species subject to proposed Appendix I listings, and based on a review of the proposals, 17 do not have in situ management measures in place. Although each situation is context specific, a more appropriate first measure for these species could be the development of conservation programs in partnership with local communities, as opposed to the "blunt instrument" approach of an international trade ban.

While trade prohibitions have proven effective at reducing trade volumes for various species (Conrad 2012; Reino *et al.* 2017), difficulties in predicting their impacts complicate the application of the precautionary principle in CITES; it cannot be assumed that prohibiting international trade is the precautionary option (Cooney and Jepson 2006). Consequently, we argue that evaluation of CITES listing proposals should involve scenario analyses to explore feasible outcomes, explicitly considering market and socioeconomic factors, and highlighting areas of uncertainty.

The use of CITES Appendix I as a conservation tool will be most effective if proposals (1) are informed by knowledge of markets for the species and products concerned and socioeconomic factors associated with harvest and supply as well as biological and trade criteria, and (2) feature an evidence-based theory of change explaining how the listing decision is expected to contribute to improving the status of species. All Appendix I proposals should be given appropriate consideration in CITES meetings, so that Parties are confident that, if adopted, there is a high probability that they will be effective.

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Truffles on the move

Range shifts in the distribution of plant and animal species have been associated with climate change (Lenoir *et al.* 2008; Chen *et al.* 2011; Gottfried *et al.* 2012), and a temperature-induced northward movement of European fungal fruiting patterns has been evident since the mid-20th century (Kauserud *et al.* 2012; Boddy *et al.* 2014; Andrew *et al.* 2017). However, understanding the relationship between belowground processes and species occurrences, including the growth and abundance of hypogeous (underground) fungi, is still limited (Trappe and Claridge 2010).

Here, we report what we believe to be the first scientific discovery – detection, excavation, and identification – of Piedmont white truffles (*Tuber magnatum* Pico; hereafter PWT) north of the European Alps. Of the three main *Tuber* species, PWT is the most aromatic and valuable (Vita *et al.* 2018), often exceeding several thousand Euros per kilogram. Nevertheless, the life cycle of this ectomycorrhizal fungus remains enigmatic (Riccioni *et al.* 2016; Iotti *et al.* 2018). While the phylogeny of the genus *Tuber* indicates that the *magnatum* group belongs to the oldest lineage originating from an area that later became Europe (Jeandroz *et al.* 2008), Rubini *et al.* (2005) suggested that the geographic distribution of PWT tracks the postglacial expansion of its host plants (mostly hardwood trees such as oak [*Quercus* spp]) from a refugium in central Italy. Until now, observations of PWT fruiting have been restricted to a few natural habitats in northern Italy and parts of the Balkan Peninsula. Given that successful cultivation of PWTs has yet to be confirmed (Iotti *et al.* 2018), the iconic species seems particularly vulnerable to environmental changes, and predicted warming represents a substantial economic threat.

On different dates during six growing seasons between October 2012 and November 2018, 15 PWTs were detected by Giano, a trained truffle dog (breed name: Lagotto romagnolo), under a dominant beech (*Fagus sylvatica*) tree in the city of Geneva, Switzerland (Figure 1). No fruiting bodies were found in 2014. The spatial locations of the 15 PWTs – each weighing between 5 and 50 g – were mapped shortly after their excavation at soil depths from 8 to 40 cm; findings from a preliminary examination of spore size and fruiting body ornamentation were suggestive of *Tuber magnatum* (Figure 1). Subsequent laboratory analysis – including DNA extraction from samples of fresh gleba (spore-bearing tissue) of two PWTs from 2012 and 2018, as well as DNA sequencing of the fungal ITS region (internal transcribed spacer of the nuclear ribosomal DNA; Leuchtmann and Clémençon 2012) – revealed 100% accordance with *Tuber magnatum*. Genetic sequences have been deposited in the GenBank database (http://ncbi.nlm.nih.gov/genbank), which is hosted by the National Center for Biotechnology Information, under accession numbers MK5
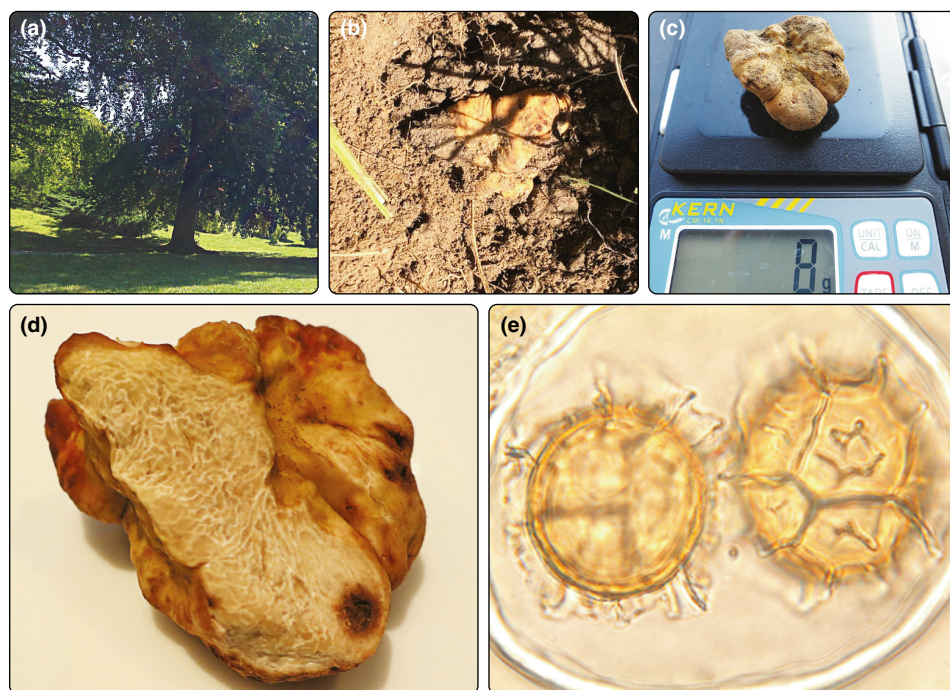
Figure 1. (a) A park in the city of Geneva, Switzerland (around 46°12′N, 06°08′E and 420 m above sea level), where 15 PWTs were found since 2012 in the vicinity of an old beech tree. (b) The half-excavated, in situ, fruiting body on 16 August 2018, which (c) weighed eight grams after cleaning and (d) contained a mature gleba with (e) microscopically visualized ripe spores.

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74864 and MK557927; specimens for DNA extraction are available at the Herbarium of ETH Zurich (ZT Myc 30425 and ZT Myc 59985).

Soil samples taken from the upper 20 cm next to the PWT detected on 16 August 2018 revealed biologically active soil (a carbon:nitrogen ratio of 8.5:1) with a moderate soil pH (H_2O) at 6.8, a low content in total calcium oxide (4711 mg CaO per kilogram of soil), and a very high concentration of magnesium oxide (424 mg MgO per kilogram of soil). Though growing in symbiosis with plants (Rubini *et al.* 2001), no *Tuber magnatum* mycorrhizae were detected at any of the fine root tips extracted from our soil samples, analyzed both morphologically and genetically. This finding agrees with our own observations from southwest Hungary and those from previous studies (Murat *et al.* 2005).

The first record of PWTs north of the Swiss Alps, where botanic, climatic, and edaphic (soil-related) conditions are comparable to those of the southern habitats, raises more questions than it provides answers. Do our findings imply a warming-induced range shift? Was the fungus already co-existing with its sym-biotic partners long before it produced fruiting bodies, or were the latter simply undetected? What are the biotic and abiotic requirements for fruiting body formation and maturation? What are the potential host species and the main vectors of spore dispersal? What is the species' eco-physiological plasticity and evolutionary origin? In addition to a better understanding of the molecular phylogeny and historical biogeography of the genus *Tuber* (Jeandroz *et al.* 2008), further insights are expected from genotyping numerous PWT fruiting bodies, together with genetic studies of northern and southern populations (Rubini *et al.* 2005). The genome sequence of the PWT (Murat *et al.* 2018) will offer new molecular markers to trace the origin of this species, down to single fruiting bodies.

The coincidence of an unusually early harvest in August 2018 and exceptionally warm and dry conditions over Europe during this period should inspire interdisciplinary research to continue exploring the various direct and indirect effects of climate change on the hidden truffle world (and its symbiotic plant partners) at different spatiotemporal scales.

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FrontiersEcoPics

Life, in a nutshell

While studying coconut crabs (*Birgus latro*) – the world's largest terrestrial invertebrate and specialized consumer of the iconic fruits of the coconut palm (*Cocos nucifera*) – on Chagos Archipelago in the Indian Ocean, I found hundreds of terrestrial hermit crabs (*Coenobita brevimanus*) living inside empty coconut shells, all leftovers from the coconut crabs. Despite having studied hermit crabs for over a decade at tropical locations around the world, I had never previously seen a hermit crab using a coconut as a shell. Notably, all these other tropical locations lacked coconut crabs, even though coconuts had been introduced by humans. The presence of coconut crabs seems to afford novel housing opportunities for hermit crabs. Coconut crabs access coconuts by completely tearing off the husk, then breaking a hole in the shell, out of which they scrape the white meat and leave behind a spherical shell cavity, nearly identical to the hollowed out, architecturally remodeled seashells preferred by terrestrial hermit crabs. The coconut shells that housed large hermit crabs on Chagos were orders of magnitude bigger and more spacious than most of the seashells inhabited by smaller hermit crabs. The large dimensions of coconut shells can therefore enable hermit crabs to grow to extreme sizes. Coconut shells are also lighter than the seashells, and come fully remodeled (without the inner spiral of seashells, which must be carved out when terrestrial hermit crabs remodel), so this saves the crabs substantial work. All these qualities (bigger, easier to carry, fully remodeled) make coconut shells potentially ideal homes. However, coconut crabs are known predators of smaller crustaceans, and given that coconut crabs originally opened up these shells, it is well within their capacity to break them open again to prey upon their new inhabitants. Thus, moving into these predator-provided shelters could entail a complicated cost–benefit calculus.

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