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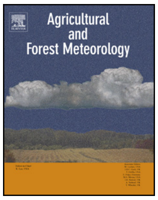

Long-term monitoring reveals a highly structured interspecific variability in climatic control of sporocarp production

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ABSTRACT

Understanding factors triggering fungal sporocarp productivity responses to climate at an individual species level is critical to predicting future species composition and abundance under global climate change scenarios. Different climatic responses at a species level may lead to shifts in species turnover and in the relative contributions of different species, which may in turn have strong impacts on community functional attributes. We used sporocarp production data compiled over 15 years of weekly sampling during the mushroom fruiting season in a continental Mediterranean climate pine forest to estimate: (i) the interspecific variability on the climatic factors constraining fungal sporocarp productivity, (ii) the relationship of this variability linked to mushroom phenology and trophic guilds, and (iii) the impact of different species responses on sporocarp community composition and diversity under projected climate change scenarios. Fungal fruitbody production was closely correlated with climatic conditions throughout the year, indicating that sporocarp development may be controlled by processes occurring well before the fruiting season. The large interspecific variability in the climatic factors controlling sporocarp production was highly structured with differences inlength of the temporal window controlling this process, and the timing of the summer-autumn rainfall climatic signal being the most relevant factors. Climatic response was unrelated to fungal phenology or trophic guild. When individual models are applied to future climate scenarios (2021–2080), they predict a decrease in total sporocarp productivity, which agrees with community based models, as well as a shift in community composition, leading to less species-diverse assemblages.

1. Introduction

Mediterranean pine forests are a hot spot of fungal biodiversity, harboring a large number of endemic species (Tedersoo et al., 2014). Ectomycorrhizal fungi diversity peaks at intermediate latitudes and under low rainfall (Tedersoo et al., 2014,2012), a phenomenon that may reflect the fact that they evolved with Pinaceae hosts at higher latitudes, which could have led to them being inferior competitors under tropical conditions (Tedersoo and Nara, 2010). Enhanced water acquisition provided by ectomycorrhizal symbionts is critical for tree performance in drought-prone Mediterranean environments (Vásquez Gassibe et al., 2015), but some ectomycorrhizal fungi taxa are also of high economic value in their own right, such as *Tuber* spp., *Amanita caesarea* (Scop.) Pers. and *Lactarius deliciosus* (Boa, 2004; De Román and Boa, 2006). In contrast to the high abundance of the ectomycorrhizal guild, saprophytic species are relatively scarce here compared to more mesic environments (Baptista et al., 2015; Martínez-Peña et al., 2012; Tedersoo et al., 2014), probably as a consequence of dry conditions limiting fungal activity in the more superficial soil levels in which saprotrophs dominate (Lindahl et al., 2007), and by the fact that mycorrhizal

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fungi and saprotrophs play opposing roles in soil organic matter formation (Averill et al., 2014; Clemmensen et al., 2013).

Mushroom production is characterized by a high interannual variability that is closely linked to variations in weather conditions from one year to the next (Ágreda et al., 2014; Boddy et al., 2014). Mushrooms generally flourish under warm and wet conditions, but the constraining factor of mushroom productivity differs depending on regional climate characteristics. In temperate environments where soil humidity is maintained throughout the year, mushroom yields are positively related to mean temperature, with rainfall only playing a secondary role (Büntgen et al., 2012b, 2013; Sato et al., 2012). In contrast, under Mediterranean climate, rainfall is the major factor determining fungal productivity (Büntgen et al., 2012a; Salerni et al., 2002), being essential for the initiation of fungal fructification (Ágreda et al., 2015; Martínez de Aragón et al., 2007; Salerni et al., 2002), and this is inhibited during dry summers (Pinna et al., 2010). However, under continental Mediterranean climate, where low temperatures limit biological activity during a large part of the year, fungal productivity seems to be limited both by rainfall and temperature (Ágreda et al., 2015).

Changes in climatic conditions associated with global warming are altering the fruiting patterns of mushrooms, fungal productivity (Büntgen et al., 2012b; Gange et al., 2011; Sato et al., 2012; Yang et al., 2012), fruitbody size (Büntgen et al., 2015), geographical distribution (Kauserud et al., 2010; Wollan et al., 2008) and phenological patterns (Diez et al., 2013; Gange et al., 2007; Kauserud et al., 2008, 2010, 2012; Mattock et al., 2007; Yang et al., 2012). Boddy et al. (2014) showed that in general fruiting phenology is changing, with extended fruiting seasons, shifting hosts, and increasing variability in annual yields. Most of this research has been performed by evaluating productivity or abundance at a community level (Büntgen et al., 2012a, 2012b, 2013; Boddy et al., 2014; Kauserud et al., 2008; Diez et al., 2013; Gange et al., 2013; Sato et al., 2012). Less effort has been devoted to functional guilds (Ágreda et al., 2015; Diez et al., 2013; Kauserud et al., 2012; Sato et al., 2012) and individual taxa response has been almost entirely restricted to edible species with high economic value (Bonet et al., 2008; Büntgen et al., 2011, 2012a; Hernández-Rodríguez et al., 2015; Martínez de Aragón et al., 2007; Martínez-Peña et al., 2012; Mihail et al., 2007; Vaario et al., 2015; Yang et al., 2012).

Fungal community response to environmental change depends on the often contrasting environmental constraints of multiple individual species and their respective life-histories (Hawkes and Keitt, 2015). Diversity of limiting factors, species-specific plasticity and adaptative potential (Malcolm et al., 2008) may cause heterogeneous responses determining changes at community level, with shifts in species relative abundance and species turnover (Deslippe et al., 2011). Changes in fungal community characteristics may have strong impacts on their functional attributes: modifying carbon cycling (Clemmensen et al., 2013), altering the bacterial community (Nuccio et al., 2013), and disrupting mycorrhizal interactions (Hawkes et al., 2011) with effects cascading up to higher trophic levels (Classen et al., 2015; Walther, 2010). Thus, evaluating fungal species response to climatic variability is critical in order to understand soil response to global change.

Mushroom abundance has been used as surrogate for fungal abundance for saprotrophic and ectomycorrhizal groups (Boddy et al., 2014). Although this approach has limitations compared with the direct measurement of fungal presence in the soil using molecular techniques, it allows larger areas to be sampled with higher frequency and replication, and provides accurate taxonomic information, and is therefore considered to be a valid alternative (Zambonelli et al., 2012). Moreover, these records are an excellent tool to help evaluate the effect of interannual variability in mushroom productivity. Our aim was to achieve a better understanding of the climatic control of fungal productivity processes and its interspecific variability, and to achieve this we analyzed a long-term data set of fungal productivity, compiled over 15 years of weekly sampling during the mushroom fruiting season of a *Pinus pinaster* Ait. forest growing under a continental Mediterranean climate in central Spain. This data set allows us to formulate several basic questions about the behavior of epigeous fungal species and their productivity under Mediterranean climatic conditions: (i) How do the climatic factors that constrain fungal productivity, estimated through mushroom production, vary across the different species?, (ii) Is this variability linked to mushroom phenology and/or trophic guilds?, and (iii) How might projected climate change scenarios affect sporocarp community composition and diversity when individual species responses are considered?

2. Material and methods

2.1. Study area

Research was conducted in the south of the province of Soria, in the Castilla y León region of central Spain. Altitude ranges from 1000 m to 1200 m a.s.l., and climate is subhumid Mediterranean but affected by continental features. Records of mean monthly temperatures and total monthly precipitation (P) were obtained from the Soria meteorological station (41°46′N, 02°28′W; 1082 m altitude, 40 km away) for the period 1948–2011. The data was carefully quality-controlled and homogenized using relative methods by means of neighboring stations. Annual mean temperature is 10.4 °C, the coldest month being January (mean daily minimum temperature of −1.8 °C) and the warmest July (mean daily maximum temperature of 28.1 °C). Average annual rainfall is 556 mm, with a summer drought period typically occurring from mid July to August (Fig. 1). We calculated monthly water balance (WB) as the difference between precipitation and atmospheric evaporative demand (AED). We estimated the AED by means of the Reference Evapotranspiration (ETo) Hargreaves formulation (Hargreaves and Samani, 1985). This is based on maximum and minimum temperature data and provides accurate estimates of the AED in Spain (Vicente-Serrano et al., 2014).

Soils in the study area are arenosols and regosols developed over Tertiary and Quaternary sands, which are characterized by an excessive permeability and low nutrient content. Vegetation is dominated by *Pinus pinaster*. Understory is formed by different shrubs (*Cistus laurifolus* L., *Juniperus communis* L., *Erica arborea* L., *Calluna vulgaris* (L.) Hull.) and *Quercus pyrenaica* Willd. resprouts. The rotation of *P. pinaster* is 80 years, with trees felled in two phases. Until the 1970s, resin was the main product of these forests, but the decline of its market led to a shift towards wood production. Recently, mushroom harvesting has become a major activity, focused primarily on *Lactarius deliciosus*, but also including *Hygrophorus* (Fr.) and *Tricholoma* (Fr.) Staude species.

2.1.1. Sampling design

We sampled fungal production in an 11,000 ha *Pinus pinaster* forest. In order to avoid tree stand age effects, we performed a random stratified sampling design. On a 1:20,000 scale map, we superimposed a 1-ha grid, classifying every cell into one of seven age classes, according to the forest management plan: 0–10 (regenerating but with a proportion of parent trees), 11–20, 21–40, 41–60, 61–90, and older than 90 years old. Every grid cell was numbered and cells corresponding with every age class were selected randomly; three plots per age class were chosen, providing a total of 21 sampling plots. Selected cells were located in the field and were checked to confirm whether they met the strata assumptions, and if they did not, another random cell was selected. Within each