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

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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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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.

Material and methods

Study site

Fieldwork was conducted in a natural Scots pine forest in the Central Spanish province of Soria (Fig 1A). The so-called PG forest reserve is situated near the species' southern distribution limit (Fig 1B). As part of the Sistema Ibérico mountain range, this habitat of monospecific and even-aged Scots pine stands is located between ~1 100 and 1 500 m asl (Aldea *et al.* 2012), covers an area of ~12 500 ha, and belongs to the Ebrillos River basin, located at the headwaters of the Duero River. The vegetation comprises meso-hygrophilous heather lands of *Erica vagans* and *E. tetralix* among pastures of *Cespitose gramineae*, mainly *Nardus stricta* on siliceous substrata, such as conglomerates, quartzite and sandstone from the Lower Cretaceous. Soils in the PG reserve are Regosols, Luvisols, Cambisols and Umbrisols (FAO 1998), often altered by anthropogenic intervention such as silvicultural treatment. The pH is markedly acid (4–5), the texture is sandy to sandy loam, with limited water holding capacity and low fertility levels. Site conditions, forest characteristics and dendrochronological features are detailed in Table S1. The semi-arid climate is continental Mediterranean with a mean annual rainfall and temperature of approximately 530 mm and 10.6 °C (Fig 1C), respectively. Although yearly values are fairly moderate, Jun.–Aug. summer precipitation totals of 87 mm and a corresponding mean temperature of 18.7 °C are indicative of frequent summer droughts.

Based on a clear cutting system (Matthews 1989; Madrigal 1994), the forestry management of PG was approved in 1907. The adopted regeneration period is 20 yr with a rotation period of 100 yr (Lucas and Barrio 1996). The applied even-aged silvicultural management consists of strip clear-cutting with soil movement and sowing when necessary, and aims to optimize timber production. In fact, the main forestry exploitation activity is Scots pine timber, followed by the use of pastures for extensive livestock farming, mainly beef cattle, as well as hunting for *Capreolus capreolus* and *Sus scrofa*. Tourism, which has slowly increased during the last decades, has affected the commercial value of picking and the growing number of myco-tourists. Harvesters collect an average of 4.3 kg d^{-1} of *B. edulis* and 25 harvesters km^{-2} d^{-1} are registered in good years (Martínez-Peña 2003).

Mushroom inventory

Since 1995, trained mycologists conducted weekly inventories of mushroom production within 18 geographically distinct plots in PG (Fig 1D, E; Table S1A). This unique setting reflects a random stratified sample by tree age classes: <15 yr, 16–30 yr, 31–70 yr, 71–90 yr and >90 yr. This stratification was possible

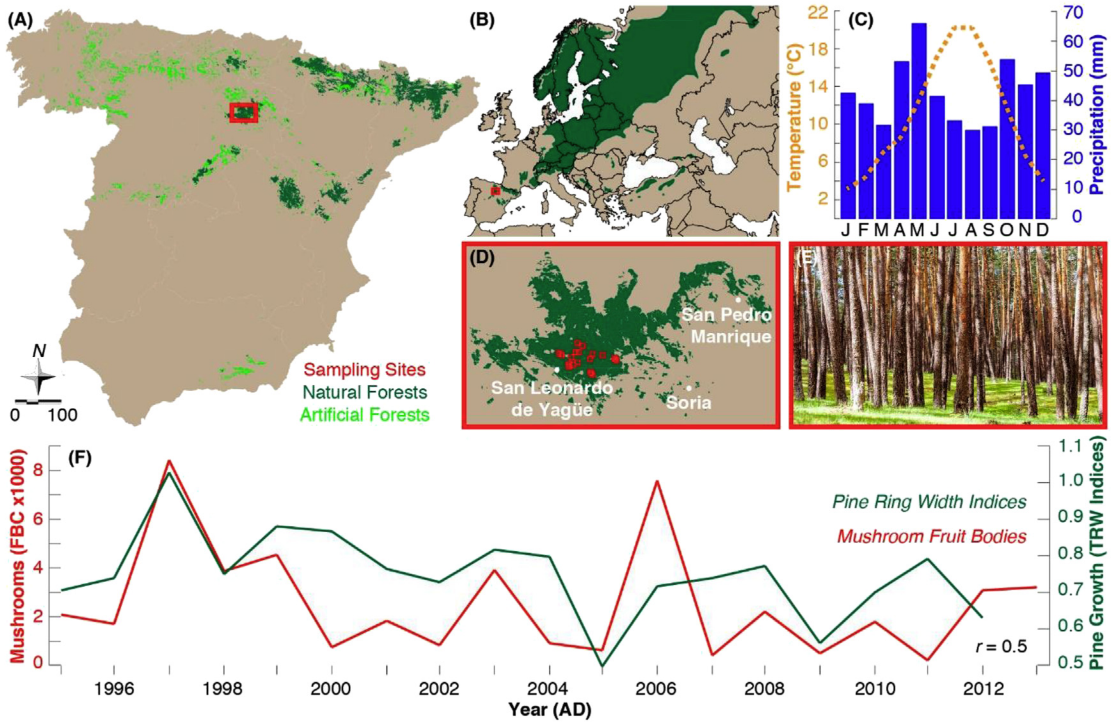

Fig 1 – (A) Spatial distribution of natural and artificial Scots pine forests in Spain, with the red rectangle indicating the PG reserve at 41°53′ E, 2°56′ W and 1 225 m asl. (B) Location of the study site near the southern distribution limit of Scots Pine (http://www.euforgen.org/distribution_maps.html), and (C) a simple climate diagram based on instrumental temperature and precipitation measurements from the nearby Soria station (41°46′30″N, 2°28′59″W′ and 1 082 m asl) from 1976 to 2012. (D) Precise location of the 18 individual fungal plots (red squares) northwest of the regional capital Soria, and (E) a typical image of PG. (F) Year-to-year and longer-term changes in both the mushroom (fruit body counts; red) and forest (pine ring width indices; green) productivity.

due to the clear cutting system used in PG, which produces a mosaic of regular stands organised in space and time. The size and shape of each of the 18 plots was adapted from previous studies (Ohenoja 1989; Kalamees & Silver 1988) that used a rectangular design with a minimum sampling area of 100 m^2. In the case of the PG reserve, permanent 35 × 5 m^2 plots fenced with 2 m-high game-proof netting were established to prevent trespassing by cattle and wild animals, as well as harvesters. Mushroom sampling was restricted to a surface area of 150 m^2, because each plot was subdivided into six 5 × 5 subplots separated by 1 m, which in total represents a sample area of 150 m^2. Environmental factors such as altitude, slope and orientation were recorded for each of the 18 plots (see Table S1 for details).

All fully developed sporocarps between weeks 35 and 50 – corresponding to the main autumnal mushroom fruiting season – were collected, weighed fresh and identified to species level using macro- and/or microscopic characters (following Index Fungorum; http://www.indexfungorum.org) (see Martínez-Peña *et al.* 2012a for details). Fruit bodies were simultaneously collected on a weekly basis in each of the 18 plots between 1995 and present. The spring fruiting season in this region is short and insignificant relative to the autumn, so was not considered in this study. The ongoing mushroom harvesting nor associated trampling is expected to not affect fruit body production (Egli *et al.* 2006).

Long-term average trading and market prices according to regional surveys from commercial mushroom harvesters were estimated for the economically most important species *B. edulis* and *L. deliciosus* (∼7 and ∼6 € kg^{-1}) (Aldea *et al.* 2014; Martínez-Peña *et al.* 2007, 2011). Several quantities were calculated to evaluate intra- and interannual patterns in mushroom fruiting, including accumulated weekly fruit body counts (FBC), fruit body weights (FBW), total fruit body weight (TFW), species diversity (SDV), and the weighted week of appearance (WWA) (Büntgen *et al.* 2012b, 2013b). The WWA was calculated as the sum of the products of calendar weeks and their corresponding counts divided by the total annual fruit body counts, which represent the intra-annual peak of mushroom fruiting. The annual sum of all weekly fruit body counts (FBC) revealed year-to-year changes in mushroom productivity. The three fungal indices (FBC, FBW and WWA) were separately calculated for the two functional guilds of mycorrhizal and saprotrophic fungi (Myc and Sap), and for edible and non-edible species (herein refereed to as Edi and NoE). Additional analyses were performed for the economically most important edible species (*B. edulis* and *Lactarius* spp., with the later including 1,617, 162 and 2 fruit bodies of *L. deliciosus*, *L. quieticolor* and *L. semisanguifluus*, respectively). All indices of fungal production were calculated for two independent early (1995–2004) and late (2004–2013) time periods. Although this technique implies a 1 yr overlap between the two split-periods, it is the best way to have equally long intervals. This simple split period approach is less prone to statistical artefacts due to extreme values located at the margins of a time-series. Mean, standard deviation and standard error were computed for all indices and the two intervals. As an additional test of whether mushroom production can be related to climate variation, univariate and multiple regression models were used to search for combined effects of Jun.–Aug. precipitation and temperature on WWA, FBC and FBW.

Tree-ring assessment

Dendrochronological samples were taken from all individual Scots pines within the 18 forest plots, resulting in a total of 871 ring width cores of 5 mm diameter (Table S1C). Sampled trees ranged in age from 6 to 175 yr, with individual start and end dates between 1837 and 2011 (see Büntgen *et al.* 2013a for further details). Mean segment length (MSL) of all data was 40 yr and mean growth rate (AGR) was 2.16 mm yr^{-1} (Table S1C). After power-transformation (PT; Cook & Peters 1997), the Regional Curve Standardization method was applied to remove non-climatic, biological-induced growth trends (so-called age trends) from the raw ring width measurements (RCS; Esper *et al.* 2003). The pith offset for each sample, i.e., the number of innermost missing rings per core sample, was estimated to ensure an appropriate operation of the RCS method. The RCS technique has been demonstrated to be particularly suitable for growth-climate response analyses and climate reconstructions as it allows lower frequency information to be preserved in the final chronology (Büntgen *et al.* 2008), for which index values were calculated as residuals between the original measurements and their corresponding curve fits. Mean chronologies were computed using a bi-weight robust mean and their variance was stabilized over time (Osborn *et al.* 1997).

In addition to the PG dataset and its subsequent RCS master chronology (PGRCS; containing all 871 samples and using RCS detrending after PT), we also developed two well-replicated datasets and their corresponding master chronologies from nearby maritime pine (*P. pinaster*) and holm oak (*Quercus ilex*) forests, following the same sampling technique and detrending method. These two species are the most relevant conifer and evergreen broadleaf species surrounding PG. A total of 658 samples were collected from the Maritime pine forest 'Almazán' ∼50 km southeast of PG, and 480 samples were extracted from holm oaks, growing ∼20 km southeast of PG. The 'Almazán' forest is located between 950 and 1 200 m asl on arenosols and regolsols developed over Tertiary and Quaternary sands, with moderate acidic reaction (pH 5–7). The holm oak stands are located ∼1 200 m asl on well-drained calcareous bedrock. With its diffuse to semi-ring-porous wood formed between Apr. and Jul. (Barbero *et al.* 1992; Montserrat-Martí *et al.* 2009), holm oak is the main host species for the Périgord black truffle (*T. melanosporum*) across the western Mediterranean region. Climatic conditions of the maritime pine and holm oak forests are similar to those previously described for PG.

Warm season (Apr.–Sep.) and summer (Jun.–Aug.) averages of gridded (0.25° × 0.25°) temperature means, precipitation totals and the diurnal temperature range (E-OBS v10.0; updated from Haylock *et al.* 2008), extracted over the area 41.5–42.0° N and 2.5–3.0° W, were used to calculate climatological trends over two independent early (1995–2004) and late (2004–2013) split periods.

To unravel the ecological complexity of our dataset and to best visualize the various direct and indirect relationships between fungal phenology, productivity and diversity, as well as tree growth and climate, non-metric multidimensional scaling (NMDS) was applied (Rabinowitz 1975). NMDS is an explanatory or ordination method whose purpose is to provide a visual representation of the pattern of proximities (i.e. similarities or distances) among a set of objects. More related or similar objects are depicted near to each other and dissimilar objects are found further apart from each other. One single NMDS run, accounting for the ranking of distances between objects, was applied for all individual parameters.

Results

Comprising a total of 48 348 weekly resolved and precisely located counts of epigeous sporocarps of macromycetes between 1995 and 2013, the PG fungal inventory provides a unique dataset for the analysis of long-term changes in the phenology, productivity and diversity of mushrooms under Mediterranean climate conditions. This exceptional compilation includes 33 396 mycorrhizal and 14 952 saprotrophic mushroom counts of 98 and 62 species and 27 and 39 genera, respectively. These numbers equal 12 581 edible and 35 767 non-edible specimens, with the first group including 1 586 and 1 617 *B. edulis* and *Lactarius* spp. (i.e. *deliciosus*, *quieticolor* and *semisanguifluus*), respectively.

Split period (1995–2004/2004–2013) comparison of the weighted week of appearance (WWA) of all mushrooms revealed a substantial autumnal delay from week 43.6 ± 0.4 to 44.7 ± 0.5 (Fig 2). This phenological trend is further reflected in the WWA of both nutritional modes (mycorrhizal and saprotrophic), as well as by the edible and non-edible subgroups. The most significant ($p = 0.03$) delay was found for the edible cohort, with peak fruiting in weeks 42.6 and 44.1 before and after 2004, respectively. At the same time, mean annual fruit body counts (FBC) of the two split periods decreased by nearly one-third from 2 880 to 2 045. This overall long-term decline in productivity was consistent among all species except the saprotrophic guild, which exhibited a slight rise in FBCs. The greatest loss in mushroom numbers was observed for edible mushrooms, which declined by a factor of almost three. In addition, the total weight of fruit bodies has also declined since 1995. With a drop of nearly 10 tons, the mean annual fruit body weight (FBW) of all mushrooms changed from 36 700 kg to 27 340 kg yr^{-1}, a consistent but insignificant trend in all subgroups. Comparison over the early/late-split periods not only revealed a generally delayed fruiting of fewer mushrooms in the later period, but also slightly lower species diversity (51 instead of 55).

In addition to the observed long-term changes in PG mushroom phenology, productivity and diversity, there was a reduction in ring width of *P. sylvestris*, *P. pinaster* and *Q. ilex*, the three main tree species of the broader study area (Fig 3). This forest growth decline coincided with a Spanish-wide decrease in truffle harvest (Büntgen *et al.* 2012a, 2015). At the same time, warm season (Apr.–Sep.) and summer (Jun.–Aug.) temperature means and precipitation totals increased and decreased, respectively. The observed shift towards more arid conditions over the Iberian Peninsula was further reflected in an enlargement of the diurnal temperature range during warm seasons and particularly the summer months, implying more clear sky days and less cloud cover.

A more detailed view of the intra and interannual behaviour of the two most expensive marketable fungal species under a warmer and drier Mediterranean climate confirmed the overall observed pattern (Fig 4). The reduced numbers of *B. edulis* and *Lactarius* spp. fruit bodies later in autumn lowered their total annual harvest (Fig 4A–C). Conversely, the mean fruit body weight (MFW) of *B. edulis* increased significantly ($p = 0.00$) from 70 to 123 gr (Fig 4D), whereas the MFW of *Lactarius* spp. remained nearly constant (see Fig S1 for details on the linear relationship between fruit body counts of *B. edulis* and *Lactarius* spp.). Intra and interannual changes in the phenology (later) and productivity (lower) of these gastronomic flagship species are best explained by fluctuating Jul.–Sep. precipitation totals over large parts of the Iberian

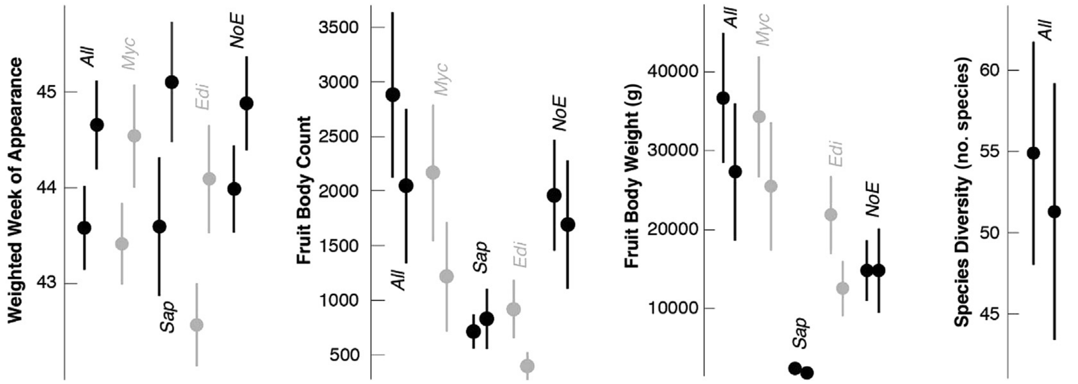

Fig 2 – Long-term changes in the weighted week of appearance (WWA), mean annual fruit body counts (FBC), mean annual fruit body weights (FBW), and species diversity (SDV) averaged for all, mycorrhizal and saprotrophic (All, Myc, Sap), as well as edible and non-edible (Edi, NoE) mushrooms during 1995–2004 and 2004–2013 (left and right hand circles in each pair, respectively). Vertical lines show ±1 standard error. Although most trends are coherent, Wilcoxon tests revealed non-significant changes for all pairings at the $p < 0.05$-level (Holm-Bonferroni corrected), likely because of the relatively short monitoring periods.

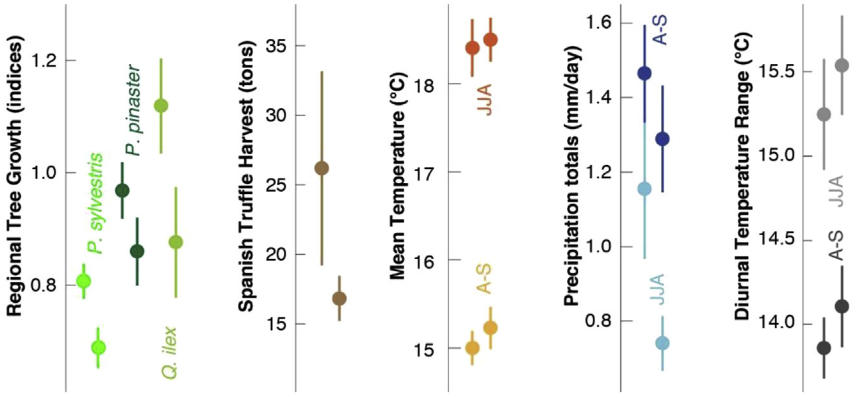

Fig 3 – Long-term changes in nearby tree growth (*Pinus sylvestris*, *Pinus pinaster*, *Quercus ilex*), Spanish truffle harvest (*Tuber melanosporum*), and regional climate from Jun.–Aug. and Apr.–Sep. (JJA, A-S). Although most trends are coherent, Wilcoxon tests revealed non-significant changes for all pairings at the $p < 0.05$-level (Holm-Bonferroni corrected), likely because of the relatively short monitoring periods.

Peninsula, and northwest Spain in particular (Fig 5), including the study site itself. In this regard, it is important to note that most of the mushrooms fruit between early Sep. and mid Nov. (from week 37–47), which is at least 2 months after the critical period of summer rainfall in this region. Further information on the monthly and seasonal-resolved temperature and precipitation sensitivity of both intra- and interannual changes in PG mushroom phenology and productivity, as well as on the

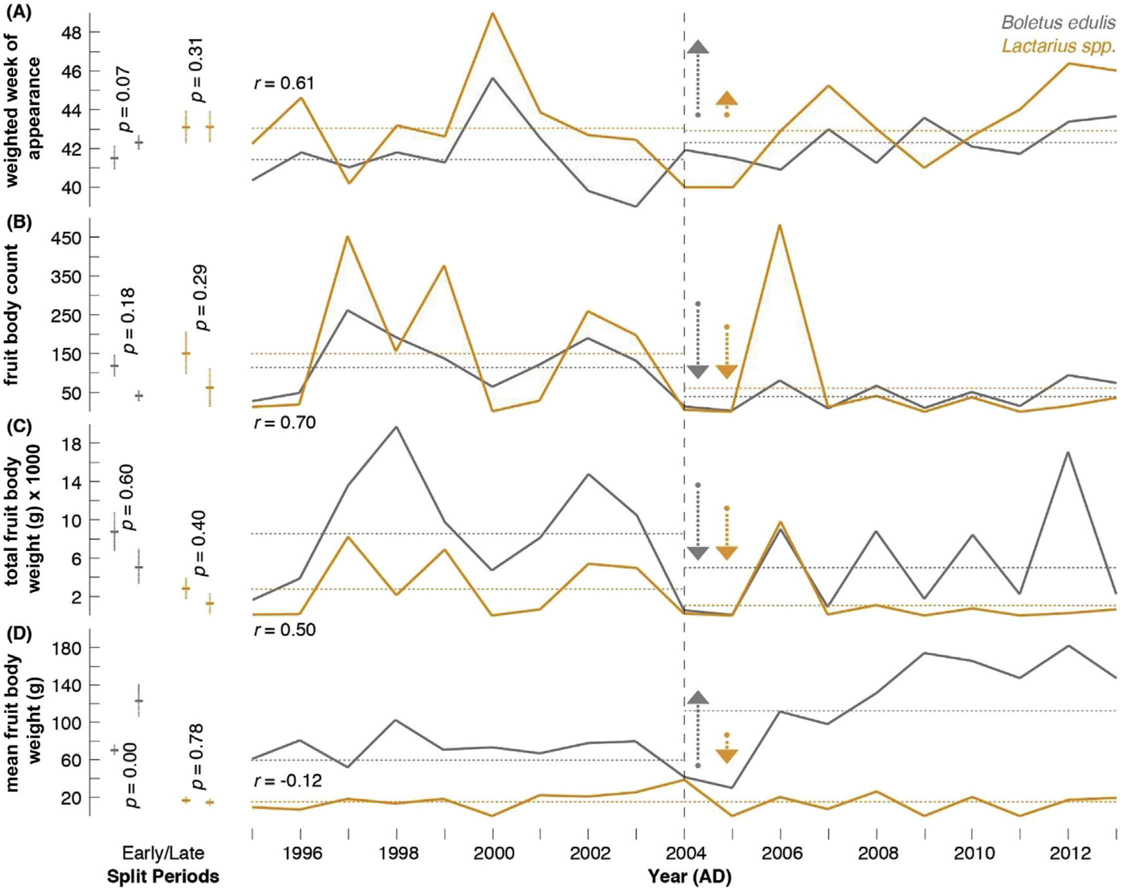

Fig 4 – (A–D) Long-term changes in the weighted week of appearance (WWA), fruit body count (FBC), total fruit body weight (TFW), and mean fruit body weight (MFW) averaged for *Boletus edulis* and *Lactarius* spp. (grey and orange) over two periods (1995–2004 and 2004–2013), as indicated by the horizontal dashed lines. FBCs P values on the left side (A–D) refer to Mann–Kendall tests, whereas arrows and their corresponding lengths denote differences between the pre and post 2004 periods.

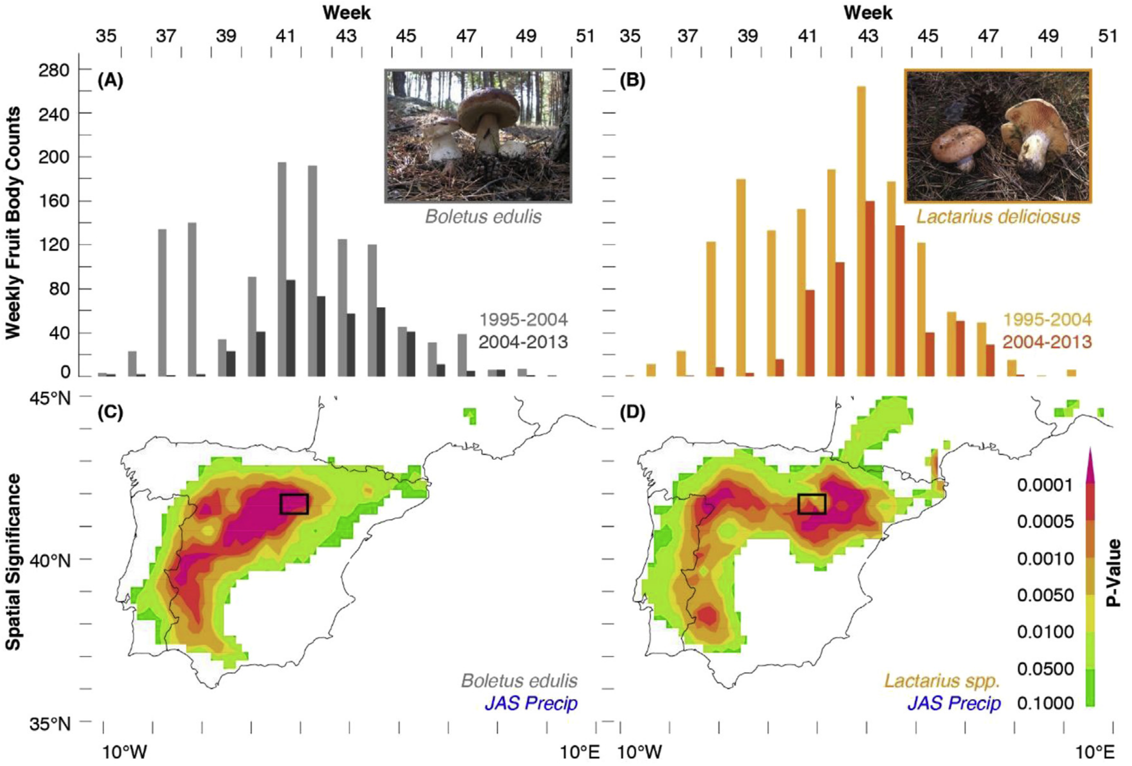

Fig 5 – (A–B) Weekly fruit body count (WFC) of *Boletus edulis* and *Lactarius* spp. summed over 1995–2004 and 2004–2013 (colour codes). Photographs are selected examples of *Boletus edulis and Lactarius deliciosus*, the most common edible species in the PG fungal reserve, which are represented by 1 586 and 1 617 fruit bodies, respectively. (C–D) Significance patterns for spatial correlation fields of the annual changes in fruit body count (FBC) of *Boletus edulis* and *Lactarius* spp. computed against high-resolution (0.25° × 0.25°) Jun.–Sep. precipitation totals over the southwest European continent and the period 1995–2013 (E-OBSv10.0; Haylock *et al.* 2008, updated). The fractions of associations with $p < 0.10$ are 39.7 % and 45.3 % for *Boletus edulis* and *Lactarius* spp., respectively. Black rectangles indicate the location of PG.

growth-climate relationship of PG Scots pine is summarized in Figs S2–S4, respectively.

Regression models verified these relationships between climate variability and fungal productivity and phenology of the edible species. Overall, precipitation was a more useful variable than temperature for explaining both phenology and productivity (Fig 6). On its own, temperature was not a significant explanatory variable for any of the responses, whereas precipitation was significant for explaining WWA, FBC and TFW of all edible species. However, multiple regressions revealed that temperature could be a significant explanatory variable once the effects of precipitation were accounted for (Table 1). In summary, these edible species fruited earlier, more abundantly, and with overall greater biomass in warm and wet years.

Ordination statistics based on non-metric multidimensional scaling (NMDS; see methods above) revealed a high level of similarity in the behaviour of TFW and FBC of all fungal species independent of their functional and toxicological guilds (Fig S5). Species diversity was also closely related to TFW and FBC. The productivity of *B. edulis* as well as the Périgord black truffle (*T. melanosporum*) was most closely linked to summer precipitation totals, whereas the yield of *Lactarius* spp. was slightly less rainfall dependent. Tree-ring widths of all conifer and evergreen broadleaf species (*P. sylvestris*, *P. pinaster* and *Q. ilex*) were associated with Apr.–Sep. precipitation totals. The strongest dependency on warm season rainfall was for the PG Scots pine stands. Mean temperature and the diurnal temperature range formed an autonomous cluster. Fungal phenology, most separated from forest productivity including mushrooms and trees, was related to summer and warm season temperature and the diurnal temperature range. Interestingly, the WWA of *B. edulis* and *Lactarius* spp. was slightly disconnected from the WWA of all other fungi species.

Discussion

This study, based on the longest weekly, continuous mushroom inventory known for a Mediterranean environment, highlights ongoing changes in fungal ecology, which are either directly or indirectly related to climate variability. Overall, this study not only reveals later fruiting in the year, but also a reduced number, weight and diversity of wild mushrooms over the past decade. Based on regression analyses, these changes are significantly correlated with periods of summer drought, warmer temperatures and declining forest growth.

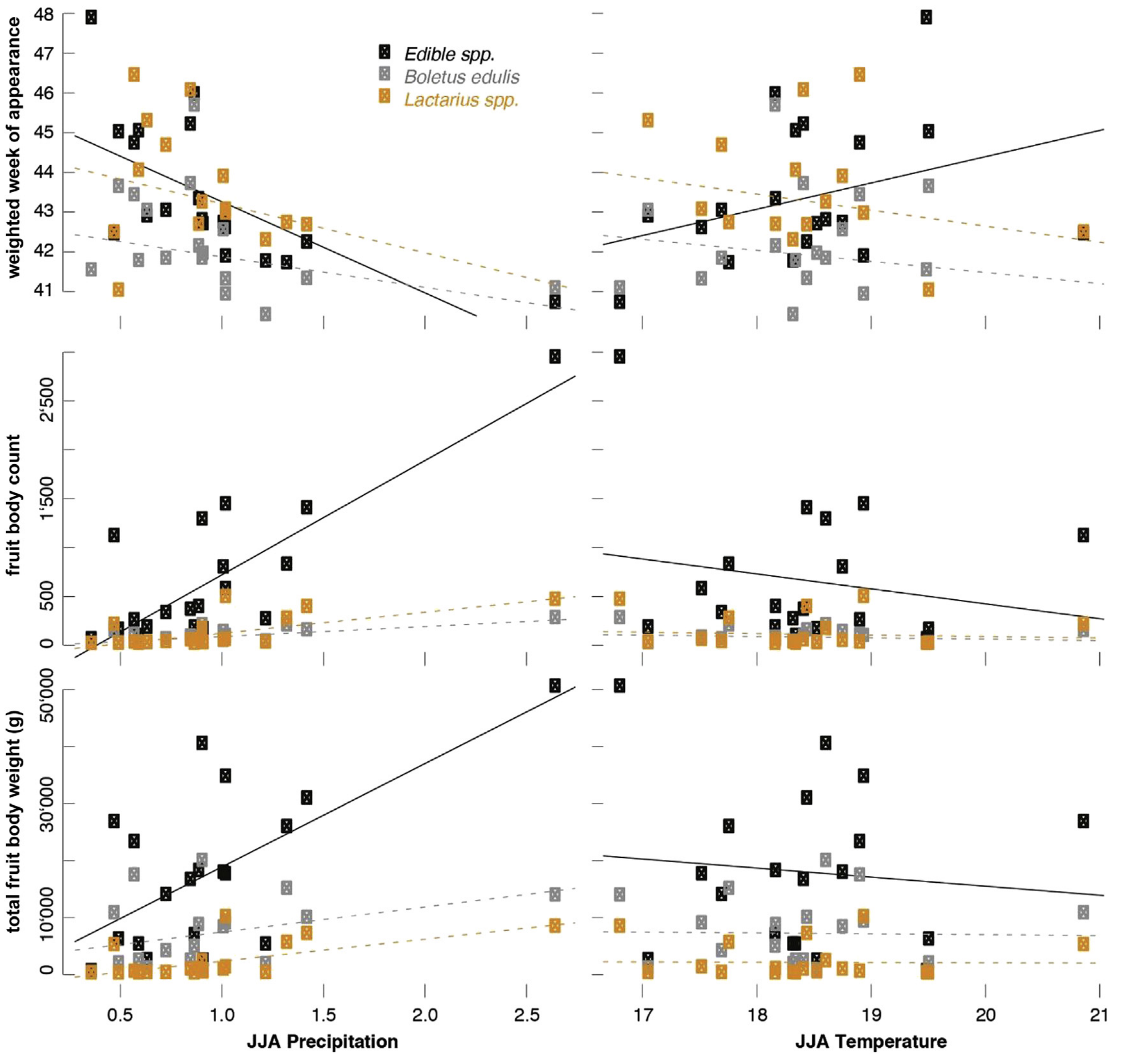

Fig 6 – Univariate regressions of mushroom phenology and productivity in relation to climate variables. Solid lines represent significant ($p < 0.05$) univariate relationships and dashed lines are not significant (see Table 1).

Nonetheless, even the unique PG monitoring program of 20 yr is still not of sufficient duration to allow statistically robust quantifications of the observed long-term changes in fungal phenology, productivity and diversity. This drawback emphasizes the importance of well replicated, long-term and highly resolved field inventories, which are still under-represented in drought-prone arid environments (Mohan *et al.* 2014). A continuation of the PG inventory, ideally aided by various laboratory experiments and other field observations (Boddy *et al.* 2014; Büntgen & Egli 2014), including molecular approaches and monitoring systems, is thus essential with respect to a broad spectrum of scientific and economic demands.

Possible reasons for the observed trends in fungal ecology are manifold and other drivers beside climate should be considered. For instance, mushroom fruiting is often affected by the endogenous development of forest stands, such as tree aging and/or canopy closure, as well as by varying forest management strategies, including the harvesting of timber and non-timber products, e.g. forest thinning and mushroom picking. Since 2011, PG has belonged to a regional mushroom picking project (Regulation and Marketing of Mycological Resources of Castilla and León; www.micocyl.es), in which annual harvesting permits are issued to control harvesting pressure in public forests and ensure a sustainable usage of mycological resources (Aldea *et al.* 2012).

The observed patterns of mushroom fruiting at intra and interannual time-scales vary considerably from species to species (Martínez-Peña *et al.* 2012a). Their responses to changing climate may also depend on the varied nutritional modes and life history characteristics of soil fungi (Andrew & Lilleskov 2009; Büntgen *et al.* 2013b; Diez *et al.* 2013; Boddy *et al.* 2014). Although significant changes in fungal community composition over time have not been detected in PG yet, there is a clear correlation between species diversity and climate variability. Therefore, a continued drying may indeed lead to a decrease in species richness over the longer term. The observed decrease in biodiversity over time could be connected with the overall decrease in mushroom production if rare species do not fruit during years of lower production,

Table 1 – Results from multiple regression analyses (significance codes: *** = p < 0.01; ** = p < 0.05; * = p < 0.1; n.s. = non-significant; red = negative effect; blue = positive effect). The weighted week of appearance (WWA), as well as the accumulated weekly fruit body counts (FBC) and the total fruit body weight (TFW) were used as response variables.

Fungal group	Response variable	JJA precipitation	JJA temperature
Edible species	WWA	**	n.s.
	FBC	***	**
	TFW	***	*
Boletus edulis	WWA	*	n.s.
	FBC	***	*
	TFW	*	n.s.
Lacarius spp.	WWA	*	*
	FBC	***	**
	TFW	***	**

since the highest species diversity is found when the total production is maximal (Bonet *et al.* 2004, 2010).

To fully understand potentially drought-induced increases in the mean weight of *B. edulis* sporocarps, it may be important to also understand the dynamics of belowground mycelium under changing environmental conditions (Mohan *et al.* 2014). However, we still have little knowledge of multi-trophic effects induced by changes in the distribution and activity of fungal mycelium or fruit bodies (A'Bear *et al.* 2013). This points to the need for combined field observation studies and laboratory experiments (Boddy *et al.* 2014). For example, isotopic labelling that traces symbiotic carbon, nutrient and water pathways for different species (host-fungus/fungus-host), environments and climates, can lead to a better understanding of the relationships between plant growth and ectomycorrhizal fungus energy capture and partition. Bioinformatic sensor technologies, such as metagenomic and/or metatranscriptomic analyses or biochemical assays, can also be useful to measure belowground functional hyphal activity and compare these data with intra-annual tree-ring patterns (Büntgen & Egli 2014). Current studies using molecular approaches have made some progress in this regard (De la Varga *et al.* 2011).

Since fungal fruiting is mediated by many factors including fungal and host physiology and changes in resource availability and competition among host trees, one strategy of reproduction could be a faster development and maturation of fruit bodies when environmental conditions are suitable. *B. edulis* seems to be more sensitive to summer drought than *Lactarius* spp. Moreover, *B. edulis* and *Lactarius* spp. show very different fruiting patterns regarding the tree stand age (Martínez-Peña *et al.* 2012a). Consistent with this hypothesis, Ortega-Martínez *et al.* (2011) found fewer fruit bodies in forests 30 + years old, so a high proportion of stands of this age in PG could explain a decline. Another difference between both species is that *B. edulis* mainly grows in stands with a closed canopy, whilst *Lactarius* spp. grows in open young stands without canopy closure (Martínez-Peña *et al.* 2012a). Hence, the development of forest stands towards either a more closed or more open canopy can influence the composition of fungal communities. Furthermore, in cultivated (saprotrophic) mushrooms, fruit body growth is clearly driven by the availability of nutrients (Straatsma *et al.* 2013), especially if species tend to grow in groups as in the case of *Flammulina velutipes* (Gruen 1983). Due to competition, single fruit bodies tend to grow bigger than several growing in a group, and those in smaller groups are bigger than those in larger groups. The total weight of the individual groups of 3–7 fruit bodies each, however, did not differ significantly. Gruen (1983) anticipated that such competitive behaviour may also be the case for other species of higher fungi growing on a shared mycelium.

In fact, our results for *B. edulis* are consistent with this theory: TFW did not differ significantly between the first and second monitoring periods, even though MFW was higher and FBC were lower in the second period. Why did *B. edulis* fruit bodies grow larger in the second period compared with the first? Whereas the knowledge about the factors influencing fruit body size of cultivated mushroom is extensive (e.g. Straatsma *et al.* 2013; Yang *et al.* 2013), very little is known about what governs the size of mycorrhizal fungi growing in the wild. For *Dermocybe uliginosa*, a mycorrhizal species associated with willow, final fruit body size is inversely proportional to the length of the growing period (Kotilova-Kubickova *et al.* 1990a), but the average FBW varies widely between different habitats and years (Kotilova-Kubickova *et al.* 1990b). It is common knowledge among mushroom growers that very moist substrata produce fewer (and perhaps bigger) fruit bodies than moderately moist substrata (Straatsma *et al.* 2013). However, this does not explain our results since the second period was drier compared with the first.

Placed in a broader geographical context, our findings diverge from studies showing increased fungal activity in more temperate habitats north of the Alpine arc (Kauserud *et al.* 2008, 2010, 2011, 2012; Büntgen *et al.* 2012b; Boddy *et al.* 2014), where a warmer but not drier climate also tends to improve tree growth (Büntgen *et al.* 2011). It appears noteworthy that a statistically significant positive relationship between autumnal fungal fruiting and summer tree-ring width was observed in PG, whereas non-significant correlations were found between mushroom fruiting and tree growth in Switzerland (Büntgen *et al.* 2013b). In fact, it is well known that a drier than average summer climate can affect both tree and mushroom growth (Büntgen *et al.* 2012a, 2013a), either directly or indirectly through reduced carbon allocation. Therefore, the positive association between tree growth and fungal production in PG is likely indicative of a carbon and water limited ecosystem, whereas their production may be more independent in more mesic ecosystems (e.g. Switzerland; Büntgen *et al.* 2013b).

The PG inventory not only provides an ideal test case for better understanding high to low-frequency aspects of fungal ecology in a drought-prone Mediterranean environment, but it also shows the economic importance of non-woody forest products in rural areas of the Iberian Peninsula. Intensive harvesting of *B. edulis* and *Lactarius* spp. had already begun in the 1950s, and now >62 % of the local population surrounding PG is actively involved in the collection of mushrooms and their subsequent trade (Martínez-Peña *et al.* 2011). Consequently, forest owners and managers recently agreed to incorporate myco-silvicultural criteria into their management plan to mitigate the effects of forest stand regeneration on wild edible mushroom production. In doing so, they made an important step from traditional forest management towards a multi-functional management (www.micosylva.com). The integration of myco-silvicultural criteria may also help mitigate the effects of global warming by taking into account the role of mycelial systems of ectomycorrhizal roots on uptake and transport of water and nutrients (Brownlee *et al.* 1983). PG belongs to a group of mycological parks (the Micosylva Forest network), whose ultimate aim is to economically appraise mycological resources.

At a regional-scale, hundreds of tons of edible forest mushrooms – mainly *B. edulis* and *Lactarius* spp. – are sold annually in local markets, generating an economic value of several million Euros (Martínez-Peña *et al.* 2011; Voces *et al.* 2012). This financial gain is particularly important for the rural development of the forested areas of Spain and other southern European countries (Martínez de Aragón *et al.* 2011; Bonet *et al.* 2014; de-Miguel *et al.* 2014). The economic benefit of mushroom harvesting, in tandem with (myco-) tourism and gastronomy, may even exceed the fiscal profit obtained from traditional timber products (Palahí *et al.* 2009; Aldea *et al.* 2012; Frutos *et al.* 2012). More than 250 000 myco-tourists attracted by mushroom harvesting (68 %), myco-gastronomy (31 %) and myco-culture (1 %), already generate a total of 32 million Euros per year in Castilla and León (Latorre 2014). This tendency is increasing.

The Mediterranean basin has been identified as a hotspot of future drying in response to rising greenhouse gases (Kelley *et al.* 2012; Hoerling *et al.* 2012; Barkhordarian *et al.* 2013).In seeking to prevent ecological and financial loss under predicted climate change, we suggest summer irrigation and stand thinning to reduce direct and indirect water competition within and between the host vegetation and its symbiotic fungal partners (Büntgen *et al.* 2014). Moreover, future forest management strategies aimed at safeguarding prosperity in an era of rapid drying (i.e. a combination of warmer temperatures and less precipitation) require region-specific understanding of how productivity, sustainability and diversity of forest resources are likely to change. Long-term observational datasets such as that being collected at PG are critical and should be supplemented by modelling approaches to improve empirical understanding of agricultural and forest system functioning.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.funeco.2015.03.008.

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