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LETTER

Mast seeding in European beech (*Fagus sylvatica* L.) is associated with reduced fungal sporocarp production and community diversity

Talia J. Michaud[1] | **Ian S. Pearse**[2] | **Håvard Kauserud**[3] | **Carrie J. Andrew**[4] | **Peter G. Kennedy**[1]

[1]Department of Plant and Microbial Biology, University of Minnesota, St. Paul, Minnesota, USA
[2]U.S. Geological Survey, Fort Collins Science Center, Fort Collins, Colorado, USA
[3]Department of Biosciences, University of Oslo, Oslo, Norway
[4]Natural History Museum, University of Oslo, Oslo, Norway

Correspondence
Talia J. Michaud, Department of Plant and Microbial Biology, University of Minnesota, St. Paul, MN 55108, USA.
Email: talia.michaud@gmail.com

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Abstract

Mast seeding is a well-documented phenomenon across diverse forest ecosystems. While its effect on aboveground food webs has been thoroughly studied, how it impacts the soil fungi that drive soil carbon and nutrient cycling has not yet been explored. To evaluate the relationship between mast seeding and fungal resource availability, we paired a Swiss 29-year fungal sporocarp census with contemporaneous seed production for European beech (*Fagus sylvatica* L.). On average, mast seeding was associated with a 55% reduction in sporocarp production and a compositional community shift towards drought-tolerant taxa across both ectomycorrhizal and saprotrophic guilds. Among ectomycorrhizal fungi, traits associated with carbon cost did not explain species' sensitivity to seed production. Together, our results support a novel hypothesis that mast seeding limits annual resource availability and reproductive investment in soil fungi, creating an ecosystem 'rhythm' to forest processes that is synchronized above- and belowground.

KEYWORDS
fungal phenology, historical ecology, mast seeding

INTRODUCTION

Mast seeding, or the synchronous production of an outsized seed crop in a population of plants, is a well-documented, global phenomenon (Kelly, 1994). Mast seeding is often investigated as a resource input, wherein large seed crops increase the local abundance of seed predators (Bogdziewicz et al., 2016) and are a labile substrate for decomposers (Zackrisson et al., 1999), frequently causing cascading effects on food webs (Ostfeld et al., 2000). The altered fate of the resources necessary to produce a mast seed crop—including water, nitrogen and carbon—also causes resource limitation within the mast seeding plant (Pearse et al., 2016). Many tree species switch resources away from vegetative growth to produce a mast seed crop (Pearse et al., 2016), evidenced by negative correlations between tree ring growth and seed production (Koenig & Knops, 1998). In a mast year, the flux of resources redirected towards seed production may limit resource availability to organisms that are dependent on trees or soil from which the trees draw resources.

Forest-dwelling fungi span many ecological niches and are often categorized according to their trophic mode or guild. For instance, saprotrophic fungi decompose a variety of organic matter types, while root-associated ectomycorrhizal fungi are sustained by a combination of photosynthate from host plants and nutrients held in soil inorganic and organic matter (Smith & Read, 2010). Their complementary life cycles drive forest nutrient cycling globally (Baldrian et al., 2023): saprotrophic fungi possess uniquely powerful mechanisms that degrade recalcitrant organic matter (Baldrian, 2008), while mycorrhizal fungi mediate the transfer of nutrients to trees (Hoeksema et al., 2010; Näsholm et al., 2013), thereby influencing primary productivity.

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These differences may determine their sensitivity to mast seeding events. Because ectomycorrhizal fungi are dependent on trees for carbon, we anticipate that ectomycorrhizal fungi will be more sensitive to mast seed production than saprotrophic fungi. Like mast seed crops, ectomycorrhizal sporocarp production depends on recent photosynthate (Hobbie et al., 2021; Högberg et al., 2001). Accordingly, ectomycorrhizal fungi appear more proximally affected by tree resource availability compared to saprotrophic fungi: Collado et al. (2018) found that ectomycorrhizal sporocarp production was correlated with vegetative growth of trees in that year, while saprotrophic sporocarp production was linked with growth 2 years earlier. Additionally, ectomycorrhizal fungal sporocarp production is typically more seasonal than sporocarp production of saprotrophic fungi, evidenced by a unimodal peak in sporocarp production during peak tree productivity compared to the more stable pattern of production across the season among saprotrophs (Ponce et al., 2023; Sato et al., 2012). Resource switching during masting may reduce resource allocation belowground (Nikolova et al., 2011), or require increased nitrogen and/or water uptake by trees (Pearse et al., 2016), both of which may more immediately affect ectomycorrhizal fungi than saprotrophic fungi (Kranabetter et al., 2019).

Ectomycorrhizal fungal activity and root presence, however, can influence saprotrophic fungal activity (Frey, 2019). For instance, ectomycorrhizal fungal activity is posited to reduce saprotrophic fungal activity through competition for nitrogen and/or water in the same substrates when resources are sufficiently scarce, a phenomenon commonly referred to as the ‘Gadgil effect’ (Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971). Roots, on the other hand, may prime saprotrophic fungal activity by exuding labile carbon-containing compounds (Dijkstra et al., 2013; Huo et al., 2017). Thus, if during a mast year, trees decrease belowground carbon allocation and/or increase nitrogen and water uptake facilitated by ectomycorrhizal fungi, this may reduce resource availability to saprotrophic fungi, despite their ‘free-living’ designation.

Ectomycorrhizal fungi also differ in the magnitude of their own resource demand (Bidartondo et al., 2001; Hobbie & Colpaert, 2003), which may influence their sensitivity to masting. For instance, species that are more sensitive to atmospheric nitrogen pollution (nitrophobic versus nitrotolerant) are thought to require more carbon from their tree hosts, although other possible explanations exist (Bidartondo et al., 2001; Lilleskov et al., 2019; Wallander, 1995). Additionally, ectomycorrhizal fungi with mycelial growth that extends further into the soil are thought to require more carbon and other nutrients (Agerer, 2001; Fernandez et al., 2017; Lilleskov et al., 2011). These differences may render species that are more resource-demanding more sensitive to potential resource limitation induced by mast seeding.

Studying fungal sporocarp production has been central to the field of fungal ecology for decades, especially as a proxy for fungal resource availability. While sporocarp production is not a perfect proxy for fungal resource availability, fruitification ultimately represents carbon and nutrient investment in sexual reproduction, which fungi cannot do without the necessary resources (i.e., photosynthate and/or organic matter). Tree vegetative growth is linked to sporocarp production, both experimentally (Andrew & Lilleskov, 2009) and in observational studies (Collado et al., 2018; Egli et al., 2010), reifying our hypothesis that mast seeding and consequent resource switching in trees may reduce resource availability and fruitification by extension among forest-dwelling fungi.

To evaluate the potential relationship between mast seeding in trees and fungal resource availability, we coupled two high-resolution, long-term ecological time series datasets: (A) a fungal fruiting census spanning 1977–2006 from Payerne, Switzerland and (B) a contemporaneous time series reconstruction of seed production in the dominant overstory tree species, European beech (*Fagus sylvatica* L.). We analysed the data at three ecological scales: (1) total sporocarp production, (2) guild-level sporocarp production and (3) species-level sporocarp production. We expected a negative relationship between beech seed production and sporocarp production and for ectomycorrhizal sporocarp production to be more negatively associated with seed production than saprotrophic sporocarp production. We tested whether (1) total sporocarp production, community composition and diversity decreased with increasing beech seed production and (2) the relationship between sporocarp and beech seed production differed at the guild level between ectomycorrhizal and saprotrophic fungi. At the species level, we tested (3a) whether the proportion of species with significant relationships with masting differed between ectomycorrhizal and saprotrophic fungi and (3b) if ectomycorrhizal species' sensitivity was explained by traits putatively corresponding to resource demand.

METHODS AND MATERIALS

Site description

The fungal census was conducted in the 75-hectare La Chanéaz Fungal Reserve, established in 1975, near Payerne, Switzerland (Swiss Federal Institute for Forest, Snow and Landscape Research WSL; 46 degrees 47′55″ to 46 degrees 48′10”N and 6 degrees 59′52″ to 7 degrees 00′30″E (Straatsma et al., 2001)). The site is an old-growth forest on the Swiss Central Plateau (mean altitude 585 m), dominated by multi-story beech (*Fagus sylvatica*), with interspersed spruce (*Picea abies*), larch (*Larix decidua*), oak (*Quercus robur*), pine (*Pinus sylvestris* and *Pinus strobus*), maple (*Acer pseudoplatanus*) and ash (*Fraxinus*

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excelsior) growing on calcaric cambisol. The study area was enclosed by 2-m fences to deter mushroom pickers and other large animals from harvesting the fruiting fungi.

From 1977 to 2006, a total of 106,521 epigeous sporocarps from fungi with macroscopic sporocarps were recorded and identified. Surveys were conducted on a weekly basis, during the May to November growing season, among five 300 m^2 plots. These plots were subdivided into three 100 m^2 subplots, each of which experienced a distinct mushroom surveying/harvesting procedure: picking, cutting and no harvest (Egli et al., 2006). From the years 1980 to 1983, only edible species were recorded. Data from these years were excluded from analyses of annual sporocarp production. Species taxonomies were updated by Andrew et al. (2016), and included synonymies and nomenclatural changes based on Index Fungorum and Species Fungorum (http://www.indexfungorum.org; www. speciesfungorum.org). Further information on the mushroom sampling procedure is detailed in Straatsma et al. (2001) and Egli et al. (2006). Sporocarp counts and presence/absence data were both modelled in this current study, detailed in the statistical analyses section below (Andrew et al., 2016).

Beech masting record compilation

Beech seed production records were compiled from the MASTREE+ database (Hacket-Pain et al., 2022). The temporal dynamics of beech seed production show high synchrony within large portions of the species' range (Vacchiano et al., 2017), in which mast seed production is predicted by spring temperatures in the 2 years preceding the mast crop and is affected by long-term climate oscillations on decadal scales (Ascoli et al., 2017). We compiled all >5-year records of seed production within the 'southern region' identified by Vacchiano et al. (2017), resulting in 80 unique time series of beech seed production (Table S1). These datasets were from Switzerland, Italy and France. Records were constrained to those of beech seed or fruit production, such that records of pollen or flower abundance were dropped. In the region of our dataset, the frequency of mast years of beech has increased over the time period of the dataset, though to a lesser degree than in Great Britain (Bogdziewicz et al., 2020; Nussbaumer et al., 2016). To combine these datasets, we standardized each dataset to its range, resulting in a seed production score from 0 to 1 for each year (e.g. Pearse et al., 2020). Or, where *Ast* is standardized annual seed production, *A* is one observation in a long-term seed production time series (*SP*):

$$\mathrm{Ast} = (\mathrm{A} - \min(\mathrm{SP})) / (\max(\mathrm{SP}) - \min(\mathrm{SP})).$$

We used the annual mean of datasets as the region-level index of mast seeding (Figure 1). The mast index was strongly positively correlated ($r=0.6$, $p<0.0001$) with the long-term (1986–2011) estimate of seed production nearest to the fungal study site, MASTREE record 3149, suggesting that the mast index accurately represents local seed production.

Meteorological record compilation

Historical daily precipitation and temperature data from 1977 to 2006 were compiled from the nearest weather station (Meteo Payerne, 7 km away; 46 degrees 48′42”N, 6 degrees 56′33″ E; 490 m altitude) of the Federal Office of

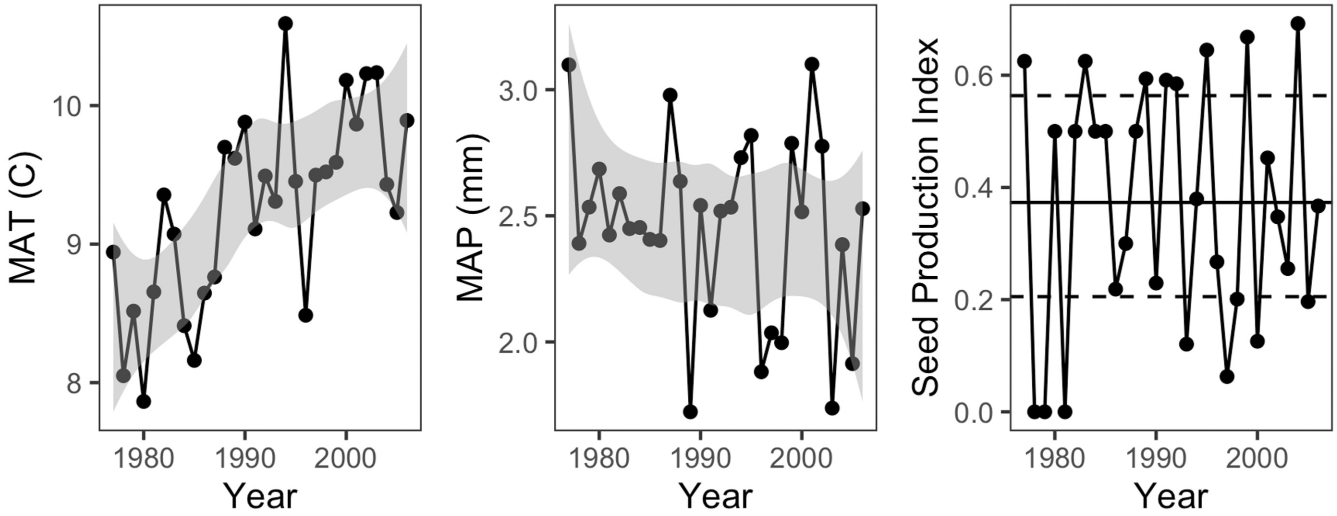

FIGURE 1 Climate (panels one and two) and beech seed production (third panel) data from 1977 to 2006 for Payerne, Switzerland. For mean annual temperature (MAT) and mean annual precipitation (MAP), the shaded region represents the 95% confidence interval around a loess curve fit to the data. For beech seed production, each point represents an annual index of beech seed production derived from MASTREE+. Dotted lines represent the interquartile range of the data.

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Meteorology and Climatology, MeteoSwiss (http://www.meteoschweiz.admin). Daily temperature and precipitation were averaged across the years and included in models of sporocarp production (Figure 1).

Species traits compilation

The FungalTraits database was used to assign guild to species (Põlme et al., 2020). For ectomycorrhizal species (*n* = 200), extraradical mycelial exploration type was assigned at the genus level using literature sources (Agerer, 2006; Lilleskov et al., 2011; Tedersoo & Smith, 2013). Species with long-distance, medium-distance fringe and medium-distance mat exploration types typically produce hydrophobic extraradical mycelium and were designated hydrophobic, while those with contact, short-distance and medium-distance smooth types were designated hydrophilic (Agerer, 2001; Unestam & Sun, 1995). Potential ectomycorrhizal fungal nitrophobicity was assigned to 24 species using literature sources (van Strien et al., 2018; van der Linde et al., 2018).

Data analyses

All analyses were performed in R (R Core Team, 2023). To evaluate the relationship between total sporocarp production and interannual variability in beech seed production, we calculated total annual sporocarp counts (115,417 sporocarps) and guild-level annual sporocarp counts (54,583 ectomycorrhizal sporocarps, 38,811 saprotrophic sporocarps) across the 15 subplots at La Chanéaz. Because records from 1980 to 1983 were incomplete, we excluded these data (93,329 remaining sporocarp observations). For models of total and guild-level annual sporocarp production, we constructed negative binomial regression models using the glmmTMB package (Brooks et al., 2017) and the nbinom1 family parameterization. Our models included annual sporocarp counts as our response variable, with mean annual temperature, precipitation and annual beech seed production index as fixed effects. Pairwise correlations between fixed effects were examined prior to modelling, and showed no significant correlations, consistent with general observations that annual seed production and current-year weather are relatively decoupled (Figure S1). For both models, plot and subplot were included as random effects, with the subplot nested within plot to reflect the study site design. Residuals were simulated using DHARMa (Hartig & Lohse, 2022) and inspected for non-linearity, heteroscedasticity and zero inflation. For the analysis of total sporocarp production, residual non-linearity was detected; specifically, a hump-shaped relationship was detected between residuals and mean annual temperature. To address this, we introduced natural splines in our temperature predictor using the splines R base package (R Core Team, 2023) with two degrees of freedom. At the guild level, we included fixed intercept terms for guild and interactions between guild and seed production. We also included a dispersion formula with guild as the response variable to address varying dispersion between guilds. For both models, predicted sporocarp counts at different levels of seed production, mean temperature and precipitation were generated using the ggeffects package (Lüdecke, 2018). Partial residuals for visualization were generated using the 'partialize' function in the jtools package (Long, 2023) and subset below the maximum observed counts to aid visualization.

We also examined relationships between beech seed production, current-year weather and sporocarp community composition, diversity and richness. We used the 'capscale' function in the ape package (Paradis & Schliep, 2019) to perform a distance-based redundancy analysis (dbRDA) using the Bray–Curtis dissimilarity metric with mean annual precipitation, mean annual temperature and seed production as predictors (Paradis & Schliep, 2019). We performed an analysis of variance (ANOVA) on the overall model fit and the terms of the model with 999 permutations. We then calculated annual fungal species richness and diversity (Shannon-Weiner) at the plot level (to mitigate excessive zeros, n = 5 plots per year) and regressed these values against annual seed production, mean annual temperature and mean annual precipitation with plot as a random effect. We modelled species richness with a negative binomial regression ('nbinom1' family in glmmTMB) and diversity with a gaussian distribution in glmmTMB (Brooks et al., 2017).

To evaluate species-level responses to seed production, temperature and precipitation, we modelled annual sporocarp production for each species using logistic regression with mixed effects. For edible species whose occurrences were recorded from 1980 to 1983, we included data from these years. Using the package glmmTMB, we modelled presence-absence data (0, 1) based on beech seed production, mean annual temperature and mean annual precipitation. Because sample sizes became limited at the species level, we scaled temperature and precipitation variables to enhance model convergence. Plot and subplot were included again as random effects, with subplot nested within plot. To capture species' sensitivity to these environmental variables, we ran logistic regression models for each species sequentially, ordered by decreasing species' frequency. We fit models to 250 species before species-level data became too sparse to fit models. We extracted z scores associated with each predictor for each species. The z score is the statistic associated with the likelihood of observing the estimated coefficient given the variability in the input data and the null hypothesis. Given an alpha level of 0.05, if the absolute value of the z score is greater than 1.96, the likelihood of observing the estimated coefficient is sufficiently low (below 0.05) to reject the null hypothesis that there is no relationship

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between the response variable and the predictor. In context, a sufficiently low z score associated with beech seed production indicates that there is evidence that a species is less likely to be observed at high levels of seed production, i.e., a mast year. This analysis yielded z scores associated with 151 species of ectomycorrhizal fungi and 96 species of saprotrophic fungi. Fisher's exact tests were used to test whether the proportions of species associated with beech seed production versus unassociated varied across guilds. Among ectomycorrhizal fungi, this test was performed to detect whether the proportion of species significantly associated with seed production varied by ectomycorrhizal exploration type, mycelial hydrophobicity and potential nitrophobicity.

RESULTS

Total sporocarp production was strongly negatively related to beech seed production (coefficient ± standard error: -1.15 ± 0.20 log(sporocarp count) per unit seed production, $z = -5.660$, $p < 0.001$) (Figure 2a). Conversely, sporocarp production was positively related to temperature and precipitation (temperature, first spline: 2.18 ± 0.28 log(sporocarp count)°C^{-1}, $z = 7.811$, $p < 0.001$; temperature, second spline: 0.42 ± 0.15 log(sporocarp count)°C^{-1}, $z = 2.845$, $p < 0.01$; precipitation: 0.57 ± 0.15 log(sporocarp count) mm^{-1}, $z = 5.882$, $p < 0.001$). Total sporocarp counts declined by an average of 55% based on seed production, from an average of 406 sporocarps at lowest seed production (95% Confidence Interval (CI): 305.97–539.36 per $100\,\text{m}^2\,\text{year}^{-1}$) to an average of 183 sporocarps at highest seed production (95% CI: 140.47–238.47 per $100\ \text{m}^2\,\text{year}^{-1}$), at mean levels of temperature and precipitation. The composition of the total sporocarp community was also significantly related to mean annual temperature ($F = 5.497$, $p = 0.001$), mean annual precipitation ($F = 3.340$, $p = 0.001$) and beech seed production ($F = 2.279$, $p = 0.002$; dbRDA, $F = 3.705$, $p = 0.001$) (Figure 3). Mean annual precipitation and seed production were oppositely related to community composition (Figure 3). Species richness was negatively associated with seed production (-0.59 ± 0.23 log(species) per unit seed production, $z = -2.569$, $p = 0.010$), and positively associated with mean annual temperature (0.40 ± 0.06 log(species)°C^{-1}, $z = 6.265$, $p < 0.001$) and mean annual precipitation (0.31 ± 0.11 log(species) mm^{-1}, $z = 2.623$, $p = 0.009$). Specifically, from the lowest to highest level of seed production, species richness declined 34% on average, from 39 species (28.26–53.06 per $100\,\text{m}^2\,\text{year}^{-1}$)

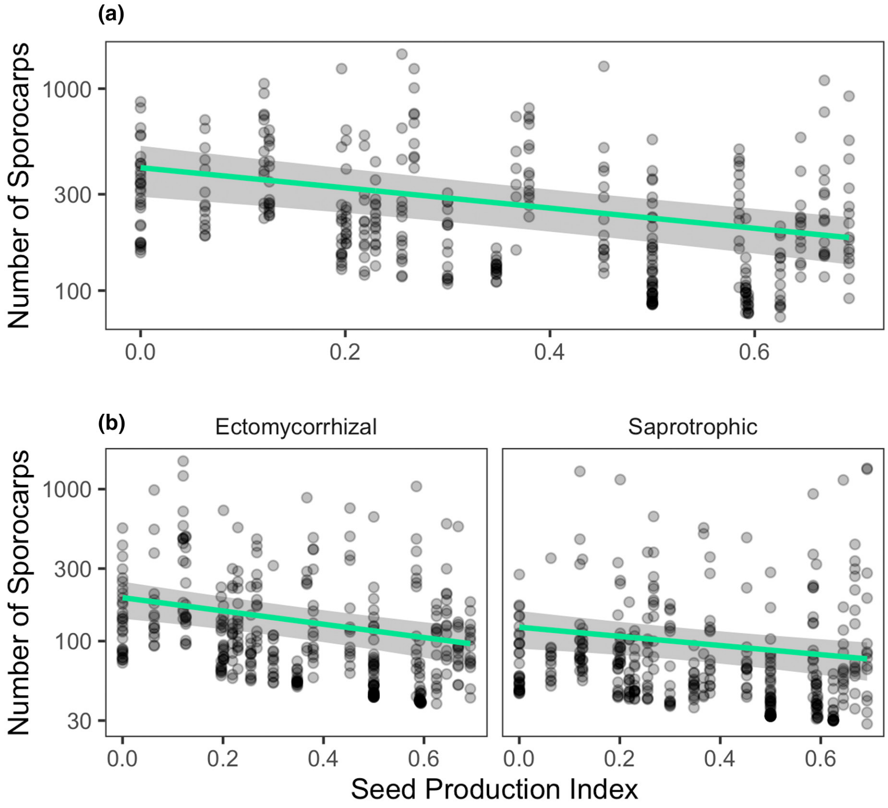

FIGURE 2 Relationship between beech seed production and (a) total fungal sporocarp production and (b) guild-level sporocarp production from 1977 to 2006. Points represent residual variation in sporocarp production after accounting for variation arising from mean annual precipitation and mean annual temperature. The green line represents the mean line estimated for the relationship between beech seed production and sporocarp production predicted via negative binomial multiple regression. The shaded intervals represent 95% confidence intervals around the mean lines.

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to 26 species (18.69–35.27 per 100 m^2 year^{-1}). Shannon-Weiner diversity was also negatively associated with seed production (-0.57 ± 0.24 per unit seed production, $z = -2.331$, $p = 0.022$), positively related to temperature ($0.35 \pm 0.07\,^{\circ}\mathrm{C}^{-1}$, $z = 4.731$, $p < 0.001$) and positively related to precipitation ($0.27 \pm 0.13\,\mathrm{mm}^{-1}$, $z = 2.035$, $p = 0.042\,\mathrm{mm}^{-1}$; Figure S2).

At the guild-level, sporocarp production was negatively associated with seed production among both ectomycorrhizal and saprotrophic fungi (ectomycorrhizal: -1.01 ± 0.22 log(sporocarp count) per unit seed production, $z = -4.625$, $p < 0.001$; saprotrophic: -0.69 ± 0.22 log(sporocarp count) per unit seed production, $z = -3.18$, $p = 0.001$). The relationship between seed production and sporocarp production trended more negative for ectomycorrhizal fungi, compared to saprotrophic fungi, although this was not significant (-0.31 ± 0.30 log(sporocarp count) per unit seed production, $z = -1.041$, $p = 0.298$). Ectomycorrhizal sporocarp counts declined by 50%, on average, from 193 sporocarps (95% CI: 193.11–96.16 per 100 m^2 year^{-1}) with lowest seed production to 96 sporocarps per 100 m^2 year^{-1} (95% CI: 72.50–127.54 per 100 m^2 year^{-1}) with greatest seed production, at mean temperature and precipitation. Saprotrophic sporocarp production declined by 38%, on average, from 123 sporocarps per 100 m^2 year^{-1} (95% CI: 93.39–163.13 per 100 m^2 year^{-1}) with lowest seed production to 76.42 sporocarps per 100 m^2 year^{-1} (95% CI: 57.60–101.38 per 100 m^2 year^{-1}) at highest seed production (Figure 2b).

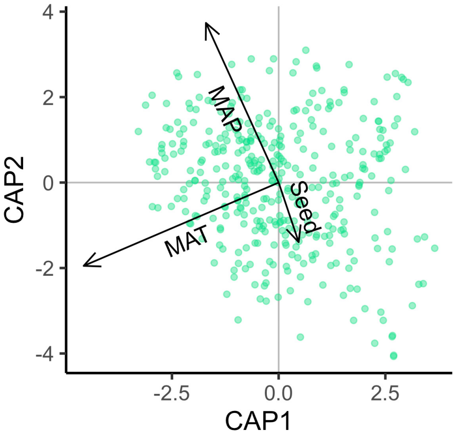

FIGURE 3 Distance-based redundancy analysis showing the relationships between fungal sporocarp community composition and mean annual precipitation (MAP), mean annual temperature (MAT) and beech seed production (Seed).

At the species level, out of the 280 ectomycorrhizal and saprotrophic species that fruited adequately to fit models, 27 species (10%) were significantly less likely to produce fruitbodies as beech seed production increased (z score < -1.96; Figure 4). These species produced 29% of all the fruitbodies recorded at the fungal reserve ($n = 30{,}918$). One terrestrial saprotrophic fungal species (*Gymnopus ocior*) was more likely to be observed as beech seed production increased (z score > 1.96, $n = 189$). Across guilds, however, there were no significant differences in the proportion of species with significant associations with beech seed production (Fisher's exact test, $p = 0.786$): 15/172 (9%) of ectomycorrhizal fungal species and 12/108 (11%) of saprotrophic fungal species were significantly less likely to produce fruitbodies during a mast seeding event (Figure 4). The top 25 most abundant species and information about their relationship with beech seed production is presented in Table 1. Among ectomycorrhizal fungi, neither potential nitrophobicity, mycelial hydrophobicity, nor extraradical mycelial exploration type explained species' fruiting response to masting (Fisher's exact test, $p = 0.32$; $p = 0.88$, $p = 0.96$).

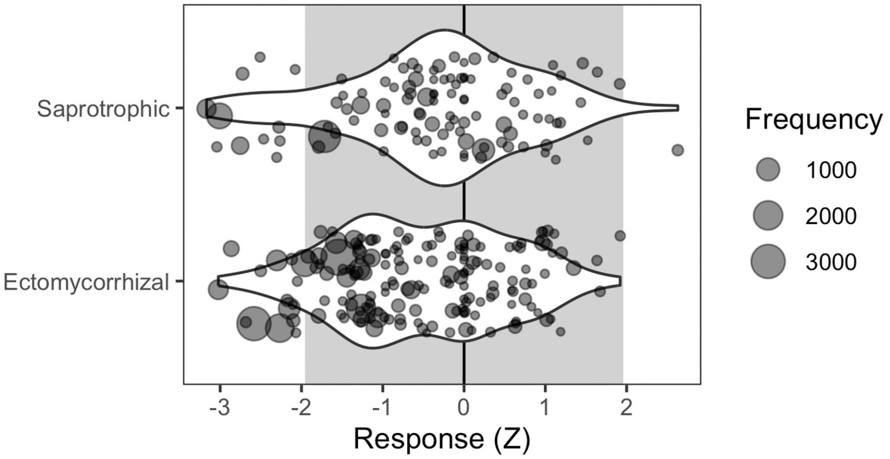

FIGURE 4 Variation in fungal species' relationships with beech seed production derived from multiple logistic regression models. Each point represents the z score associated with the modelled relationship between one species' presence and beech seed production from 1977 to 2006. The shaded interval shows the range of non-significant z scores using an alpha level of 0.05 (cutoffs: −1.96, 1.96). Point size corresponds to the total number of presences or the frequency of observation for a species.

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TABLE 1 Top 25 most abundant fungal species observed at La Chanéaz, with reference to their total abundance (Total Fruitbodies), ecological guild (Guild), whether they showed a significant association with European beech seed production (Association: Seed Production), their habitat (Habitat, broadleaf and/or conifer).

Species	Total Fruitbodies	Guild	Association: Seed production	Habitat	Exploration type	Nitrophobicity
Cortinarius caperatus	3399	Ectomycorrhizal	Not	Broadleaf/Conifer	Medium-distance fringe	Nitrophobic
Cortinarius flexipes	1767	Ectomycorrhizal	Not	Broadleaf/Conifer	Medium-distance fringe	
Craterellus cornucopioides	8634	Ectomycorrhizal	Negative	Broadleaf	Short-distance delicate	
Craterellus tubaeformis	1702	Ectomycorrhizal	Not	Conifer	Short-distance delicate	Nitrophobic
Hygrophorus eburneus	1759	Ectomycorrhizal	Negative	Broadleaf	Contact	
Inocybe petiginosa	1003	Ectomycorrhizal	Not	Broadleaf	Short-distance delicate	
Laccaria amethystina	12,073	Ectomycorrhizal	Not	Broadleaf/Conifer	Short-distance delicate	
Laccaria laccata	1627	Ectomycorrhizal	Not	Broadleaf/Conifer	Short-distance delicate	Tolerant
Lactarius blennius	2846	Ectomycorrhizal	Negative	Broadleaf	Medium-distance smooth	
Russula cyanoxantha	935	Ectomycorrhizal	Not	Broadleaf/Conifer	Contact	Tolerant
Russula fellea	1330	Ectomycorrhizal	Negative	Broadleaf	Contact	
Russula nobilis	2848	Ectomycorrhizal	Not	Broadleaf	Contact	
Russula ochroleuca	5530	Ectomycorrhizal	Negative	Broadleaf/Conifer	Contact	Tolerant
Xerocomellus chrysenteron	2475	Ectomycorrhizal	Negative	Broadleaf/Conifer	Long-distance	
Clitocybe gibba	1859	Saprotrophic	Not	Broadleaf/Conifer		
Entoloma rhodopolium	927	Saprotrophic	Not	Broadleaf	Medium-distance smooth	
Gymnopus confluens	1115	Saprotrophic	Not	Broadleaf/Conifer		
Gymnopus dryophilus	1641	Saprotrophic	Negative	Broadleaf/Conifer		
Hypholoma fasciculare	7209	Saprotrophic	Not	Broadleaf/Conifer		
Kuehneromyces mutabilis	6946	Saprotrophic	Not	Broadleaf/Conifer		
Mycena galopus	1353	Saprotrophic	Negative	Broadleaf/Conifer		
Mycena pura	3154	Saprotrophic	Negative	Broadleaf/Conifer		
Pholiota squarrosa	848	Saprotrophic	Not	Broadleaf/Conifer		
Rhodocollybia butyracea	6242	Saprotrophic	Not	Conifer		

Note: For ectomycorrhizal fungi, exploration type and association with atmospheric nitrogen deposition (nitrophobicity), if known, is included.

DISCUSSION

Our findings suggest that both the magnitude of fungal sporocarp production and sporocarp community composition are tightly linked to interannual variability in overstory tree seed production. Specifically, the highest level of annual seed production in European beech was associated with a 55% reduction in total fungal sporocarp production. High seed production in beech was also associated with reduced fungal sporocarp species richness and diversity as well as shifts in community composition. Together, this pattern is consistent with the hypothesis that tree investment in a mast seed crop decreases resource availability to fungi, limiting fungal reproductive investment. Although the magnitude of ectomycorrhizal sporocarp production was marginally more negatively related to seed production than in saprotrophic fungi, both guilds showed reduced fruiting in mast years. This finding suggests that the relationship between interannual variability in seed production and fungi extends beyond the ectomycorrhizal fungal community, highlighting the dependence of multiple guilds of soil fungi on trees (Koide et al., 2014). Indeed, similar proportions of ectomycorrhizal and saprotrophic fungal species had significant relationships with seed production.

Our findings are consistent with the causal hypothesis that mast seeding temporarily depletes tree and soil resources, resulting in reduced fungal fruiting. However, as an observational study, it is important to consider alternate explanations of the negative correlation between annual seed production and fungal fruiting. First, it could be imagined that both fungal fruiting and seed production could respond to the same set of environmental drivers (environmental covariation).

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In beech, however, this is unlikely because beech seed crops are strongly predicted by high temperatures in July in the year preceding seed production (Y-1) and low July temperatures in the year preceding that (Y-2; Bogdziewicz et al., 2023). Temperature at these lagged time periods has not been shown to affect fungal sporocarp production, which is more strongly associated with recent weather conditions (Sato et al., 2012). Collado et al. (2018) did find that saprotrophic sporocarp production was linked to tree growth 2 years previous, however, suggesting that lagged environmental conditions may play a role in fungal fruiting. However, the direct role of lag effects to fruiting-year carbon availability, versus indirect effects to other aspects relating to fungal biology (e.g., root dynamics, compositional interactions, spore germination or vegetative growth) that then impact future fruiting, remains, at this point, unexplored. Second, it may be possible that high fungal sporocarp production could inhibit masting in non-mast years (reversed causation). Again, this is unlikely because beech mast events are largely determined by the number of flower primordia produced, an event that happens over a year prior to the seed crop and fungal fruiting event (Gruber, 2003). It is possible that high fungal biomass or production, indicated by high sporocarp production, could limit plant nutrient availability and thereby primordia production through nutrient immobilization (Näsholm et al., 2013; Tanentzap et al., 2012), but we did not find a relationship between seed production the year previous and fungal fruiting (data not shown). Finally, we note that seed production data were inferred from many historical records instead of measured at the site. This introduces uncertainty in our analysis, since masting behaviour at the site may have differed somewhat from the record we assembled. We stress, however, that masting is by definition synchronous, and at large geographic scales (Koenig & Knops, 1998; Vacchiano et al., 2017). Taken together, although the results support our causal hypothesis, we maintain that these findings are correlative and require further investigation.

Analysis of fungal sporocarp community composition revealed that mean annual precipitation and seed production were oppositely related to community composition (Figure 3). This suggests that fungal community composition during a dry year resembled that during a year of high seed production. During a drought year, microbial activity is stymied by reduced water availability (Schimel, 2018). Our finding could indicate that high seed production necessitates greater water uptake from soil, resembling drought conditions. The effects of mast seeding on soil conditions and processes, however, have rarely been studied (Zackrisson et al., 1999), rendering this supposition speculative. Long-term monitoring of soil moisture and nutrient availability in forests where masting is also recorded could improve understanding of the links among soil resource availability, masting and fungal community composition. This monitoring is particularly important in the context of shifting climatic conditions, which have already been shown to negatively affect the magnitude of masting in European beech forests (Bogdziewicz et al., 2020, 2023). If, for example, masting frequency decreases, but the same forests experience more frequent droughts, it seems likely that the interannual community shifts we observed here may be a harbinger of future fungal sporocarp composition in European beech forests.

Among ectomycorrhizal fungi, we evaluated whether differences in fungal traits putatively associated with resource demand explained whether species showed significant relationships with seed production. Previously, ectomycorrhizal species with prolific, highly ramified and hydrophobic exploratory mycelia have been assumed to be more costly to their hosts because they purportedly require more carbon and nutrients to sustain vegetative tissue production (Karst et al., 2021; Lilleskov et al., 2011). This logic has been used to explain why many fungal species with these convergent traits are sensitive to nitrogen deposition (Lilleskov et al., 2011); nitrogen deposition is assumed to decrease photosynthate availability to ectomycorrhizal fungi and, hence, limit those that require substantial carbon. This explanation, in turn, has reified a link between species' nitrophobicity and carbon cost (Lilleskov et al., 2019). Here, we found evidence that mast seeding may reduce resource availability to ectomycorrhizal fungi, as evidenced by decreased sporocarp production. Yet, the mycelial traits associated with high resource demand did not explain the species-level relationships with mast seeding. For example, similar proportions of species showed significant relationships with seed production across extraradical mycelial exploration types, groups with hydrophobic versus hydrophilic extraradical mycelia, and putative nitrophobicity. Among the 15 ectomycorrhizal species significantly negatively associated with seed production (Table 1), both species with hydrophobic and hydrophilic exploratory hyphae were present. Additionally, among the taxa with significant associations with beech seed production was *Russula ochroleuca*, a putatively nitrotolerant species (van Strien et al., 2018; van der Linde et al., 2018; Table 1). These findings suggest that current traits that have been previously linked to resource demand in ectomycorrhizal fungi are not sufficient to describe species' sensitivity to resource scarcity across more diverse situations of carbon availability (Bidartondo et al., 2001; Jörgensen et al., 2023; Wallander, 1995).

Our findings open a novel line of research at the intersection of mast seeding and fungal ecology. In general, we speculate that masting may have wide-ranging effects on soil processes, though these have only rarely been explored (Zackrisson et al., 1999). These hypotheses could be tested by monitoring soil moisture levels, rates of nutrient cycling and hyphal production and turnover

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during mast and non-mast years or by experimentally altering mast crops or root connections within the soil. Similarly, it would be useful to explore the geographic, taxonomic and environmental scope of the connection between masting and fungal fruiting. This effort will be aided by widespread records of long-term seed production (e.g. Hacket-Pain et al., 2022) and comparable multi-decadal sporocarp surveys (e.g. Bonet et al., 2012; Sato et al., 2012; van Strien et al., 2018). Additionally, we suggest that quantification of sporocarp production by other fungal guilds may also reveal important insights about the scope of masting effects. For example, we hypothesize that fungi that are pathogens on living trees, such as the 'humongous fungus', *Armillaria mellea*, may also experience significant decreases in sporocarp production in mast years, while fungi living on dead trees, i.e. wood decay fungi, may have no relationship with masting-related resource shifts. Finally, assessing how masting is related to the size, biomass and stoichiometry of sporocarps would further clarify how changes in resource availability impact fungal fructification (Hobbie et al., 2021). Answering this latter question might be possible using careful measures of herbarium specimens (Andrew et al., 2019), which provide an underappreciated resource for studies of fungal responses to altered environmental conditions.

CONCLUSIONS

This study is the first to evaluate the potential linkage between mast seeding and fungal sporocarp production. We have demonstrated a strong inverse relationship between beech seed production and fungal sporocarp production, diversity and species richness. We have also shown that ectomycorrhizal and saprotrophic fungi show comparable declines in fruitification with increasing beech seed production, despite key differences in their ecology. Mast seeding has been linked to the abundance and feeding habits of numerous animals that consume seeds or have trophic links to those that do (e.g. Ostfeld et al., 2000; Stephens et al., 2019), resulting in a 'rhythm' to many aboveground forest processes (Pesendorfer et al., 2021). Our findings suggest that this 'rhythm' extends belowground, amplifying the ecological significance of masting. This rhythm may be disrupted as climate change alters the frequency and magnitude of masting (Bogdziewicz et al., 2020, 2023). The results of our study also suggest that masting may create a broad 'pull' on soil resources that significantly alters resource availability for fungal (and likely other microbial) guilds. Indeed, the composition of the sporocarp community during a mast year resembled that during drought conditions. Whether this pattern emerges across diverse forests remains unknown, as do the proximal mechanisms driving decreased sporocarp production. We argue that mast seeding may be an underappreciated driver of fungal activity and call for further research.

AUTHOR CONTRIBUTIONS

TJM and ISP conceived of the project. CJA performed data curation. TJM performed statistical analyses with input from ISP, HK, CJA and PGK. TJM wrote the manuscript with input from ISP, HK, CJA and PGK.

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DATA AVAILABILITY STATEMENT

The data supporting these results and R code are available at DRYAD (https://doi.org/10.5061/dryad.fxpnvx10p).

ORCID

Talia J. Michaud https://orcid.org/0000-0002-7295-6808

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