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REVIEW ARTICLE

Endozoochorous seed dispersal by cattle—an option for species enrichment in deintensified grasslands?

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Cattle are relatively good endozoochorous seed dispersers. Could feeding cattle with the seeds of endozoochorous target species be used as a method to floristically enhance species-poor, de-intensified grasslands? Based on the five stages of seed dispersal, the possibilities and limitations of endozoochorous species establishment are outlined. The process of establishment after cowpat deposition involves a multitude of imponderables due to the multifactorial structure of the effects. Nevertheless, a number of authors report encouraging findings regarding seedling establishment from cattle feces under field conditions. The methods available for introducing target species into species-poor grasslands are summarized, and a seed-feeding method is classified with respect to the existing range of measures. The new procedure is cost-effective and could be incorporated into the grazing system as a repeatable routine. A number of open questions are addressed, the exploration of which could help optimize the process and better assess the chances of success.

Key words: endozoochory, restoration success, seed feeding, seed transfer

Implications for Practice

- Cow dung offers a number of properties (consistency, large surface area, comparatively low mortality rates of the contained seeds) that make the process of targeted seed transfer using grazing cattle interesting for practical use.
- Direct seed feeding to grazing animals makes the method independent of seed ripening time and species abundances in donor plots.
- However, optimization of the process and a more comprehensive scientific analysis of the limiting constraints during the establishment process are still needed to assess its practicality.

Introduction

Intensification of grassland use in the past has contributed to species impoverishment in Europe (Busch et al. 2019). Subsequent extensification will not necessarily result in the desired short- to medium-term restoration success if the target species are no longer present in the current vegetation or soil seed bank (Bakker & Berendse 1999). From a conservation perspective, the use of native species is recommended in these cases. Common methods include seeding autochthonous wild species or transferring mown material from species-rich target vegetation (Kiehl et al. 2010). Endozoochorous species transfer (i.e. dispersal of diaspores via digestion and fecal excretion by animals) has played a little role as a targeted restoration tool so far due to comparatively high seed loss rates. However, cattle, as endozoochorous seed dispersers, may offer some advantages. They are common grazing animals in many countries around the world and can be deployed over large areas. On average, more diaspores survive intestinal passage in cattle than in horses, sheep, or goats (Bonn & Poschlod 1998). Softer feces, such as cattle dung, help seeds to survive (Lennartz 1957). Cow dung has good water retention, which is important for seed germination (Mouissie et al. 2005). The cow dung pat covers, on average, a large contiguous area of approximately 600 cm^2 (Marsh & Campling 1970). Studies on deer, sheep, and cattle in New Zealand showed that deer and sheep dung decomposed after only a few weeks, but cow dung had only visibly disappeared from the surface after 12 months (Williams & Haynes 1995). The size and delayed decomposition of cow dung pats may reduce aboveground plant biomass and lead to gap formation (Malo & Suarez 1995), increasing the chances of establishing species transmitted by zoochory provided that the positive effects outweigh the negative side effects, which I will discuss below. The above aspects indicate the potential chances of success of endozoochory in cattle. Targeted feeding of germinable seeds from typical grassland species could provide an opportunity to improve the botanical diversity in species-poor grasslands. A distinctive feature of cow dung is the formation of a hard dry crust on the surface of cowpats (Weeda 1967), which may have negative effects on the germination and development of endozoochorous seeds in the dung (Milotić & Hoffmann 2016a). Similarly, horse dung can also cover a large area but is less prone to dry surface crusting because of its fibrous structure (Milotić &

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Hoffmann 2016a). However, these advantageous characteristics are hindered by the specific grazing behavior of horses such as deep and pronounced selective browsing and latrine behavior, which means the deposition of feces in tall sward areas that are then avoided (Fleurance et al. 2022). This type of grazing behavior may reduce the chances of germinable seeds establishing in horse dung. Free-ranging wild mammals such as fallow deer and roe deer also have high potential for endozoochorous seed dispersal; this potential is lower for forest species and greater for grassland and ruderal species (Heinken et al. 2002). In principle, the idea of adding seed to wildlife feed is also possible. In this article, however, I will limit my discussion to grasslands, where agricultural wildlife management has been more of a niche practice. For the above reasons, cattle have been selected as the model species for the proposed seed-feeding process. Endozoochorous species transfer is a multistage process. To understand this process, identify research gaps, and assess application strategies, the main stages and special features of the dispersal process are outlined below.

Stages of the Endozoochorous Dispersal Process

Wang and Smith (2002) developed a scheme of animal-mediated seed dispersal and recruitment in terms of a loop. The approach was very comprehensive, including different animal species, habitats, and types of zoochorous seed dispersal. Following the idea of a schematic presentation, I have outlined the main stages and their influencing factors that are important for the process of endozoochorous dispersal and establishment on cattle pastures (Fig. 1). In contrast to Wang and Smith, the process proposed here is not considered a cyclic system, but it ends with the successful germination and establishment of seeds dispersed by zoochory. This is justified by the fact that seeds in the proposed process are supplemented. The steps of the process are explained in more detail below.

(1) *Grassland growth and seed development*.

It is well established that the abundance of seeds in vegetation is the determining factor in the number of seeds ingested and the number of germinable seeds in feces (Bonn 2004; Bruun & Poschlod 2006; Albert et al. 2015a). Studies of grazing herbivores have revealed a trend toward a negative correlation between seed release height and seed quantity in feces (Bonn 2004; Bakker et al. 2008; Stroh et al. 2012). In addition to the natural occurrence of diaspores in grassland vegetation, there is also seed material introduced into the dispersal process by supplementary feeding. This exogenous seed source is the focus of the present study. Feeding seeds of typical grassland species to cattle is aimed at the species enrichment and diversification of species-poor grasslands. When species of the pasture reach seed maturity, seeds of the existing vegetation would be eaten by the grazing animals, creating a competitive situation with the externally fed seeds during the stage of seedling establishment in the cow dung.

(2) *Intake of seeds by grazing cattle*.

Feed preferences determine how many and which seeds are ingested (Gilhaus et al. 2017). This also influences the competitive situation for seedling establishment in cowpats (see stage 1). Cattle graze less selectively than sheep, goats, or horses, especially with regard to preference for the leaf and stem parts of a plant (Matches 1992). The chewing and digestion process increases the mortality of the seeds or affects their ability to germinate.

(3) *Seed passage*.

After feed intake, the seeds are first exposed to damage from chewing (Gardener et al. 1993). Exposed to anaerobic conditions, a low pH of 2.5, and proteolytic and cellulolytic enzymes in the digestive tract of grazing animals, seeds are subjected to severe stress conditions that not all species can survive (Gardener et al. 1993). Intestinal passage has been regarded as a particularly critical stage for seed survival (Cosyns et al. 2005b). There has been no shortage of attempts to relate different morphological seed characteristics to the digestive resistance of seeds in order to develop models for estimating germinable seeds in feces. Feeding experiments have yielded contradictory results. The numerous studies on this topic are not discussed here. A possible explanation for these contradictory results could be multifactorial dependencies between mortality rates and different traits (D'hondt & Hoffmann 2011). It is undisputed that hard-shelled seeds survive much better than softer seeds (Neto & Jones 1987; Gardener et al. 1993). However, there are also species whose seeds have better germination rates after passing through the digestive tract (Samuels & Levey 2005). In grasslands, this effect occurs mainly in species with hard and impermeable seeds, such as legumes (Russi et al. 1992). The retention time of seeds in the digestive tract of cattle ranges from 8 to 10 hours to a maximum of 8–10 days, with the majority of excreted seeds after 1–3 days (see table 40 in Bonn & Poschlod 1998). Forage quality and seed traits influence the retention time (Jones & Neto 1987; Gardener et al. 1993; Cosyns et al. 2005b). Increased forage quality (i.e. digestibility) of the forage shortens the retention time.

(4) *Dung deposition*.

According to findings by White et al. (2001), the density of fecal deposition is correlated with the length of stay of cattle. Resting places of livestock are therefore preferred endozoochorous dispersal sites (Welch et al. 1990). Studies in cattle have also shown that fecal deposition reflects habitat preferences (Cosyns et al. 2005a; Kohler et al. 2006). However, adapted management practices could cause a more even distribution of cowpats; e.g. a rotational grazing system with subdivision into smaller paddocks. The rotational system has to be adapted to the retention time of the seeds (see above).

(5) *Seed germination and seedling establishment*.

Stages 3 and 5 are the "bottlenecks" in the endozoochorous dispersal process. While many studies have been conducted on Stage 3, there are still gaps in knowledge with respect to stage 5. Many publications to date have focused on the determination of germinable seed content in animal feces, which does not yet allow conclusions to be drawn about the actual establishment success of species. As a result, the contribution of endozoochory to seedling establishment has often been overestimated (Pakeman & Small 2009; Karimi et al. 2020). Nevertheless, a number of authors report encouraging findings regarding seedling establishment from cattle feces under field conditions (e.g. Spain: Malo & Suarez 1995; Traba et al. 2003; Netherlands: Mouissie

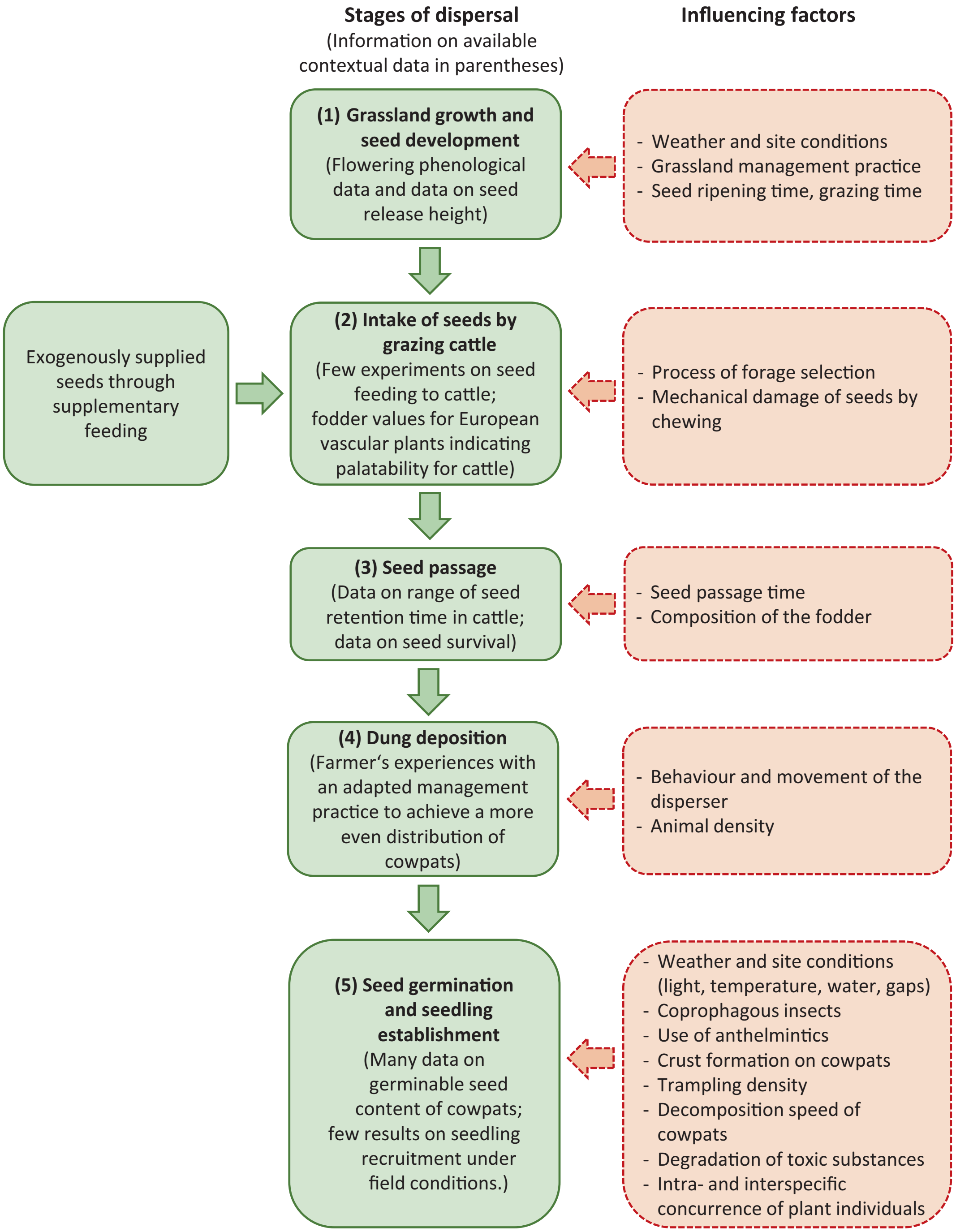

Figure 1. Stages of the endozoochorous dispersal process and influencing factors.

et al. 2005; Germany: Hofmann et al. 2007). Notably, observations of cowpat colonization may be associated with uncertain discrimination regarding the origin of the plants (soil seed bank, current vegetation, or seeds in feces).

Research from past decades has shown that the establishment success of seeds from feces depends on a variety of factors. Colonization of cowpats by plants depends strongly on the rate of fecal decomposition. Older studies showed that the main factors in fecal decomposition are microbial degradation, weather conditions, exposure to invertebrates and birds foraging for insect larvae, and consumption and removal of feces by insects (mainly dung beetles) and earthworms (reviewed in Marsh & Campling 1970). The use of anthelmintics to control livestock parasites has a negative effect on these insects (Beynon et al. 2012). In addition, Eichberg et al. (2016) reported a negative effect of anthelmintics on seed germination in three tested grassland herbs. The more liquid dung patches with a higher water content decompose more rapidly (Weeda 1967). The consistency of cattle dung can vary considerably as a result of differences in feed and physiological status of the animals (Dickinson et al. 1981). A distinctive feature of cattle dung is the rapid crust formation on the surface of cowpats during dry, warm weather, which significantly delays decomposition and lowers the leaching effect of rainwater (Weeda 1967). Under the Atlantic climatic conditions of England, cowpats deposited in early fall decomposed more rapidly than those deposited in spring, whereas decomposition in summer depended on variable rainfall during that season (Dickinson et al. 1981). Wetter weather conditions resulted in more rapid decomposition of cowpats. The displacement of seeds into the soil close to the surface caused by trampling can also promote establishment (Rotundo & Aguiar 2004; Eichberg et al. 2005). This impact has been demonstrated predominantly at dry sites, while cattle trampling has not been equally effective for species colonization in wet lowland pastures (Stammel & Kiehl 2004). However, trampling could break up the crust of the cowpats and thus contribute to the acceleration of dung decomposition. The extent to which this process influences the establishment of zoochorous seeds on wetter sites has hardly been investigated. Species with higher Ellenberg N indicator values appeared to germinate more readily in dung under field conditions (Mouissie et al. 2005). However, it should be noted that under natural grazing conditions, the seed proportions of the species ingested by the animals are not equivalent, as would be possible in an exact seed feeding experiment. Other studies have shown that the openness of grassland swards is of great importance for the establishment success of germinated seeds (Malo & Suarez 1995; Cosyns et al. 2006). In this context, gap size has a differentiating effect on recolonization (Bullock et al. 1995). In semiarid environments, significantly more species germinate on thin-layered cowpats than on thick-layered cowpats (Malo & Suarez 1995; Gokbulak & Call 2004). In the rainy Scottish moorland, pat thickness had no effect on the number of plants on cowpats (Welch 1985).

Germination conditions in dung are complex. On the one hand, the cover of cowpats helps to eliminate competition from extant swards and may exert a beneficial fertilizing effect on seedlings (Olff & Ritchie 1998). On the other hand, dung also extends the time until seedlings emerge (Milotić & Hoffmann 2017) because it contains toxic and germination-inhibiting substances (Marambe et al. 1993; Edney & Rizvi 1996); therefore, rapid dung decomposition could promote seedling establishment. Moreover, different feeding strategies can considerably affect the phytotoxicity of dung (Hoekstra et al. 2002). Studies of seeds added to dung have suggested that the growth-promoting benefits of dung deposition are not apparent for most species until later life stages (Milotić & Hoffmann 2016b).

Endozoochory as a Restoration Tool

The individual stages of endozoochorous seed dispersal act as a selective species filter. This reveals the potential and limitations of endozoochory with regard to its use in grassland restoration. The filtering effect of stages 1 and 2 can make direct endozoochorous seed transfer by grazing a species-rich donor grassland and subsequently moving the animals to the target site inefficient. For a potentially effective transfer, donor species would need to be abundant, have produced many seeds at the time of grazing, and, where possible, be preferred as forage by grazing herbivores. However, these difficulties can be overcome by feeding the seeds of the target species directly to the grazing animals. This would also have the advantage of allowing the post-ripening process required for some species to break physiological dormancy (Baskin & Baskin 2014) to no longer have a limiting effect on dispersal events. Not every species can be spread by endozoochory. Data on the endozoochorous dispersal potential of many species are available for northwestern Europe (e.g. Will & Tackenberg 2008; Albert et al. 2015b). Endozoochory information on a variety of species is also available in the LEDA database (Kleyer et al. 2008). These data can be used to assess the chances for plant species to have successful endozoochorous dispersal and to select seeds that are appropriate for feeding to cattle. According to research by Baasch et al. (2016), regionally propagated target species should be preferred due to their better establishment success. Some seeds, such as hard and impermeable legume seeds, have germination advantages during the digestion process (Neto & Jones, 1987; Russi et al. 1992; Gardener et al. 1993). However, in many cases, the passage through the digestive tract and exposure to digestive enzymes result in reduced seed viability (Cosyns et al. 2005b; Milotić & Hoffmann 2016c), which raises the question of the advantage of endozoochorous transfer over direct seeding. Notably, seeding involves expenses, requires ground preparation, and sometimes must be repeated if weather conditions are unfavorable for seed establishment. The method of seed feeding, on the other hand, can easily be repeated the following year if the weather conditions are unfavorable. Complete removal of previous vegetation is usually undesirable for nature conservation and environmental protection related reasons. Therefore, of the many seeds sown, very few will become established under the competitive pressure of the existing vegetation. Soil disturbance, e.g. by power harrowing, improves the seedling establishment (Edwards et al. 2007). Hofmann et al. (2007) found only minor differences in seedling emergence between seeds from overseeding and seeds fed to animals. This could be explained by the negative influences of mastication and digestion being compensated by the more favorable establishment conditions (reduced competition from extant vegetation by cowpat covering and the establishment-promoting nutrient supply). Repeated seed feeding to grazing animals requires little effort. The animals spread the seeds by themselves. Cowpats scattered on the paddock are initial sites for further spread. Many grassland species are perennial and have runners (Huyghe et al. 2008). Few but well-distributed seedlings over the pasture may be sufficient to initiate colonization. Another advantage is that it is easy to vary the application time according to the needs of the species. Whether seed feeding to cattle is a practical method for species enrichment in grasslands depends on further testing and optimization of the process. Adding seeds of the target species to animal feed could be impractical and wasteful if the seeds become segregated from the feed. An adhesive is therefore needed to prevent this segregation. A suitable agent for this purpose would be molasses from the sugar industry. In addition, molasses also has a beneficial effect on the digestibility of feed in ruminants and improves feed intake (Mordenti et al. 2021). Because of the negative effects mentioned above, anthelmintics should not be used just before or after seed feeding.

Other Existing Techniques of Seed Introduction and Possible Applications for the New Method

With the decline of species-rich grassland habitats and increasing efforts to restore species diversity, various methods have been developed over the last three decades to specifically introduce species from extensively used grasslands. These methods and techniques have been described in various review articles (e.g. Klimkowska et al. 2007; Hedberg & Kotowski 2010; Kiehl et al. 2010; Török et al. 2011; Scotton et al. 2012) and are therefore listed only briefly here.

(1) Seeding of target species: direct seeding or slot seeding by a sowing machine;
(2) Transfer of seed-containing fresh or dry hay from a species-rich donor site to a recipient site;
(3) Planting juveniles is a recommended method of introducing rare species.
(4) Transfer of turves or seed-containing topsoil from a donor site.

The success of these measures depends on the initial conditions and soil preparation. On bare soils, seedlings are not exposed to the competitive pressure of preexisting vegetation. Therefore, the success of species introduction is usually better on open ex-arable fields than on grassland sites (Donath et al. 2007). Sufficient soil disturbance, especially in lowland grasslands, is considered essential (Pywell et al. 2007; Schmiede et al. 2012; Bischoff et al. 2018).

The transfer of fresh hay obtained from suitable species-rich donor grasslands is considered a very promising measure for the establishment of new target species (Buchwald et al. 2007; Bischoff et al. 2018). The transferred plant material also provides protection against desiccation of seeds and seedlings (Donath et al. 2007). However, the use of this method is limited by the insufficient availability of suitable donor communities and by different dates of seed maturity for different species; thus, the entire spectrum of the desired species is usually not present in the hay or some species are present only in low quantities. Therefore, a combination of hay transfer and sowing is recommended (Török et al. 2012).

In general, nonregional herb seeds and seeds of highly competitive cultivars should never be used for the restoration of species-rich grasslands (Conrad & Tischew 2011). During the establishment phase of the introduced species in the first year, clearing the plant stands by frequent mowing is important for the successful establishment (Hofmann & Isselstein 2004; John et al. 2016). With regard to the endozoochorous seed dispersal, a short sward in the following year would also be advantageous to avoid shading effects on seedlings of the cowpats.

The cost range of restoration measures is very wide. Their selection will have to be made on a project-by-project basis, depending on the site conditions, availability of propagules or donor sites, and availability of funds (Török et al. 2011). Very expensive measures, such as topsoil removal, have a high chance of success, but are only possible in small areas due to the high costs involved. Török et al. (2011) proposed a differentiated approach depending on the size of the area to be restored: In very large areas, low-cost, low-diversity seed mixtures are used. Smaller areas, on the other hand, are suitable for more expensive, high-diversity seed mixtures combined with more intensive soil tillage. The authors proposed a combined procedure involving sowing low-diversity mixtures in a large area and high-diversity mixtures in small blocks to create biodiversity hotspots for further colonization.

Now the proposed method of seed feeding can be evaluated in comparison with the other methods. This method is intended to complement existing methods for larger grassland areas. It also uses less expensive, low-diversity mixtures, but the species spectra of these mixtures are adapted to endozoochory. The procedure is cost-effective and less labor-intensive, does not require the use of machinery, and could be incorporated into the grazing system as a repeatable routine. Compared to the transfer method of green hay, seed feeding to cattle is independent of seed ripening time and is not dependent on the availability of species-rich donor areas, as regionally adapted wild seeds can be purchased commercially. The new procedure could be preferred on sites where preparatory ground tillage is not desirable (e.g. peatlands). The seed-feeding method can also be combined with the method of sowing high-diversity mixtures on small disturbance gaps within a large paddock (see Valko et al. 2016).

Further Need for Research

Important questions remain to be answered: How does the rate of dung decomposition affect the establishment process? At what stage of decomposition do the germination-inhibiting properties of cattle feces disappear and the positive fertilizing effects predominate? Under which climatic and site-specific conditions is enrichment of endozoochorous species most promising? Which boundary conditions are critical for establishment success (weather conditions, crusting of the cowpat, etc.)? What is the most favorable transfer time for each donor species to achieve a high establishment rate? To what extent are species with low N indicator values (compared to species with high N values) disadvantaged in phase 5 of the establishment process? Ideally, species not found in the experimental paddock should be tested. This will help to verify the origin of the species dispersed by endozoochory. The necessary investigations should be carried out under natural conditions and, if possible, at several test sites in order to obtain valid and transferable results.

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