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Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists

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To elucidate the genetic bases of mycorrhizal lifestyle evolution, we sequenced new fungal genomes, including 13 ectomycorrhizal (ECM), orchid (ORM) and ericoid (ERM) species, and five saprotrophs, which we analyzed along with other fungal genomes. Ectomycorrhizal fungi have a reduced complement of genes encoding plant cell wall–degrading enzymes (PCWDEs), as compared to their ancestral wood decayers. Nevertheless, they have retained a unique array of PCWDEs, thus suggesting that they possess diverse abilities to decompose lignocellulose. Similar functional categories of nonorthologous genes are induced in symbiosis. Of induced genes, 7–38% are orphan genes, including genes that encode secreted effector-like proteins. Convergent evolution of the mycorrhizal habit in fungi occurred via the repeated evolution of a ‘symbiosis toolkit’, with reduced numbers of PCWDEs and lineage-specific suites of mycorrhiza-induced genes.

Fungi are often described as either saprotrophs, which degrade complex organic substrates, or biotrophs, which obtain carbon compounds from living hosts. Among the latter, ECM fungi provide crucial ecological services in interacting with forest trees. They are portrayed as mutualists trading host photoassimilates for nutrients and having limited capacity to decompose soil lignocellulose1–3, as a result of their reduced repertoire of PCWDEs4–6. However, recent studies are challenging this view7–10. An improved understanding of the ability of ECM fungi to decompose lignocellulose is needed to resolve mechanisms of nutrient cycling in forests. The ECM lifestyle in Laccaria bicolor is associated with the expression of new mycorrhiza-induced small secreted proteins (MiSSPs) that are required for establishment of symbiosis11,12. Mycorrhizal symbioses have arisen repeatedly during fungal evolution and include not only ECM associations but also those with ORM and ERM mycorrhizae13. It is not known whether these symbioses share the genomic features found in L. bicolor4 and Tuber melanosporum5. Here we assess whether there

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are general evolutionary and functional properties of mycorrhizal Basidiomycota and Ascomycota, using comparative analysis of 18 newly sequenced genomes (Supplementary Tables 1 and 2), including 13 from ECM, ERM and ORM fungal symbionts.

Genomes of mycorrhizal fungi range in size from approximately 38 to 125 Mb, and their predicted gene contents range from approximately 15,000 to 23,000 genes (Supplementary Tables 3 and 4). We combined the 18 new genomes with 31 others and performed phylogenomic analyses (Supplementary Note, Supplementary Tables 1 and 5–10, and Supplementary Figs. 1–23). An organismal phylogeny resolved six to eight independent lineages of ECM and two lineages of ORM symbionts in Agaricomycetes as well as two mycorrhizal lineages in Ascomycota (Fig. 1). Molecular-clock analyses have suggested that the Pezizomycotina and Agaricomycetes are approximately 400 and 300 million years old, respectively. In contrast, the Pinaceae lineages in Ascomycota (Fig. 1) are general  evolutionary and functional properties of mycorrhizal Basidiomycota and Ascomycota, using comparative analysis of 18 newly sequenced genomes (Supplementary Tables 1 and 2), including 13 from ECM, ERM and ORM fungal symbionts.

Genomes of mycorrhizal fungi range in size from approximately 38 to 125 Mb, and their predicted gene contents range from approximately 15,000 to 23,000 genes (Supplementary Tables 3 and 4). We combined the 18 new genomes with 31 others and performed phylogenomic analyses (Supplementary Note, Supplementary Tables 1 and 5–10, and Supplementary Figs. 1–23). An organismal phylogeny resolved six to eight independent lineages of ECM and two lineages of ORM symbionts in Agaricomycetes as well as two mycorrhizal lineages in Ascomycota (Fig. 1). Molecular-clock analyses have suggested that the Pezizomycotina and Agaricomycetes are approximately 400 and 300 million years old, respectively. In contrast, the Pinaceae lineages in Ascomycota (Fig. 1) are approximately 15,000 to 23,000 genes (Supplementary Tables 3 and 4), and the arbuscular mycorrhizal fungus *Rhizophagus irregularis* demonstrated substantial losses in PCWDE genes. To assess the diversity of lignocellulose-decay capabilities of other mycorrhizal lineages, we cataloged 28 gene families and subfamilies encoding oxidoreductases and carbohydrate-active enzymes (CAZymes) associated with plant cell wall degradation (Fig. 2, Supplementary Note, Supplementary Tables 7–10 and Supplementary Fig. 3). Among Agaricomycetes, saprotrophs (including white-rot decayers, which can degrade lignin as well as cellulose), *Botryobasidium botryosum*, *Jaapia argillacea* and soil and litter saprotrophs possess on average 133 gene copies across all PCWDE families, whereas brown-rot species (which lack the ability to degrade lignin) possess 81 gene copies, and ECM species maintain 62 gene copies on average. Thus, the evolution of ECM parallels that of brown-rot lineages, with both guilds having lost much of the plesiomorphic enzymatic apparatus of white rots (Supplementary Note).

To reconstruct the evolution of decay capabilities, we performed tree species tree reconciliation for 16 gene families encoding oxidoreductases and carbohydrate-active enzymes (Supplementary Note and Supplementary Figs. 4–23). Here we focus on enzymes acting on lignin and crystalline cellulose, including class II peroxidases (PODs), glyoxal oxidase (GLX; an accessory enzyme that generates H₂O₂ as a substrate for PODs), GH6 and GH7 (cellulohydrolases) and lytic polysaccharide monooxygenases (LPMOs) (Supplementary Figs. 4–23). Expansion of LPMO genes, from 4 copies in the ancestor of Basidiomycota to 27 copies in the ancestor of Agaricomycetes, preceded the initial duplication of ligninolytic POD genes and the origin of the GLX...
gene, which are localized to the lineage leading to the ancestor of Auriculariales (Fig. 1). From that point, multiple copies of genes encoding LPMOs, PODs and GLXs, as well as GH6 and GH7, are reconstructed in the 'backbone' nodes of the Agaricomycete phylogeny (Fig. 1), thus suggesting that white rot was a conserved trait in the early evolution of mushroom-forming fungi.

Although all ECM species have reduced complements of PCWDEs (Figs. 1 and 2, and Supplementary Figs. 3–23), they have arisen from functionally diverse saprotroph precursors and have retained distinct suites of PCWDEs. For example, within the Agaricales, the ECM *Amanita muscaria* is nested within a group of soil and litter saprotrophs, including *Amanita thiersii*, which lacks PODs, whereas another ECM species, *Hebeloma cylindrosporum*, is nested within a group of white-rot decayers that have multiple POD, GLX, GH6, GH7 and LPMO enzymes (Fig. 1 and Supplementary Figs. 12–16). *A. muscaria* has lost genes encoding GLXs, GH6 and GH7, and it has a reduced complement of LPMO genes; both may be consequences of a shift to ECM, but the loss of POD genes in *A. muscaria* preceded (and therefore could not have been caused by) the evolution of the ECM habit. In contrast, *H. cylindrosporum* has three POD genes encoding manganese peroxidases (Supplementary Fig. 4), thus suggesting that it may possess ligninolytic capabilities similar to those in *Cortinarius glaucopus*.

The most densely sampled clade of ECM species in our analysis, the Boletales, contains six ECM species that are nested within a paraphyletic assemblage of brown-rot wood decayers lacking PODs and GLXs (Fig. 1). The ECM Boletales have further lost all copies of GH6 and GH7 genes and have no more than five copies of LPMO genes, thus suggesting that they have limited capacity to degrade lignocellulose (Fig. 1 and Supplementary Figs. 22–23). Gene tree–species tree reconciliations of LPMOs and other decay-related CAZymes suggest that parallel losses of brown-rot saprotrophy have occurred in the three ECM lineages in Boletales (Boletineae, Suillineae and Tulasnelliinae; Supplementary Figs. 15–23), although the ability to oxidize organic matter remains in *Paxillus involutus*.

Cantharelales and Sebacinales are early-diverging lineages of Agaricomycetes that include the ORM symbionts *Sebacina vermifera* and *Tulasnella calospora*. In contrast to ECM taxa in Boletales and

| Phylum | Subphylum | Species | Ecology 1 | Ecology 2 | Oxidoreductases | CAZymes | CBM1 |
|--------|-----------|---------|-----------|-----------|-----------------|---------|------|
| Basidiomycota | Agaricomycotina | Amanita muscaria | Biotroph | 29 | 28 | 0 |
| | | Hebeloma cylindrosporum | Ectomycorrhizal | 22 | 19 | 2 |
| | | Laccaria bicolor | 34 | 47 | 1 |
| | | Paxillus involutus | 23 | 39 | 0 |
| | | Paxillus rubicundulus | 24 | 35 | 0 |
| | | Pholiotina croceum | 41 | 50 | 0 |
| | | Pisolithus microporus | 17 | 29 | 0 |
| | | Poietus tinctorius | 22 | 26 | 0 |
| | | Scleroderma citrinum | 24 | 25 | 0 |
| | | Suillus lutescens | 29 | 40 | 0 |
| | | Tremella mesenterica | 8 | 14 | 0 |
| | | Sebacina vermifera | 21 | 121 | 50 |
| | | Tulasnella calospora | 9 | 178 | 110 |
| | | Phleotomospora indica | 15 | 103 | 64 |
| | | Auricularia delicata | 60 | 140 | 42 |
| | | Botryobasidium botryosum | 16 | 97 | 29 |
| | | Formitiporia mediterranea | 40 | 81 | 10 |
| | | Galea maritima | 77 | 128 | 52 |
| | | Heterobasidion annosum | 35 | 65 | 17 |
| | | Hypholoma sublateritium | 52 | 83 | 28 |
| | | Jaapia argilacea | 17 | 102 | 24 |
| | | Phanerochaete chrysosporium | 31 | 75 | 28 |
| | | Pileusosaurus oreas | 43 | 111 | 31 |
| | | Plicaturopis crispa | 21 | 70 | 9 |
| | | Punctulatus stipitatus | 46 | 93 | 26 |
| | | Schizophyllum commune | 8 | 103 | 5 |
| | | Sphaerobolus stellatus | (0/1) | (1/0) | 0 |
| | | Trametes versicolor | 50 | 94 | 23 |
| | | Coniophora puteana | 16 | 80 | 3 |
| | | Dacryopinax sp. | 14 | 50 | 1 |
| | | Fomitopsis pinicola | 16 | 65 | 0 |
| | | Gloeophyllum trabeum | 13 | 61 | 1 |
| | | Hydnocarpus polyrachi | 21 | 86 | 16 |
| | | Serpula lacrymans | 12 | 52 | 8 |
| | | Agaricus bisporus | 47 | 65 | 13 |
| | | Amanita thiersii | 27 | 71 | 10 |
| | | Coprinopsis cinerea | 41 | 96 | 44 |
| | | Gymnoporus luxurians | 66 | 118 | 32 |
| Ascomycota | Ustilaginomycotina | Ustilago maydis | Plant pathogen | 6 | 22 | 0 |
| | | Pucciniomycotina | Melanomaia lari-pupila | 91 | 71 | 0 |
| | | | Tuber melanosporum | 5 | 19 | 3 |
| | | | Oidiodendron maius | 31 | 119 | 36 |
| | | | Cryphonectria parasitica | 18 | 102 | 12 |
| | | | Stagonospora nodorum | 16 | 104 | 10 |
| | | | Aspergillus nidulans | 9 | 83 | 6 |
| | | | Trichoderma reesei | 10 | 39 | 14 |
| | | | Sphingobolus stellatus | 2 | 10 | 0 |
| | | | Botryobasidium botryosum | 3 | 5 | 0 |
| | | | Ectomycorrhizal | 5 | 19 | 3 |
| | | | Encod symbiont | 5 | 19 | 3 |
| | | | Soil, litter or other Saprotroph | 10 | 39 | 14 |
| | | | Plant pathogen | 2 | 10 | 0 |
| | | | Animal pathogen | 3 | 5 | 0 |
| | | | Biotroph | 6 | 22 | 0 |
Agaricales, symbiotic members of Cantharellales and Sebacinales have a robust apparatus for degradation of crystalline cellulose, particularly T. calospora, which has 7 GH6, 27 GH7 and 33 LPMO genes (even more than its putatively saprotrophic sister taxon, B. botryosum) (Fig. 1 and Supplementary Figs. 15 and 16). Moreover, proteins with a cellulose-binding domain (CBM1) are rarely detected in ECM, whereas they are abundant in the ORM and ERM symbionts (Fig. 2 and Supplementary Table 7). Unlike typical ECM fungi, ORM fungi transfer carbohydrates to their hosts in the juvenile state of orchids, and they exploit nonliving organic substrates to feed their host16. Similarly, the ERM Oidiodendron maius (Ascomycota) maintains multiple copies of GH6, GH7 and LPMO genes (Fig. 1 and Supplementary Table 7), thus explaining its saprotrophic ability in Sphagnum peat17. Reconciliation analyses suggest that the divergence of Cantharellales and Sebacinales occurred before the diversification of PODs in Agaricomycetes and the origin of white rot (Fig. 1). The well-developed capacity to attack crystalline cellulose in these lineages and in the Ascomycota may reflect a primitive mode of symbiotic life substantially relying on the saprotrophic ability to decay nonwoody substrates with modest lignin content.

In L. bicolor, symbiosis requires lineage-specific genes encoding small secreted effector proteins that control host-plant development and immunity4,11,12. By sequencing RNA from free-living mycelia and mycorrhizal roots, we identified genes regulated by symbiosis development in the ECM A. muscaria, H. cylindrosporum, P. involutus, P. croceum, S. luteus, the orchid mycorrhizal T. calospora, the ericoid mycorrhizal Oidiodendron maius, the endophytic S. vermifera and the brown-rot S. lacrymans are shown in Supplementary Figure 25, whereas double-hierarchical-clustering heat maps of symbiosis-downregulated genes are shown in Supplementary Figure 26. Species abbreviations are in Supplementary Table 1.

Figure 3 Presence and sequence similarity of symbiosis-upregulated genes from L. bicolor in 55 genomes of saprotrophic (white rots, brown rots, soil and litter decayers), mycorrhizal (ECM, ERM and ORM), pathogenic and endophytic fungi. The heat map depicts a double-hierarchical clustering of 588 symbiosis-upregulated L. bicolor genes (rows, fold change >5, false discovery rate–corrected P < 0.05; Supplementary Data Set 1) based on their percentage sequence identity (color scale at left) with their orthologs (if any) in selected fungal species (columns). Right, color-coded gene clusters (clusters I to VI), with dots representing differentially expressed genes upregulated >100-fold; for genes with regulation less than 100-fold, the fold-change value is set to 1 (majority of the genes). The x-axis is a logarithmic scale of the fold change in gene expression (natural algorithm with Euler’s number). Genes of cluster VI are L. bicolor-specific (orphan) genes, whereas genes of cluster V have sequence similarity only with predicted proteins of the sister species L. amethystina. Double-hierarchical-clustering heat maps of symbiosis-upregulated genes for the ECM A. muscaria, H. cylindrosporum, P. involutus, P. croceum, S. luteus, the orchid mycorrhizal T. calospora, the ericoid mycorrhizal Oidiodendron maius, the endophytic S. vermifera and the brown-rot S. lacrymans are shown in Supplementary Figure 25, whereas double-hierarchical-clustering heat maps of symbiosis-downregulated genes are shown in Supplementary Figure 26. Species abbreviations are in Supplementary Table 1.
induced orphan genes have homologs in both Supplementary Fig. 25 thus suggesting that they are used to penetrate host cells. Colonization of the host root apoplastic space (CE8), hemicellulose (GH30) and cellulose (GH5_5 and LPMOs) are obscured, a phenomenon frequently observed for effector genes 19, or diverged so far that their similarities to other sequences have been specific orphan genes may represent either ancestral genes that have the ECM habit species within a genus continued to develop a specific gene complements have been adapted to the ECM lifestyle. For example, de novo Fig. 3. The latter diverged from the L. bicolor lineage ~20 million years ago18, thus indicating that even after the evolution of the ECM habit species within a genus continued to develop a specific symbiosis protein ‘toolkit’ and to diverge from each other. Lineage-specific orphan genes may represent either ancestral genes that have diverged so far that their similarities to other sequences have been obscured, a phenomenon frequently observed for effector genes19, or genes formed de novo from previously noncoding sequences20. Orphan fungal genes are over-represented among up- and downregulated genes found in mycorrhizal roots (Figs. 3 and 4, and Supplementary Figs. 25 and 26). To assess whether previously uncharacterized but highly induced genes may represent candidates for secreted effector proteins (CSEPs), we assessed which and how many of these genes encode proteins that possess properties (for example, predicted signal peptide, size <300 amino acid residues and no sequence similarity) common to known secreted effectors, such as mycorrhiza-induced small secreted protein of 7 kDa (MiSSP7)11,12. Of the induced genes, 8–28% encode proteins with a predicted signal peptide, a significantly higher fraction than the 3–7% of noninduced and non-symbiosis-related genes that encode a protein with a signal peptide (P = 2.04 × 10−6 to <2.20 × 10−16, Fisher’s exact test; Fig. 4 and Supplementary Fig. 25). Except for S. verrunfera, there is a significantly higher proportion of genes encoding secreted proteins of <300 amino acid residues (4–11% compared to 1–2% in the noninduced set; P = 0.0033 to <2.20 × 10−16, Fisher’s exact test; Fig. 4 and Supplementary Fig. 25).

Serpula lacrymans is a member of a paraphyletic clade of brown-rot lineages from which the ECM Boletales are derived (Fig. 1). S. lacrymans is able to form a loose hyphal mantle around pine roots, and this may provide clues to the antecedent condition of ECM21. Transcript profiling of the root-associated mycelium showed a significant proportion of root-induced transcripts, but we detected no small secreted proteins, whereas ECM Boletales expressed a large set of MiSSPs (Supplementary Fig. 25). Although proteins known to interact with host immunity and development, such as MiSSP7, are not the only functional class to be over-represented among lineage-specific short secreted proteins, the prevalence of CSEPs among symbiosis-induced genes suggests that at least some of these genes encode new symbiosis-related effectors.

Mycorrhizal symbioses evolved from ecologically diverse decayer precursors and radiated in parallel, following the origins of their host-plant lineages (Fig. 1). Polyphyletic evolution of the ECM lifestyle is marked not only by convergent losses of different components of the ancestral saprotrophic apparatus but also by rapid genetic turnover in symbiosis-induced genes (Fig. 3), some of which may reflect lineage-specific functional innovations, such as MiSSPs. In contrast, ERM and ORM fungi retained an extensive decay apparatus that is probably exploited indirectly by the plant for carbohydrate supply, thus explaining their known saprotrophic ability17. The available genome sequences of mycorrhizal fungi will represent foundational information for understanding symbiosis development and functioning. These resources will facilitate field studies aiming to predict responses of mycorrhizal communities to environmental shifts, such as altered forest-management practices and climate change.

METHODS

Methods and any associated references are available in the online version of the paper.

Accession codes. Genome assemblies and annotations for the organisms used in this study are available via the JGI fungal genome portal MycoCosm22 (Supplementary Tables 2 and 3). In addition, the newly sequenced genome assemblies and annotations have been deposited in GenBank under the following accession codes and BioProjects, respectively: A. muscaria Koide BX008, JMDV00000000 and PRJNA207684; Gymnopus luxurians FD-317 M1, JINP00000000 and PRJNA68535; H. cylindrosporum h7, JMDQ00000000 and PRJNA207849; Hydnum rutilus var. rutilus FD-334 SS-4, JMSK00000000 and PRJNA207871; Hypholoma sublateralum FD-334 SS-4, JMSK00000000 and PRJNA70685; L. amethystina LaAM-08-1, JMSL00000000 and PRJNA196025; O. miusz. JMPD00000000 and PRJNA74727; P. involutus ATCC 200175, JOMD00000000 and PRJNA60449; Paxillus rubicundulus WO68 2h10, JMDR00000000 and PRJNA243391; P. croceum F 1598, JMDN00000000 and PRJNA61203; Pisolithus microcarpus 441, JDMN00000000 and PRJNA60815; Pisolithus tinctitans Marx 270, JMDD00000000 and PRJNA207840; Plicaturopsis crispa FD-325 SS-3, JOMB00000000 and PRJNA207847; Sclerotodea citrinum Foug A, JMDU00000000 and PRJNA207859; S. vermifera MAFF 305830, JMDH00000000 and PRJNA207844; Sphaerobolus stellatus SS14, JOMA00000000 and PRJNA207858; S. luteus UH-SL-Lm8-n1, JMSM00000000 and PRJNA242126; T. calospora MUT 4182,
JMDT0000000 and PRJNA207843). Electronic files of the phylogenomic and phylogenetic analyses have been deposited in the Dryad Repository under doi:10.5061/dryad.2gq0f. The complete gene expression data sets have been submitted to Gene Expression Omnibus (superset series GSE63947). For L. bicolor and S. lacrymans, microarray data4,21 were reanalyzed (GSE9784, GSE27839 and GSE63929).

Note: Any Supplementary Information and Source Data files are available in the online version of the paper.

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AUTHOR CONTRIBUTIONS
E.M. conceived and guided the entire Mycorrhizal Genomics Initiative. I.V.G. directed all genome-sequencing and analysis efforts at JGI. D.S.H. directed the phylogenomic analyses. A. Tunlid coordinated the P. involutus genome project. F.M., D.S.H., I.V.G. and A. Kohler wrote the paper with contributions and input from all project members. A. Kohler performed overall management of biological materials and DNA and RNA preparations at INRA. K.W.B. performed overall project management at JGI. N.C., M.D.C., J.D., D.F., T.J., U.L., E. Martino, M.P., J.R. and M.T. extracted genomic DNA for sequencing. J.D., N.H., M.G., M.T., H.-R.K., S.H., U.L., E. Martino, U.N., J.M.P. and F.R. provided RNA for transcript profiling. A. Kohler, E. Morin, F.M., C.M., C.V.-F., G.G., S.H., S.P., M.G., A.Z., F.R., J.C., R.M. and A.P. analyzed genomic and transcriptomic data. C.C. and C.Y.N. performed genome sequencing. A. Clum, A. Copeland, K.L., A. Trift and H.S. assembled the genomes. A. Kuo, R.A.O., R.R. and A.S. annotated and analyzed the genomes. B.C. and F.S. analyzed the P. involutus genome. E.A.L. and A. Lipzen performed transcriptome sequencing and analysis at JGI. L.G.N., D.F. and D.S.H. performed organismal phylogeny and analyzed evolution of decay-related gene families. A. Kuo and E. Morin performed protein clustering analysis. B.H. and A. Levasseur annotated the CAZyme and fungal oxidative lignin enzyme (FOlyme) families. J.H. analyzed the repeated elements in A. massarica.

COMPETING FINANCIAL INTERESTS
The authors declare no competing financial interests.

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ONLINE METHODS

Sequencing, assembly and annotation. The 18 new genomes were sequenced with a combination of the Sanger, 454, Illumina and PacBio sequencing platforms (Supplementary Note and Supplementary Tables 2 and 3). All genomes were assembled in a platform-dependent manner and annotated with the JGI Annotation Pipeline23, which combines several gene prediction and annotation methods with transcriptomics data and integrates the annotated genomes into MycoCosm22, a web-based fungal resource for comparative analysis (Supplementary Note).

Transcript profiling. Gene expression in mycorrhizal root tips and free-living mycelium from the ECM A. muscaria, H. cylindrosporum, P. involutus, P. croceum and S. luteus, the ERM O. maius and the ORM S. vermifera and T. calospora was assessed with RNA-seq (Supplementary Note and Supplementary Table 11).

Protein sequence clustering. Predicted protein sequences were clustered with the Markov Cluster Algorithm (MCL) program24, with an inflation parameter of 2.0 (Supplementary Note).

Phylogeny. From protein sequence clustering, we identified single-copy gene families (1,809 clusters) that contained genes for >15 species (Supplementary Note and Supplementary Fig. 1). We found 617 such clusters, 5 of which contained suspected nonorthologous genes and were excluded. The remaining 611 gene families were retained, and ambiguously aligned sites were removed by 3 different settings altogether (with GBlocks and PRANK posterior probabilities). The single-gene alignments were then concatenated to result in 3 data sets with 19,567 sites and 149 loci (PRANK, 1.0 exclusion threshold), 114,814 sites and 542 loci (PRANK, 0.95 exclusion threshold) and 34,323 sites in 259 loci (MAFFT + GBlocks) (Supplementary Fig. 2). We then inferred maximum-likelihood and Bayesian trees by using RAxML 7.2.8 and PhyloBayes 3.3, respectively. The inferred trees were largely congruent across data sets and analyses. The inferred maximum-likelihood tree (data set PR0.95; Supplementary Fig. 2) was used for subsequent analyses.

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Corrigendum: Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists

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In the version of this article initially published online, the Online Methods indicated that 612 single-gene families were included in the phylogenetic analysis. However, one gene family was excluded because of significant topological conflict, and the total number of gene families included was therefore 611. The error has been corrected for the print, PDF and HTML versions of this article.