

gridded maps of biomass to be produced over time⁶.

Radar backscatter is sensitive to vegetation fresh biomass⁷. At long wavelengths (0.7 m or longer), radar penetrates deep into the canopy and the backscatter energy depends on a combination of variables including the size, number density, and the water content and wood specific gravity of branches and stems. However, radar backscatter suffers from gradual loss of sensitivity as biomass increases. The phenomenon referred to as 'saturation' occurs often in radar backscatter at shorter wavelengths, but is not unique to radar and forests, and can occur in all types of remote-sensing measurements, even for non-woody vegetation. However, at longer wavelengths (>0.7 m), radar backscatter remains sensitive to a wide range of AGB.

Variation in tree density may impact radar backscatter, but does not cause loss of sensitivity. In spatially heterogeneous forests, the largest source of error in deriving the relationship between radar backscatter and biomass is from the geometry of measurement and the difference between the biomass sensed by radar and that sampled on the ground. The

ground data are too often based on small inventory plots, leading to large errors that are often ignored. By increasing the plot size used for remote-sensing calibration, the relationship improves significantly⁵.

Woodhouse *et al.*¹ criticize the use of regression models that convert the backscatter into AGB, which are derived using collections of sites spanning a range of forest types. Mixing data across forest types to sample a wider range of AGB is a common statistical approach used not only in most remote-sensing studies but also repeatedly in field estimation, where inventory data from a limited number of trees is used to predict AGB values over the full range of trees from different regions. Regardless of the type of models used, prediction never implies accuracy.

A systematic radar observation at long wavelengths from space, as recommended by European Space Agency's BIOMASS mission, accompanied by remote-sensing-specific field inventory data provides the only way to circumvent the limitations of field inventory-only biomass monitoring at the global scale. Extending current studies beyond the landscape scale is a priority if radar remote sensing is to fulfil its potential in the context of the Reducing Emissions

from Deforestation and Forest Degradation programme (www.un-redd.org). □

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CORRESPONDENCE:

Drought-induced decline in Mediterranean truffle harvest

To the Editor — With a price of up to €2,000 kg⁻¹ the Périgord black truffle (*Tuber melanosporum*; hereinafter truffle) is one of the most exclusive delicacies¹. However, harvests of this ectomycorrhizal ascomycete have declined in its natural Mediterranean habitat², despite cultivation efforts since the 1970s³. Satisfying explanations for the long-term decrease in both natural and planted truffle yields are lacking. Understanding microbial below-ground processes remains challenging because experimental settings generally don't have the necessary degree of real-world complexity⁴, long enough mycological observations are scarce⁵ and quantitative information from natural truffle habitats and plantations is usually not available^{2,3,6}.

Here we seek to understand how climate can affect truffle production, either directly, or indirectly via their

symbiotic host plants. We did this by analysing annual inventories of regional truffle harvests from northeastern Spain (Aragón), southern France (Périgord), and northern Italy (Piedmont and Umbria) (Supplementary Fig. S1 and Table S1). We found that changes in truffle production (tons yr⁻¹ from 1970–2006) were most similar between Aragón and Périgord ($r = 0.59$; $p < 0.001$), and non-significant between Périgord and Piedmont–Umbria ($r = 0.12$). The observed regional-scale coherency probably originates from common climatic cues that synchronize truffle fruiting among large parts of the western Mediterranean Basin. Spanish and French truffle harvests showed significant positive correlation with summer rainfall ($r = 0.72$ and 0.43 ; $p < 0.001$), whereas lower agreement was found between Italian truffle production and precipitation ($r = 0.22$; Supplementary Fig. S2).

These different sensitivity levels seem reasonable as the Italian truffières are generally experiencing twice as much summer rainfall as the Spanish areas, with the French sites ranging in between (Supplementary Fig. S3).

When averaging the three truffle records (Supplementary Table S1), their subcontinental mean correlates positively and negatively at the 99.9% significance level with gridded June–August precipitation totals and temperature maxima ($r = 0.60$ and -0.57), respectively (Fig. 1a,b). Natural and cultivated Mediterranean truffle yields — seasonally restricted to November–February³ — depend on variations in summer climate⁶, with wet and cold conditions promoting fruit body formation. Given the symbiotic fungi–host association⁷, we postulate that competition for summer soil moisture between host plants and their mycorrhizal

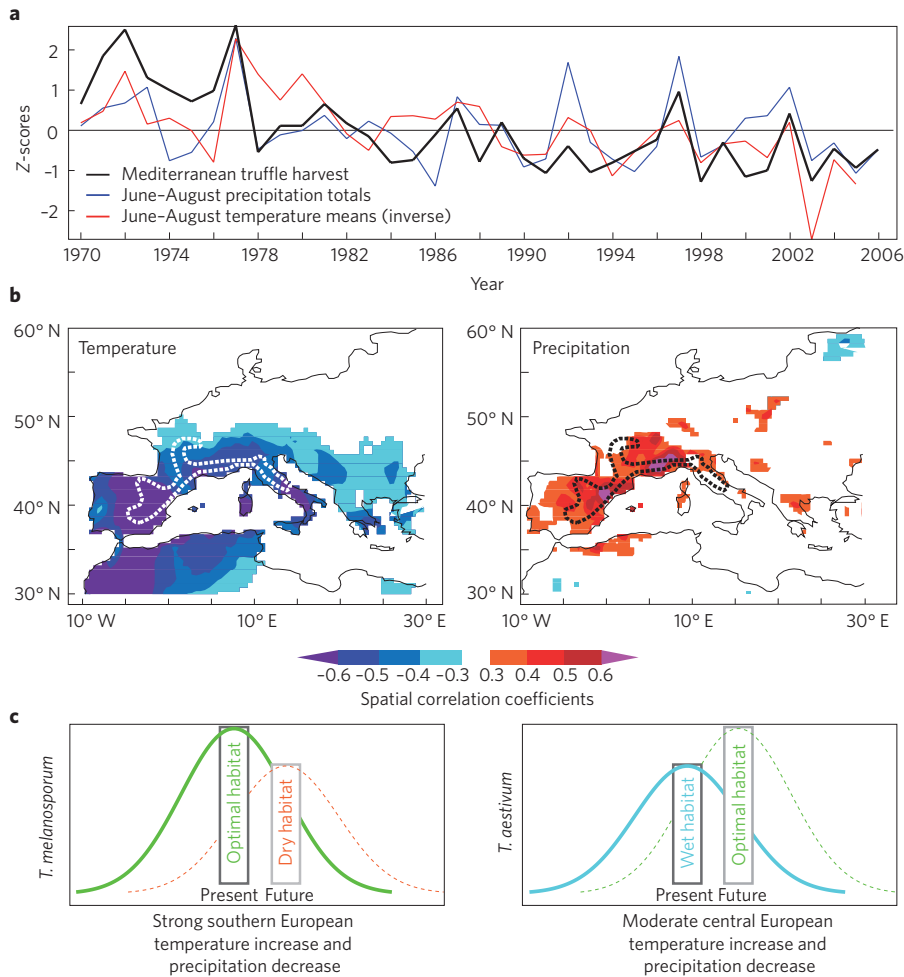


Figure 1 | Truffle yield and climate change. **a**, Comparison of Mediterranean truffle harvests (tons yr⁻¹) and variations in June–August temperature means (inverse) and precipitation totals averaged over 35–50° N and 10° W–20° E (see Supplementary Information for details). All time series were normalized to have means of 0 and standard deviations of 1 over their common period 1970–2006. Annual truffle harvest correlates at the 99.9% significance level with inverse temperature means ($r = 0.59$) and precipitation totals ($r = 0.60$) over 1970–2006. First-order autocorrelation ($lag-1$) of the truffle, precipitation and temperature time-series is $r = 0.48$, $r = -0.05$ and $r = 0.33$, respectively. **b**, Corresponding spatial field correlations (1970–2006) of the Mediterranean truffle record and gridded ($0.5^\circ \times 0.5^\circ$) European summer (June–August) temperature means and precipitation totals (over 30–60° N and 10° W–30° E). Dashed contours indicate the natural distribution of *T. melanosporum*. **c**, A schematic overview of the observed and expected southern European *T. melanosporum* and central European *T. aestivum* fruit body (ascocarp) productions (left and right). The diagram indicates a shift from presently optimal Mediterranean growth conditions for *T. melanosporum* toward less productivity in a drier future. In contrast, *T. aestivum* growth is likely to benefit from a slightly warmer and drier climate north of the Alpine arc.

partners might be a critical factor for truffle fruit body production, particularly in semi-arid environments.

The observed response delay emphasizes complex mechanisms of carbohydrate allocation from the host plants to their fungal symbionts^{6,8}. An adequate carbohydrate flux from the host tree to its roots during the vegetation period might stimulate soil mycelium growth and

fruit body initialization, which is likely a prerequisite for rich winter truffle harvests. An additional carbon source for fungi fruit body production might derive from those carbohydrates that were allocated in the host trees' stem and roots during the warmer vegetation period⁹. In fact, Spanish tree growth (that is, oak ring width; Supplementary Table S2), which mainly occurs from May–July and depends

on the amount of precipitation during this period (Supplementary Fig. S4), correlated positively at the 99.9% significance level ($r = 0.62$; 1970–2006) with truffle yield (Supplementary Fig. S5). This relationship implies ring width variations are a reasonable proxy for truffle fruit body production.

A suite of 12 climate models projects increasing mean temperatures and decreasing precipitation totals for the Mediterranean Basin until the end of the twenty-first century¹⁰ (Supplementary Figs S6,S7), which subsequently denotes intensified potential summer evapotranspiration. The simulated climate envelope for southwest Europe for the past decades matched the observed decline in Mediterranean truffle harvest. It remains unclear if plant physiological and biogeochemical processes relevant for truffle fruit body formation and maturation will behave in a state-dependent, nonlinear way or if critical thresholds — so-called tipping points — at which a system shifts abruptly from one state to another will be reached under projected climate change¹¹. Nevertheless, we assume that the Mediterranean truffle yield will continue to decline in response to amplified summer dryness (Fig. 1c), and we believe that calcareous regions north of the Alpine arc will possibly transform into more suitable habitats^{12,13}.

Spatial and seasonal alterations in future precipitation regimes and associated summer aridity will be important for the adaptation and evolution of *T. melanosporum* across its native distribution range, perhaps favouring drought-resistant strains³. An expected decline in Mediterranean truffle harvests — impacting rural tourism, regional agriculture and global prices^{2,14} — may also enhance the value of other species that are more plastic in their metabolism and less deterministic in their ecological niche requirements^{3,6}. *T. aestivum* cultivation in more temperate environments north of the Alps (Fig. 1c), as well as market demand for supplies from non-traditional Périgord black-truffle-producing countries outside Europe, will probably increase. □

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Author contributions

U.B. designed the study with input from W.T., U.S., L.S. and S.E. Analyses were performed by U.B. with support of J.J.C. and E.M.F. All authors contributed to discussion, interpretation and writing.

Additional information

Supplementary information is available in the online version of this paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence should be addressed to U.B.

Competing financial interests

The authors declare no competing financial interests.

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CORRESPONDENCE:

Arctic contaminants and climate change

To the Editor — In a recent Letter¹, Ma *et al.* analysed eight persistent organic pollutants (POPs) at an Arctic monitoring station (Mount Zeppelin, 474 metres above sea level, Svalbard). They identified inclines in the latter parts of the linearly detrended concentration time-series (1993–2009). Their interpretation is that many POPs (besides the more volatile polychlorinated biphenyls and hexachlorobenzene) have become remobilized from Arctic repositories into the atmosphere as a consequence of climate change. However, it should be emphasized that other factors can cause the reported inclines, which reflect nonlinearities (or a degree of curvature) within the data.

The eight POPs (α -HCH, γ -HCH, *cis*-NO, *trans*-CD, *o,p'*-DDE, *p,p'*-DDE, *o,p'*-DDT, *p,p'*-DDT) analyzed by Ma *et al.* exhibit declining Arctic trends due to reductions in global emissions, modified by processes such as environmental degradation and interchange between atmosphere and surface media. Ma *et al.* used a linear model to detrend the data. Notably, statistical significance of the linear fit does not preclude presence of nonlinearities within the data (indeed such nonlinearities are what lead to the reported inclines), nor does it provide information

on the origins of this nonlinearity. Factors other than climate change may also cause nonlinearity or curvature in POP decline. Incline features on linear detrending can result from nonlinear decline of global emissions, nonlinearity that occurs naturally as concentrations decay towards zero or from concentrations declining to levels at which surface-to-air exchange (revolatilization) from legacy POP repositories increasingly occurs as a response to disequilibrium^{2,3} (even in the absence of climate change), acting as a buffer and decelerating their declines.

Ma and colleagues' perturbation modelling predicts how enhanced revolatilization induced by climate change acts to relatively enhance Arctic POPs' atmospheric levels, as previously postulated^{2,4,5}. The modelled inclines showed correlations to the incline features in the detrended data, but comparison in terms of magnitudes was limited, and some discrepancies exist. For example, interannual variability for the eight POPs appears to co-vary in the model¹ (see ref. 1, Supplementary Fig. S3) but not in the detrended measurements (data visualization; J. Ma, personal communication).

With the data available at present it is very difficult to establish quantitatively

which factors (revolatilization induced by climate change, or other factors as outlined above) contribute most to nonlinearity in these eight POPs' declining trends at Mount Zeppelin. Thus, the potential for multiple sources of nonlinearity is emphasized as an important caveat to the reported identification of an observable and widespread warming-induced signature. Full visualization of the summer data analysis behind the statistics (noting differences to Fig. 1¹) would aid readers' interpretation. □

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Ma *et al.* reply — Roberts¹ argues that our linear detrending analysis for the air concentration time-series of persistent organic pollutants (POPs) collected from

the Mount Zeppelin Arctic monitoring site may not address nonlinearities within the air concentration data, though the time series of POPs data analysed in our

study² exhibited statistically significant linear trends.

However, one cannot assume that the overall impact of a combination