Comment on “Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism”

Thomas D. Bruns* and John W. Taylor

Davison et al. (Reports, 28 August 2015, p. 970) claim that virtual taxa of Glomeromycota show little endemism and that endemism that exists is similar to the levels seen in plant families. We show that this is likely due to the conservative species definition rather than to any ecological pattern.

The Glomeromycota is a globally important group of fungi that form mutualistic interactions with the roots of the majority of land plants. They cannot be grown in axenic culture, and their taxonomy is currently based on differences in spore morphology and sequences of conserved genes (1). Davison et al. (2) use partial small subunit (SSU, or 18S) ribosomal RNA gene sequences to argue that their “virtual taxa,” which are “approximately species-level taxonomic units” of Glomeromycota fungi, have very limited endemism compared with larger organisms and that their pattern is more similar to that seen at the plant family level. However, there is a logical error in their methods, because they compare fungal taxa defined by partial SSU sequence to species in plants defined by multiple criteria and assume that they are comparing equivalent units.

We ask the question of what SSU-defined virtual taxa would look like if this approach were applied to animals or plants. To do this, we retrieved the human sequence for the same 520-base pair region, starting immediately after the NS51 primer, of the SSU gene used by Davison et al., and then used Basic Local Alignment Search Tool (BLAST) on this sequence to see the taxonomic depth that would be captured by a 97% identity threshold, the criteria they used. We found that the human gene fragment was a 99% match to house mouse (Mus musculus), pig (Sus scrofa), white-tailed deer (Odocoileus virginianus), western European hedgehog (Erinaceus europaeus), and horse (Equus caballus), and a 97% match to the common wombat (Vombatus ursinus) and several other marsupials. Thus, SSU-defined virtual taxa, if applied to mammals, would also show little or no endemism because most or all would be a single unit. Furthermore, if all species of mammals were defined by morphological differences in their egg cells, which are within the same scale as spore of the Glomeromycota, we would expect to see few, widely dispersed species that might well be correlated with the slight differences in the SSU gene.

We repeated this process by retrieving the homologous region from wheat (Triticum) and applying BLAST to it. We found that all available genera in family Poaceae (Oryza, Zea, Lolium, Festuca, Allotetraposis, Sorghum, Lecomella, and Anarthria) had SSU regions 98 to 99% identical to Triticum. Furthermore, at 96% identity, members of several Eudicot family were retrieved, including Caryocar glabrum (Caryocaraceae), Ackama rosfolla, Calotelia paniculosa, Opocunonia papuana (Cononiacese), and Hevea brasiliensis (Euphorbiaceae). With these results in mind, Davison et al.’s finding that Glomeromycota virtual taxa had similar levels of endemism to plant families makes sense, but only because similar levels of molecular divergence are then being compared in both groups; there is no evidence that one group has less endemism than another.

It is conceivable that fungal species have less conservation SSU genes, but when we used the SSU region from Neotria, from the well-sampled order Hypocreales, we found 99% identity with all sampled genera in the order. Thus, the entire order would be equivalent to one SSU-defined virtual taxon.

Morphologically defined species in the Glomeromycota have always been delimited by the characters available in their spores, and these “species” do correlate fairly well with SSU-defined units, but that does not mean that they are comparable to species in other groups. Knowing that these SSU-defined taxa are actually equivalent to family- or order-level taxonomic units in plants, animals, and other fungi should give us pause to consider the alternative: that all of these “species” in the Glomeromycota are actually collections of fairly distantly related taxa.

The main problem with respect to the Glomeromycota and all other small organisms is that there are very few observable phenotypic characters that allow us to distinguish and classify them. As a result, taxonomic concepts from species to phyla end up being much broader than those applied to larger, better-studied organisms. Broad species concepts led to hypotheses that, for small organisms, such as bacteria and protists, there is no endemism because “everything is everywhere” (3, 4). When more variable DNA sequences are used for comparison in small organisms, it has been shown that almost nothing is everywhere, whether fungi (5), protists (6), bacteria (7), or archaea (8). Now, population genomics is showing that natural barriers to fungal gene flow occur over geographic distances well below the size of continents (9–12), with dispersal limitation playing a key role in the assembly of fungal communities (12). When similar variable markers and population genomics can be applied to arbuscular mycorrhizal fungi, we predict that narrowly endemic species and populations will be discovered to be the rule, and what we now call species will be revealed to be collections of distantly related taxa.

Certainly, SSU-defined taxa are very useful in the Glomeromycota, and they currently provide one of the only ways to begin to catalog their global patterns. Furthermore, the correlation of these SSU taxa with other ecological parameters, and the modest level of endemism they reveal, is impressive and provides good evidence that they capture some of the evolutionary signal. However, claims of differences in endemism between them and macroscopic plants or animals only demonstrate how different the taxonomic concepts are; they say nothing about the comparative ecology of these organisms.

REFERENCES AND NOTES

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