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The role of wild ungulates in nutrient cycling in Mediterranean ecosystems: a pending issue

El papel de los ungulados en el ciclo de nutrientes en ecosistemas mediterráneos: una asignatura pendiente

Laura Barbero-Palacios[1], José Antonio Carreira[2], Elena Baraza[3], Jennifer Adams Krumins[4], Matthew Brolly[5], Niall G. Burnside[5], Jordi Bartolomé[6], Santiago Lavín[1], Juan Antonio Calleja[7,8,9], João Carvalho[10], Rita Tinoco Torres[10], Isabel C. Barrio[11], Ramón Perea[12] & Emmanuel Serrano[1*]

1. Wildlife Ecology & Health Group (WE&H) and Servei d'Ecopatologia de Fauna Salvatge (SEFaS), Departament de Medicina i Cirurgia Animals, Facultat de Veterinària, Universitat Autònoma de Barcelona (UAB), 08193 Bellaterra, Barcelona, Spain.
2. Departamento de Biología Animal, Vegetal y Ecología, Universidad de Jaén, 23071 Jaén, Spain.
3. Departament de Biologia, Universitat de les Illes Balears, 07071 Palma de Mallorca, Spain.
4. Department of Biology and Molecular Biology, Montclair State University, Montclair, NJ, USA.
5. School of Environment & Technology, University of Brighton, Lewes Road, Brighton BN2 4JG, UK.
6. Grup de Recerca en Remugants, Departament de Ciència Animal i dels Aliments, Universitat Autònoma de Barcelona (UAB), 08193 Bellaterra, Barcelona, Spain.
7. Universidad Autónoma de Madrid, Departamento de Biología (Botánica), 28049 Madrid, Spain.
8. Universidad Autónoma de Madrid, Centro de Investigación en Biodiversidad y Cambio Global, 28049 Madrid, Spain.
9. Centre de Recerca Ecològica i Aplicacions Forestals CREAF, 08290 Cerdanyola del Vallès, Barcelona, Spain.
10. Department of Biology & CESAM, University of Aveiro, Campus de Santiago, Aveiro, Portugal.
11. Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Árleyni 22, Reykjavik, IS-112 Iceland.
12. Departamento de Sistemas y Recursos Naturales, Universidad Politécnica de Madrid, 28040 Madrid, Spain.

*Corresponding author: emmanuel.serrano@uab.cat

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Since the end of the Second World War, wild ungulate populations have experienced a substantial increase in both their number and range in almost all European countries (Apollonio *et al.* 2010), an expansion facilitated by a decrease on traditional livestock activity, especially in southern Europe (San Miguel-Ayanz *et al.* 2010). A total of 23 different species of wild ungulates live in Europe, and as a consequence at least 12 million bison, deer, ibex and boar trample, defecate, urinate, graze, browse, transport seeds and drive plant recruitment within a range of ecosystems, shaping the vegetation structure and nutrient dynamics from the Tundra to the Mediterranean. Because of their number and impact, ungulates are probably one of the main ecological processes' drivers of the terrestrial ecosystems. Although the role of ungulates in nutrient cycling is beginning to be understood in other ecosystems, comparatively little is known about their impacts in the Mediterranean basin. The consequences that the increased numbers of wild ungulates will bring and whether they will substitute up to some point the environmental function of the extensive livestock is still a pending issue in this habitat.

Ungulates are ecosystem engineers

In the last decades ungulates have become increasingly recognised as ecosystem engineers (Gordon & Prins 2007), because their activity may trigger significant modifications in the composition and structure of plant communities, soil properties and below ground biodiversity. One of the main mechanisms by which ungulates drive ecosystem structure and functioning is through defoliation.

Defoliation of grasses (i.e., grazing) in fertile productive soils with a vegetal cover of palatable plants stimulates above and belowground biomass, enhancing root exudation and increasing nitrogen mineralization and plant uptakes (Bardgett & Wardle 2010). Conversely, similar levels of grazing in unproductive soils can result in catastrophic soil degradation (Fig. 1). In these scenarios, where nutrient rich and palatable plants are scarce, selective feeding usually modifies vegetation composition and structure and subsequently soil properties and nutrient cycling (Gordon & Prins 2007). Further, in high numbers, trampling by large herbivores can cause soil compaction and denude vegetation cover, exposing soils to erosion. Such effects have been widely reported for domestic ungulates, but less is known about the effect of high densities of wild ungulates on ecosystems. Ungulates also represent an important prey for large carnivores, allowing their natural expansion and minimizing their impact on livestock (Apollonio *et al.* 2010). Moreover, ungulates' carcasses provide an important food supply for scavengers and can cause concentrated pulses of nutrients into the soil (Bardgett & Wardle 2010 and references therein). Ultimately, because ungulates are primary consumers, they drive the fluxes of energy from primary production to the upper levels of the food chain and the cascading effects of their activity unleashes important top down and bottom up regulations on the ecosystem.

Figure 1. Adult male deer (*Cervus elaphus*) browsing a holm oak (*Quercus ilex*). Ungulates can affect vegetation composition, nutrient cycling, and soil biogeochemistry through multiple grazing behaviours. Illustration by Carlos García Poveda (Poveda & López 2018).

Ungulates as drivers of nutrient cycling and plant nutrient uptake

Historically, biogeochemistry has focused on the role of plants and microorganisms in regulating nutrient cycling in terrestrial ecosystems. It has taken a long time to recognise the role of animals in carbon and nutrient cycling (i.e., zoogeochemistry) by selectively feeding and browsing, disturbing soil properties, and releasing carbon and nutrients through excretion, egestion, and the decomposition of carcasses (Schmitz *et al.* 2018). The impacts that animal waste can cause on ecosystem biogeochemistry should be given special attention, due to the significant amount of biomass that it can represent, and its increased rates of decomposition, particularly when compared to litter. For example, a roe deer individual can produce 20 pellet groups per day (Acevedo *et al.* 2010); considering that densities above 0.21 deer/ha are common in central Spain, and that deer faeces contain around 2% of nitrogen (Hewison *et al.* 2009), that results in a release on the ground of 8g of N/ha. Although nutrient inputs from dung may be not high in terms of total land surface, and little is known about the total amount of nutrients translocated to the plants, these inputs occur in a highly concentrated where droppings accumulate, thus generating a strong effect at micro-meso-scale and contributing to heterogenized the environment. Therefore, ungulates play an important role in the transfer of these nutrients and in the creation of a spatio-temporal variability within ecosystems. At a landscape scale, wild ungulates migrate between distant regions, or perform seasonal migrations across elevations tracking the temporal variation on plant phenology and forage quality. At a finer scale, ungulates will select feeding areas, moving between patches where forage is more abundant or nutritious.

There are numerous ways in which herbivores affect nutrient fluxes and pool sizes within ecosystems, however, the carbon cycle has typically been the central focus due to the growing interest in climate change mitigation (ecosystem enhanced

C sequestration and reduced GHG emissions). Interestingly, wild ungulates have received scant consideration as part of the solution, yet their significant feedback effect on carbon cycling is becoming more evident (Schmitz *et al.* 2018). The omission of wild ungulates could result in substantial under or over-estimates in the capacity of ecosystems to sequester carbon. However, the mechanisms and magnitude of the effect of wild herbivores on nutrient cycling and soil chemistry are ecosystem-specific and operate at different spatial scales (Forbes *et al.* 2019).

Limited understanding in Mediterranean ecosystems

Although the role of ungulates in nutrient cycling is beginning to be understood in other ecosystems such as grasslands, temperate and boreal forests and Arctic tundra (Bardgett & Wardle 2010 and references therein), little information and understanding exists in Mediterranean biomes. Mediterranean ecosystems are highly complex habitats with elevated rates of erosion, poor soils, predominant sclerephilous vegetation and high frequency of short dry-rewetting pulses which affect organic matter decomposition and nutrient mineralisation (San Miguel-Ayanz *et al.* 2010). Examples of these Mediterranean-type ecosystems are predominant in the Iberian Peninsula. Although ungulate overabundance is common in many regions of the Iberian Peninsula, very little information exists on the role of increasing wild ungulates populations on nutrient availability and cycling in this region. Whether ungulates can ameliorate or exacerbate this process opens a new field of research and debate with strong implications for wider ecosystem management. The last report from the International Panel on Climate Change (Unite Nations 2019) highlighted that the Mediterranean was one of the most vulnerable regions to the impacts of climate warming and the capacity for soils to regenerate, and longer and more severe droughts are expected in the Iberian Peninsula in the next years. Observational and experimental studies on the role of ungulates on soil functioning and preservation are a pressing scientific issue, and these studies are acutely needed in the Iberian Peninsula.

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