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Black truffle winter production depends on Mediterranean summer precipitation

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Abstract

The unprecedented price inflation of Black truffles, recently exceeding 5000 Euro kg^{-1} (in Zurich), is a combined result of increasing global demands and decreasing Mediterranean harvests. Since the effects of long-term irrigation and climate variation on symbiotic fungus-host interaction and the development of belowground microbes are poorly understood, the establishment and maintenance of truffle plantations remains a risky venture. Using 49 years of continuous harvest and climate data from Spain, France and Italy, we demonstrate how truffle production rates, between November and March, significantly rely on previous June–August precipitation totals, whereas too much autumnal rainfall affects the subsequent winter harvest negatively. Despite a complex climate-host-fungus relationship, our findings show that southern European truffle yields can be predicted at highest probability ($r = 0.78$, t-stat $= 5.645$, prob $= 0.000\,01$). Moreover, we demonstrate the reliability of national truffle inventories since 1970, and question the timing and dose of many of the currently operating irrigation systems. Finally, our results suggest that Black truffle mycorrhizal colonization of host fine roots, the sexualisation of mycelium, and the formation of peridium are strongly controlled by natural summer rainfall. Recognising the drought-vulnerability of southern Europe's rapidly growing truffle sector, we encourage a stronger liaison between farmers, politicians and scientists to maintain ecological and economic sustainability under predicted climate change in the Mediterranean basin.

Introduction

Approximately 16 km^2 of arable land in northeastern Spain and southern France are transformed each year into new plantations of the (Périgord) Black truffle (*Tuber melanosporum* Vittad, an Ascomycota; hereinafter 'truffle'), with slightly smaller units in north-central Italy. This booming industry substantially contributes to rural economies and cultural identity (Samils *et al* 2008, Büntgen *et al* 2017). An estimated 110 000 kg yr^{-1} of truffles that are growing in wild habitats and ~40 000 ha of scattered plantations in Spain, France and Italy generate ~50 million Euro annually (Oliach *et al* 2019). The rapidly growing and wide-ranging economic sector includes the production of mycorrhized plants in nurseries, the harvest of wild and cultivated truffles, truffle dog training, the marketing of fresh and processed truffles, the transformation of truffles into secondary products, mycotourism (i.e. truffle-tourism), mycological gastronomy, interdisciplinary research, and producer extension services (Büntgen *et al* 2017). The total asset, in France alone, has been estimated at ~67 million Euro yr^{-1}. With an increasing trend, cultivated fruitbodies already account for up to 80% of all commercially traded truffles (Murat 2015, Reyna and Garcia-Barreda 2014). Due to the hidden belowground lifecycle of this iconic culinary species (Trappe and Claridge 2010), and its complex host interaction (Büntgen *et al* 2015), as well as potential direct and indirect climatic (e.g. precipitation and temperature, respectively) impacts (Büntgen *et al* 2012, Molinier *et al* 2013, Le Tacon *et al* 2014, 2016, Thomas and Büntgen 2019, Baragatti *et al* 2019), truffle cultivation in southern Europe is still associated with high ecological and economic risks. Although many plantations are now irrigated, an increase in the frequency and intensity of Mediterranean summer droughts is expected to affect both, the quality and quantity of the subsequent truffle winter harvest (Büntgen *et al* 2012, Thomas and Büntgen 2019). This is particularly alarming since warming in southern Europe is predicted to exceed global rates by 25% (Cramer *et al* 2018), notably with summer temperatures rising at a pace 40% larger than the worldwide mean (Lionello and Scarascia 2018). This trend will be associated with more heatwaves and a reduction in summer precipitation of around 10%–15% over the Mediterranean truffle producing regions (Fischer and Schär 2010, Büntgen *et al* 2012, Jacob *et al* 2014, Vautard *et al* 2014, Thomas and Büntgen 2019).

Despite a putative sensitivity bias, due to a substantial increase in irrigation intensity and refined cultivation practices during the past years (Olivera *et al* 2014a, 2014b, Oliach *et al* 2019), as well as the common belief that national truffle production data are very noisy because of uncoordinated trading and often-unofficial marketing (Reyna 2012), in addition to many other biases (Le Tacon *et al* 2014, Baragatti *et al* 2019), this study aims to understand the dependency of truffle productivity on rainfall variability. To reconstruct the effects of Mediterranean climate change on truffle harvest, we collected annual estimates of the fungus' fruitbody yield from Spain, France and Italy between 1970 and 2017/18, and compared these values with monthly resolved and spatially explicit temperature and precipitation indices. Time series analyses, spatial field correlation coefficients and a suite of calibration-verification trials were applied to quantify the relationship between truffle production and climate variation at different spatiotemporal scales.

Data and methods

Three continuous, 49 year-long records of the approximate annual truffle production from southern Europe's main truffle producing regions in northeastern Spain, southern France and northcentral Italy is analysed and compared against high-resolution, gridded climate indices of the same three regions. Though still associated with wide uncertainties (see discussion below), data from the national harvest inventories represent a substantial update in the number of years studied from initial 37 (1970–2005/6) in Büntgen *et al* (2012) to the current 49 years from 1970 to the latest complete truffle harvest between November 2017 and March 2018 (supplementary online material is available online at stacks.iop.org/ERL/14/074004/mmedia). Information on the winter truffles harvest from northeastern Spain and southern France was compiled by the national Truffle Grower Associations and the Groupement European Tuber (Courvoisier 1992, Callot 1999, Reyna 2012, Oliach *et al* 2019). The French Ministry of Agriculture gathered yields from across France until 1988, whereas data afterwards are restricted to the most important markets, from which the French National Truffle Grower Association calculated the nationwide harvest. Truffle information from northcentral Italy was collected and published by the National Institute for Statistics until 1990, and afterwards from the Groupement European Tuber (Oliach *et al* 2019). While allowing year-to-year variability to be analysed, the limited resolution of the truffle data does not reflect any intra-seasonal changes.

For comparison against regional and Mediterranean-wide climate variability, monthly and spatially resolved gridded temperature means and precipitation totals were extracted from the E-OBS v8.0 reanalyses dataset (Haylock *et al* 2008). In addition to European-scale field correlation analyses (as commonly applied in high-resolution (paleo)climatic studies through the KNMI server; http://climexp.knmi.nl/), regional climate indices were derived by averaging the E-OBS grid cells over 41–42 °N and 2–0 °W for northeastern Spain, over 44–45 °N and 3–5 °E for southern France, and over 44–45 °N and 10–12 °E for northcentral Italy. The normalized grid cell averages (i.e. Z-scores with a mean of zero and a standard deviation of one over 1970–2018), climatically representative of the truffle producing regions in each country, were used as predictors of similarly normalized truffle production (mean of 0 and STDV of 1). Pearson's correlation coefficients were used to determine those months (i.e. each individual monthly value of the year of truffle growth) and/or seasons (i.e. averages of two or more consecutive months prior to truffle harvest) when regional climate indices are significantly correlated ($p < 0.05$) with truffle harvests (see supplementary online material for details). To test the statistical robustness and temporal stability of the relationship between monthly climate and fruitbody production this experiment is performed three times for each region, once for the first half of the truffle and climate data's common period (1970–1993), once for the second half (1994–2017), and once for the full period (1970–2017). Dividing the period shared by both the harvest and precipitation data into an early-period and a late-period, and using the linear model estimates derived from the information in one to verify the unused values in the second, and visa-versa, is called split period calibration/verification. This method of establishing a robust linear model between an instrumental quantity and an independent time series of measurements is common practice in dendroclimatology (Esper *et al* 2016).

The skill with which modelled estimates of truffle winter production, derived from climate values in the calibration period, replicates the observed variance of production in the validation period, is expressed by the performance of the coefficient of efficiency (CE) and reduction of error (RE) statistics. Both RE and CE are measures of the shared variance between actual and estimated values (with CE being the more rigorous statistic). Positive values of RE and CE suggest the model has predictive skill (Frits 1976, Cook *et al* 1994). As often used in high-resolution palaeoclimatology, the Durbin–Watson (DW) statistic assesses temporal stability in the calibration models (DW; Durbin and Watson 1951). DW tests for lag-1 autocorrelation in model residuals. A DW value > 1.00, for $n = 47$, represents an acceptable degree of first-order autocorrelation in the residuals ($p < 0.05$).

To guard against inflated correlations due to covariance in trend (low-frequency), all further modelling experiments are performed on both first-differences (FD; high-frequency), and undifferenced (UD; actual values) data. The calibration and verification exercises, using monthly and seasonal precipitation totals as predictors of truffle production, are the final step before accepting any model's hind or forecast ability. These experiments are performed on the FD transformations of seasonal precipitation and winter production of the truffle, as well as their original UD values. Once again, the classical split period approach is applied independently for each of the truffle producing regions. When both periods produce verifiable estimates, significantly correlated with only positive error reduction, the relationship between predictor and predictand is considered robust, and a reconstruction or prediction may be performed.

Results

None of the monthly and seasonal temperature means reveal significantly ($p < 0.05$) positive relationships with any of the regional or Mediterranean-wide truffle winter yields (figure 1). However, Pearson's correlation coefficients between truffle winter production and monthly summer precipitation reveal significantly ($p < 0.05$) positive values at both the regional and sub-Mediterranean scales. Despite current irrigation efforts, truffle harvests in northeastern Spain, southern France and northcentral Italy exhibit their highest correlations with rainfall in slightly different summer months (figure 1). Moreover, precipitation totals between October and November have significant ($p < 0.05$) negative effects on the subsequent fungal yield. The total truffle harvest of all three regions is significantly positively correlated with total June–August precipitation (figures 1, 2; table 1). This association is confirmed by DW statistics of 1.1056, 1.1569 and 1.3795 for Spain, France and Italy, respectively. Over the full 1970–2017/18 period (figure 2(A)), the Spanish harvest has the highest correlation with summer precipitation ($r = 0.68$), followed by France and Italy ($r = 0.59$). All three regions display a long-term decline in both, summer rainfall and winter truffle yield, from the mid-1970s until around 2000. While there is a sharp rise in Spanish summer precipitation and truffle winter production from 2012 to present, the French data present a much slower, though continuous increase since around 2003. This positive trend is less distinct in Italy, where truffle production peaked between 2012 and 2014. Most surprising is the strong dependency of truffle winter production on previous summer precipitation in Spain since 1994 ($r = 0.75$), the driest region and period in which irrigation is most intense. Another surprising result is the high agreement between truffle data from Spain and those from France and Italy ($r = 0.52$ and 0.47), which is not mirrored by their corresponding precipitation records ($r = 0.48$ and 0.17). In addition to the temporally stable association between truffle winter production and June–August precipitation (figure 2(A)), European-wide field correlations of each of the three production regions exhibit remarkably strong spatial coverage of explained summer rainfall variability (figure 2(B)). The highest correlations are again found over Spain, from the Iberian System in the south to the foothills of the Pyrenees in the north, followed by two clusters in southern France, west and east of the Rhone Valley, and along a north-to-south transect in Italy between the Po Valley in the north and the Apennine Mountains in the south. Another interesting finding are the negative correlations between truffle production and precipitation between September/October and November (figure 1), which are distinct in all three countries.

Full period modelling using the optimal seasonal precipitation averages as a predictor of truffle winter harvest reveals statistically significant solutions (figure S1), the most robust of which is that for the Spanish harvest (table 1). Time series analysis of model residuals (figure S1), in all instances, shows there is still unaccounted persistence manifest by the rather low DW statistics. This suggests that, in addition to the

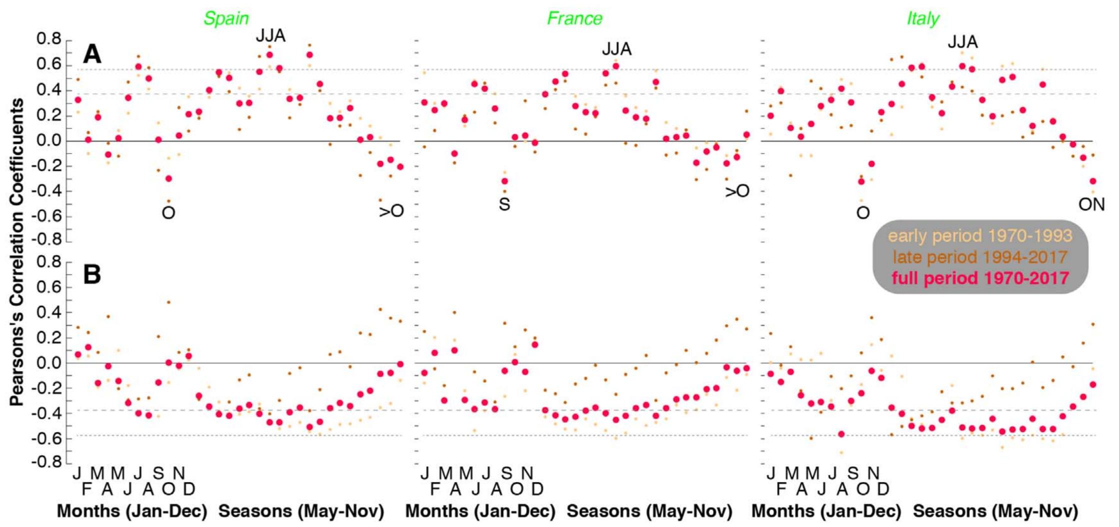

Figure 1. Regional truffle production and precipitation and temperature variation. Pearson's correlation coefficients between (A) normalized monthly and seasonal (any combination between June and November prior to harvest) precipitation totals averaged over 41–42 °N and 2–0 °W in Spain, 44–45 °N and 3–5 °E in France, and 44–45 °N and 10–12 °E in Italy (E-OBS v8.0) and normalized truffle winter yields in northeastern Spain, southern France and northcentral Italy (table S4) over three time periods (1970–1993, 1994–2017 and 1970–2017). The 99% significance levels for the full (0.38) and split (0.59) periods are shown by the dashed lines. (B) Similar to (A) but using temperature means.

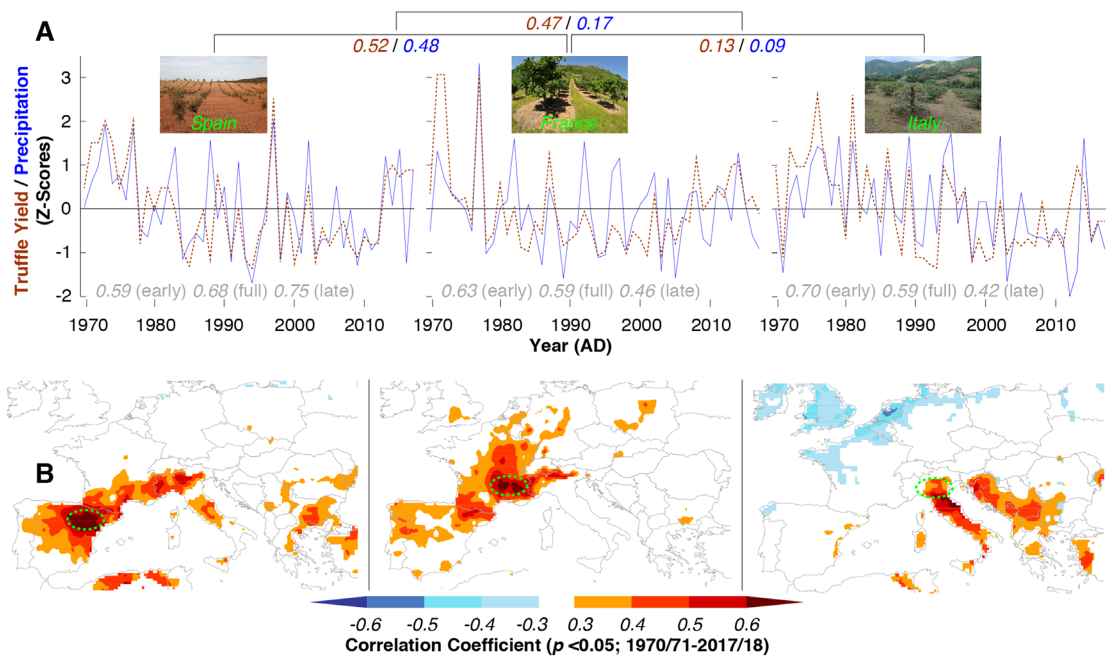

Figure 2. Regional patterns of precipitation totals and truffle yields. (A) Truffle winter yields for northeastern Spain, southern France and northcentral Italy (dashed lines) together with summer (June–August) precipitation totals from the same regions (blue lines). Time series are normalized over the common period 1970–2017 (see table S4 for data), and precipitation totals are averaged over 41–42 °N and 2–0 °W in Spain, 44–45 °N and 3–5 °E in France, and 44–45 °N and 10–12 °E in Italy. Photos show a gradient from arid to semi-arid truffle plantations in Spain (Teruel in Aragón), France (Aveyron in Occitanie) and Italy (Ascoli Piceno in Marche), and the correlation coefficients refer to relationships between regional truffle winter yield (brown) and summer precipitation (blue) from 1970 to 2017. Correlation coefficients at the bottom of the three graphs (grey) indicate temporal changes in the relationship between truffle harvest and rainfall from 1970 to 1993 (early), 1970 to 2017 (full) and 1994 to 2017 (late). (B) Maps of significant ($p < 0.05$) spatial field correlation coefficients between truffle winter yields from Spain, France and Italy (dashed circles) and gridded June–August precipitation totals over Europe and the 1970–2017 period (see table 1 for statistics). For the Spanish, French and Italian data, the fraction of the map with $p < 10.00\%$ is 38.44%, 33.82% and 36.19%, respectively.

variation accounted for by precipitation there is in fact an additional, unaccounted, factor affecting fruitbody production that is transient in nature (see Discussion below).

The best prediction model is that which explains the Spanish truffle winter production (figure S2). The French model is also arguably acceptable, however, it is clear that the Italian model, though a robust

Table 1. Linear regression models for regional precipitation totals and truffle yields. Spanish, French and Italian Summer (June–August) precipitation totals as a predictor of truffle production in the corresponding countries between 1970 and 2017 explains 46.22%, 28.43% and 25.62% variance, respectively.

	Corr.	t-stat	Prob.	RSQ	Cum. RSQ	Adj. RSQ	Adj. RE	AIC
Spain	0.680	6.288	0.0000	0.462	0.462	0.451	0.439	−25.51
France	0.533	4.274	0.0001	0.284	0.284	0.269	0.254	−11.79
Italy	0.506	3.981	0.0003	0.256	0.256	0.240	0.225	−9.94

Table 2. Calibration/verification models for Mediterranean precipitation totals and truffle yields. Combined Spanish, French and Italian Summer (June–August) precipitation totals as a predictor of total Mediterranean truffle production for two early/late split periods. All statistics are calculated for normalized undifferenced and pre-whitened values (first-differenced), with positive reduction of error (RE) and coefficient of variation (CE) values suggesting strong verification results (see tables S1–S3 for the regional calibration/verification models). The verification period, RE is an implementation of Allen's PRESS statistic (Allen 1974), which employs a leave-one-out calculation between actual and estimated values, similar to the leave-one-out iterative calculations commonly used in cross-validation tests.

Calibration period results (undifferenced data 1970–1993)									
Pearson	*Prob.*	*Robust*	*Prob.*	*Spearman*	*Prob.*	*RE*	*CE*	*MedRE*	*MedCE*
0.606	0.001	0.601	0.001	0.606	0.000	0.368	0.368	0.365	0.337
Calibration period results (1st-differenced data 1970–1993)									
Pearson	*Prob.*	*Robust*	*Prob.*	*Spearman*	*Prob.*	*RE*	*CE*	*MedRE*	*MedCE*
0.607	0.001	0.432	0.001	0.451	0.001	0.324	0.324	0.269	0.242
Verification period results (undifferenced data 1994–2017)									
Pearson	*Prob.*	*Robust*	*Prob.*	*Spearman*	*Prob.*	*RE*	*CE*	*MedRE*	*MedCE*
0.551	0.000	0.525	0.000	0.416	0.000	0.475	0.149	0.461	0.091
Verification period results (1st-differenced data 1994–2017)									
Pearson	*Prob.*	*Robust*	*Prob.*	*Spearman*	*Prob.*	*RE*	*CE*	*MedRE*	*MedCE*
0.776	0.000	0.768	0.000	0.701	0.000	0.517	0.506	0.448	0.438

predictor of annual variation, lacks the most credibility in predicting low-frequency behaviour (tables S1–S3). Repeating the calibration and verification experiment using the averages of all three regional summer precipitation totals, and the average of the three national truffle winter production records, produces another verifiably robust model (figure S3). All verification statistics of RE and CE are positive for each period, and at both the high and low-frequency domains (table 2). This strong sub-Mediterranean dependency of truffle winter production to previous summer precipitation is mirrored in the spatial correlation fields of the averaged data (figure 3). When calculated over the full period 1970–2017/18, significantly ($p < 0.05$) positive correlations cover most of the truffle producing regions in all three countries (figure 3(A)), with an overall increase in this relationship towards present (figures 3(B), (C)).

Discussion

To some degree, our results call into question the timing and dose of those irrigation systems that already operate. This is particularly the case for north-eastern Spain since the 1990s, which represents the driest period and region of this study. Although the current irrigation prescription seems ineffective, we argue that a simple increase of the amount of water might not be helpful (Bonet *et al* 2006, Olivera *et al* 2014a, Büntgen *et al* 2015), since the formation and maturation of truffle fruitbodies is likely enhanced by periodic drought-stress (Garcia-Barreda *et al* 2019). Since temporally adjustable belowground watering systems might be more efficient than traditional aboveground sprinklers, such techniques could reduce the burden of current water-use allowances, which are predicted to become more restrictive as the frequency and severity of Mediterranean summer droughts increases (Fischer and Schär 2010, Trnka *et al* 2018). While deficit irrigation might be an alternative (Fereres and Soriano 2006, Sears *et al* 2018), it requires understanding of the fungus' full lifecycle (Baragatti *et al* 2019).

Consistent with previous findings (Gallot 1999, Büntgen *et al* 2012, 2015, Le Tacon *et al* 2014, 2016, Thomas and Büntgen 2019, Baragatti *et al* 2019), our results highlight the importance of summer precipitation for truffle winter production. High precipitation totals and low temperature means between June and August are expected to stimulate (a) mycorrhizal colonization of host fine roots, (b) formation and sexualisation of mycelium, and (c) development of peridium. We further assume that the truffles'

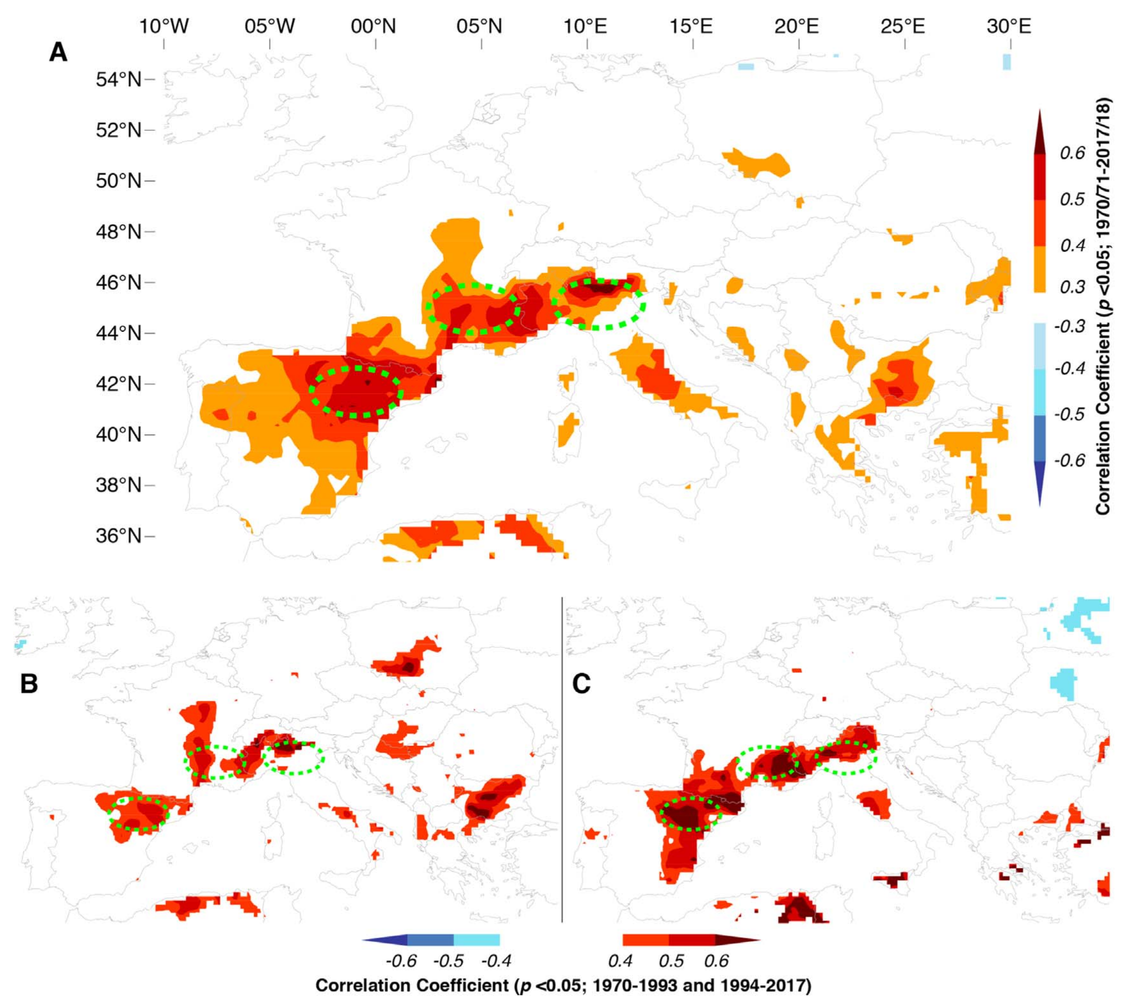

Figure 3. Spatiotemporal patterns between precipitation totals and truffle yields. (A) Map of significant ($p < 0.05$) spatial field correlation coefficients between total Mediterranean truffle winter yields aggregated from northeastern Spain, southern France and northcentral Italy (dashed circles) and gridded Summer (June–August) precipitation totals over Europe and the 1970–2017 period. (B)–(C) Similar to (A) but independently calculated over the early and late 1970–93 and 1994–2017 split periods (see table 2 for calibration-verification statistics). For the full, early and late period, the fraction of the map with $p < 10.00\%$ is 39.71%, 24.24% and 23.83%, respectively.

associated tree partners not only provide an important carbon pool, but also act as the principal source of water in dry periods during fruitbody formation and maturation. We speculate that the host plants, water stressed themselves, may possibly also provide compensation to the fungi during drought spells through increased hydraulic lifting. A better understanding of the potential hydraulic redistribution of soil water by direct nocturnal water transfer from host trees to their mycorrhizal symbionts is, however, needed (Querejeta *et al* 2003, Warren *et al* 2008). Favouring environments of contrasting drought-stress (Garcia-Barreda *et al* 2019), truffles can survive dry periods of up to 30 d (Ricard *et al* 2003). Our own observations of *T. aestivum* in Switzerland and southern Germany suggest that fruitbodies can mature in totally dried-out soils, where other epigeous ectomycorrhizal species have already stopped fruiting. Another interesting finding is the inverse relationship between winter truffle yields and precipitation totals in October and November (figure 1), which indicates that wetter and cooler autumns negatively affect the subsequent truffle harvest. Furthermore, we did not find any significant positive effects of monthly and/or seasonal temperature means (figure 1), which supports the idea that truffles can grow under much cooler (or warmer) conditions than previously thought (Thomas and Büntgen 2017). It is important to note that June–August precipitation totals and temperature means in Spain, France and Italy are significantly negatively ($p < 0.05$) correlated ($r = -0.46$, -0.47 and -0.62, respectively). While the obtained truffle-climate relationships appear most reasonable in a myco-bio/ecological perspective (Büntgen *et al* 2015), the role of host plants is largely unknown (Büntgen and Egli 2014), and some bias may emerge from imprecise meteorological measurements that were aggregated over broad spatiotemporal scales rather than reflecting the environmental conditions of the exact locations and periods of truffle growth.

In addition to the direct negative effects of a dryer future on the growth and development of truffles and

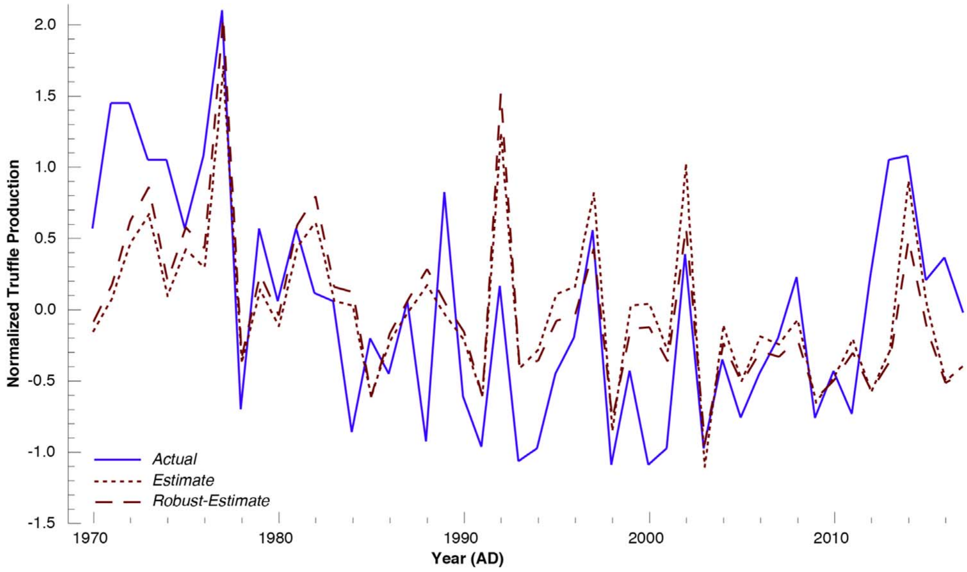

Figure 4. Actual and modelled Mediterranean truffle winter harvest. Average, regional truffle winter production (northeast Spain, southern France and northcentral Italy) from 1970 to 2017 (blue line) and two model estimates based on the combined average summer (June–August) precipitation totals over the same three regions, in the same period. The dotted red-line is the simple linear estimate, the dashed red-line is the Robust estimate, computed using the bi-weight means of X (precipitation total) and Y (truffle harvest). The robust estimate is one that attempts to minimize the disproportionate influence of outliers.

their hosts—similar to other ectomycorrhizal fungi (Köhler *et al* 2018), there are several indirect, temperature-induced, factors (Baragatti *et al* 2019), such as wildfires, pathogens and diseases (Thomas and Büntgen 2019), as well as phenological mismatch in trophic interactions that may disrupt current ecological systems (Renner and Zohner 2018), and cause economic damage. A longer fire season combined with more frequent large fires is expected as a result of increasing summer temperatures, drought and land-use changes (Khabarov *et al* 2016, Ruffault *et al* 2016). Forest fires not only kill trees but also impact soil chemistry, which affects ectomycorrhizal fungal communities (Mediaviella et al 2017). Similarly, the wide range of insect pests and destructive pathogens, such as *Phytophthora cinnamomi* that feed on oaks, are expected to expand their distribution under warmer winter temperatures (Bergot *et al* 2004, Barredo *et al* 2015). In addition, insect pest may also directly affect truffle fruitbodies and thus pose a serious threat to the emerging industry (Rosa-Gruszecka *et al* 2017), because warming increases both population growth and metabolic rates of insects (Deutsch *et al* 2018), and even small larvae infestations already cause large damage. Almost ironically, a warmer and dryer future implies more flood hazards (Cramer *et al* 2018), which can trigger massive surface erosion and sediment relocation, associated with reductions in the richness and abundance of ectomycorrhizal fungi (Barnes *et al* 2018).

Conclusions

This study shows that inventories of truffle yield from Spain, France and Italy, rather than reflecting mainly noise, are reliable since 1970, and that winter truffle harvests significantly depend on previous summer rainfall, whereas too much autumnal precipitation has negative effects. Our findings question the timing and dose of the existing irrigation systems, and call for both management and conservation action to mitigate a multitude of unprecedented ecological and economic risks under predicted climate change. The various threats might be particularly severe for rural Mediterranean cultivators that are most vulnerable to a warmer and dryer future (Büntgen *et al* 2017, Cramer *et al* 2018).

Ultimately, we provide a robust tool for predicting sub-Mediterranean truffle winter production from previous summer precipitation at highest probability. The degree of statistical significance afforded by our model ($r = 0.78$, t-stat $= 5.645$, prob $= 0.000\,01$) rivals that of the best high-resolution climate proxy records (Esper *et al* 2016), for instance. Considering, the number of environmental factors not accounted for in this linear model, such as the inverse relationship with summer temperature (Thomas and Büntgen 2019, Baragatti *et al* 2019), it is remarkable to find summer precipitation alone can explain 36.76% of the subsequent truffle winter production (table 2; figure 4). If handled responsibly, this information can help stabilize production and pricing from regional to international scales, thereby contributing to the maintenance of sustainable harvests and markets. The likelihood to forecast truffle production from summer to winter, however, does not enable long-term projections since host density and irrigation intensity in plantations can (and should) be adapted to changing environmental conditions. Since a drought-induced collapse of the system would also trigger biodiversity losses, a critical review of the current plantation practices deems timely and calls for a vibrant liaison between academia, policy and economy at local to international levels. Finally, we hope that our study will stimulate more detailed work to explore the species' full lifecycle, such as yearlong, fine-scale excavating technique from archaeology as a new approach in ectomycorrhizal research to gain unique insights into the hidden belowground truffle kingdom.

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