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Kathryn E Bushley

University of Minnesota Twin Cities

Yong-Ping Yang

Chinese Academy of Sciences

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Letter to the Editor

Regarding the social–ecological dimensions of caterpillar fungus (*Ophiocordyceps sinensis*) in the Himalayas – Reply to Shrestha and Bawa

Shrestha and Bawa's (2013) recent study has proliferated in popular media as evidence of a "rapid decline" in caterpillar fungus (*Ophiocordyceps sinensis*) abundance in Nepal due to trade-induced overharvesting. Drawing from field research in Tibetan Yunnan, China, from 2007–2011, and scientific literature on *O. sinensis*, we disagree that the data presented in Shrestha and Bawa's recent study unequivocally demonstrates that there is (1) an overall decline in caterpillar fungus abundances, and that (2) trade-induced over-harvesting is "almost certainly responsible for declining populations." Here we clarify that Shrestha and Bawa have usefully provided three *indications* that there is *potentially* an overall decline in fungal abundance, and it remains uncertain whether trade-induced harvesting influences caterpillar fungus abundance because research on the relative importance of asexual versus sexual reproduction in propagating new caterpillar fungus infections is lacking.

First, Shrestha and Bawa document a *per capita* decline in caterpillar fungus collection among harvesters in Nepal from 2007–2011, which they rightly clarify *does not indicate an overall decline* in caterpillar fungus because the number of collectors has increased during the same time period. Our field research in Yunnan from 2007–2011 has similarly found that harvesters have experienced a per capita decline during the past decade, which most harvesters attribute to the increased number of collectors, driven by rapid price increases.

Second, Shrestha and Bawa report a 28% decline in trade volume per trader from 2007–2011, but fail to clarify how the overall number of traders has changed during the same time period. If Nepal has seen a 900% - 2300% increase in price during the last decade, the number of buyers has likely consonantly increased, indicating that there has been a *per capita* decline in trade volume among traders but not necessarily an overall decline in caterpillar fungus.

Third, Shrestha and Bawa use official district and national level revenue figures from the Government of Nepal to substantiate their claim that there is a "sharp decline" in overall harvest of caterpillar fungus. While the authors note that there is likely a high uncertainty and margin of error in the official government reports of trade volumes due to the "secrecy" of the informal caterpillar fungus economy, they fail to elucidate how the formal figures are contingent upon whether traders use official channels and sell their volumes in Kathmandu or other government centers. Traders can alternatively sell their collections directly to Tibetan traders in harvesting areas, who likely offer higher prices.

Furthermore, contrary to Shrestha and Bawa's claim that fungal decline is due to overharvesting, it remains uncertain how increased harvesting influences caterpillar fungus viability. Shrestha and Bawa claim that harvesting "inhibits caterpillar fungus reproduction" based on their findings that 94.4% of 1257 sampled individuals were "reproductively immature" when they were harvested because they "lacked spores in their stromata at the time of harvest." Their interpretation is somewhat misleading: if collected individuals lack spores in their stromata at the time of collection, this indicates that harvesting precedes *sexual reproduction*. Like all fungi, however, the caterpillar fungus may propagate both sexually *and asexually*, and each reproductive pathway is independent of the other. Many fungi are known to reproduce primarily asexually with infrequent sexual reproduction.

While little is known about the ecology of the caterpillar fungus' asexual stage (anamorph) *Hirsutella sinensis*, it has been suggested that *H. sinensis* asexual spores (conidia) could play key roles in caterpillar fungus infections since it has been difficult to produce caterpillar-fungus infections in the laboratory by inoculating host larvae with *O. sinensis* sexual spores (ascospores) or mycelium alone. This suggests that environmental factors likely facilitate host parasitism. Host *Thitarodes* (Hepialidae) ghost moth larvae are root-boring and live underground in tunnels. Using gut content analysis, Lei et al. (2011) more frequently detected *H. sinensis* in larvae that were preferentially foraging on certain high alpine plant roots, and the authors conclude that it is possible that larval consumption of *H. sinensis* can lead to infection with *O. sinensis* and development of the caterpillar fungus fruiting body. Peng et al.'s (2013) recent soil analysis of *O. sinensis* DNA distribution further suggests that infection likely occurs in *Thitarodes* tunnels. These studies suggest that asexual reproduction and infection in subterranean habitat associations may play more significant roles in caterpillar fungus propagation than is currently understood.

While overall levels of caterpillar fungus may indeed be declining, more evidence is needed to justify the claim that caterpillar fungus is in "rapid decline" due primarily to overharvesting. Other factors such as global climate change, host *Thitarodes* population fluctuations and parasites may also influence fungal propagation and further long term integrated studies are needed to quantify changes in total abundance of the caterpillar fungus.

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Michelle O. Stewart
Department of Geography,
University of Colorado at Boulder,
Boulder,
CO 80309,
USA
E-mail address: Michelle.O.Stewart@colorado.edu

Kathryn E. Bushley
Department of Botany and Plant Pathology,
Oregon State University,
Corvallis, OR 97331,
USA

Yang Yongping
Kunming Institute of Botany,
Chinese Academy of Sciences,
Kunming,
China