: ‘Genera (like families, orders, etc.) are monophyletic if synapomorphies are found to identify them as such. Surely it is strange to speak of a “cause” of a genus.’

Two respondents neatly distinguished two facets of evolutionary reality but differed in whether they felt higher taxa exhibited the second facet:

‘Two meanings of “real, evolutionary groups”. One is just “clades” – lots but not all genera are certainly clades. The other is “evolutionary entities that, as an entity, play a role in evolutionary processes”. This is more controversial. I suspect many genera are like this but certainly far from all of them; I think they form by adaptive transitions and radiation.’

‘What do you mean with “evolutionary group”? Two reproductively isolated biospecies (no gene flow) of the same genus do not share a common evolutionary fate. Thus it is not an evolutionary group. . . (?) However, in ill-defined morphospecies with considerable gene flow. . . a common evolutionary fate of the genus seems quite likely. . . ? . . . IMHO: No taxonomic units higher than “species” can acts [*sic*] as a unit in evolution. (?) . . .’

To paraphrase, species share both evolutionary history and fate. Higher taxa share evolutionary history (when monophyletic) but are not widely thought to share evolutionary fate. However, both

respondents identify that levels above the species might share evolutionary fate in some circumstances.

III. Empirical evidence for species and higher taxa with shared evolutionary fate

The motivation behind the original Anderson survey was that empirical evidence was unavailable to address whether genera are natural units. Hence, the best that could be done was a survey of opinion. Despite enormous progress in empirical approaches to species and speciation, the questions raised by the survey have rarely been the focus of targeted study, even at the species level: it is clear that opinions still hold sway and vary widely. Most studies take species units for granted and seek to understand mechanisms for their divergence, for example by identifying genes responsible for reproductive isolation or ecological divergence. A rare exception was the study by Rieseberg *et al.* (2006), which compared taxonomic species names with measures of reproductive isolation and morphological clustering. They found that most recognized plant species did correspond to reproductively isolated and morphologically distinct clusters – and that there was no evidence that plant species were less well defined than animal species.

With growing data available across entire clades, it is now possible to go further and test directly for signatures of independent evolution (Barraclough *et al.*, 2003), such as reproductive isolation and divergent selection. These tests can compare a 'species model' with discrete species units (Fig. 1b) to a null model of no discrete units (Fig. 1a) or perhaps of a gradual decline in sharing of evolutionary processes rather than a discrete break (such as the exponential decline in homologous recombination frequency between bacterial isolates). For example, Fontaneto *et al.* (2007) found evidence for independent evolution in bdelloid rotifers and for divergent selection acting on quantitative measures of morphology. Similar methods have since been used widely to delimit species in animals and bacteria (Barraclough *et al.*, 2009; Monaghan *et al.*, 2009), but there are fewer studies in plants because of the difficulty of obtaining variable markers at the species

level. One example is detection of discrete clustering indicative of the species level in tropical orchids and subtropical shrubs (Lahaye *et al.*, 2008).

Above the species level, identifying shared evolutionary history is now a well-honed discipline through phylogenetics. There have been few studies, however, testing for evolutionary reality in terms of shared evolutionary fate at higher levels (Fig. 1). Scopece *et al.* (2010) tested for reproductive isolation within species versus within genera. They found that post-zygotic isolation in orchids was low within *Orchis* and within *Androrchis*, but high between the genera. Our impression is that such cases are widely known among botanists, but more systematic studies are needed to compare reproductive isolation between species and genera and to identify whether processes define discrete levels. In a genic view of speciation, there might be extensive gene flow across much of the genome with just a few regions targeted by divergent selection in ecologically divergent species (Ellegren *et al.*, 2012). Some genes might cross species boundaries readily and share evolutionary fate at higher levels, while others are restricted to particular species by divergent selection.

Recently we extended ideas for delimiting species to test for the emergence of independently evolving groups at higher levels (Barraclough, 2010; Humphreys & Barraclough, 2014). Using simulation models, we showed that clades can share evolutionary fate when there is species turnover through continual speciation and extinction, yet turnover operates independently in different clades. One scenario is clades isolated in different geographic areas. Over a sufficiently long time, turnover in each region leads to the emergence of monophyletic clades restricted to each geographic area, with each clade's crown age determined by the rate of species turnover, and divergence between clades increases linearly with time. A similar pattern can arise if sister clades occupy different ecological guilds. The outcome is phylogenetic clusters separated by long stem branches (Fig. 1c) – as long as the migration rate between geographic regions or shifts between ecological guilds are below a threshold value. We used statistical methods developed for delimiting species (generalized mixed-Yule coalescent (GMYC) method; Pons *et al.*, 2006; Fujisawa & Barraclough, 2013) to

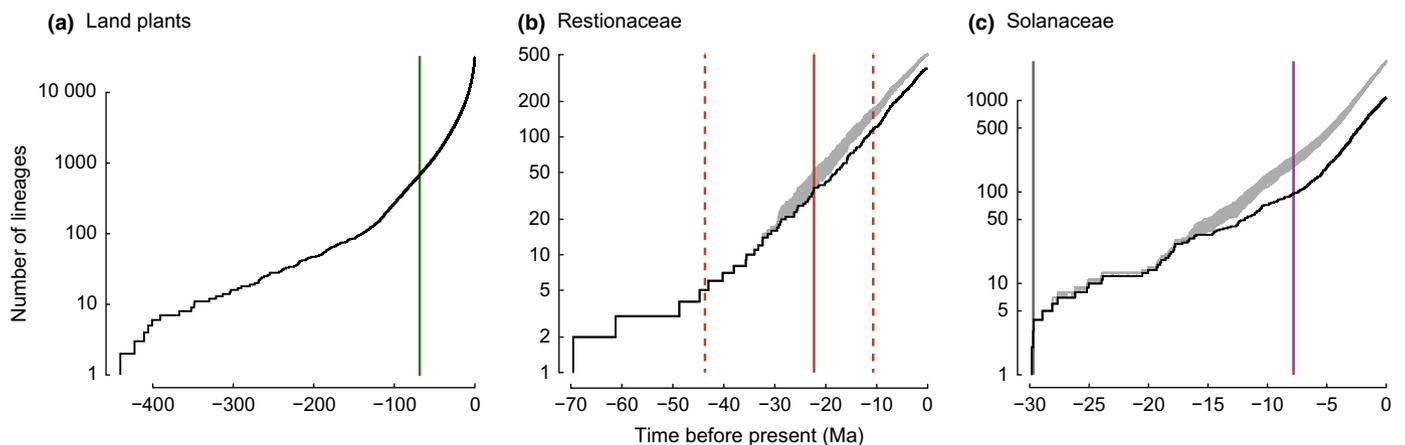


Fig. 3 Results of testing for higher evolutionarily significant units (hESUs). Black line, log number of lineages over time from root node to present; gray lines, log number of lineages over time when missing species are added randomly within their subfamilies (b; 500 replicates shown) or genera (c; 100 replicates shown). (a) Land plants. Green vertical line, single threshold age of hESUs for c. 10% sampled tree. (b) Restionaceae. Brown vertical line, median crown age of hESUs; dashed lines, 95% confidence limits of ages of hESUs across multiple threshold solutions. (c) Solanaceae. Purple vertical line, single threshold age of hESUs for 40% sampled tree; gray vertical line, single threshold age of hESUs for analysis with missing species added. Ma, million years ago.

Table 1 Summary of results of generalized mixed Yule-coalescent (GMYC) analyses testing for higher evolutionarily significant units (hESUs) in plants

Clade	Rank	Tips in tree (% of species)	hESUs	Threshold time (Ma)	Rank of hESUs
Land plants	Subkingdom	31 749 (9)	682	68.5	(Family)
Restionaceae	Family	382 (77)	11	22.3 (10.7–43.7)	Genus or above
Restionaceae – complete ¹	Family	496 (100)	10	23.0 (15.0–26.9)	Genus or above
Solanaceae	Family	1075 (c. 40)	96	7.8	Genus or below ²
Solanaceae – complete ¹	Family	2695 (c. 100)	2	29.7	Within family

¹For 'complete' Restionaceae trees, number of hESUs is the median estimate across 500 trees and threshold times are the median estimate across each tree. For Solanaceae, results are for the single threshold analysis only and there was no variation among the 100 'complete' trees analysed. The Restionaceae taxonomy was taken from Briggs & Linder (2009), updated with species numbers in Litsios *et al.* (2014), and the Solanaceae taxonomy from Olmstead *et al.* (2008) and The Plant List (2014).

²For Solanaceae, the below-genus count is mainly driven by *Solanum* being split. Most other hESUs correspond to genera. Ma, million years ago.

demonstrate a pattern consistent with independently evolving higher evolutionarily significant units (hESUs) in mammals, found roughly at the taxonomic level of families (Humphreys & Barraclough, 2014).

Our preliminary analyses indicate that similar units are found in plants (Figs 3, S1; Table 1). We first analysed the land plant tree of Zanne *et al.* (2014). We detected a transition in branching rate indicative of phylogenetic clusters separated by longer stem branches around the level of families: we found 682 hESUs compared with 642 recognized families (The Plant List, 2014). Many families, such as Fabaceae, Ericaceae, Brassicaceae and Orchidaceae, were identified as hESUs. This analysis is premature because only < 10% of species are represented in this tree, and we anticipate that, as more species are added, this might lead to detection of more recent hESUs (c.f. Humphreys & Barraclough, 2014). We also analysed the better sampled Restionaceae (phylogeny from Litsios *et al.*, 2014; 77% sampled) and Solanaceae (phylogeny from Särkinen *et al.*, 2013; 40% sampled). In Restionaceae we identified 11 hESUs. To investigate the possible effects of missing species, we added the remaining species randomly within the subfamilies that they belong to (Table S4; repeated for multiple random placements). The result remained unchanged and therefore appears to be robust to missing species in this case. By contrast, analysing only 40% of the species in Solanaceae greatly overestimated the number of hESUs compared with when missing species were added.

IV. Conclusions

These results provide preliminary methods of determining, and evidence for, evolutionarily significant higher units. Further analyses are needed to confirm the existence of such units in plants. These should include geographic ranges and trait data to infer possible causes of phylogenetic discreteness. For example, any hESU associated with occupation of a particular ecological guild should be associated with low variation in traits defining membership of that guild, for example, succulence in a clade restricted to arid regions (Evans *et al.*, 2014) or clustering of occupied floral morphospace in a clade with a single pollination syndrome (Chartier *et al.*, 2014). These patterns relate to those detected in searches for evidence of adaptive radiation (e.g. Etienne & Haegeman, 2012; Rabosky, 2014) or species selection (Rabosky

& McCune, 2010), but differ because high species richness or diversification rates are not necessary to detect an independently evolving hESU (Schenk *et al.*, 2013). Some hESUs could have low species richness because of limited opportunities in that region or ecological zone. Similarly, imbalance is not required: two clades could be detected as distinct hESUs even if they contained the same number of species. Independence would be indicated by recent crown ages and unexpectedly long internal stem branches (similarly to detecting independent evolution at the species level; Fujisawa & Barraclough, 2013).

Although final resolution of higher units awaits comprehensive analyses of well-sampled clades, we return to the question of whether species or genera (or higher taxa) are the more natural unit, that is, more reflective of shared evolutionary fate. Analyses of DNA barcodes indicate a steep upturn in genealogical branching rate occurring around the level of species (Acinas *et al.*, 2004; Pons *et al.*, 2006; Lahaye *et al.*, 2008). This marks the transition from between-species branching (determined by speciation and extinction events) to within-species branching (determined by effective population size, demographic changes and natural selection on the marker). This provides clear evidence of the reality of the species boundary and is typically far steeper than shifts observed at deeper levels in the tree. We do already therefore have evidence for the importance of the species level, at least for variation in organelle markers.

Opinions have shifted since the 1940s towards the greater reality of plant species than genera. However, there remain many researchers who believe that genera are more evolutionarily real than species in plants. There are now empirical tools available to test these ideas by comparing observed variation to predictions with or without the existence of units linked by shared evolutionary fate. As gaps in our sampling of plant diversity are filled in, it will be possible to test whether higher taxa with shared evolutionary fate exist. Our view is that the species level (sometimes blurring into higher levels in species complexes) will be found to be the main unit structuring variation, but this remains to be tested. Only when we understand the structure and units of biodiversity can we begin to understand evolutionary processes responsible for its generation.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 An estimate of higher evolutionarily significant units (ESUs) in Restionaceae and Solanaceae.

Table S1 Survey questions

Table S2 Number of responses to the survey obtained from each institution

Table S3 Survey responses

Table S4 Number and position of unsampled species added to Restionaceae and Solanaceae

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