

# Unraveling environmental drivers of a recent increase in Swiss fungi fruiting

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## Abstract

Disentangling biotic and abiotic drivers of wild mushroom fruiting is fraught with difficulties because mycelial growth is hidden belowground, symbiotic and saprotrophic supply strategies may interact, and myco-ecological observations are often either discontinuous or too short. Here, we compiled and analyzed 115 417 weekly fungal fruit body counts from permanent Swiss inventories between 1975 and 2006. Mushroom fruiting exhibited an average autumnal delay of 12 days after 1991 compared with before, the annual number of fruit bodies increased from 1801 to 5414 and the mean species richness doubled from 10 to 20. Intra- and interannual coherency of symbiotic and saprotrophic mushroom fruiting, together with little agreement between mycorrhizal yield and tree growth suggests direct climate controls on fruit body formation of both nutritional modes. Our results contradict a previously reported declining of mushroom harvests and propose rethinking the conceptual role of symbiotic pathways in fungi-host interaction. Moreover, this conceptual advancement may foster new cross-disciplinary research avenues, and stimulate questions about possible amplifications of the global carbon cycle, as enhanced fungal production in moist mid-latitude forests rises carbon cycling and thus increases greenhouse gas exchanges between terrestrial ecosystems and the atmosphere.

**Keywords:** climate change, forest ecology, fungi-host interaction, global carbon cycle, plant phenology, tree growth

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## Introduction

Terrestrial biomass production and carbon sequestration are highly dependent on symbiotic associations between host plants and mycorrhizal fungi (Treseder & Allen, 2000; Smith & Read, 2007; Clemmensen *et al.*, 2013), as well as the effects of saprobes and invertebrates on soil organic matter decomposition (Rousk & Baath, 2011; Lubbers *et al.*, 2013). Host plants provide their mycorrhizal partners with photosynthetic assimilates, in exchange for improved access to soil nutrients and phosphorus, as well as protection against pathogens (Smith & Read, 2007). Yet, relatively little is known about possible contributions of saprobic organisms to this complex fungi-host interplay (the mycorrhizal relationship) (Treseder & Allen, 2000; Leake *et al.*, 2002), and how climate change may impact overall ecosystem processes (via various effects on fungi productivity and phenology) that subsequently can affect biosphere-atmosphere exchanges of carbon (Orwin *et al.*, 2011; Cheng *et al.*, 2012; Clemmensen *et al.*, 2013; Lubbers *et al.*, 2013), nitrogen (Zak *et al.*, 2011), and methane (Lenhart *et al.*, 2012).

Despite two recent studies from Asia (Sato *et al.*, 2012; Yang *et al.*, 2012) and a pioneering work from the US (Diez *et al.*, 2013), most reports of climate-induced changes in fungal fruiting patterns, including both alternations in productivity and phenology originate from Europe. Ranging from local surveys (e.g., Egli *et al.*, 2006; Gange *et al.*, 2007; Büntgen *et al.*, 2012b) to national and even international networks (Kausserud *et al.*, 2010, 2012), there is clear evidence for a longer European mushroom fruiting season in temperate forest ecosystems, which parallels an overall extended vegetation period (Menzel *et al.*, 2006). Although the length of the fruiting season tends to increase on average, there remains considerable variation between ecological groups, species and countries, depending on the types of data used and the methods applied (e.g. Gange *et al.*, 2013; Kausserud *et al.*, 2013) – a comprehensive state-of-the-art review is still missing.

Moreover, the relationship between environmental factors including climate and mushroom fruiting patterns, as well as host phenology is highly complex. Unraveling biotic (host plants and fungal partners), abiotic (climate, pollution, land cover), and combined edaphic (soil) drivers of mushroom fruiting therefore poses a scientifically useful (Gange *et al.*, 2007; Kausserud *et al.*, 2012) but also still a substantial challenge because of the need for consistent data collected over

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sufficient time (Hall *et al.*, 2003; Kausserud *et al.*, 2008). Biological interaction between mycelial growth and soil fauna (invertebrates and small mammals) complicates our understanding of how mycorrhizal and saprotrophic organisms may react (directly or indirectly via host plants) to changes in their environment. The absence of high-resolution, long-term field surveys challenges the detection of external fingerprints on the activity and plasticity of hidden belowground mycelia (fungi) and their ephemeral macroscopic fruit bodies (mushrooms). Cross-disciplinary effort and its expected insight will become particularly useful to adapt silvicultural and agricultural systems (and services) in a climatologically changing world.

In this study, we seek to better understand how the productivity and phenology of wildlife mycorrhizal and saprotrophic mushrooms fluctuated at different time-scales, and how these alternations were driven by environmental factors. We therefore compiled and assessed the world's longest continuous fungal inventory, which comprises 64 695 and 50 722 weekly resolved records of mycorrhizal and saprotrophic mushrooms belonging to 282 and 186 taxa from 29 to 71 genera, respectively. Intra- and interannual fluctuations in the number of emerging mushrooms and their fruiting time, together with variations in radial stem growth of 136 beech trees from the same monitoring plots, were related to nearby meteorological observations and plant phenological indicators. Gridded climate indices, in tandem with split period approaches and linear regression models were used to detect spatiotemporal variability in the response patterns of wildlife mushroom fruiting.

## Material and methods

Between 1975 and 2006, weekly inventories of mushroom production were recorded in five disjunct 300 m<sup>2</sup> plots in the protected multi-storied, mixed beech (*Fagion*) fungus reserve 'La Chanéaz' (Figure S1). This unique setting covers 75 ha of temperate forest in western Switzerland. Permanent, continuous and 2 m high fences prevented the 1500 m<sup>2</sup> large study area from any interference of mushroom pickers and forest animals. The protected area is located on calcaric cambisol at around 585 m asl between 6°59'52" to 7°00'30" East and 46°47'55" to 46°48'10" North. The dominant beech trees (*Fagus sylvatica*) in this temperate forest have heights between 28 and 44 m.

A total of 115 417 epigeous sporocarps of macromycetes (Figure S2), each marked with methylene blue when counted to avoid errors when recording in the field, were macro- and/or microscopically identified. The protected reserve was periodically managed before and during the survey to correct for stand-closure and to ensure natural regeneration by autochthonous species. Further details on the so-called 'femel system' forest management strategy that was applied, as well as on the long-term mushroom inventory that was conducted

are provided in Egli *et al.* (2006) and in Büntgen *et al.* (2012b). Our fungi monitoring is likely representative for most of the Swiss mixed beech forests, which cover at least 50% of the country's total forested area (Wohlgemuth *et al.*, 2008), and with a similar ratio likely also represent most of the temperate, water-saturated Central European and comparable mid-latitude forest ecosystems (FAO, 2011, [www.mcpfe.org](http://www.mcpfe.org)).

Accumulated weekly fruit body counts (WFC) were used to evaluate intra-annual patterns in both symbiotic and saprotrophic mushroom fruiting. Weekly fruiting of the two functional guilds was divided by the corresponding total annual fruit body counts, and the weighted week of appearance (WWA) was computed to assess temporal changes in mycorrhizal and saprotrophic mushroom phenology. The WWA thus represents the sum of the products of calendar weeks and their corresponding counts divided by the total annual fruit body counts (i.e. the intra-annual peak of mushroom fruiting). In contrast to the above within-year variability revealed the sum of all annual fruit body counts (AFC) year-to-year changes in mushroom productivity, and the number of mean weekly species (MWS) indicated the associated species diversity.

All fungi indices were independently calculated for mycorrhizal and saprotrophic mushrooms over the full period, as well as over two independent early (1975–1990) and late (1991–2006) split periods (of equal length but without overlap). It should be noted that the split period approach herein applied, which is one of the simple techniques, is, however, also less prone to spurious results caused by extreme values possibly located toward a time-series margin. Mean, standard deviation, and standard error of the six fungi indices (i.e. WWA mycorrhiza, WWA saprophytes, AFC mycorrhiza, AFC saprophytes, MWS mycorrhiza, MWS saprophytes) were independently computed over the early/late split intervals. Linear regression models and significance tests were additionally applied to reveal trends in fungi productivity and phenology over the full period 1975–2006.

Distinct core samples of 136 beech (*Fagus sylvatica*) trees of all age-classes (Figures S3 and S4), ranging from 17 to 164 years, were collected in November of 2011 within each plot of the fungus reserve. Annual ring width variations were precisely measured and absolutely dated following standard dendrochronological techniques. Two different mean chronologies were developed for the 1848–2011 period (Figure S5). One without detrending and one after power-transformation in combination with the application of negative exponential or straight-line functions for the removal of biological-induced age trends. The new tree-ring width evidence was correlated against the different mushroom indices, as well as against an array of phenological indicators.

A total of 20 different spring-autumn phenological records (via MeteoSwiss) from the neighboring village of Posieux were considered for comparison (Figure S6). The majority of 16 individual parameters refers to spring-summer phenology (before July), whereas four parameters indicate autumn phenology (after September). Sixteen phenological spring-summer observations are: Hazel blossoming, Coltsfoot blossoming, Larch leaf development, Cuckooflower blossoming, Hazel leaf development, Hawbit blossoming, Cherry blos-

soming, Chestnut leaf development, Pear blossoming, Beech leaf development, Apple blossoming, Spruce leaf development, Chestnut blossoming, Hay harvest, Chrysanthemum blossoming, and Elder blossoming. Four phenological autumn observations are: Chestnut leaf discoloration, Beech leaf discoloration, Chestnut leaf fall, and Beech leaf fall. Note that their chronological order reflects their average intra-annual time of appearance. See supplement for additional information on the temporal behavior of the different phenological parameters.

We used local meteorological measurements (via MeteoSwiss) from the nearby village of Payerne (Figures S7–S9), and correlated them against the various mushroom, tree-ring and phenological indices. High-resolution gridded ( $0.5^\circ \times 0.5^\circ$ ) and monthly resolved climate indices from the CRUTS3 database (Jones *et al.*, 2012) were used for spatial field correlation analysis at the European-scale (Büntgen *et al.*, 2010).

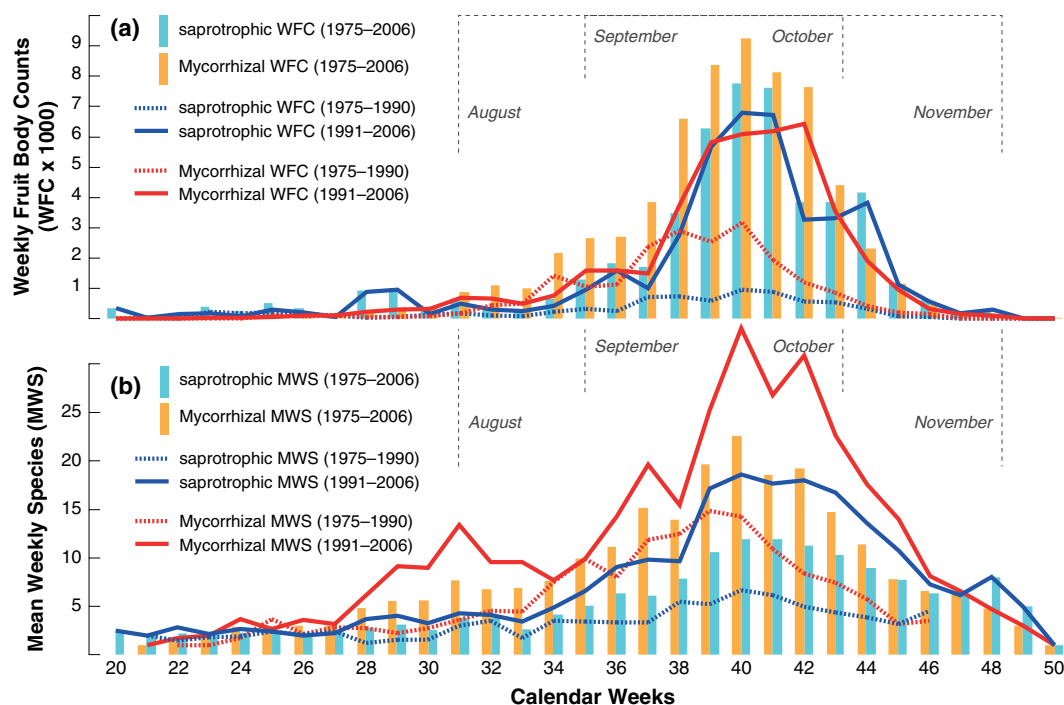
## Results

The continuous fungal inventory covers the period 1975–2006 and comprises a total of 115 417 weekly resolved and precisely located mushroom counts. This exceptional compilation, which is representative for most mid-latitude temperate forest ecosystems, includes 64 695 (50 722) mycorrhizal (saprotrophic) mushrooms of 282 (186) taxa and 29 (71) genera.

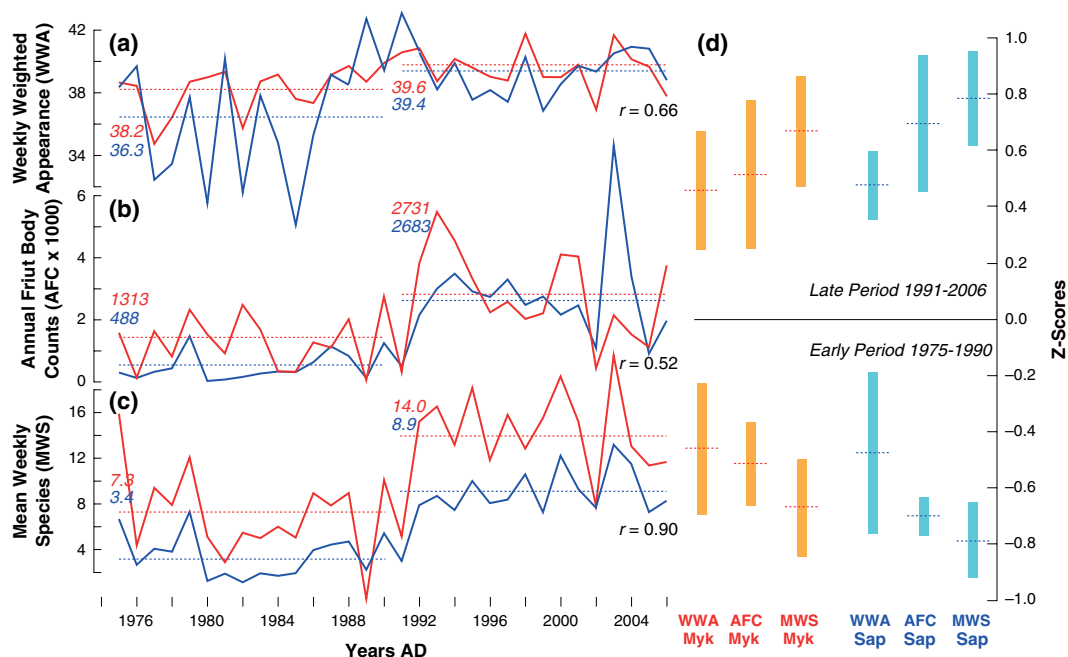
Mushroom counts of both nutritional modes show similar intra-annual fruiting behavior with major

productivity peaks between September and October (Fig. 1a). The WFC correlate highly within years ( $r = 0.93$ ;  $P < 0.0001$ ). An average autumnal productivity delay of 12 days, observed in both functional guilds between 1975 and 2006, coincided with a massive rise in fruit body counts and a distinct increase in the number of mean weekly species (MWS) over time (Fig. 1b).

A most simple split period (1975–1990/1991–2006) comparison of the weighted week of appearance (WWA), which is likely also less prone to outlier-induced biases, further reveals a substantial delay from week 38.2 to 39.6 and from week 36.3 to 39.4 for mycorrhizal and saprotrophic mushrooms, respectively (Fig. 2a). Mean annual fruit body counts (AFC) before and after 1991 increased by a factor of two (1313–2731) and five (488–2683) for symbiotic and saprotrophic fungi, respectively (Fig. 2b). The number of mean weekly species (MWS) also increased from 7.3 to 14.0 for mycorrhizal and from 3.4 to 8.9 for saprobic mushrooms over the entire survey (Fig. 2c). After normalizing the six different fungi indices over their common period 1975–2006 (i.e. adjusting their mean and standard deviation to 0 and 1), the corresponding standard errors of the early/late intervals revealed significant changes in the time-series' temporal behavior (Fig. 2d). Biggest differences between the early/late periods are found for MWS, whereas smallest, though



**Fig. 1** (a) Weekly fruit body counts (WFC) of mycorrhizal (red) and saprotrophic (blue) mushrooms summed over the full 1975–2006 period, and the early/late 1975–1990/1991–2006 split periods (dashed lines). (b) Corresponding mean values of weekly mycorrhizal (red) and saprotrophic (blue) fungal species (MWS).



**Fig. 2** (a) The weekly weighted appearance (WWA), (b) annual fruit body counts (AFC), and (c) mean weekly species (MWS), independently computed for mycorrhizal (red) and saprotrophic (blue) mushrooms, with the horizontal dashed lines referring to their independent early/late split period means (1975–1990/1991–2006). (d) Mean and standard error (dashed lines and shadings) of the three different mycorrhizal and saprotrophic early/late mushroom z-score indices after normalizing the individual time-series (i.e. adjusting their mean and variance to 0 and 1 over the 1975–2006 period). (See Fig 3 for additional statistical insight).

still significant differences are characteristic for WWA. Linear regression models (1975–2006), separately applied to each of the normalized fungi records (Fig. 3), indicate that all data contain significant positive trends ( $P < 0.05$ ). The increasing amount of MWS over the past four decades is particularly strong for saprophytes ( $P = 0.000001$ ), whereas the rise in mycorrhizal AFC is less pronounced ( $P = 0.0028$ ). The observed changes in fungi productivity and phenology were accompanied by a long-term increase in the radial growth of 136 beech trees from the same monitoring plots (Fig. 4 and Figure S5). Superimposed on interannual growth variability exists an overall positive trend, with the most significant increase occurring during the past decade.

The amount and timing of fruit bodies of the two functional guilds, however, suggest different relationships with local tree growth, climate, and plant phenology (Figs 5 and 6). Saprotrophic AFC was most strongly correlated with April to August mean temperature (0.72), and mean spring–summer plant phenology (−0.54). Saprotrophic MWS parallels tree growth (0.58). Agreement between saprotrophic productivity, plant phenology and ring width variability is somewhat indicative for a common external (i.e. climatic) forcing upon the different ecological components (Figure S10). The strongest relationship was found between March to April mean temperature variability and early

spring–summer plant phenology (−0.73). A significant correlation of 0.46 between mean autumnal plant phenology and the intra-annual timing of mycorrhizal fruit body production (WWA) agrees well with the symbiotic concept of fungi–host interaction. However, since mycorrhizal WWA shows highest correlation with mean August temperatures (0.71) and autumnal plant phenology correlates strongest with mean August to September temperatures (0.63), it remains unclear whether the mycorrhizal fruiting peak is directly driven by temperature or indirectly via a temperature-dependent host phenology.

Variation in spring–summer temperatures was found to be most important for the productivity, diversity and phenology of saprobic mushrooms and ring width variability (Figure S11). Significant correlations between the fungal and climate data suggest that synoptic fluctuations in June to August temperature impact saprobic yield and tree growth, and that August temperatures over southwestern Europe likely influence mycorrhizal phenology in Switzerland (Fig. 7). Augmented autumnal mycorrhizal mushroom yield also coincided with increased September to October precipitation totals (Figure S12). It should be noted that effects of more complex, and integrative meteorological parameters, such as drought metrics and indices of vapor pressure, were found to be less suitable to explain both, year-to-



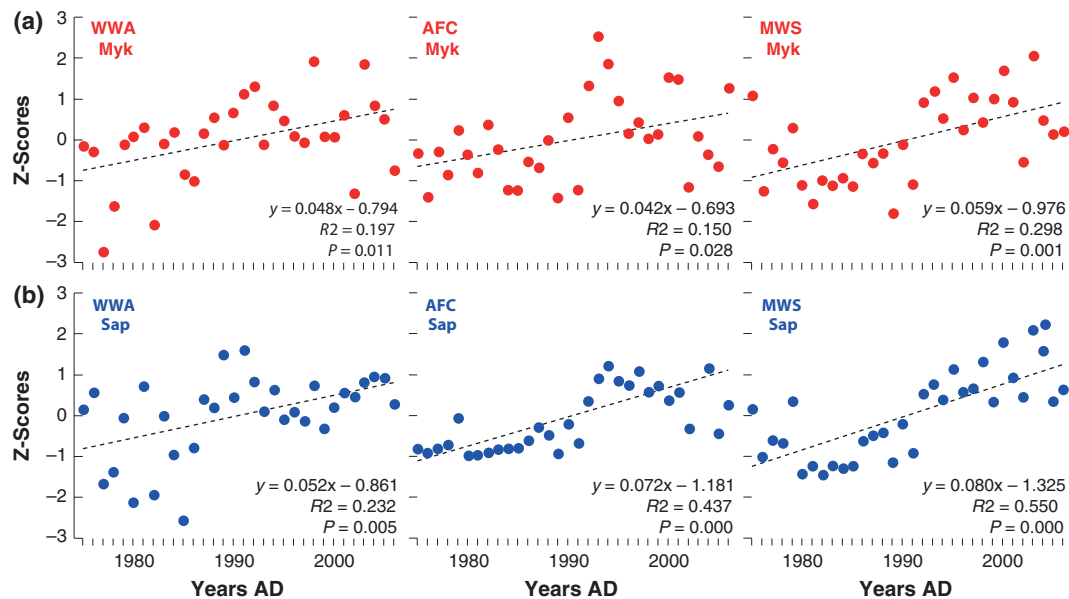


Fig. 3 Linear regression models of the weekly weighted appearance (WWA), annual fruit body counts (AFC), and mean weekly species (MWS), separately computed for (a) the mycorrhiza and (b) the saprotrophic mushroom species based on their individual time-series after normalizing (i.e. adjusting their mean and variance to 0 and 1 over 1975–2006).

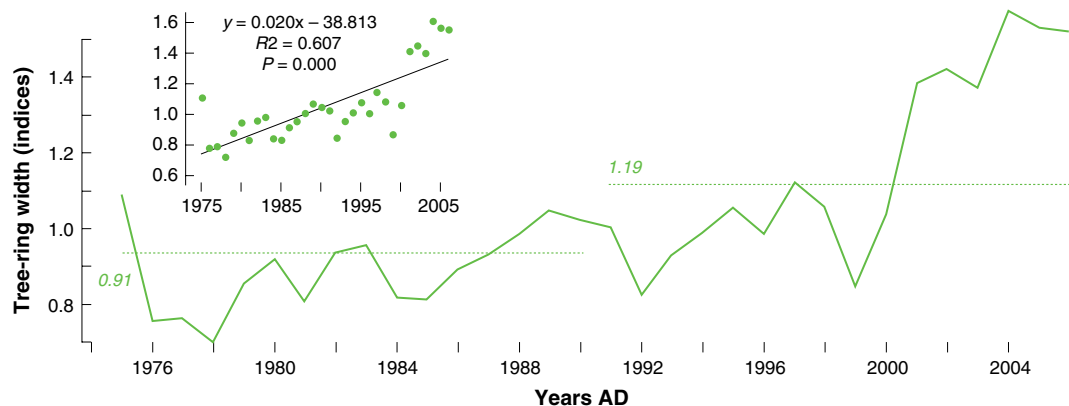


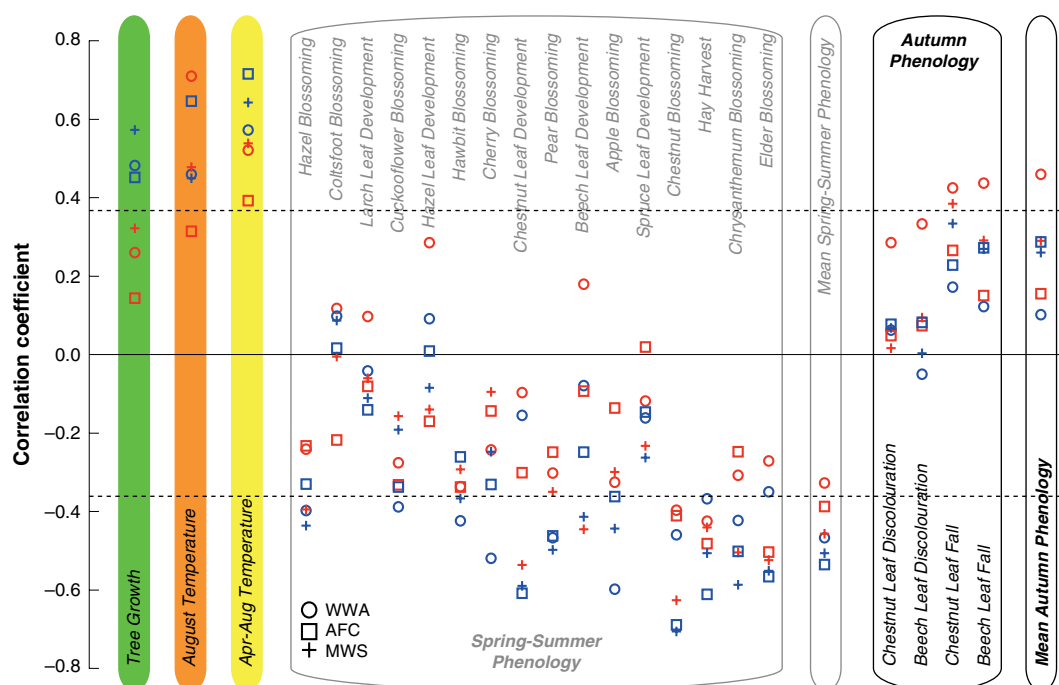
Fig. 4 Interannual and longer term variations of the oak tree-ring width chronology, using power-transformation and detrending with negative exponential or straight-line functions (see supplementary information for details).

year and decadal-long variations in mushroom fruiting, a finding that is in line with the observations reported by Büntgen *et al.* (2012b). Further complexity originates from the fact that mycorrhizal mushroom fruiting not only depends on the host-fungi carbon flux but also on the associated water flow between the nearby trees and its surrounding fungal partners. A schematic overview of the complex fungal web is provided in figure 8.

## Discussion

On top of the climatic factors described are additional external factors that can impact fungi productivity and phenology at different intensity depending on the functional guild. In fact, the relatively stronger

enhancement of saprophytes may originate from either direct (or indirect via the host plant) harmful influences of atmospheric nitrogen deposition on mycorrhizal mycelial growth and its subsequent fruit body production (Peter *et al.*, 2001; Högberg *et al.*, 2003; Gillet *et al.*, 2010). It is also notable that after the 2003 summer heat (from June to August) (Luterbacher *et al.*, 2004; Schär *et al.*, 2004; Büntgen *et al.*, 2011), significantly more autumnal saprobes (primarily the parasitic/saprobic species *Armillaria ostoyae*) contributed to the observed convergence of the two AFC time-series (Figure S13). To which degree and in which direction changes in forest growth, litter input, root biomass production, and/or rhizodeposition though affect the fruit body production of both nutritional modes remains debatable (Jones



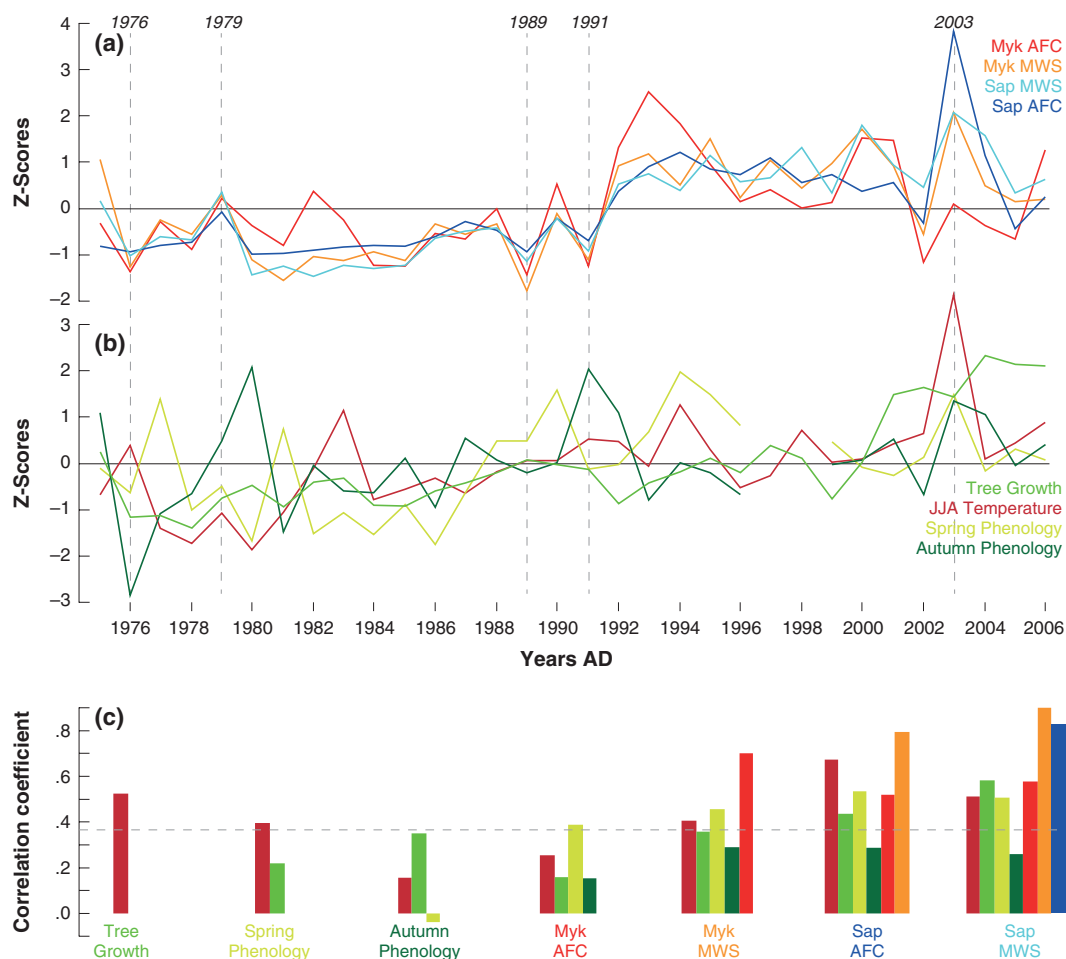
**Fig. 5** Correlation coefficients of three different mycorrhizal (red) and saprotrophic (blue) mushroom indices weekly weighted appearance (WWA, fruit body counts AFC and mean weekly species MWS) computed against local tree growth (green), August and April–August temperature means (orange and yellow), and phenological spring–summer and autumn (gray and dark gray) indicators, which were ordered after their average intra-annual occurrence date. Dashed lines indicate the 95% significance level corrected for lag-1 autocorrelation in the time-series.

*et al.*, 2009). It is also unclear how alternations in the proportion of mycorrhizal vs. saprobic soil mycelia may influence carbon budgets among various spatio-temporal scales (Clemmensen *et al.*, 2013), let alone effects on soil invertebrates (Lubbers *et al.*, 2013).

Little differences in the intra-annual emergence of mycorrhizal and saprobic mushrooms, together with non-significant correlations between mycorrhizal fruiting and tree growth are likely indicative for a carbon and precipitation-saturated ecosystem. The almost synchronized intra-annual fruiting distribution of both functional guilds somewhat contradicts the fact that saprotrophic mushrooms generally emerge throughout the entire warm season Sato *et al.* (2012). Possible offset between our findings and those reported by (Sato *et al.*, 2012) might be caused by different climatic conditions of the two studies (i.e. oceanic vs. continental). Mushroom growth under a balanced oceanic climate is perhaps more closely related to bio-ecological rules (saprophytes all over the year, mycorrhizal restricted to host plant phenology), where heat waves and drought spells are less important. Mushroom phenology in continental environments, however, is expected to be generally shorter and fruiting patterns of both functional guilds are likely more directly affected by ambient climatic factors. In our case, warmer summers stimulate both

functional guilds with similar intensity. Extended summer seasons, later frost events and a delayed snow cover also enhance belowground soil activity in tandem with aboveground mushroom productivity. The synchronous timing of autumnal fruit body production of specific mycorrhizal and saprobic species may partly be related to common climatic drivers of mushroom fruiting. Since the mycorrhizal lifestyle does not show a monophyletic origin but is arisen many times from saprobic ancestors (Hibbett *et al.*, 2000; Tedersoo *et al.*, 2010), common climatic and/or other external drivers of fruit body production of both lifestyles may describe a possible explanation. If fruit body production of both functional guilds is indeed mainly determined by carbon allocation (Högberg *et al.*, 2010), it would support the growing evidence that carbon acquisition of both functional guilds (Leake *et al.*, 2002) is closely intermingled via priming effects and decomposer abilities inherent of mycorrhizal fungi (Talbot *et al.*, 2008; Janssens *et al.*, 2011; Subke *et al.*, 2011; Veneault-Fourrey & Martin, 2011).

A long-term increase in the radial growth of beech trees from the mushroom monitoring plots provides additional independent evidence of enhanced ecosystem productivity in temperate forests north of the Alpine arc (Büntgen *et al.*, 2013), and thus supplements recent findings from Central Europe (Luterbacher *et al.*, 2004;



**Fig. 6** (a) Mushroom (annual fruit body counts and mean weekly species), as well as (b) vegetation (tree growth and plant phenology) and temperature (mean June–August) variability after normalizing the individual time-series (i.e. adjusting their mean and variance to 0 and 1 over the 1975–2006 period). (c) Cross-correlation of each parameter computed over the 1975–2006 period. Mean spring phenology is inverted, and the dashed horizontal line refers to the 95% significance level corrected for lag-1 autocorrelation.

Büntgen *et al.*, 2011, 2012a,b; Stobbe *et al.*, 2012). Such beneficial circumstances are likely representative for most of the mid-latitudinal temperate forest zones (FAO, 2011, [www.mcpfe.org](http://www.mcpfe.org)), if precipitation (i.e. soil moisture availability) is not a limiting factor (Allen *et al.*, 2010). In fact, it is well known that higher temperatures can stimulate mushroom productivity and host vitality in carbon and precipitation-saturated environments (i.e. under conditions where both factors are not limiting; Kauserud *et al.*, 2008, 2010; Kauserud *et al.*, 2013; Büntgen *et al.*, 2012b).

Saprobic species are more directly affected by external factors, including climate (Fig. 8). Less agreement between mycorrhizal mushroom yield and ambient climate may possibly result from the symbiotic fungi–host interaction that allocates carbon for fruit body production (Högberg *et al.*, 2001; Egli *et al.*, 2010), and may also deliver cues for their fruiting activity (Kües & Liu, 2000). Saprotrophic mushrooms, in contrast, acquire

carbon mainly by temperature-dependent and moisture-limited decomposition processes (Rousk & Baath, 2011), whereas mycorrhizal fruiting relates more directly to their host's carbon supply (Högberg *et al.*, 2001; Egli *et al.*, 2010). Overall lower effects of climate on the timing and the amount of mycorrhizal sporocarps might also result from the location of mycelia in deeper soil layers (Fig. 8), less prone to climatic factors such as drought (Baldrian *et al.*, 2012; Clemmensen *et al.*, 2013). Water exchange from the host plants to its fungal partners may enable compensation of sporadic soil moisture deficits throughout the vegetation period (Querejeta *et al.*, 2003; Lilleskov *et al.*, 2009).

Projected increases in atmospheric greenhouse gases and terrestrial fertilization rates will have complex and possibly also non-linear effects on the net primary production of the biosphere, including tree growth and mushroom yield. Moreover, if we assume that higher mushroom productivity goes along with stronger

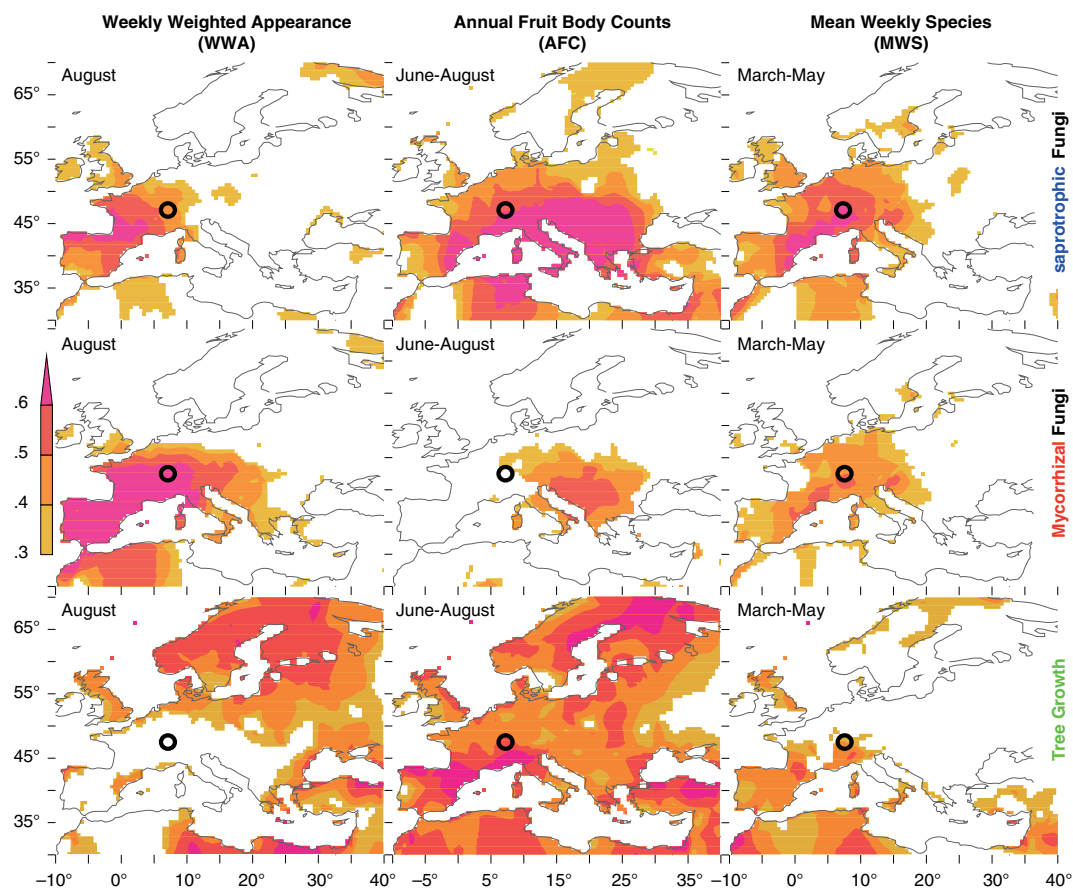


Fig. 7 Spatial correlation fields of the saprotrophic (blue) and mycorrhizal (red) mushroom data, as well as tree growth (green) computed against August (8), June–August (6–8) and March–May (3–5) temperature means. Black cycles indicate locations of the fungus reserve (ca. 47°N and ca. 7°E).

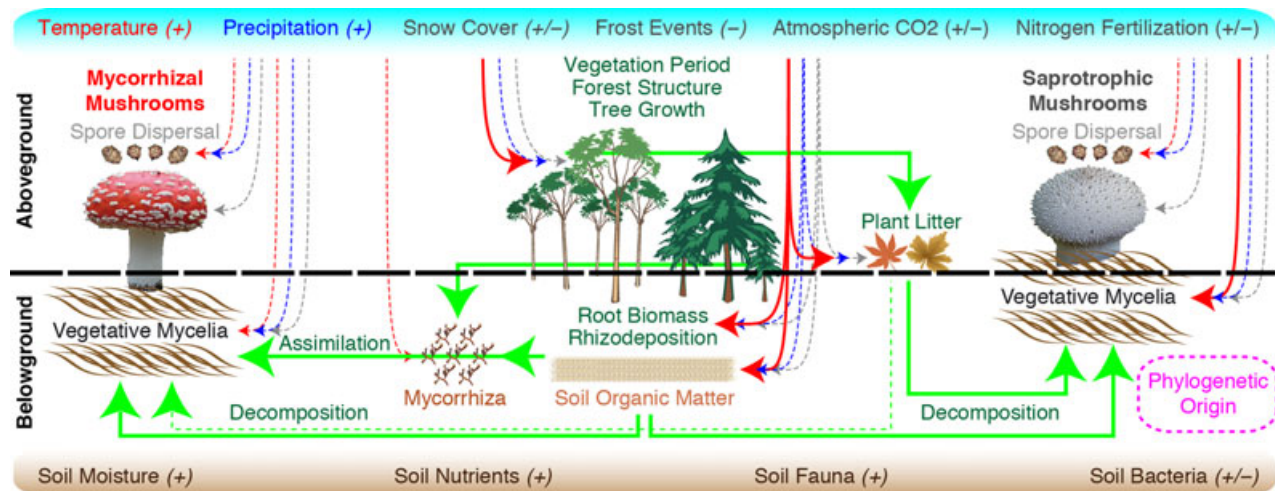


Fig. 8 Climatic drivers of the mycorrhizal and saprotrophic fungal web, including biotic (e.g., host plants and fungal partners) and abiotic (e.g., environmental change) factors as well as above and belowground processes and pathways.

mycelial decomposition activities, it is reasonable that different fungi with different nutritional modes and different decomposition routes will have different

effects on carbon sequestration, resulting in even more complex fluxes between forest ecosystems and the atmosphere. Associated effects on the global carbon



cycle (Cheng *et al.*, 2012; Clemmensen *et al.*, 2013) and possibly even also on methane fluxes (Lenhart *et al.*, 2012) are likely to occur under predicted climate change (van der Heijden *et al.*, 2008; Orwin *et al.*, 2011). Amplified photosynthetic activities possibly lead to augmented carbon resources for mycorrhizal fungal growth. Clemmensen *et al.* (2013) showed that a substantial amount of this root- and mycorrhiza-derived carbon is sequestered in soils. On the other side, increased and prolonged activity of both functional guilds in a warmer but not drier world may stimulate a faster degradation and a reduced accumulation of soil organic matter (Davidson & Janssens, 2006; Cheng *et al.*, 2012), and thus likely also alters the atmospheric composition. However, it is also known that the presence of mycorrhizal fungi can result in decreased rates of soil organic matter decomposition (Gadgil & Gadgil, 1971; Koide & Wu, 2003; Lindahl *et al.*, 2010; McGuire *et al.*, 2010), and it is thus not clear if increased activity of both functional guilds would indeed enhance soil organic matter degradation at the ecosystem level.

Likely unaffected by the organism's circadian rhythm and photobiology (Körner & Basler, 2010), our results demonstrate the importance of long-term mushroom inventories to capture high- and low-frequency variability in their phenology and productivity. The observed long-term increase in WFC and MWS, likely representative for most precipitation-saturated, temperate forest ecosystems of the mid-latitudes, provides independent evidence that supplements previously reported long-term changes in mushroom populations, such as drought-induced productivity reductions in truffle (Hall *et al.*, 2003; Buntgen *et al.*, 2012a) and matsutake (Okada *et al.*, 2011; Yang *et al.*, 2012). In this regard, our study emphasizes the importance of linking ecological changes to environmental factors, and suggests careful assessments of intertwined carbon pathways within and between different nutritional fungi modes and their symbiotic host partners.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Sampling site. Location of the Swiss fungus reserve 'La Chanéaz', and pictures of the typical temperate forest (upper right) and the protection fence (lower right).

**Figure S2.** Mushroom examples. The upper row provides examples of typical mycorrhizal fruit bodies from the reserve 'La Chanéaz': *Boletus edulis* (King Bolete) has a cosmopolitan distribution and is one of the most sought-after edible mycorrhizal mushrooms worldwide.

**Figure S3.** Tree-ring samples. (a) Temporal distribution (start and end years) of the 136 beech core samples, with each horizontal bar representing one individual ring width measurement series (the trees' life span).

**Figure S4.** Chronology characteristics. Temporal changes in mean series length, tree age, and sample replication of the beech chronology based on 136 core samples.

**Figure S5.** Tree-ring variation. Bi-weight robust mean chronology of the 136 beech measurement series following different chronology development approaches: (a) without detrending and (b) after power-transformation and detrending with negative exponential or straight-line functions.

**Figure S6.** Plant phenology. Inter-annual variations (1975–2006) in local phenology from Posieux (46°46'00"N, 7°6'00"E, 670m asl) nearby the fungus reserve.

**Figure S7.** Climatic background. Annual course of monthly resolved temperature means and precipitation totals recorded in Payerne and computed over the full and early/late split periods to emphasize slight temporal changes.

**Figure S8.** Climate variability. Interannual August (bold) and June-August (thin) climate variability recorded in Payerne.

**Figure S9.** Cloudiness and wind-speed. Monthly averages of daily mean cloudiness (%) and daily mean wind-speed (m/s) recorded in Payerne.

**Figure S10.** Temperature forcing. Correlation coefficients (>0.0; 1975–2006) between monthly and seasonal temperature means, mycorrhizal (red) and saprophyte (blue) mushroom data (WWA, AFC and MWS), as well as tree growth (green) using the beech chronology after power-transformation and detrending with negative exponential or straight-line functions.

**Figure S11.** Fungi-heat response. Correlation coefficients (1975–2006) between monthly and seasonal measurements of temperature, sunshine and evapotranspiration and mycorrhizal (red) and saprophyte (blue) mushroom timeseries.

**Figure S12.** Fungi-hydrological response. Correlation coefficients between monthly and seasonal measurements of humidity, precipitation and cloudcover and mycorrhizal (red) and saprophyte (blue) mushroom timeseries.

**Figure S13.** Nutritional-mode offset. Difference between weekly counts (WC) of mycorrhizal and saprotrophic fungi (saprotrophic minus mycorrhizal counts).