bridge the gap between functional traits, plant performance and life-history strategy (Fig. 1).

Amy E. Zanne1* and Daniel S. Falster2

1Department of Biology, University of Missouri, St Louis, St Louis, MO 63108, USA; 2Biological Sciences, Macquarie University, NSW 2109, Australia

(*Author for correspondence: tel +1 314 516 6672; email aezanne@gmail.com)

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General latitudinal gradient of biodiversity is reversed in ectomycorrhizal fungi

Tropical rainforests support a tremendous biodiversity of animals and plants, but because of difficulties in observation and identification, little is known about the richness patterns of microbes, including fungi. The general latitudinal gradient of diversity (LGD) demonstrates that nearly all terrestial and marine macroorganisms studied so far have peak richness at low latitudes (Hillebrand, 2004). Indeed, recent research in the Americas revealed that neotropical rainforests comprise the highest diversity of endophytic fungi. Plant taxa harbor different endophyte communities and therefore fungal diversity increases with host diversity (reviewed in Arnold, 2008). Similar patterns may enhance the diversity of ectomycorrhizal fungi (EcMF) in the temperate zone (Bruns et al., 2002; Ishida et al., 2007; Tedersoo et al., 2008), but the relevance of this and other potential factors remain unknown in tropical ecosystems because of a lack of published studies. In this issue of New Phytologist, Peay et al. (pp. 529–542) address the biotic and abiotic factors driving the composition of an EcMF community in a Bornean rainforest that comprises one of the highest plant diversities in the world.

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Do tropical and temperate EcMF communities differ? Extensive fruit-body surveys have revealed that tropical and temperate forests share many common EcMF lineages, such as the /boletus, /cantharellus, /clavulina, /russula–lactarius, /tomentella–thelephora, etc. (reviewed in Tedersoo
et al., 2010a). However, EcMF fruit-bodies do not provide useful data for quantitative comparisons of the local EcMF diversity among studies, because of their strongly seasonal and yearly unpredictable production and ephemeral habit. Several common EcMF lineages, such as the tomentella–thelephora, piloderma and hysteronium, produce either resupinate fruit-bodies on the underside of debris or hypogeous sporocarps that remain unnoticed unless specifically searched for. Moreover, many ascomycete lineages and some basidiomycete lineages probably lack fruit-bodies. The development of molecular techniques has facilitated the identification of EcMF from root tips and mycelia that can be found in soil throughout the year. Rapidly advancing sequencing and microarray technologies enable quantitative analyses of EcMF diversity and ecology based on numerous independent soil or root samples. Peay et al. collected 101 soil samples from seven 400-m² plots at Lambir Hills, Borneo, and recovered 105 EcMF species, most of which belong to the russula–lactarius, boletus and tomentella–thelephora lineages. These data are valuable for shedding light on EcMF diversity and community composition in tropical habitats, but do not represent all tropical forests that differ in historical biogeography and composition of ectomycorrhizal host lineages. To address differences in EcMF diversity and community structure between temperate and tropical rainforests, we supplemented the data from Lambir Hills with three data sets from different tropical regions (Africa, South America and South East Asia) and compared them with the results of temperate studies that employed generally similar methods for sampling and identification (Table 1).

Across these studies, the most species-rich lineages were thelephora–tomentella and russula–lactarius, followed by cortinarius, sebacina, clavulina, boletus and inocybe (Supporting Information Fig. S1). Surprisingly, the relative richness of only two EcMF lineages differed significantly between tropical and temperate habitats – russula–lactarius (t-test: t = 18.8; P = 0.005) and inocybe (t = 8.4; P = 0.027), which were relatively more diverse in tropical and temperate forests, respectively. However, the statistical significance collapsed when adjusted using the Bonferroni correction for multiple tests.

In contrast to the compositional similarity of EcMF, the diversity of EcMF in tropical sites was lower than that in temperate sites, as revealed by the rarefied species richness (Fig. 1a; t-test: t = 61.3; P < 0.001) and minimal richness estimators – Jackknife 2, Chao2 and ICE (Fig. S2). This pattern in EcMF strongly contradicts the negative LGD (Hillebrand, 2004). Thus, many of the proposed causal mechanisms, such as the mid-domain, geographical area and climatic stability effects that have been developed to explain the general LGD pattern (Lomolino et al., 2006), may be inapplicable to EcMF or need substantial modification.

What, then, causes the lower EcMF richness in tropical ecosystems? Although the information available is scant, we propose three possible mechanisms. First, historical and biogeographical effects may partly explain the differences in EcMF richness pattern observed between tropical and temperate ecosystems. Many EcMF lineages occur in both tropical and temperate biomes. While several temperate lineages are notably absent from tropical forests, no strictly tropical lineages are known (Tedersoo et al., 2010a). The EcMF community data support this observation: temperate forests harbor more EcMF lineages than tropical forests (Fig. 1b; t-test: t = 345.4; P < 0.001). The strictly temperate EcMF lineages probably evolved at higher latitudes with the Pinaceae hosts, but may be inferior competitors in tropical conditions. However, this can only partly explain the observed pattern, because these temperate lineages are relatively species-poor and usually form a minor component in temper-
ate forests (except for the amphinema–tylospora and strictly Pinaceae-specific suillus lineages).

Second, when both soil and roots are regarded as habitats for EcMF, the lower diversity and abundance of these habitats may account for the lower EcMF diversity in the tropics. EcMF hosts are an obligatory energy source for all EcMF. Therefore, the co-existence of different hosts enhances habitat diversity. With certain exceptions (Morris et al., 2008), host preference is rarely evident at the host species level, but is probably more important at higher taxonomic levels, that is, from genus to phylum (Ishida et al., 2007). While tropical forests are often dominated by a single ectomycorrhizal host lineage, such as the Dipterocarpaceae or certain groups of Fabaceae, temperate habitats are often composed of multiple codominant host lineages, for example, Fagales, Pinaceae and Salicaceae. Although many different dipterocarp or leguminous host species co-exist in a tropical site, their phylogenetic habitat difference is lower compared with temperate forests. Similarly, the soil habitat is less diverse in the tropics than in temperate forests. In tropical forests, the soil profile is usually poorly differentiated and has thin organic and litter layers as a result of the rapid consumption of organic matter by mesofauna and the fast decomposition rates that occur in constantly warm and humid conditions. Many temperate EcMF species display niche differentiation by soil horizons (e.g. Lindahl et al., 2007) and EcMF communities accumulate more species in better developed soils (Nara et al., 2003).

Third, resource availability and fragmentation may explain the observed pattern of EcMF richness. Many temperate forests are exclusively dominated by suitable host trees that may account for 100% in basal area or the number of stems. Conversely, EcMF hosts usually contribute < 75% to the basal area in South East Asia and in monodominant patches of other tropical regions. Tropical EcM hosts are most often distributed sparsely, forming small isolated host islands in non-EcM vegetation. Fragmentation and availability of fewer EcM roots may reduce the population size of EcMF and eventually result in fewer co-existing EcMF species (Peay et al., 2007; Tedersoo et al., 2010b).

The comparison of temperate and tropical forests demonstrates that the EcMF richness pattern is an exception to the general LGD. The underlying mechanisms of the EcMF richness pattern may include historical–biogeographical factors, habitat diversity and resource availability–fragmentation. Accumulating EcMF data from seasonal tropical and subarctic ecosystems will probably improve our understanding of these causal mechanisms and the entire shape of the latitudinal gradient of EcMF diversity. In addition to high-quality DNA sequence data, collection of various environmental and biological data for each study site is essential to develop a general model of EcMF diversity and community composition on a global scale (Lilleskov & Parrent, 2007).

Leho Tedersoo1* and Kazuhide Nara2

1Institute of Ecology and Earth Sciences and Natural History Museum of Tartu University; 40 Lai, 51005 Tartu, Estonia; 2Asian Natural Environmental Science Center, The University of Tokyo, Midori-cho 1-1-8, Nishi-Tokyo, Tokyo 188-0002, Japan

(*Author for correspondence: tel +372 56 654 986; email leho.tedersoo@ut.ee)

References


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Supporting Information

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

Fig. S1 Relative contribution of 13 most common lineages of EcMF to the local species richness in tropical and temperate forests.

Fig. S2 Rarefied accumulation curves of minimal species richness estimates for the eight study sites in tropical and temperate forests.

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**Figure S1.** Relative contribution of 13 most common lineages of ectomycorrhizal fungi (>1% total relative frequency) to the local species richness in tropical (open bars) and temperate (shaded bars) forests. Bars denote S.E. \((n = 4)\). The lineages are ranked based on their relative species richness across the eight study sites. Differences were calculated by use of \(t\)-tests: *, \(P<0.05\); **, \(P<0.01\). Note that after accounting for multiple comparisons by use of the Bonferroni test, all differences became non-significant. Therefore, any patterns shown here must be interpreted with caution.
Figure S2. Rarefied accumulation curves of minimal species richness estimates (a-c) for the eight study sites. a) Jackknife2; b) Chao2; c) ICE; brown, Tagamõisa, Estonia; green, Mt. Field, Australia; blue, Huizteco, Mexico; black, UC Sierra Foothill, CA; purple, Lambir Hills, Malaysia; red, Monts de Cristal, Gabon; orange, Bukit Bangkirai, Indonesia; pink, Yasuni, Ecuador. The minimal richness estimates were calculated based on original data sets by use of a computer program Estimate S (Colwell, 2006; EstimateS: statistical estimation of species richness and shared species from samples. Version 8. Persistent URL <purl.oclc.org/estimates>) and 1000 replicates.

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