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Title: Are ungulates in forests concerns or key species for conservation and biodiversity? Reply to Boulanger et al. (DOI: 10.1111/gcb.13899)

Running Title: Ungulates: concerns or key species?

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Boulanger et al. investigated the effect of ungulate grazing on forest understory plant community composition using exclosures in forests, mainly plantations, over a 10 year period. They found increasing richness of herbaceous plant species with grazing, promoting light-demanding species, while shrub richness decreased. Although grazing did not cause changes to forest-specialist species richness, the authors conclude that ungulate grazing - even at relatively low densities - is detrimental to forest-specialists, and contributes to a landscape-level biotic homogenization. Thus, they suggest ungulates to be of concern in biodiversity conservation.

Boulanger et al. assess the ecosystem effect using the current managed state of the forest as a baseline, i.e., more light-demanding species in the forest is a change of state and therefore also a concern. However, for biodiversity conservation, we would advocate for baselines informed by a macroecological and evolutionary perspective. Most of the current biodiversity in Europe has evolved in the Pleistocene or earlier (Lang, 1994), and in ecosystems markedly influenced by dynamic natural processes, including grazing (Coope, 2004; Kurtén, 1968; Sandom, Ejrnaes, Hansen, & Svenning, 2014; Svenning, 2002). With this baseline for European ecosystems, ungulate grazing must be considered a potential key instrument for biodiversity conservation. Applying this baseline to the study of Boulanger et al. would not necessarily have changed the analyses and results, but most likely the conclusions and

perspectives as regards the plant diversity dynamics in their study. More importantly, an evolutionary informed baseline may change the formulation of study questions and designs in the future. Ungulates and other large herbivores contribute to biodiversity by creating variation in abiotic conditions and diversification of resources, such as dead wood, dung, carcasses etc. Investigating biodiversity effects of ungulates therefore entails a broader aspect of biodiversity, including specialized fungi and insects etc. as well as quantifying the abiotic variation (Brunbjerg et al., 2017).

The study finds that "ungulates tend to favor ruderal, hemerobic, epizoochorous and non-forest species". However, the properties of plant species hitchhiking on ungulates are extremely dependent on the landscape matrix. Deer are important dispersal vectors for plant species, and if the landscape matrix is mainly farmland, ruderal plants will, of course, be introduced to forest fragments. In contrast, if deer were more or less restricted to natural areas, one should primarily expect dispersal of grassland and wetland herbs into forest glades. In addition, ruderal and hemerobic plant species that today are perceived as negative indicators of conservation status, actually occurred naturally in European landscapes throughout the Pleistocene (see Appendix B in Svenning (2002)), albeit likely at lower densities than in farmland.

Applying the evolutionary informed baseline render unjustified the concerns about increased prevalence of light-demanding plant species in forests, as such, unless it is at the large-scale expense of forest specialists. Many threatened species are associated with high-light forest environments such as forest glades and edges, as these have strongly declined at least partially due to the decline of large herbivores in European forests, first the wild species and more recently also free-roaming livestock. Notably, many declining and extinct butterfly species are associated with open woodland habitats (Eskildsen et al., 2015). Thermophilous saproxylic and coprophilic beetles, epiphytic lichens and rare tall herbs confined to the forest-

grassland ecocline, are favored by open grazed woodland with ancient trees, as are a suite of bird species (e.g., Bergmeier, Petermann, & Schröder, 2010). Hence, existing evidence points to moderate grazing in forests as an ecological baseline and conservation target rather than a concern. Therefore, results from highly managed forests landscapes focused on taxonomically or functionally narrow aspects of biodiversity, e.g., such as the focus on herbaceous plants and shrubs presented by Boulanger et al., should be considered with caution in relation to nature conservation. This said, field-based evidence on large-herbivore effects on overall biodiversity in contemporary intensively used landscapes are sparse, and further research is much needed.

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References

Bergmeier, E., Petermann, J., & Schröder, E. (2010). Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. *Biodiversity and Conservation, 19*(11), 2995-3014. doi:10.1007/s10531-010-9872-3

Boulanger, V., Dupouey, J.-L., Archaux, F., Badeau, V., Baltzinger, C., Chevalier, R., . . . Ulrich, E. Ungulates increase forest plant species richness to the benefit of non-forest specialists. *Global Change Biology*, n/a-n/a. doi:10.1111/gcb.13899

Brunbjerg, A. K., Bruun, H. H., Broendum, L., Classen, A. T., Fog, K., Froeslev, T. G., . . . Laessoee, T. (2017). A systematic survey of regional multitaxon biodiversity: evaluating strategies and coverage. *bioRxiv*, 158030.

Coope, G. (2004). Several million years of stability among insect species because of, or in spite of, Ice Age climatic instability? *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 359*(1442), 209-214.

Eskildsen, A., Carvalheiro, L. G., Kissling, W. D., Biesmeijer, J. C., Schweiger, O., & Høye, T. T. (2015). Ecological specialization matters: long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Diversity and Distributions, 21*(7), 792-802. doi:10.1111/ddi.12340

Kurtén, B. (1968). *Pleistocene Mammals of Europe*. London: Weidenfeld and Nicolson.

Lang, G. (1994). Quartäre vegetationsgeschichte Europas: methoden und ergebnisse.

Sandom, C. J., Ejrnaes, R., Hansen, M. D., & Svenning, J. C. (2014). High herbivore density associated with vegetation diversity in interglacial ecosystems. *Proc Natl Acad Sci U S A, 111*(11), 4162-4167. doi:10.1073/pnas.1311014111

Svenning, J.-C. (2002). A review of natural vegetation openness in north-western Europe. *Biological Conservation, 104*(2), 133-148. doi:http://dx.doi.org/10.1016/S0006-3207(01)00162-8

Figures

Figure 1. Examples of grazing in forests and its importance for biodiversity. Grazed woodlands (Løvenholm, Denmark, top-right and bottom-right and New Forest, England, bottom-left) with typical forest-species and light-demanding species in a mosaic with high biodiversity (Photo: Morten DD Hansen, Jacob Heilmann-Clausen, Jens-Christian Svenning). Veteran oak established c. 700 years ago in a grazed woodland and slowly withered away as

grazing ceased (top-left, Jægerspris, Denmark, Wikimedia commons public domain). Thermophilous Hermit Beetle (*Osmoderma eremita*, Photo: Magne Flåten, Wikimedia Commons, https://creativecommons.org/licenses/by-sa/3.0/, blended in using Office Picture Tools) and Noble chafer (*Gnorimus nobilis*, Photo: Morten DD Hansen) both associated with old trees and threatened by forestry and few remaining light-exposed veteran trees. Ilex Hairstreak (*Satyrium ilicis*) associated with oak woodlands and threatened by the disappearance of forest edges (Photo: L. B. Tettenborn, Wikimedia Commons, https://creativecommons.org/licenses/by-sa/3.0/, blended in using Office Picture Tools) and Heath Fritillary (*Melitaea athalia*, Photo: Morten DD Hansen) associated with forest glades and meadows (Photo: Morten DD Hansen). Minotaur Beetle (*Typhaeus typhoeus*, Photo: Morten DD Hansen) associated with forest glades, bare ground and lives primarily on ungulate dung.

Figure 1