

NEWS AND VIEWS

PERSPECTIVE

Scaling up: examining the macroecology of ectomycorrhizal fungi

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Ectomycorrhizal (ECM) fungi play major ecological roles in temperate and tropical ecosystems. Although the richness of ECM fungal communities and the factors controlling their structure have been documented at local spatial scales, how they vary at larger spatial scales remains unclear. In this issue of *Molecular Ecology*, Tedersoo *et al.* (2012) present the results of a meta-analysis of ECM fungal community structure that sheds important new light on global-scale patterns. Using data from 69 study systems and 6021 fungal species, the researchers found that ECM fungal richness does not fit the classic latitudinal diversity gradient in which species richness peaks at lower latitudes. Instead, richness of ECM fungal communities has a unimodal relationship with latitude that peaks in temperate zones. Intriguingly, this conclusion suggests the mechanisms driving ECM fungal community richness may differ from those of many other organisms, including their plant hosts. Future research will be key to determine the robustness of this pattern and to examine the processes that generate and maintain global-scale gradients of ECM fungal richness.

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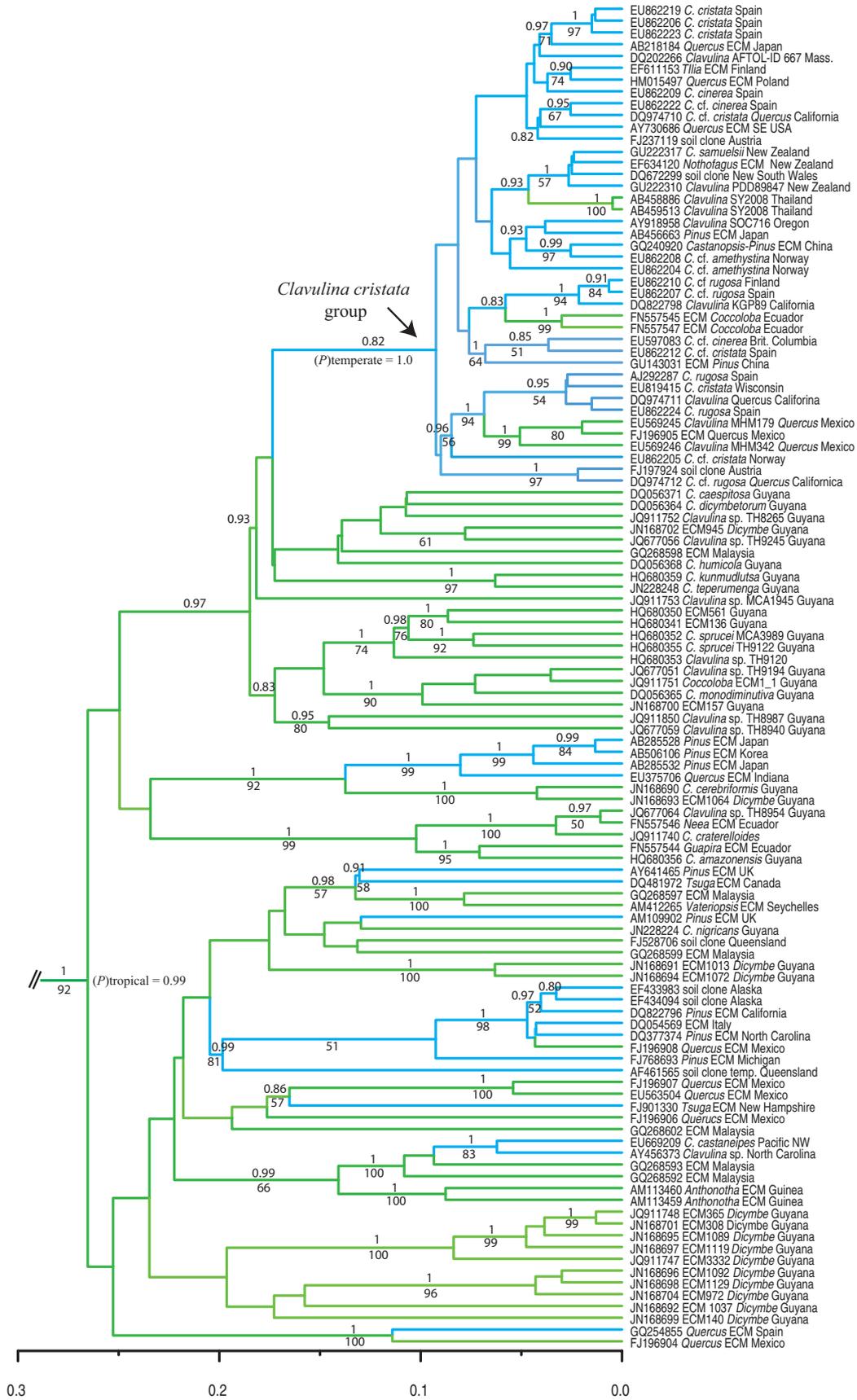
To better understand the causes of the classic latitudinal diversity gradient (LDG), researchers have proposed either evolutionary or ecological explanations, although the two are not mutually exclusive (Sherratt & Wilkinson 2009). From an evolutionary perspective, two main hypotheses,

among others (Wiens *et al.* 2006), have been invoked to explain the classic LDG: the time and area hypothesis and the diversification rate hypothesis (Mittelbach *et al.* 2007). The former suggests the tropics are more species-rich because tropical lineages are older and inhabit a larger area providing more opportunities for diversification. The latter suggests greater richness is observed in the tropics because lineages there exhibit higher net rates of diversification possibly due to low extinction rates, shorter generation times or higher extinction rates at high latitudes (Cardillo *et al.* 2005). Indeed, the diversification rate hypothesis was recently supported in a study on a group of butterflies (Condamine *et al.* 2012). However, species richness may be independent of clade age (Rabosky 2009) refuting the time and area hypothesis.

To explore whether the reversed LDG observed by Tedersoo *et al.* may be caused by differential rates of diversification between temperate and tropical ectomycorrhizal (ECM) fungal clades, we examined the genus *Clavulina* (order Cantharellales), a monophyletic group that contains 74 described species (Henkel *et al.* 2011b; Uehling & Henkel 2012). This analysis represents a robust test of a reversed LDG observed for ECM fungi because *Clavulina* contains more known species from tropical regions than temperate ones (Henkel *et al.* 2005). The data set we used includes ITS sequences from voucher-specimens as well as environmental samples from root tips or soils sampled from temperate and tropical latitudes. Although not all known species of *Clavulina* are represented by ITS sequences, our expectation is that any bias introduced by incomplete taxon sampling should be mitigated by efforts to include samples from a wide range of geographic locations as well as from ECM root tips and soil hyphae.

Our analysis of *Clavulina* raises doubts about both the time and area and diversification rate hypotheses. We do find that *Clavulina* is ancestrally tropical (Fig. 1). Consistent with the time and area hypothesis, we observe that tropical taxa are also older and that temperate lineages are nested among tropical clades. However, the rate of relative speciation is higher in one large inclusive clade containing 41 species (species delimitation follows Smith *et al.* 2011) distributed primarily in temperate zones (out of 114 total species excluding outgroups). For convenience, we refer to this clade as the *Clavulina cristata* group (see caption to Fig. 1 for methodological details). The *C. cristata* group exhibits a relative speciation rate approximately 2.6 times higher than the remainder of the tree, which is characterized by tropical lineages and seven considerably less rich temperate lineages. The rate of extinction in the *C. cristata* clade is also higher than elsewhere in the tree, but estimated extinction rates are so low that such differences are for all purposes practically negligible. The fact that clade age

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is not associated with richness in this analysis suggests that differences in speciation rates between temperate and tropical clades may drive greater species accumulation observed in temperate areas.

The finding that *Clavulina* is ancestrally tropical and has given rise to a rapidly diversifying clade in temperate areas may not be unique (Matheny *et al.* 2009). Buyck *et al.* (1996), based on field observations, highlighted several ECM fungal lineages distributed across the neotropics, tropical Africa and south-east Asia. These include *Amanita*, Boletaceae, Russulaceae, Inocybaceae, *Cantharellus* and *Scleroderma* (Boletales). We now add *Clavulina* to this list and make the prediction that these groups may be ancestrally tropical in origin with subsequent internal (possibly rapid) radiations in temperate regions. If nested temperate clades exhibit elevated rates of diversification, then this would be an important complement to the general observation that ECM fungal communities are more species-rich at temperate latitudes. At the minimum, such an endeavour is worth exploring, but will require substantial global taxonomic inventories and collaborative efforts in systematics (specimen-based research), community ecology (environmental sampling), biogeography (modes of dispersal) and evolutionary biology (phylogenetic and diversification rate-based research).

We note that several caveats and challenges may weaken the results in this example. Statistical support for nodes throughout the *Clavulina* phylogeny is generally weak, taxon sampling of known species is not yet complete, ancestral state reconstruction was performed only on a single topology, only one single gene region was sampled, and some other feature (perhaps intrinsic) may be associated with the increase in speciation rate observed here. Moreover, we were unable to detect any significant increase in diversification rate for seven other (small) temperate clades of *Clavulina*. Nevertheless, we find it encouraging (and predictive) that our approach can be refined, applied more broadly to other ECM clades, and help to better understand the evolution and macroecology of ECM fungi.

From an ecological perspective, Tedersoo *et al.* (2012) suggest that one major difference between tropical and

temperate environments is soil heterogeneity. In particular, they argue that temperate soils typically have more vertical heterogeneity than their tropical counterparts, which could provide a greater number of niches and therefore support a larger number of ECM fungal species. Peay *et al.* (2010) recently found that ECM fungal species richness was significantly higher in vertically heterogeneous sandy soils than in more homogenous clay soils at adjacent sites in the lowland tropical rainforests of Borneo. Similarly, Smith *et al.* (2011) showed that ECM species richness was high in a Neotropical forest where soils contained a robust litter/humus layer. While both of these studies support, the idea that soil heterogeneity could be an important driver of ECM fungal richness, looking at richness patterns across varying soil profile gradients in temperate forests, is needed to strengthen this explanation (i.e. are poorly differentiated soils in temperate areas notably ECM fungal species-poor?). Furthermore, experimental manipulations that control for confounding factors will be necessary to fully evaluate the role of soil heterogeneity in promoting ECM fungal richness.

Another significant result from the Tedersoo *et al.* (2012) meta-analysis was determining the relative importance of different factors in explaining the variation in ECM fungal composition across study locations. Using 19 different predictor variables, they found that host family explained 30% of the variation in fungal species composition, while all others explained <5%. Given this finding and that host lineages often differ between temperate and tropical forests, future studies that explicitly control for host phylogeny will provide deeper insight into the effects of abiotic factors on ECM community structure. For example, it would be interesting to compare the richness of ECM fungal communities in lowland tropical Fagaceae forests of Central America and south-east Asia with their congeneric counterparts in temperate regions. If ECM fungal richness were similar between tropical and temperate Fagaceae forests, it would indicate that the reversed LDG is driven largely by differences in host-lineage distributions and not abiotic factors.

Along with host family composition, it also seems important to consider the effects of host density. Four

Fig. 1 An ultrametric phylogenetic tree produced from ITS sequences for the ectomycorrhizal (ECM) genus *Clavulina*. A log-normal distribution with the mean set to 1.0 was used to model for rate differences between branches, and a Yule model of speciation was used as a prior for node heights. Together with a GTR + I + G model of nucleotide substitution, the tree was produced in BEAST and represents a consensus of 20 005 trees sampled from a posterior distribution from five independent runs using target node heights. After a burn-in of 1000 trees from each run, posterior probabilities were calculated in TreeAnnotator. Posterior probabilities >0.8 are shown above branches. Maximum likelihood (ML) bootstrap values from 200 bootstrap replicates conducted in RAxML are shown below branches. A parsimony ancestral state reconstruction was performed in MacClade under conditions of equal symmetry. In addition to parsimony, we reconstructed the ancestral area using ML, comparing a symmetric and asymmetric model in Mesquite. Both models generated results very similar to the parsimony analysis, with a proportional likelihood (P) = 1.00 for a temperate ancestor of the *C. cristata* group and (P) = 0.99 for a tropical ancestor for *Clavulina* as a whole. Branches reconstructed under parsimony as tropical are green; branches reconstructed as temperate are blue. Six sequences of Cantharellaceae (*Sistotrema coronilla* DQ397337, *Sistotrema confluens* DQ267125, *Hydnum albomagnum* DQ218305, *Hydnum repandum* AJ547871, *Hydnum repandum* AJ783968 and *Hydnum rufescens* AJ547868) were used for outgroup purposes but are pruned from the tree. *Clavulina* was found to be monophyletic with significant measures of statistical support. Diversification rate comparisons were performed using MEDUSA. The black arrow indicates an increase in net diversification rate by approximately 2.6 compared to the rest of the tree.

recent studies that have examined ECM fungal communities in tropical forests with high host density have found ECM fungal richness levels comparable to those in temperate forests (Peay *et al.* 2010; Tedersoo *et al.* 2010a; Henkel *et al.* 2011a; Smith *et al.* 2011). In contrast, Tedersoo *et al.* (2010b) found much less ECM fungal richness in a tropical forest with extremely low host density. As noted by the authors of the current study, many temperate forests have high host density, which may also help explain consistently higher ECM fungal richness. Unfortunately, the statistical models in their meta-analysis did not include host density as a predictor variable, but the aforementioned results suggest that host density may be a key latitude-independent predictor of ECM fungal richness.

In conclusion, the meta-analysis of Tedersoo *et al.* (2012) makes an important contribution in scaling up our understanding of ECM fungal richness and community composition. Future studies that test the various roles of different biotic and abiotic factors using a combination of experimental manipulations and other approaches will be key to determine the processes underlying global patterns for ECM fungi.

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