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Drought-induced changes in the phenology, productivity and diversity of Spanish fungi

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ARTICLE INFO

Article history:
Received 24 November 2014
Revision received 11 March 2015
Accepted 19 March 2015
Available online 27 May 2015
Corresponding editor:
Jacob Heilmann-Clausen

Keywords:
Dendroecology
Climate change
Ecosystem functioning and productivity
Edible mushrooms
Iberian Peninsula
Mediterranean drought
Non-wood forest products

ABSTRACT

Mushrooms are amongst the most important of non-timber forest products, with growing economic value in many rural areas of the Mediterranean region. At the same time, the effects of climate variability on fungal ecology and productivity are insufficiently understood, because the belowground life cycle of fungi is mediated in many different ways and observational field surveys at the community level are generally too short. Here, we assess records of 48, 348 mycorrhizal and saprotrophic fungal fruit bodies that were recorded at weekly intervals between 1995 and 2013 in Pinar Grande, the largest Spanish Scots pine forest. Autumnal fruiting was delayed by one week after 2004 compared with the period before, the mean annual number of sporocarps dropped from 2 880 to 2 045, and mean species richness declined from 55 to 51. Trends in the phenology and productivity of *Boletus edulis* and *Lactarius* spp., the most profitable edible species, were associated with decreasing Jul.–Sep. precipitation totals, whereas the mean fruit body weight of *B. edulis* significantly increased from 71 to 123 g (pre and post 2004). In tandem with declining Spanish tree growth and truffle harvest since the 1970s, this study reveals a strong dependency of drought-prone Iberian forest ecosystem productivity on hydroclimatic variability. In light of a predicted drier Mediterranean climate, our results further emphasize the importance of long and well-replicated field inventories at high spatio-temporal resolution for informing forest service and management strategies, as well as gastronomy and tourist industries.

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http://dx.doi.org/10.1016/j.funeco.2015.03.008

Introduction

Wild edible and medicinal mushrooms are among the most important non-timber forest products (Hall *et al.* 2003; Boa 2004; Wang & Hall 2004), with growing economic value in many rural areas of Spain (Bonet *et al.* 2008, 2014; Palahí *et al.* 2009; Voces *et al.* 2012; Martínez-Peña *et al.* 2011; Aldea *et al.* 2012; Latorre 2014). The drought-prone Mediterranean region, and particularly the Iberian Peninsula, contains several gastro-mycological hotspots, such as the Périgord black truffle (*Tuber melanosporum*) orchards in northeastern Spain (Samils *et al.* 2003, 2008; Olivera *et al.* 2011, 2014a, b, c; Büntgen *et al.* 2015), and the southern foothills of the Pyrenees where wild *Boletus edulis* (ceps or porcini) and *Lactarius* spp. (saffron milk caps) reach highest economic value (De Roman & Boa 2004; Martínez de Aragon *et al.* 2007; Voces *et al.* 2012).

In Castilla and León, an autonomous community of ~9.5 million ha (with 4.5 ha of forested area) in north-central Spain, the average gross annual production of edible wild mushrooms – excluding truffles – is ~34 000 tons, equivalent to ~80 million € (Martínez-Peña *et al.* 2011). The harvesting of a wide range of edible mushroom species, including *B. edulis*, *Lactarius deliciosus*, *Amanita caesarea* and *Cantharellus cibarius* has been gaining more attention among the local population since the 1950s. Today, a total of 35 small agro-food companies are involved in processing and trading mycological products, such as fresh, dried and frozen mushrooms and pâtés-oils-cheeses made of mushrooms. Moreover, myco-tourism represents an important source of revenue, particularly for rural societies in the numerous forested areas across north-central Spain. To better manage and control the commercial usage of mycological resources in this part of the Iberian Peninsula, mushroom harvesting is now controlled in a region >400 000 ha (www.micocyl.es). This regulation aims to establish and support a sustainable myco-tourism industry (Martínez-Peña *et al.* 2011).

Despite these recent moves toward regulation, fungal resources have not yet been sufficiently integrated into multi-objective forest management plans (Martínez-Peña *et al.* 2012a, b), and effects of climate variability on fungal ecology are still poorly understood (Boddy *et al.* 2014). The role that fungi may play in ecosystems responding to global change is particularly debatable for the subtropics and warm temperate biomes (Mohan *et al.* 2014), because datasets with adequate temporal and spatial coverage are scarce. The absence of high-resolution, long-term monitoring programs limits the ability to detect climatic and management effects on belowground fungal activity and ephemeral fruit bodies (mushrooms). In fact, the belowground life cycle of fungi is mediated in numerous different ways, and time-series of observational field surveys at the community level are generally too short and of limited geographical distribution (Mohan *et al.* 2014). Cross-disciplinary efforts will therefore become exceptionally useful to adapt silvicultural and agricultural management plans (and services) for predicted climate change (Büntgen *et al.* 2015). In addition, the relationship between environmental factors including climate and mushroom fruiting patterns (Büntgen *et al.* 2012b; Diez *et al.* 2013), as well as host phenology is highly complex (Büntgen *et al.* 2013b). Unravelling biotic (host plants and fungal partners), abiotic (climate, pollution, land cover) and combined edaphic drivers of mushroom fruiting has proven scientifically useful (Gange *et al.* 2007; Kauserud *et al.* 2012, 2013), but also challenging (Hall *et al.* 2003; Kauserud *et al.* 2008).

These shortfalls in our understanding of fungal ecology appear particularly urgent since instrumental observations show that most of the Mediterranean basin has been drying since the 1970s (Büntgen *et al.* 2012a, 2013a, 2015; Luterbacher *et al.* 2012). State-of-the-art model simulations further predict a continuation of this trend in response to rising concentrations of greenhouse gases (Kelley *et al.* 2012; Hoerling *et al.* 2012; Barkhordarian *et al.* 2013). Indications of ongoing and projected climate change are strongest for the Iberian Peninsula (Büntgen *et al.* 2012a, 2013a), where future rates of temperature increase and precipitation decrease will most likely accelerate aridification (Fischer & Schär 2010; Xoplaki *et al.* 2012). Ecological consequences are manifold and may include: biodiversity loss (Carnicer *et al.* 2011; Anderegg *et al.* 2013), phenological alteration (Peñuelas *et al.* 2002), species-specific range shifts (Peñuelas *et al.* 2007), decreasing forest productivity (Martínez-Vilalta & Piñol 2002; Jump *et al.* 2006; Galiano *et al.* 2010; Linares & Camarero 2012), as well as reduced carbon accumulation (Vayreda *et al.* 2012). These effects will be accompanied by socio-economic costs related to the transition from traditional timber harvest to a more diversified utilization of non-woody forest products and resources (Hanewinkel *et al.* 2013; Hanewinkel & Peyron 2014). Drought risk and water resource management strategies will thus become essential to inform future public policy and scientific activity (Courtenay-Botterill & Hayes 2012). Specifically related to the province of Soria where this study is located, it is well known that the annual stem growth of most forest trees, including pine, oak and juniper, is highly sensitive to summer drought (Büntgen *et al.* 2012a, 2013a, 2015; Esper *et al.* 2014). Similar observations on the increasing relevance of summer water stress for the functioning and productivity of forest ecosystems have been made for many species across most of the Iberian Peninsula (Rozas *et al.* 2011; Galván *et al.* 2014, 2015; Camarero *et al.* 2015).

Here, we aim to improve understanding of long-term changes in Mediterranean fungal ecology and to assess the role of climate variation in shaping the observed patterns. We use a database of 48 348 wild fungal fruit body counts that were recorded at weekly intervals between 1995 and 2013 in the 'Pinar Grande' fungal reserve (hereinafter PG), the largest Spanish Scots (*Pinus sylvestris*) pine forest. We compare interannual to decadal fluctuations in the phenology, productivity and diversity of this unprecedented inventory of fungi with local to regional-scale climate variability, as well as rates of nearby tree growth and the Spain-wide truffle harvest. We discuss the importance of well-replicated and highly resolved field inventories, which are still underrepresented in drought-prone arid environments. Focusing on the hydro-climatic dependency of Iberian forest ecosystems and their non-woody fungal products, we define priorities for silvicultural service and management strategies under predicted Mediterranean drying.