# Some ecological implications of Agaricomycete phenology

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## Abstract

Macrofungi, and specifically Agaricomycetes, are important drivers for nutrient partitioning and cyling in terrestrial ecosystems and other ecosystem processes. Fruiting patterns of saprotrophic and ectomycorrhizal taxa bear implications for the maintenance of fungal assemblages that interact with their environment. While fruiting patterns have been investigated in a few cases, biome-wide studies across a comprehensive number of Agaricomycete species with a special focus on their temporal ecology, are lacking. Based on a of more than 2000 ectomycorrhizal and saprotrophic Agaricomycetes, the phenologies of both guilds have been investigated. The phenologies of either guilds coincide to a large extent. Surprisingly, the course of fruiting is bimodal, i.e. showing minima in spring, July and autumn. Possible explanations, in particular avoidance of fungivores and of evading activities of competing microorganisms are discussed.

## Introduction

Macrofungi, and specifically Agaricomycetes, are important drivers for nutrient partitioning and cyling in terrestrial ecosystems and other ecosystem processes (Trappe & Luoma 1992). During their life cycle, the development of fruit bodies is crucial for reproduction and dispersal (Dix & Webster 1995), i.e. for the maintenance of fungal assemblages that interact with their environment. Among other traits, temporal patterns of fruiting (phenology) may be of ecological relevance because it is often part of assembly rules (Morin 2011). Fruit bodies are, for example, important nutrient sources for micro- and macrofauna (Straatsma et al. 2001), and temporal correlations are likely to contribute to the functioning of food webs.

While the timing of fruit body production is commonly triggered by precipitation, temperature and nutrient availability (Moore et al. 2008, Boddy et al. 2014), a good part of the phenology of Agaricomycetes is genetically controlled (Selosse et al. 2001). Most species in temperate to boreal biomes seem to fructify towards autumn, some already in early spring (Boddy et al. 2014). There are indications that ectomycorrhizal taxa fructify during a narrower time range towards the end of a year than saprotrophs (Khasa et al. 2009). Typical spring, summer and autumn fruiters are shown in Fig. 1.

To further clarify the ecological implications of differences in fruiting phenologies, more data on fruiting patterns across a wider taxonomical and ecozonal range are needed. I therefore compiled and analysed a database of Agaricomycetes, and interpreted the results with respect to fungal life strategies, trophic modes and interactions with associated invertebrates.

**Fig. 1** – Top row – Saprotrophic: *Strobilurus esculentus* (Wulfen) Singer (Image Thomas Pruß (cc)), *Pluteus romellii* (Britzelm.) Sacc. (Image Landsnorkler (cc)), *Flammulina ononidis* Arnolds (Image Gerhard Koller (cc)). Bottom row – Ectomycorrhizal: *Tylopilus alboater* (Schwein.) Murrill (Image Martin Livezey (cc)), *Chroogomphus rutilus* (Schaeff.) O.K. Mill. (Image H. Krisp (cc)), *Porphyrellus porphyrosporus* (Fr. & Hök) E.-J. Gilbert (Image A. Kunze (cc)); size bars 2 cm

## Materials & Methods

A compilation of 1026 ectomycorrhizal and 1262 saprotrophic mushroom phenological information extracted from the Funga Nordica (Knudsen & Vesterholt 2012) served as a database. By using only one source, the integrity of data was ensured. The phenological information was converted to months (Table 1).

**Table 1** Matching seasonal information with months based on the Funga Nordica

| Season | Days | Month |
|---|---|---|
| Early spring | 87.5 | II |
| Spring | 112.5 | III |
| Late spring | 137.5 | IV |
| Early summer | 166.7 | V |
| Summer | 198.0 | VI |
| Late summer | 229.3 | VII |
| Early autumn | 258.3 | VIII |
| Autumn | 283.0 | IX |
| Late autumn | 307.7 | X |
| Early winter | 350.5 | XI |
| Winter | 409.5 | XII |

To visualize the fruiting patterns of the ectomycorrhizal and the saprotrophic guild during the seasons, species numbers per fruiting month were plotted as a bar chart.

To elucidate the species distribution of both guilds along the annual seasons, a t-test was applied, and basic statistical parameters were calculated using PAST version 3.21 (Hammer et al. 2001).

To show phenological differences among the genera, mean fruiting months of all species of each taxon were calculated.

To show phylogenetic patterns, the phenological data of the genera were aggregated to the next higher taxonomic and assigned to the respective branches of the current phylogenetic tree weighted by species means (Hibbett 2007).

**Results**

Ectomycorrhizal and saprotrophic taxa show differing bi-modal fruiting patterns (Fig. 2).
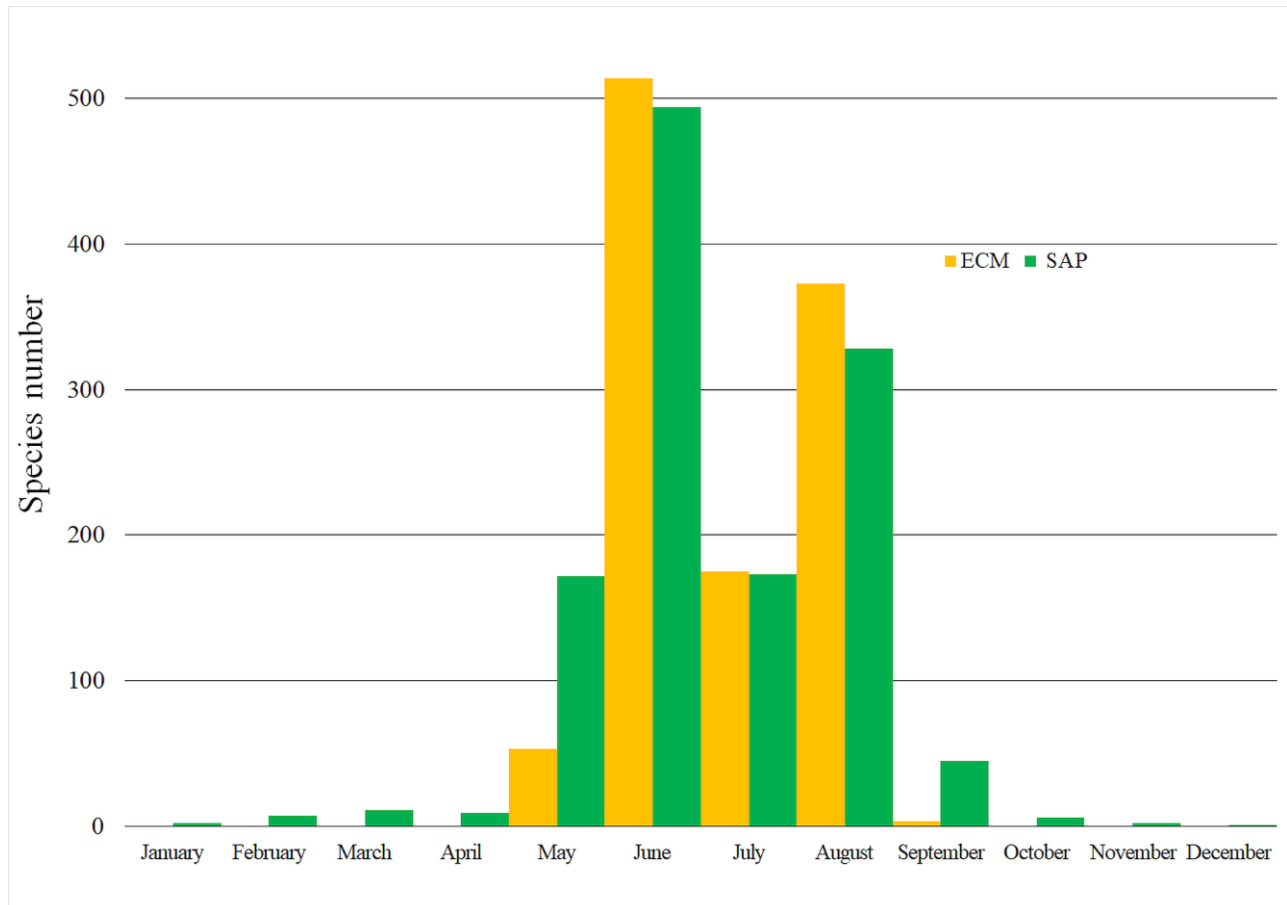


**Fig. 2** – Comparison of the numbers of the ectomycorrhizal (orange) and saprotrophic (green) species during a year.

The t-test came up with a probability of p=0.14 (Monte Carlo) for equal means. The statistical results are shown in Table 2.

**Table 2** Comparison of mean saprotrophic (SAP) and ectomycorrhizal species fruiting months by basic statistical parameters

|         | Sample size | Mean | Standard error | Median | Skewness |
|---------|-------------|------|----------------|--------|----------|
| **SAP** | 1263        | 6.8  | 0.038          | 6.5    | 1.38     |
| **ECM** | 1026        | 6.9  | 0.026          | 6.5    | -0.23    |

The fruiting patterns for all Agaricomycete genera in the data set are presented in Tables S1, S2. The compilation of phylogenetic phenology patterns largely revealed close similarities among the clades (Fig. S1).

See supporting material: https://osf.io/dzu4n/?view_only=1dbbc66a805445d48b027ee8a594807f

## Discussion

Compared to the ectomycorrhizal species, the saprotrophic species show a wider temporal fruiting range, even though in both guilds the fruiting peaks coincide (Fig. 2, Table 2). The more compressed fruiting season of the ectomycorrhizal guild is probably controlled by species-specific cues of the hosts (Dickie et al. 2010, Kauserud et al. 2012) in connection with carbon (photosynthate) availability (Sato et al. 2012). This holds true even for taxa that exhibit saprotrophic capacities (Lindahl & Tunlid 2015), e.g. Cortinarius because they degrade soil organic compounds predominantly to capture nutrients other than carbon (Hupperts et al. 2017).

There are indications that primary production and precipitation are drivers for early fruiting ectomycorrhizal species, while temperature drives fruiting of early saprotrophic and late saprotrophic as well as late ectomycorrhizal taxa (Andrew et al. 2018). Generally, early colonisers among saprotrophic taxa (r-selected, e.g. Strobilurus, see Table S1) fruit more proficiently and are smaller than K- or S-selected late fruiters (Boddy et al. 2014). Moreover, late fruiters are rarer than early appearing mushrooms (Simmel & Poschlod 2017)

Clade-related fruiting patterns generally do not show conspicuous clustering, perhaps with the exception of the agaricoid clade which has the broadest range of three months. The latter may be explained by the high proportion of species in the data set (Table 3).

**Table 3** Phenology range and species number of the clades investigated

| Clade | Phenology | Species no. |
|-------|-----------|-------------|
| Agaricoid | July-September | 1180 |
| Tricholomatoid | July-August | 664 |
| Marasmioid | August | 105 |
| Amanitaceae | September | 37 |
| Pluteoid | August | 39 |
| Hygrophoroid | August | 48 |
| Incertae sedis | August | 24 |
| Boletales | August-September | 83 |
| Russulales | August-September | 248 |
| Polyporales | August | 3 |

Phylogenetic patterns and the seasonal fruiting distribution of both ectomycorrhizal and saprotrophic taxa point at common drivers. Generally, sufficient precipitation is a precondition for developing fruit bodies (Chacón & Guzmán 1995, Pinna et al. 2010), while the course of temperature controls the timing (Straatsma et al. 2001). This is corroborated by the effect of climate change (warming!) which leads to shifts in fruiting seasons across a large number of taxa (Kauserud et al. 2008, Büntgen et al. 2011, Kauserud et al. 2012, Boddy et al. 2014).

At an individual level, fruiting is commonly triggered by disturbances, for example when mycelia reach substrate edges, nutrients become depleted or injured (Moore et al. 2008). Another common fruiting stimulator is cold-shock, i.e. a sharp temperature drop below a certain threshold over a certain period of time (Pinna et al. 2010).

On the other hand, genetic factors may modulate patterns induced by weather and climate. It is, for instance, striking that fungal and insect fungivore phenologies only marginally overlap. In Greenland, fungal fruiting peaks around July/August (Petersen 1977), while Mycetophilidae and Muscidae in Greenland and Arctic Canada, both taxa being predominantly fungivores, have their peak season about one month earlier (Høye & Forchhammer 2008, Bolduc et al. 2013) with an overlap of ca. two weeks. This suggests that the fungi have adapted to avoiding damage by insect fungivores (Hanski 1989, Boddy & Jones 2008). On the other hand, entirely avoiding associated insects could lead to a critical impoverishment of vectors. Insects are supposed to be important

dispersers, particularly for ectomycorrhizal taxa (Halbwachs & Bässler 2015). Therefore, the overlap between fungal and insect fungivore phenologies in the Arctic could be a trade-off between damage and dispersal. In this context, it should be noted that species with larger fruit bodies withstand destruction longer than smaller ones (Hanski 1989). However, global warming leads to shifts in mushroom fruiting (Boddy et al. 2014) which could disrupt, e.g. interactions with animals. It remains to be seen if the phenotypic and genotypic plasticity of all interacting organisms can counteract detrimental effects. In this vein, phenotypic variance may be induced by hosts (Dickie et al. 2010), and genetically-based phenology shifts as observed in *Laccaria bicolor* (Selosse et al. 2001).

The surprising result that fruiting of both guilds follows a bi-modal course is, at first glance, suggestive of common environmental drivers. However, typical temperature and precipitation patterns in Scandinavia do not fit the main fungal fruiting seasons in June and August. Highest long-term precipitation and temperature values occur in most Scandinavian areas during July (Diebel et al. 2018). Another possibility of the bimodal fruiting could be avoidance of the peak activity of fungivorous insects. Insect activity is temporally constricted in boreal settings, mainly driven by temperature and day length (Danks & Foottit 1989), but only a few relevant studies on fungivorous insects are available (Põldmaa et al. 2015). Some are suggestive of asynchronous phenologies (e.g. Shorrocks & Charlesworth 1980), others not (e.g. Bechev 2000). In this vein, it has been observed that *Leccinum albostipitatum*, when already fruiting in July, becomes infested by fungus gnats (Holmberg & Marklund 2018). It appears that the phenology of mushroom-associated flying insects underlies multiple influences of the abiotic and biotic environment (Danks & Foottit 1989), and not intrinsic factors as host-specificity (Koskinen et al. 2018). Moreover, when looking at soil-dwelling fungivores, such as epigeic Collembola (Hanski 1989), a temporal connection to fungal fruiting seems to be unlikely, because Collembola abundance is highest towards autumn (Turnbull 2014). Furthermore, mammals, as important fungivores and vectors (Halbwachs et al. 2016), do not show marked seasonal feeding habits, at least during the vegetation period.

There might be another (additional) explanation. Soil-dwelling microbiota, such as bacteria and soil microfungi compete for the ephemeral soil nutrient sources, especially during the summer. Also, some hypogeic fungivores (Collembola, Acari and Enchytraeidae) are active particularly around July (Burges & Raw 1967). Could it be that the mycelia of mushrooms undergo a diapause during July?

Beyond all these speculations, the bimodal fruiting pattern of mushrooms and its adaptive relevance remains an enigma.

**Conclusion**

The ectomycorrhizal and saprotrophic guild show similar bimodal phenologies which points at substantial environmental effects, particularly temperature and moisture. The narrower fruiting band of ectomycorrhizal taxa is probably induced by host cues in connection with photosynthate production. The generally adaptive character of temporal fruiting patterns is underscored by the fact that at cladistic levels deeper than genera fruiting periods hardly differ.

Early fruiters among the saprotrophic mushrooms seem to utilise litter accumulated during the preceding cold season (temporal resource partitioning, thus minimising competition, Morin 2011) which suggests an R-selected lifestyle, while S-selected late fruiters need to cope with cold stress.

The conspicuous bimodal course of fructification may be an adaptation to peak activities of fungivores and/or competing soil microorganisms, though relating data are somewhat inconsistent. This phenomenon deserves further studies that dig deeper into the phenologies of epigeic and hypogeic invertebrates associated with mushrooms and into seasonal mycelial dynamics of mushrooms.

## Acknowledgements

## Accessibility of data

The database compiled for this study can be accessed in Tables S3, S4 (https://osf.io/dzu4n/?view_only=1dbbc66a805445d48b027ee8a594807f)

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