

Chapter 2

Population Biology and Ecology of Ectomycorrhizal Fungi

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2.1 Introduction

Despite their wide diversity, physiological peculiarities and inconspicuousness of fungi have long hampered their study and recognition of their prevalence in ecosystems (Webster and Weber 2007). In forest environments, understanding of biology and diversity of ectomycorrhizal fungi (EcMF) has been challenging due to the limited availability of morphological and ecological characters to delineate species. Most Ascomycota and Basidiomycota produce conspicuous fruitbodies, but many others fruit hypogaeously (e.g. *Rhizopogon*, *Tuber* spp.), inconspicuously (e.g. corticioid and resupinate fungi) or never (e.g. *Cenococcum geophilum*). Although several early mycologists had rather advanced thinking about fungal ecology, the development of molecular tools and phylogenetic analyses in the last decades has enabled a giant step to assess species diversity (Dettman et al. 2003). At infraspecific level, there are more serious obstacles. As for other ‘non-model’ organisms, progress in EcMF population ecology is held back by the difficulty to distinguish between individuals. Fruitbodies are not representative of individuals since a mycelial genet (=genetic individual) can produce several fruitbodies, or even no fruitbody over the observation period, because of either environmental variation or sampling effort (Todd and Rayner 1980; Sélosse et al. 2001; Moore et al. 2008; Halme and Kotiaho 2012).

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The scarcity of phenotypic criteria to characterise individuals first led to the use of somatic incompatibility (SI) to distinguish among genets (e.g. Fries and Mueller 1984; Dahlberg and Stenlid 1994). Even though SI brought first insights into EcMF population ecology by enabling description of genotypes' numbers and sizes, this technique was barely sufficient to precisely differentiate among kin and fully describe genetic diversity of fungal populations (Jacobson et al. 1993; Anderson and Kohn 1998). Soon, a wide range of molecular markers (e.g. AFLP, RAPD, RFLP, SSR, SNP amongst many) were developed to identify EcMF genotypes. Population genetics studies first described patterns in local populations and explored their ecological drivers. Further technical progress in developing molecular markers and power of associated analyses broadened the scope of EcMF population studies (Anderson and Kohn 1998; Horton and Bruns 2001). Subsequent studies integrated biological features deciphered at local scale, such as mating systems and dispersal, to regional scale and up to distribution ranges. That broadening of scales helped documenting the role of wider environmental, biotic interactions and biogeographic drivers in shaping EcMF diversity.

2.2 Fine-Scale Population Genetic Structure

2.2.1 *Mating System and Colonisation Following Forest Stage*

Early population-level research aimed at tracking the persistence of inoculated ectomycorrhizal genotypes and evaluating their competitive interaction with indigenous populations (*Amanita muscaria*, Sawyer et al. 2001; *Laccaria bicolor*, Seloosse et al. 1998, 1999; *Lactarius deliciosus*, Hortal et al. 2009; *Suillus collinitus*, El Karkouri et al. 2005; *Tuber melanosporum*, Guérin-Laguet et al. 2013) or assessing the genetic diversity and origin of commercial mushrooms (*Tricholoma matsutake*, Murata et al. 2005; *Tuber magnatum*, Rubini et al. 2005). These studies also revealed the mating system and life history strategies of fungi during forest ecological succession.

The pioneer studies by Dahlberg and Stenlid (1990, 1994) investigated genet distribution of *Suillus* spp. at various forest stages with SI. Young stands were dominated by numerous small genets, whereas older stands harboured less numerous, larger genets. During the forest chronosequence, colonisation by spores would have established the first, small genets, part of which would have extended below-ground by mycelium growth, eliminating others by competition. In mature stands, large and competitive genets would dominate, potentially favoured by a greater ability to spread in soil by mycelial growth (Dahlberg and Stenlid 1994).

This paradigm was soon applied to various EcMF through mapping and genotyping of fruitbodies. These surveys were further used to distinguish EcMF species falling into 'early-stage' and 'late-stage' categories, i.e. displaying either

pioneer traits (*R*-strategists) or traits associated with later successional traits (*C* and *S*-strategists; strategies sensu Grime 1977), respectively. A ruderal strategy was observed for populations of *Russula vinosa* (Liang et al. 2004), *L. bicolor* (Selosse et al. 1999), *Russula brevipes* (Bergemann et al. 2006) and *Tricholoma terreum* (Huai et al. 2003) that formed many densely fruiting small genets (<4 m) with a prevalence of sexual reproduction and spread by sexual spores. As expected, these *R*-strategists ('early-stage') were observed in young forests, e.g. *Laccaria amethystina* in primary successional *Larix kaempferi* stands (Wadud et al. 2014), *Suillus granulatus* in a young *Pinus strobus* stand (Lee and Koo 2016) and *Rhizopogon vinicolor* in recently disturbed *Pseudotsuga menziesii* stands (Kretzer et al. 2005; Dunham et al. 2013). Typical *C/S*-strategists ('late-stage') were characterised by habitat in old stands and predominance of a few large, perennial and potentially competitive genets that suppress the establishment of conspecifics from meiospores. A population of *Russula* species from subsect. *Foetentinae* harboured dominant genets extending up to 70 m, competing with small genets producing a single fruitbody in a primary dipterocarp forest (Riviere et al. 2006). Fiore-Donno and Martin (2001) detected a single, large genet of *Xerocomus chrysenteron* (110 m-extent) and of *X. pruinatus* in a mature stand. Rubini et al. (2011) recovered a completely clonal *T. melanosporum* population, with a single strain dominating a truffle ground and likely impairing the establishment of other genets. Another noteworthy spontaneous genet, reaching a 40 m width and estimated 300 m², was described in a natural population of *Suillus pungens* in a mature *Pinus muricata* forest (Bonello et al. 1998; Table 2.1 in Douhan et al. 2011).

2.2.2 Species' Ecological Strategy and Environmental Constraints

However, using genet distribution as a proxy of species' ecological strategy and mating system soon revealed shortfalls. First, multiple discrepancies arose in the expected balance between sexual reproduction and mycelial expansion considering forest stage. Redecker et al. (2001) observed small genets of *Lactarius xanthogalactus*, *Russula cremoricolor* and *Amanita francheti* in a late successional forest, suggesting that basidiospore recruitment was more important than previously recognised. Small genets (mean size <10 m) were also displayed by *Amanita albobverrucosa* in native mature forest stands (Sawyer et al. 2003), *Cantharellus formosus* in old-growth Douglas fir stands (Dunham et al. 2003) and *Tricholoma scalpturatum* in mature stands (Carriconde et al. 2008a). Thus, EcMF colonisation strategy might be also explained by species' intrinsic features. Furthermore, various species showing a mixed pattern of mid-sized genets, occasional large individuals and numerous very small genets could not be categorised as 'early-' or 'late-stage' strategists; as a result, the

respective prevalence of sexual recombination (i.e. arrival of new spores) and vegetative growth (i.e. genet persistence and extension) could not be inferred. For instance, *Tricholoma matsutake* associated with *Pinus densiflora* formed a mosaic of numerous small mycelial genotypes intermingled with a dominant genet (Murata et al. 2005). Various EcMF species display such a mixed strategy, like *Amanita* spp. (Sawyer et al. 2003), *A. muscaria* (Bagley and Orlovich 2004), *Cortinarius rotundisporus* (Sawyer et al. 1999), *Cenococcum geophilum* (Wu et al. 2005), *Pisolithus* spp. (Anderson et al. 2001), *Russula brevipes* (Bergemann and Miller 2002), *Suillus spraguei* (Burchardt et al. 2011) and *Tuber aestivum* (Molinier et al. 2016).

Local environmental conditions and intraspecific competition are therefore a key to the local population structure. Fine-scale genet distribution patterns, that were contradicting the strategies theory, were observed in unexpected habitats. For example, Seloisse (2003) described old populations (>70 years) of *Leccinum duriusculum* composed of small genets, and a young population (<20 years) with large genets, suggesting that genet size results from the way how neighbours' density limits genet expansion and that small genets are not necessarily recently established. In mature stands, small genets were observed for *Suillus grevillei* (Zhou et al. 1999) and *Laccaria amethystina* (Gherbi et al. 1999; Fiore-Donno and Martin 2001). Genotyping of ectomycorrhizae also revealed a single large dominant *Rhizopogon vesiculosus* genet in a recently disturbed site (Kretzer et al. 2005; Dunham et al. 2013). Moreover, for some species, characterisation of conspecific populations associated to contrasted habitat characteristics further confirmed the crucial influence of forest maturity and level of disturbance on individual colonisation strategy and genetic diversity in local populations, e.g. for *Suillus* spp. (Dahlberg and Stenlid 1990, 1994) and *Hebeloma cylindrosporum* (Gryta et al. 1997, 2000; Guidot et al. 2001, 2002). Those studies do not fully invalidate Dahlberg and Stenlid's paradigm, but highlight the balance between specific biological features, infraspecific variation, site history and environmental parameters in shaping population structure.

2.2.3 Above- and Belowground Patterns of Genet Distribution

Another challenge of the use of fruitbodies to identify genets is that spatiotemporal distribution of fruiting may inaccurately reflect dynamics and abundance of genets belowground. For several species, though, comparisons of above- and belowground distribution showed strong spatial and temporal correspondence, suggesting that fruitbodies are indeed a good proxy (*H. cylindrosporum*, Guidot et al. 2001; *Suillus pictus*, Hirose et al. 2004; *L. laccata*, Wadud et al. 2014; *T. magnatum*, Murat et al. 2013). Awareness of intraspecific variability in fruiting behaviour (phenology, abundance) related to individual and microhabitat variation (*H. cylindrosporum*,

Guidot et al. 2001; *Laccaria* spp., Selosse et al. 2001; *S. pictus*, Hirose et al. 2004) motivated population surveys over several fruiting seasons. Analysis of spatiotemporal persistence confirmed rapid turnover of genets in some populations (*Pisolithus* spp., Anderson et al. 2001; *H. cylindrosporum*, Guidot et al. 2001, 2003; *L. laccata*, Wadud et al. 2008, 2014; *R. brevipes*, Bergemann et al. 2006), but also revealed some erratic fructification patterns, with often-small, ‘dormant’ (non-fruiting) genets actually persisting in soils without fruiting, e.g. for *Laccaria* (Gherbi et al. 1999; Selosse et al. 2001; Hortal et al. 2012) or *T. melanosporum* (Taschen et al. 2016). Besides validating species ecological strategies theory, the studies investigating temporal persistence confirmed the role of habitat variation, such as microdisturbance combined with infraspecific variation, in shaping population structure. In terms of infraspecific variability, not all genets persist equally as mycelium, nor expand or produce fruitbodies in similar amounts and frequencies. This also suggests infraspecific variation in competitiveness of each genet and points to the trade-off in resource allocation between sexual reproduction (fruiting) and clonal expansion (Johnson et al. 2012).

2.2.4 Local Dispersal Patterns

Beyond mating system and ecological strategy, genet mapping has contributed to basic knowledge about fungal biology, such as spore dispersal patterns (Fig. 2.1; Chap. 3). Although spore dispersal from fruitbodies is difficult to study, spatial autocorrelation analyses of kinship document the size of genetic neighbourhood and effective dispersal range (Peakall et al. 2003). Strong genetic autocorrelation among fruitbodies demonstrate the prevalence of short-distance (<20 m) dispersal of basidiospores, validating a decreasing spore deposition with increasing distance from the fruitbody (Morkkynen et al. 1997; Galante et al. 2011), which has been found in populations of *Laccaria* spp. (Wadud et al. 2014), *Tricholoma scalpturatum* (Carriconde et al. 2008a) and *Suillus grevillei* (Zhou et al. 1999, 2001). In non-agaricoid species, fine-scale spatial autocorrelation analyses revealed similar to even closer dispersal range, for example positive autocorrelation in *T. melanosporum* extends up to 6–8 m (Murat et al. 2013; Taschen et al. 2016) or up to 400 m in *Cantharellus formosus* (Dunham et al. 2006). Longer-range dispersal, probably relayed by mycophages, has been suggested for hypogaeously-fruiting species such as *Rhizopogon* spp. (no spatial autocorrelation over 5.5 km; Kretzer et al. 2005) or *Tuber* spp. (very little spatial autocorrelation over 100 km; Taschen et al. 2016; Fig. 2.1).

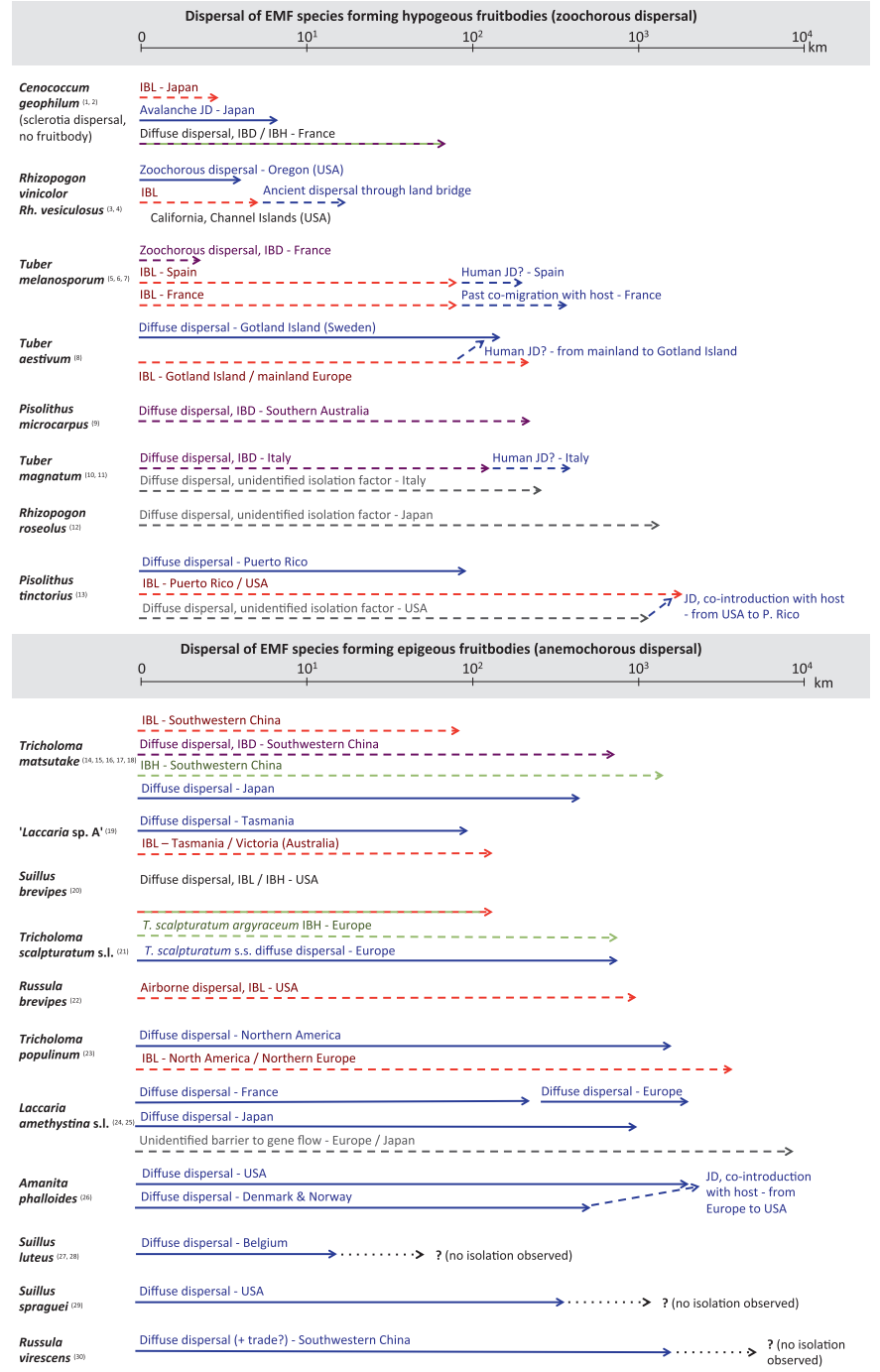


Fig. 2.1 Inferred dispersal mechanisms operating at diverse scales for several EcMF species. *Plain arrows*: uninterrupted gene flow; *dotted arrows*: discontinued gene flow. *JD* Jump Dispersal,

2.2.5 Cryptic Sexuality

Understanding of fine-scale genetic structure has enabled to shed light or re-evaluate life cycles and potential occurrence of cryptic sexual reproduction or parasexuality. The common generalist EcMF species *Cenococcum geophilum* is considered asexual (LoBuglio 1999), but its populations show unexpectedly high levels of genetic diversity and recombinant genotypes that are conflicting with the idea of clonality (e.g. Panaccione et al. 2001; Gonçalves et al. 2007; but see Douhan et al. 2007; Chap. 14). A solid cue for cryptic sexual or parasexual cycle in *C. geophilum* was recently found in Portuguese populations displaying variation in genome size and ploidy level (Bourne et al. 2014). Life cycles have been re-evaluated in *Tuber* spp. as well. Rubini et al. (2005) suggested recombination in *T. magnatum*, contradicting the so-far assumed strict selfing (Paolocci et al. 2006). Similarly, Riccioni et al. (2008) demonstrated outcrossing in populations of *T. melanosporum*, although a high inbreeding occurs in this species, due to the recruitment of sexual partners from the immediate vicinity (Taschen et al. 2016). Fine-scale studies on genetic structure have clarified autecology of EcMF species and paved the way for investigating how environmental parameters can shape population structure and genetic diversity.

2.3 Response to Environment and Biotic Interactions

2.3.1 Environmental Constraints Shape EcMF Populations

Limiting spore dispersal can lead to divergence between populations, while local standing genetic variation may allow ecological specialisation. Variation within local subpopulations can be stronger than among populations, as evidenced by analyses of molecular variance (AMOVA—*T. magnatum*, Rubini et al. 2005; *T. melanosporum*, Murat et al. 2004; *R. brevipes*, Bergemann et al. 2006). To distinguish between the effects of environmental parameters and the effects of geography, studies compared EcMF populations Spatial Genetic Structure (SGS, related to geography) to genetic structure explained by contrasted habitats.



Fig. 2.1 (continued) IBD Isolation By Distance, *IBH* Isolation By specialisation to Host/Habitat, *IBL* Isolation By Landscape. ¹Jany et al. (2002), ²Wu et al. (2005), ³Grubisha et al. (2007), ⁴Kretzer et al. (2005), ⁵García-Cunchillos et al. (2014), ⁶Murat et al. (2004), ⁷Taschen et al. (2016), ⁸Wedén et al. (2004), ⁹Hitchcock et al. (2011), ¹⁰Mello et al. (2005), ¹¹Rubini et al. (2005), ¹²Okuda et al. (2013), ¹³Rivera et al. (2014), ¹⁴Amend et al. (2009), ¹⁵Amend et al. (2010), ¹⁶Lian et al. (2006), ¹⁷Xu et al. (2008), ¹⁸Zeng and Chen (2015), ¹⁹Sheedy et al. (2015), ²⁰Branco et al. (2015), ²¹Cariconde et al. (2008b), ²²Bergemann et al. (2006), ²³Grubisha et al. (2012), ²⁴Roy et al. (2008), ²⁵Vincenot et al. (2012), ²⁶Pringle et al. (2009), ²⁷Muller et al. (2004), ²⁸Muller et al. (2007), ²⁹Rivera et al. (2014) and ³⁰Cao et al. (2013)

Gryta et al. (2006) compared the structure of populations within two *Tricholoma* species from similar-stage black poplar forests with contrasting disturbance levels (i.e. recurrent river flooding versus undisturbed). For both species, genet size, population genetic diversity and life-history strategy differed between the two habitats, pointing towards a possible specialisation to flooding. In *S. brevipes*, Branco et al. (2015) characterised genome-wide variation of two Californian populations from coastal and mountainous environments, separated by a 300 km-wide gap without host. Diversity analyses revealed robust delineation between populations from the two regions despite a low genetic divergence. Furthermore, genome-wide selection footprint analyses (F_{ST} outlier detection) detected several genomic regions diverging between populations, including the *Nha-1-like* locus that is involved in salt tolerance. These results point towards adaptive response of coastal populations to saline stress. This is a pioneering example of population genomics to characterise EcMF adaptation to local environment.

Effects of soil parameters on EcMF population diversity have been investigated more deeply. For instance, *C. geophilum* populations showed some clustering in relation to soil pH, with haplotypes specific to either calcareous or acid soil stands, suggesting adaptive response to soil acidity (Jany et al. 2002). Most studies have focused on heavy metals. *Suillus luteus* ecotypes displayed an adaptive tolerance to zinc and cadmium, mediated by metal efflux (Colpaert et al. 2000, 2011). Further research in physiological response to Zn along a gradient of soil contamination showed a correlation between Zn-tolerance and Zn level in soil, validating the hypothesis of an adaptive response to Zn pollution (Colpaert et al. 2004). However, genetic diversity in Zn-contaminated versus non-contaminated sites showed similarly high genetic diversity for neutral markers, with no genetic structure related to contamination nor geographic distance (Muller et al. 2004, 2007). Combination of sexual reproduction and effective gene flow by spore immigration may have compensated local selection of the Zn-tolerance trait and allowed local adaptation without genetic drift in contaminated sites.

Other studies focused on soils intrinsically rich in heavy metals, such as serpentine soils, which usually shape EcMF community structure (e.g. Urban et al. 2008). *Pisolithus albus* sampled in a mosaic of Ni-contaminated sites within a non-contaminated continuum revealed two genetic clusters that were related to soil type but not to geographic distance (Jourand et al. 2010). All *P. albus* isolates from non-contaminated soils were sensitive to Ni in vitro, whereas isolates from high-Ni soils were ranged from sensible to tolerant to Ni. This exemplifies the selection of ecotypes, although partly counterbalanced by gene flow from external, non-adapted populations. Similarly, isolates of *Cenococcum geophilum* from contrasting Maryland soils revealed ecotypes specific to serpentine or to non-serpentine soils, with higher genetic diversity in non-serpentine soils (Panaccione et al. 2001). Isolates from serpentine soils (Gonçalves et al. 2007, 2009) showed variable but always higher Ni tolerance in vitro compared to isolates from non-serpentine soils.

2.3.2 *EcMF Specialisation Towards Hosts*

Beyond environmental constraints, infraspecific variation in EcMF populations can be ascribed to biotic interactions due to the obligate symbiosis with their hosts. Most EcMF species are considered generalists, i.e. establishing symbiotic relationships with a variety of host tree species, genera or even families (Smith and Read 2008; Smith et al. 2009). At community level, numerous EcMF species are shared between species, forming multidimensional common ectomycorrhizal networks (Selosse et al. 2006; Bahram et al. 2014). At infraspecific level, single host trees have been shown to simultaneously associate with several genetic individuals, for example in *C. geophilum* (LoBuglio and Taylor 2002; Jany et al. 2002), *L. deliciosus* (Hortal et al. 2009), *T. terreum* (Huai et al. 2003), *R. vesiculosus* and *R. vinicolor* (Beiler et al. 2010), *T. matsutake* (Lian et al. 2006) or *T. melanosporum* (Bertault et al. 2001; Rubini et al. 2011; Taschen et al. 2016). Coexistence of several genets with different ecophysiological abilities (Hortal et al. 2012), as well as colonisation by different EcMF, can be beneficial for the host tree. This could be a key for the dominance of generalism, because it would allow the selection of the best partners by each host tree, corresponding to their ecophysiology (Douglas 1998). However, selection by host trees, if not diluted by recurrent recombination with exogenous genotypes, can lead to population specialisation and perhaps to enhanced efficiency (Bruns et al. 2002; Rochet et al. 2011). Hence, high genetic differentiation among EcMF populations could be related to host specialisation, although it cannot be related to phenotype differences (cryptic species; Taylor et al. 2006; Tedersoo et al. 2008).

To test host generalism, several studies compared genetic structure of EcMF populations associated with distinct hosts. *Laccaria amethystina* has been observed under a very broad range of temperate hosts from several deciduous families as well as Pinaceae (Fries and Mueller 1984). Comparing populations from monospecific stands, Roy et al. (2008) showed that host identity or geography each explained less than 0.90% of total variance, while diversity within populations accounted for more than 91.0% of variance (residual variance being distributed between populations within host pool or within region). Furthermore, no correspondence was observed between genotype clustering and host identity, supporting overall host generalism. Multilocus comparison of *Tricholoma populinum* populations associated with multiple poplar species from North America and Scandinavia showed no structure related to hosts (Grubisha et al. 2012). This further suggested geographic divergence of *T. populinum* after host divergence (*P. balsamifera*/*P. trichocarpa*), indicating host generalism for *Populus* spp.

Conversely, several studies revealed specialisation to a narrower range of hosts than expected. For instance, in an inoculated population of *Suillus collinitus*, cluster analysis distinguished two clades, one associated to *Pinus halepensis* only and the other to *P. sylvestris* and *P. pinea*, suggesting host specialisation (El Karkouri et al. 2005). Two sympatric genetic clusters detected in populations *Cortinarius arcuatorum* were associated with Fagaceae or conifers (Garnica et al. 2011). In

Tricholoma matsutake, significant genetic differentiation was observed among distant populations that could not be explained completely neither by climate, altitude nor geographic distance. Their distinct association with *Pinus densiflora*, *P. yunnanensis* or *Quercus monimotricha* suggested that local specialisation towards tree species was driving the genetic structure (Zeng and Chen 2015).

Hoeksema and Thompson (2007) experimentally tested host adaptation in *Rhizopogon occidentalis* by cross-inoculating multiple populations of coastal pine species (*P. contorta*, *P. radiata*) and multiple populations of the fungus. Relative performance of host and fungi were assessed based on ecophysiological traits. The host \times EcMF population interactions revealed a decline in mean fungal colonisation correlated with increasing geographic distance between plant and fungal origin, suggesting specialisation to local host populations. Such an elegant transplant experiment approach could be coupled with genomics studies to look for adaptation footprints.

Specialisation to host, if subjected to strong local selection and the lack of exogenous gene flow, may lead to (sometimes cryptic) sympatric speciation. Phylogenetic and nucleotide diversity analyses of *A. muscaria s.lat.* revealed the co-occurrence of three sympatric cryptic species, whose divergence could have been driven by host specialisation (Geml et al. 2006). Comparative phylogenies of hosts and EcMF partners also supported coevolution to be a speciation factor in fungi associated with alders, particularly in the genera *Alnicola*, *Alpova* and *Lactarius* (Rochet et al. 2011). Similarly, four cryptic, partially or totally sympatric species were detected within the *P. involutus* complex, with partly overlapping host ranges, showing a speciation driven collectively by the environment and hosts (Jargeat et al. 2013).

2.3.3 Impact of Dispersal on Population Structure

EcMF population structure can be influenced by means of dispersal of sexual and asexual propagules (Fig. 2.1) that can be mediated by wind, soil mesofauna (Lilleskov and Bruns 2005; Roets et al. 2011) and/or mammals (Johnson 1996). Then, effective dispersal of spores can be restricted by dispersers' own home range. Description of EcMF populations' SGS has allowed some inference about how means of dispersal shape EcMF populations diversity. For instance, the absence of positive spatial autocorrelation in *Rhizopogon vinicolor* and *R. vesiculosus* over 5.5 km suggests effective kilometre-scale dispersal of spores, rather than a continuous diffusion with decreasing abundance from their immediate vicinity, a pattern concordant with a dispersal by small forest mammals (Kretzer et al. 2005). Dependence of hypogeous species on such dispersal agents could shape the strong local SGS among islands by interruption of zoochory, e.g. in *Rhizopogon* spp. (Grubisha et al. 2007; Okuda et al. 2013).

In *Cantharellus formosus*, highly similar genotypes were retrieved several kilometres apart, raising the possible explanation of human or animal

mycophagous dispersal (Dunham et al. 2003). Human activities can indeed disperse EcMF propagules (Selosse et al. 1999), even unconsciously, as documented for pathogenic fungi (Fisher et al. 2012). For instance, European populations of *Tuber aestivum* revealed four genetic clusters inconsistent with geography; the absence of SGS over up to 2400 km could be explained by human dispersal via inoculated plant material (Molinier et al. 2016). Regional-scale substructure of *T. melanosporum* populations may also be related to active human inoculation and trade of plants (García-Cunchillos et al. 2014). Interestingly, Taschen et al. (2016) revealed no loss of natural regional SGS in inoculated plantations. In Puerto Rico, the founder effect (strong local SGS and reduced allelic richness) of exotic *Pisolithus tinctorius* in pine plantations points towards co-introduction with host trees (Rivera et al. 2014). The toxic and invasive *Amanita phalloides* rapidly colonised (several km/year) the west coast of North America since the nineteenth century (Pringle and Vellinga 2006). European and North American populations showed genetic differentiation but no isolation, confirming recent divergence (Pringle et al. 2009). While the European populations showed SGS, with high genetic diversity and effective population size, the North American population displayed no SGS but signs of a genetic bottleneck (low polymorphism, no private alleles), confirming the hypothesis of a recent introduction of *A. phalloides*.

A growing body of studies thus hint towards local specialisation to environment, either driven by local physical variation or by interactions with symbiotic partners and dispersers. However, some EcMF display evidence of generalism to environmental conditions and hosts. For these species, population genetic structure could be driven by dispersal efficiency over greater distances and population divergence at a broader scale.

2.4 Landscape and Habitat Distribution Shape Modern and Past Populations

2.4.1 Isolation By Distance Among Populations

Although generalist EcMF species can establish in various range of environments, their distribution range may encompass barriers to gene flow, shaping SGS at regional or continental scales. Gene flow over such distances can be mediated by long-distance dispersal (LDD), or by diffuse, continuous dispersal of propagules within the distribution area (Lomolino et al. 2010). The effects on demography of these two mechanisms entail different signatures in populations' SGS. LDD leaves a founder effect signature in small dispersed populations, including a sharp drop in neutral diversity, and posterior genetic drift. Such cues were observed in *Pisolithus* spp. populations in New Zealand, probably resulting from multiple LDD events from Australia (Moyersoen et al. 2003). A possible

ancient LDD event founded Scandinavian *T. populinum* populations, showing complete reproductive isolation from North America and strongly impoverished genetic diversity (Grubisha et al. 2012).

By contrast, diffuse dispersal represents a continuous gene flow of propagules over limited distance, where resistance to dispersal entails correlation between geographic distance and genetic distance, i.e. the characteristic Isolation By Distance (IBD) pattern. Various EcMF display IBD at variable scales. IBD was observed in *Rhizopogon* spp. over 50 km distance in California Channel Islands (Grubisha et al. 2007), in *C. geophilum* over 250 km in France (Jany et al. 2002), in *T. magnatum* over 450 km in Italy (Rubini et al. 2005), in *Pisolithus microcarpus* over 700 km in Southeastern Australia (Hitchcock et al. 2011) and in *T. scalpturatum* over 2500 km in Western Europe (Carriconde et al. 2008b). The increased reproductive isolation with longer distance can lead to lineage divergence, as revealed by combined population genetics analyses and phylogeography of wide-ranged EcMF species previously described as trans- or multicontinental (*A. muscaria*, Geml et al. 2006; *T. populinum*, Grubisha et al. 2012). Range disruption between populations can even hide cryptic speciation, as detected in *L. amethystina* across Eurasia (Vincenot et al. 2012).

2.4.2 Landscape Genetics

Beyond Euclidian geographic distance, geographic features such as mountains ranges, water bodies and watersheds and dominant airstreams can hamper dispersal of propagules (Manel et al. 2003; Zeller et al. 2012). On Mount Fuji, landscape features appear to strongly impact population structure of *Cenococcum geophilum*, whose sclerotia are not dispersed by wind. Its populations situated <10 km apart but separated by a valley were genetically differentiated (Wu et al. 2005).

Landscape effects were tested in topographically peculiar southwestern China. *Tricholoma matsutake* populations from Yunnan and Sichuan provinces displayed high genetic diversity and low but significant differentiation among populations (with significant $F_{ST} = 0.10$; Amend et al. 2010). Genetic distance did not correlate with the elevation gradient, but a significant IBD pattern appeared over 1100 km. At finer scale, strong differentiation was detected at over 65 km, and populations were significantly less diverged within than between watersheds. Landscape distance, calculated as the shortest route between populations below treeline, i.e. along suitable habitat, significantly correlated with genetic distance (Cushman et al. 2006).

In China, three geographic clusters within *Tuber indicum* are shaped by hydrographic network; one cluster corresponds to Mekong river paleoregion, whereas two other clusters are separated by the contemporary Yangtze River (Feng et al. 2016). In *T. himalayense*, by contrast, genetic structure was inconsistent with contemporary landscape. However, its populations from different watersheds were isolated due to the southward postglacial displacement of suitable habitats

that progressively decreased their connectivity (Feng et al. 2016). Thus, rivers are barriers to EcMF gene flow by spore dispersal, at least for hypogeous animal-dispersed EcMF.

2.4.3 Extensive Gene Flow

Populations of various EcMF species may display extensive gene flow in areas devoid of barriers. This was documented at regional scale in *T. aestivum* over 180 km (Wedén et al. 2004), *L. amethystina* over 450 km in France (Roy et al. 2008) and over 950 km in Japan (Vincenot et al. 2012), *T. matsutake* in China over 70 km (Amend et al. 2009) and in Japan over 450 km (Murata et al. 2005) and *S. spraguei* over 600 km (Rivera et al. 2014). Broadening of geographical scale further revealed unexpected, very extensive gene flow over thousands of kilometres. *Russula virescens* populations showed no SGS pattern over 2700 km (Cao et al. 2013). Unexpectedly, mountains and valleys of Yunnan did not act as dispersal barriers for *R. virescens* that contrast with *T. matsutake* populations (see Sect. 2.3.2). In western Europe, highly outbreeding *L. amethystina* populations have a low global F_{ST} (0.04) from Spain to Estonia, with a marginally significant signal of IBD over 2900 km (Vincenot et al. 2012), probably due to the absence of physical barriers and host generalism (Roy et al. 2008). Similarly, host generalism would favour extensive gene flow of *P. microcarpus*, associated with various acacias and eucalypts, over southeastern Australia (Hitchcock et al. 2011).

EcMF dependence on host partners requires a habitat continuum for diffuse dispersal. Even over short distances, corridors of vegetation can assist gene flow, as for *S. grevillei* (Zhou et al. 2001) or *P. microcarpus* (Hitchcock et al. 2011). While gene flow between populations of host specific EcMF species is restricted by host distribution (e.g. ‘*Laccaria* sp. A’, Sheedy et al. 2015; *Rhizopogon roseolus*, Okuda et al. 2013; *Suillus brevipes*, Branco et al. 2015), host generalism favours efficient gene flow and establishment in wide areas (Vellinga et al. 2009).

2.4.4 Co-migration with Hosts

Biogeographic analyses of EcMF population history have revealed demographic fluctuations following host populations, still reflected in modern population structure. In southern Australia, populations of ‘*Laccaria* sp. A’, specifically associated with *Nothofagus cunninghamii*, follow their host’s SGS. In Tasmania, higher genetic diversity, richness, effective population size and admixture as compared to populations from Victoria would correspond to a Tasmanian refugium for ‘*Laccaria* sp. A’ during the last glaciation, followed by postglacial co-expansion towards mainland Australia with their host (Sheedy et al. 2015). Southwestern Mediterranean truffle populations could have retreated to Italian

and Iberian glacial refugia, as present populations reflect postglacial co-expansion with their hosts. Recent gene flow was detected among *Tuber magnatum* populations from central Italy (autocorrelation up to 450 km), while those from southern and northwestern Italy differed significantly (Mello et al. 2005; Rubini et al. 2005), suggesting a glacial refugium in central Italy and a postglacial co-expansion with hosts southward and northward. *Tuber melanosporum* shows moderate differentiation between populations from central Italy, France and Spain, with highest diversities in southernmost populations, providing support to Italian and Iberian glacial refugia (Riccioni et al. 2008). Furthermore, an Italian glacial refugium for *T. melanosporum* is supported by the genetic bottleneck signature in Italian populations (Murat et al. 2004). As the distribution of *T. melanosporum* haplotypes is consistent with that of oak trees, this species may have followed the two postglacial re-colonisation routes of oaks, through the Rhone valley and through southern France to the Atlantic coast (Murat et al. 2004; Bertault et al. 2001; Payen et al. 2015). Host-associated glacial refugia for *T. melanosporum* were also found in Iberian Peninsula (García-Cunchillos et al. 2014).

These studies highlight how host demographic history shaped modern populations of EcMF species. Co-migration patterns and parallel EcMF and host biogeography enable to reconstruct the history of ectomycorrhizal forests. Populations of *T. matsutake* show unexpected isolation across the Gibraltar Strait between Europe and Morocco, perhaps due to co-migration with *Cedrus atlantica* along southern Mediterranean coast, since coalescence analysis points towards a common ancestor in Anatolia (Chapela and Garbelotto 2004). Between North America and Europe, a similar isolation was found, with significant regression with landscape distances across the Bering Strait. *Tricholoma matsutake* populations would thus have co-migrated with their hosts from North America, their centre of diversification, towards Eurasia through Beringia rather than through the Atlantic land bridge (Chapela and Garbelotto 2004). Co-migration through Beringian land bridges was also suggested for *C. arcuatorum* and *C. elegantior* (Garnica et al. 2011). Phylogeographic and coalescence analyses of American *A. muscaria* populations identified two endemic groups in Alaska, without evidence of recent gene flow from southern regions (Geml et al. 2006, 2010), again supporting a Beringian glacial refugia. Beyond documenting the history of EcMF populations, such large-scale population genetic studies contribute to understanding of EcMF biogeography.

2.5 Conclusions and Perspectives

The effective range of dispersal is an indicator of fruitbody and propagule types (Douhan et al. 2011). Fine-scale population genetic analyses clarify EcMF autecology and ecophysiology such as mycelium growth rate, persistence, reproductive biology, mating system (especially in ascomycetous EcMF whose study is now

starting) and dispersal mechanisms (Fig. 2.1). The role of microenvironmental parameters and individual plasticity on mycelium development and fructification patterns remains to be investigated, potentially with gene expression patterns at very-fine scale to re-explore the population dynamics studies of the 1990s. Currently, molecular tools can be applied to ectomycorrhizae and improve our ability to study the mycelial stage.

Nevertheless, EcMF population studies contribute to recognition of these organisms as a crucial part of ecosystem functioning and history. For instance, successful combination of demographic reconstruction, phylogenetics and paleoecology (e.g. Geml et al. 2010; Murat et al. 2004) have shown that EcMF are relevant contributors to the understanding of historical biogeography of host and associated vegetation.

Douhan et al. (2011) stated that we are reaching the era of population genomics for EcMF, giving access to adaptive traits beyond neutral traits deciphering only historical trends. Detection of selective footprints by comparing genomic structure of contrasted populations are now emerging to detect local specialisation and adaptation signatures (Bourne et al. 2014; Branco et al. 2015). This promising approach for understanding EcMF response to environmental constraints could be successfully coupled with transcriptomic analyses to identify genes actively involved in adaptation (e.g. Zampieri et al. 2011 for *T. melanosporum* cold adaptation). Another powerful combination of EcMF population genomics would associate host population genomics in order to look for genetic co-adaptation on both sides and its functional outcomes (e.g. Hoeksema and Thompson 2007). With the development of genomic and transcriptomic technologies, associating genomics and traits variation analyses in contrasted environments and hosts would open the understanding of ecology and evolution of EcMF populations.

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