



Large herbivores affect forest ecosystem functions by altering the structure of dung beetle communities



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ABSTRACT

Dramatic increases in populations of large mammalian herbivores have become a major ecological issue, particularly in the northern hemisphere, due to their substantial impacts on both animal and plant communities through processes such as grazing, browsing, and trampling. However, little is known about the consequences of these population explosions on ecosystem functions. Here, we experimentally investigated how the population density of sika deer (*Cervus nippon*) in temperate deciduous forest areas in Japan affected the decomposition of mammal dung by dung beetles, which is a key process in forest ecosystems. We measured a range of environmental variables (e.g., vegetation cover, soil hardness) and the dung decomposition rate, measured as the amount of deer dung decomposed during one week, and sampled dung beetles at 16 study sites with three different deer densities (high/intermediate/low). We then used structural equation modeling to investigate the relationships between deer density, environmental variables, the biomass of dung beetles (classified into small or large species), and the dung decomposition rate. We found that the biomass of small species increased with increasing deer density, whereas that of large species was not related to deer density. Furthermore, the dung decomposition rate was positively related to the biomass of small species but unrelated to that of large species. Overall, our results showed that an increase in deer density affects the decomposition rate of mammal dung by changing the structure of dung beetle communities (i.e., increasing the number of small dung beetles). Such an understanding of how increases in large herbivore populations affect ecosystem functions is important for accurately evaluating the ecological consequences of their overabundance and ultimately managing their populations appropriately.

1. Introduction

Dramatic increases in populations of large mammalian herbivores (hereafter, large herbivore overabundance) have become a major ecological issue, particularly in the northern hemisphere (Côté et al., 2004; Fuller and Gill, 2001; Takatsuki, 2009), due to the resulting impacts on the structure, dynamics, and processes of forest ecosystems. For example, large herbivores alter the vegetation structure and composition through browsing and bark stripping (Akashi and Nakashizuka, 1999; Rooney, 2009), with the former inducing the loss of vegetation cover and the dominance of non-palatable plant species (Rooney, 2009; Suzuki et al., 2013), and the latter leading to dieback of overstory trees (Akashi and Nakashizuka, 1999). In addition, trampling by large herbivores affects soil properties, such as hardness and saturation capacity (Kumbasli et al., 2010), and large herbivore overabundance can affect other animal species (e.g., insects and birds) by reducing the availability of food resources and changing the condition of their habitat –

the so-called “cascade effect” (Allombert et al., 2005; Iida et al., 2016a; Teichman et al., 2013).

An increase in the abundance of large herbivores can not only change the structure and composition of biological communities but can also alter the ecosystem functions that they provide (Côté et al., 2004; Takatsuki, 2009). Indeed, it is generally agreed that the alteration of biological communities, such as a decrease in functional diversity and a change in species composition, is closely linked to an ecosystem's functional ability (Elmqvist et al., 2003; Larsen et al., 2005; Naeem and Wright, 2003; Snelgrove et al., 2014; Sugiura et al., 2013). However, to date, few studies have directly investigated the effect of large herbivores on both biological communities and their ecosystem functions (Niwa et al., 2011; Stark et al., 2010; Suzuki and Ito, 2014; Vanbergen et al., 2014), particularly under natural environmental conditions in forest systems.

Insects have a wide range of ecosystem functions in forests that are crucial to maintaining ecosystem stability, including pollination, seed

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dispersal, nutrient cycling, and carcass decomposition (Brew et al., 1989; Kevan and Baker, 1983; Koike et al., 2012; Sugiura et al., 2013). Previous studies have shown that insects are one of the most likely taxa to be affected by large herbivore impacts (Iida et al., 2016a; Melis et al., 2007; Stewart, 2001; Teichman et al., 2013). For example, Teichman et al. (2013) reported that increasing ungulate densities led to a decrease in the abundance of butterflies (*Papilio canadensis*), which utilize understory vegetation as the main food resource, presumably due to resource competition and habitat destruction. Melis et al. (2007) also reported that the regional heterogeneity (β diversity) of carabid beetles decreased as the browsing pressure of moose (*Alces alces*) increased.

The decomposition of mammal dung is a key process in forest ecosystems that is largely performed by insects (Didham et al., 1996). Dung beetles are one of the main taxa involved in dung decomposition (Nichols et al., 2008), with both the larval and adult stages consuming the dung of other animals. Dung beetles break down fecal matter and often by burying it, which contributes to the transport of essential nutrients into the soil (Bertone et al., 2006; Yamada et al., 2007) and soil mixing (bioturbation) (Brown et al., 2010; Nichols et al., 2008). Dung beetles can also act as secondary seed dispersers as they bury some of the seeds that are present in dung in the soil, reducing the probability of seed predation by rodents and preventing drying (Koike et al., 2012).

An increase in the abundance of large herbivores can have both positive and negative effects on dung beetle communities, as large herbivores provide food resources (i.e., dung) to dung beetles (Iida et al., 2016b) but also change the vegetation and soil properties through browsing, which is likely to degrade the habitat conditions for dung beetles (Barbero et al., 1999; Davis et al., 2014). It is known that the magnitude and direction of dung beetle responses to an increasing abundance of large herbivores depends not only on the magnitude of the increase (see Kanda et al., 2005) but also on the life-history and ecological traits of the dung beetles, such as their feeding behavior and body size (Iida et al., 2016b; Koike et al., 2014). For example, large species are often more susceptible to the impacts of large herbivore overabundance than small species (Iida et al., 2016b; Jankielsohn et al., 2001).

Understanding how ecosystem functions respond to an increased abundance of large herbivores is essential for improving predictions of ecosystem responses to large herbivore overabundance and ultimately managing and conserving these forest ecosystems. Here, we experimentally examined how the density of sika deer (*Cervus nippon*) affects the decomposition of mammal dung by dung beetles in deciduous forest areas in Japan, where the deer population has continuously increased since the late 20th century (Uno et al., 2009), leading to the degradation of forest ecosystems, including soil erosion (Sakai et al., 2011) and the extinction or decline of several plant species (Takatsuki, 2009). We used path analysis to untangle the causal relationships between an increase in deer abundance and dung decomposition, in which we considered several pathways (Fig. 1): first, that changes in the structure of the understory vegetation and soil properties due to an increase in deer density (Fig. 1A) would modify the habitat environments for dung beetles (Fig. 1B; Barbero et al., 1999; Davis et al., 2014) and that canopy openness would also influence the structure of the understory vegetation (Fig. 1C; Tinya et al., 2009); second, that deer density would affect dung beetle communities directly through the provision of food resources (Fig. 1D; Stewart, 2001); and third, that the alteration of dung beetle communities would influence their ability to decompose dung (Fig. 1E). Since the strength of these effects can vary with the body size of dung beetles (Nichols and Gardner, 2011; Nichols et al., 2013), we expected that the response to an increased deer density would differ between beetles with different body sizes (Iida et al., 2016b; Jankielsohn et al., 2001; Koike et al., 2014).

2. Materials and methods

2.1. Study sites

This study was conducted in the Ashio-Nikko mountain area in central Japan (Fig. 2). We established 16 study sites in this region (Fig. 2), all of which were located in deciduous forest areas covered by deciduous trees (Fig. 2), dominated by *Quercus crispula*, *Acer mono*, and *Carpinus japonica*. These sites were located at 850–1450 m above sea level, with an average altitude of 1120 m. Several medium–large mammalian species are found in this region, including sika deer, Asiatic black bear (*Ursus thibetanus*), Japanese serow (*Capricornis crispus*), Japanese monkey (*Macaca fuscata*), and raccoon dog (*Nyctereutes procyonoides*).

The 16 study sites were separated into three categories according to deer density: high (> 15 deer/km²; $n = 6$); intermediate (6–15 deer/km²; $n = 5$); and low density (< 5 deer/km²; $n = 5$) (Fig. 2). Deer densities in this region have been maintained at a nearly constant level for more than 10 years (Tochigi Prefecture, 2017a), based on data derived from the Japanese Ministry of the Environment (2015). We established several study plots within each study site (5 m radius, $n = 3$ –8 depending on the area of the site), which were at least 300 m apart to minimize or eliminate the possibility of trap interference (see Larsen, 2005), giving a total of 30, 26, and 25 plots for sites with high, intermediate, and low deer densities, respectively. A preliminary analysis found no evidence of spatial autocorrelation in the data across the 21 sampling sites so we treated the data from each site as a spatially independent sample in all subsequent analyses.

2.2. Environmental conditions

In each study plot, we measured canopy openness and soil hardness from July to September, and understory cover in July (Fig. 1). To measure canopy openness, we took one hemispherical photograph from the center of each plot using a digital camera equipped with a fish-eye lens and then calculated the percentage of canopy openness using the CanopOn-2 software (Takenaka, 2009). To measure understory cover, we measured the percentage of understory vegetation cover in one subplot (1 × 1 m) per plot. We measured soil hardness at 20 or 25 different points in each study plot with a pocket penetrometer, using the penetration resistance, which ranges from 0.00 to 1.95×10^6 kPa, as an index, and then calculated the average value.

2.3. Dung decomposition rate

We measured the rate of dung decomposition (i.e., the amount of deer dung decomposed during one week) by dung beetles between late August and mid-September 2016, during which time adult dung beetle activity is most intense (Hoga, 1982; Imura and Yamada, 2011; Sonobe, 1973). Among the large mammals that inhabit this region, sika deer has one of the largest population sizes, second only to Japanese serow (Gumma Prefecture, 2016, 2017a, 2017b; Tochigi Prefecture, 2015, 2017a, 2017b). Therefore, we placed 50 fresh deer pellets on the ground in each study plot, which is equivalent to the average number of pellets per single defecation by a deer (Horino and Nomiya, 2008). Fresh pellets were collected at the deer farm in Hokkaido, northern Japan, before the experiment. Pellets were identified as fresh if they were soft with a shiny surface and without any signs of decomposition or activity of dung beetle. To prevent animal disturbance and dung breakage by rain, we covered the deer pellets with a plastic mesh cage and roof, the side of which contained a hole of approximately 30 × 60 mm to allow dung beetles to access the dung. Since the largest dung beetle species in Japan has a body length of approximately 25 mm (Ueno et al., 1985), we considered that this plastic mesh cage was unlikely to prevent dung beetles from accessing the dung. We assessed the rate of dung decomposition by counting the number of pellets that

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