Letter

Early successional ectomycorrhizal fungi are more likely to naturalize outside their native range than other ectomycorrhizal fungi

Introduction

Ectomycorrhizal fungi (EcMF) are the key symbionts of numerous woody plants in many ecosystems worldwide (Smith & Read, 2008; Tedersoo, 2017). They positively affect host plant nutrient uptake (Smith & Read, 2008) and take part in essential ecosystem processes such as carbon sequestration, nutrient cycling and decomposition of organic matter (Read & Perez-Moreno, 2003; Clemmensen et al., 2014; Shah et al., 2016). The majority of ectomycorrhizal (EcM) plants fully depend on the mycorrhizal symbionts and cannot complete their life cycle without these root associations (Smith & Read, 2008).

It has been long recognized that the absence of co-evolved EcMF can present a significant barrier to successful establishment of introduced EcM trees (Mikola, 1969; Poynton, 1979; Richardson et al., 2000a; Pringle et al., 2009). Dickie et al. (2010, 2017) proposed different strategies of alien EcM plants to overcome detrimental losses of mutualistic symbionts: (1) co-introduction of co-evolved mutualists; (2) association with familiar mutualists native to both native and alien ranges; and (3) novel associations with local species. Co-introductions of exotic EcMF with their plant hosts have been increasingly reported as a global phenomenon in recent years (Vellinga et al., 2009). In some cases, exotic EcMF can alter nutrient cycling and soil biochemistry (Chapela et al., 2001) or plant derived carbon competitive links (Wolfe et al., 2010).

EcMF introductions have been recorded in the past based on fruiting body collections (Vellinga et al., 2009). However, these aboveground sexual structures do not represent the whole EcMF communities associated with host plant roots (Gardes & Bruns, 1996; Kjøller, 2006), because many EcM fungal species produce either resupinate, hypogeous or microscopic fruiting bodies (e.g. Tomentella, Amphinema) or lack them altogether. In addition, many fungal species do not fruit frequently, making it difficult to record their presence. Therefore, methods of molecular identification are better suited for detection of many EcMF species compared to fruiting body surveys (Nilsson et al., 2019). Furthermore, in the past few years, the rise of well-developed and maintained databases such as UNITE (Abarenkov et al., 2010) and

a newly developed database of fungal next-generation sequencing studies (Větrovský et al., 2019) provide significantly improved information about the distribution and biogeography of many fungal taxa.

In plants, the EcM symbiosis has arisen independently on multiple occasions in evolutionary time since at least the Cretaceous Period (Brundrett & Tedersoo, 2018). Over 80 EcMF independent evolutionary lineages have been described to date (Tedersoo & Smith, 2017). In general, EcMF lineages differ in evolutionary age, geographic distribution, diversity, host specificity and ecology (Tedersoo & Smith, 2013). Phylogenetically, EcMF lineages mostly correspond to genus level, although some EcMF lineages are comprised of more genera. 'Early' and 'late' successional status has been recognized for some EcMF species (Mason et al., 1982; Last et al., 1984). Several fungal functional traits, such as spore germination rate, spore dormancy and spore longevity and ability to colonize tree seedlings are usually associated with early successional EcMF (Agerer, 2001; Bruns et al., 2009). Because many alien tree species have been frequently transported to new areas as seedlings along with soil from their native range (Mikola, 1969; Schwartz et al., 2006), EcMF with early successional strategy should be better preadapted to spread into new areas (Hayward et al., 2015). However, this assumption has never been tested before.

In this study, we explore the diversity of EcMF species introductions based on literature review and our own unpublished data from all continents. We expect that a relative number of naturalized EcMF species will be higher in EcMF lineages with prevalence in early successional stages.

Materials and Methods

This global-scale meta-study of EcMF co-introductions associated with alien woody plants is based on Web of Science and Google Scholar (as of 15 December 2019) search of studies, using combination of terms 'non-native', 'alien*', 'invasion*' and 'introduction*' with 'ectomycorrhiza*'. This search yielded 267 papers. In addition, we also searched for sequences of EcM mycobionts associated with exotic EcM plants in public sequence depositories, such as UNITE (Abarenkov et al., 2010) or INSD (International Nucleotide Sequence Database). The analysis included studies in which at least one EcM plant species was sampled outside its native range (corresponding to the definition of 'alien' following the criteria of Richardson et al. (2000b)) and root-associated EcMF were identified using sequencing of the internal transcribed spacer (ITS) region of ribosomal ribonucleic acid (rRNA) operon. The ITS region was chosen, because it represents the most commonly used barcoding region for fungal species (Schoch et al., 2012), which serves as a basis for molecularly defined fungal species hypotheses (SHs; Kõljalg et al., 2013). Studies with

experimentally manipulated soil treatments were excluded. If more than one alien EcM plant species per study was sampled, each species was treated as separated dataset. This procedure yielded 50 datasets from 30 studies (Supporting Information Table S1). In addition we included our seven unpublished datasets, which fulfilled all criteria listed earlier in the text.

The ITS sequences of root-associated EcMF were assigned to existing fungal SHs (version 8.0; Kõljalg *et al.*, 2013) based on BLASTN (Altschul *et al.*, 1990) search on 98.5% similarity level. Detected SHs were assigned to existing EcM lineages based on Tedersoo & Smith (2017). To determine putative native ranges of EcM SHs, we used (1) the SH distribution maps implemented in UNITE (5 November 2018), after excluding all sequences associated with non-native EcM vegetation or well known cases of EcMF introductions (i.e. introduced *Amanita phalloides* associating with native trees in North America; Wolfe *et al.*, 2010) and (2) a newly developed database of studies determining fungal community composition in natural vegetation based on next-generation sequencing (Větrovský *et al.*, 2019). Combining these two independent sources enabled us to determine the putative native ranges of EcM SHs from Sanger sequencing (UNITE) as well as next generation sequencing (NGS) based studies (Větrovský *et al.*, 2019). It gives probably the most comprehensive overview of global distribution of fungal SHs so far. Based on this information, we defined co-introduction as either concurrent or asynchronous introduction of naturalized SH with alien plant (Nuñez & Dickie, 2014; Dickie *et al.*, 2017). Putative native ranges were not defined for SHs with a low number of records in UNITE or NGS databases (less than six records). Total numbers of all SHs (on 1.5% dissimilarity level) per EcM fungal lineage were obtained from the UNITE database to calculate the proportion of naturalized EcMF SHs among all SHs in the lineage.

EcM fungal lineages were classified into early and late successional according to their appearance along the successional gradients. So far the most comprehensive review of the appearance of different EcMF genera during succession was published several years ago (Dickie *et al.*, 2013), which is a relatively long time given the rapid development of the field and its methodological tools. We extended the data provided by Dickie *et al.* (2013) with studies published since then (Table S2). If some EcMF were not recorded in studies describing EcMF communities along successional gradient, we identified their putative strategy based on the appearance on seedling roots or newly developed substrates (indicating early successional EcMF) or in mature forest vegetation (indicating late successional species).

To test whether there are differences in the share of naturalized EcMF in different EcMF lineages (based on Tedersoo & Smith, 2017), their counts were analysed by row × column contingency tables, using generalized linear models with the log-link function and a Poisson distribution of errors (Crawley, 2007). For the models that showed significant effects of the lineages, adjusted standardized residuals of G-tests were then compared with critical values of the normal distribution to ascertain the naturalized EcMF species counts per lineage that are lower or higher than expected by chance (Řehák & Řeháková, 1986; see e.g. Vinogradova *et al.*,

2018). All calculations were done in R v.3.5.0 software (R Development Core Team, 2019).

Results and Discussion

In total, 130 co-introduced EcM fungal SHs associated with roots of alien EcM plants were recorded in 57 analysed datasets worldwide (Table S3). So far, the most complete list of co-introduced EcMF compiled by Vellinga *et al.* (2009) based on fruiting bodies surveys, identified 224 co-introduced EcMF species worldwide. Interestingly, only 56 naturalized EcMF species were shared between our dataset and that of Vellinga *et al.* (2009). Collectively, these two studies identified almost 300 co-introduced EcMF species worldwide. Although 300 species represent a relatively small share of the tremendous EcMF diversity, we assume that the number of co-introduced species is much higher based on the low share of the EcMF species between the two data sets. The introductions are also probably on the rise due to increasing global trade and planting exotic material in attempts to counteract climate change effects on native trees.

The richness of naturalized species largely differed among EcMF lineages (Fig. 1). We identified numerous naturalized EcMF taxa in the /tomentella-thelephora lineage associated with both gymnosperms and angiosperms (Walbert *et al.*, 2010; Bogar *et al.*, 2015). Considering the resupinate fruiting bodies of *Tomentella* spp., these species may have been often overlooked in fruiting body surveys. Therefore, Vellinga *et al.* (2009) recognized only a few alien *Thelephora* spp., and no *Tomentella* spp., while our data indicated 18 species from the /tomentella-thelephora as co-introduced. Several of these were successfully co-introduced to more than one continent. Nonetheless, these naturalized taxa represented only a small proportion (< 1%) of all known /tomentella-thelephora SHs.

Importantly, several EcMF lineages contained a higher share of naturalized EcMF than expected by chance (Fig. 1). These lineages, /wilcoxina, /suillus-rhizopogon, /descolea, /laccaria and /pisolithus-scleroderma, likely include species with ecological traits favouring successful co-introduction with their alien EcM partners. As previously proposed by Hayward *et al.* (2015), such traits (i.e. production of resistant propagules or preferential association with widely introduced Pinaceae; Glassman *et al.*, 2015), could have allowed successful introductions of relatively small subset of EcMF in the past, which can subsequently drive host plant invasion (Policelli *et al.*, 2019). Although comprehensive databases of fungal species-level functional traits are still lacking, information about species distribution as well as their appearance during succession in previous studies enables us to estimate rough ecological strategies in EcMF. Species from the earlier-mentioned lineages were previously repeatedly detected in early successional plant communities (Table S2). With a few exceptions, members of these lineages are easily culturable and exhibit rapid mycelial growth (Chu-Chou, 1979; de la Bastide *et al.*, 1995; Kennedy *et al.*, 2011). Species from the Holarctic /wilcoxina lineage dominate on seedlings of EcM plants in tree nurseries (Mikola, 1965), early stages of succession after wildfire or following clear-cut harvesting (Barker *et al.*, 2013).
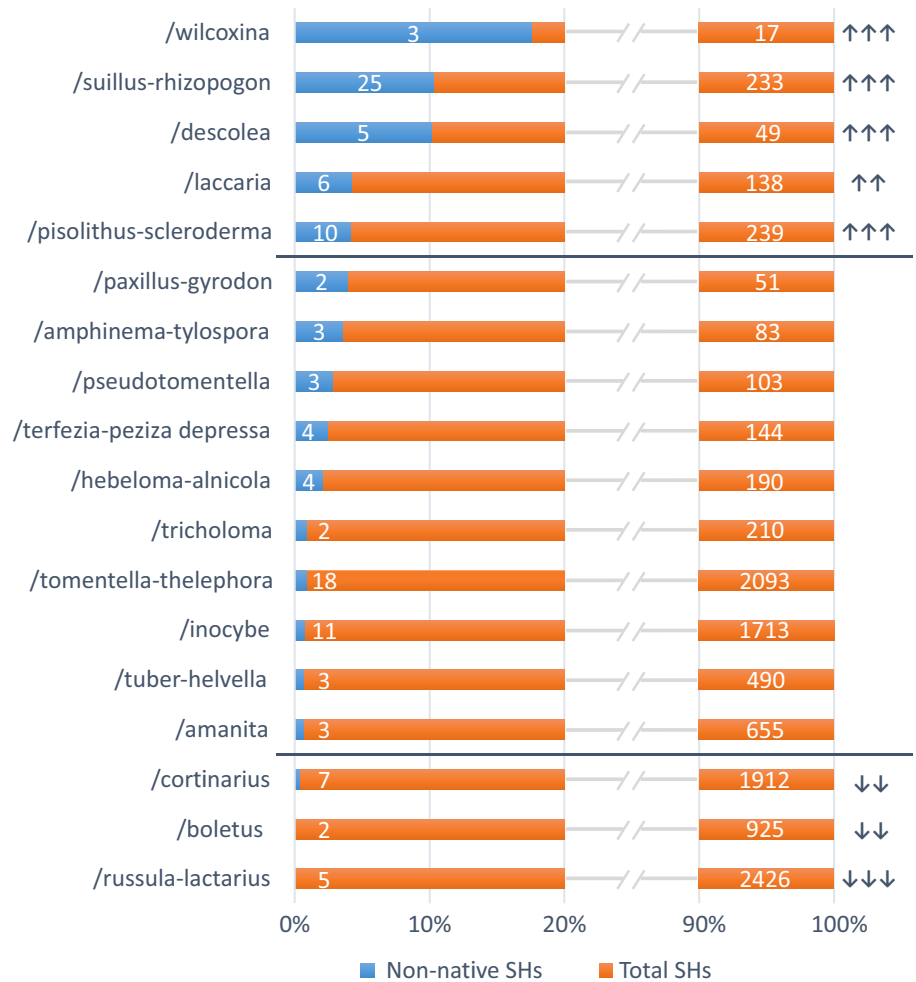
Fig. 1 Number of naturalized and all ectomycorrhizal fungal species hypotheses (SH; a molecularly defined fungal taxa used as a substitute of biological species) in different ectomycorrhizal fungal lineages. Numbers on left and right sides of the row bars indicate sums of naturalized and all ectomycorrhizal fungal SHs per lineage, respectively. Numbers on the *x*-axis correspond to the share of naturalized SHs in different ectomycorrhizal fungal lineages. Arrows indicate significant deviation of naturalized ectomycorrhizal fungi numbers from random distribution. Up arrows indicate overrepresentation and down arrows indicate underrepresentation. ↑↑↑, $P < 0.001$; ↑↑, $P < 0.01$; ↑, $P < 0.05$.

Similarly, species from the Southern Hemisphere /descolea lineage are also known as common fungal symbionts on post-fire sites (Palfner *et al.*, 2008) or on EcM plant seedlings (Kuhar *et al.*, 2017). Also other more likely co-introduced species from /laccaria lineage often occur on early successional sites (Table S2) and they are widespread in nurseries and fruit commonly on disturbed ground (Danielson, 1984). The Pinaceae-specific *Suillus* and *Rhizopogon* species are among the earliest colonizers of isolated seedlings (Peay *et al.*, 2012). *Rhizopogon* spp. build persistent, extensive spore banks in soil (Taylor & Bruns, 1999) that may support colonization of emerging seedlings after stand-replacing wild-fires (Horton *et al.*, 1998). Early successional strategy was also proposed for species from the /pisolithus-scleroderma lineage (Gardner & Malajczuk, 1988; Thompson *et al.*, 1994). However, the situation here may be more difficult, because species from both *Pisolithus* and *Scleroderma* have been widely used in commercial inoculation programmes and may have been co-introduced intentionally (Sulzbacher *et al.*, 2018). The documented ability of EcMF from all these lineages to grow on early-successional sites can be potentially explained by ease of germination of their spores and infectivity from small amounts of spores (Nara, 2009), but to identify particular functional traits that would explain why EcMF with pioneering life strategy more often become naturalized is beyond the scope of our study.

We also identified several EcMF lineages, such as /boletus, /russula-lactarius and /cortinarius, where the proportion of naturalized species was lower than expected by chance. Members of these lineages more often occur in late successional, mature forests (Table S2) and are known to colonize new hosts mostly through mycelial growth and to establish less easily from spores (Nara, 2009). Also, only a very few species of these groups can be isolated into pure culture and these few are very difficult to maintain. However, the alien EcMF can sometimes also recruit from the late successional fungi, such as *Amanita muscaria* and *A. phalloides*, which are frequently reported as co-introduced (Vellinga *et al.*, 2009) with ability to invasively spread into native vegetation in North America (Wolfe *et al.*, 2010) and New Zealand (Orlovich & Cairney, 2004; Dickie & Johnston, 2008). Although simpler recognizability of *A. muscaria* and *A. phalloides* may cause over-reporting on introduced sites relative to more cryptic EcMF species, it is clear, that late successional fungi may also naturalize outside the native range.

Importantly, our results based on the analysis of environmental DNA are in accordance with data provided by fruiting body surveys summarized in Vellinga *et al.* (2009). Re-analysis of Vellinga *et al.*'s (2009) data showed also a greater share of alien EcMF than expected by chance in EcMF genera with early successional strategy (Fig. S1). We believe that such concordance between sequencing-based data and fruiting body surveys gives strength to our conclusion that early

successional EcMF are better adapted to become naturalized than other EcMF. What particular traits associated with early successional strategy play the most fundamental role in alien EcMF introductions, remains an open question.

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Author contributions

LV, LT and PK jointly conceived the study. LV, TA and PK identified data sources, processed and analysed sequencing data. LT, TA, TV, KA, JA, MV and PK provided unpublished data. LV, TA and PK performed bioinformatics. LV, LT, PK, JP, PB and PP contributed to the development of data analysis tools and performed statistical analyses. PK drafted the manuscript along with LV and LT provided chief contributions. All authors wrote and reviewed the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Number of co-introduced and all ectomycorrhizal fungal species in different ectomycorrhizal fungal genera based on Vellinga *et al.* (2009).

Table S1 List of datasets of naturalized ectomycorrhizal fungal associated with alien ectomycorrhizal trees, included in this study.

Table S2 Frequency of observation of ectomycorrhizal fungal genera across successional chronosequences.

Table S3 Taxonomy of the naturalized ectomycorrhizal fungal species hypotheses (SHs) determined in this study with their putative native ranges.

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