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Early-stage ecological influences of population recovery of large mammals on dung beetle assemblages in heavy snow areas

Hiroto Enari[a,*], Shinsuke Koike[b], Haruka S. Enari[a], Yoshikazu Seki[c], Kei Okuda[d], Yuuji Kodera[e]

[a] Yamagata University, 1-23 Wakabamachi, Tsuruoka, Yamagata, 997-8555, Japan
[b] Tokyo University of Agriculture and Technology, 3-5-8 Saiwai, Fuchu, Tokyo, 183-8509, Japan
[c] Tamagawa University, 6-1-1 Tamagawa Gakuen, Machida, Tokyo, 194-8610, Japan
[d] Hiroshima Shudo University, 1-1-1, Ozuka-higashi, Asaminami-ku, Hiroshima, 731-3195, Japan
[e] Utsunomiya University, 350 Minemachi, Utsunomiya, Tochigi, 321-8505, Japan

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ABSTRACT

Past conservation initiatives and rapidly decreasing human populations in modern Japan have contributed to population recoveries of Sika deer (*Cervus nippon*), wild boar (*Sus scrofa*), and Japanese macaque (*Macaca fuscata*) throughout the country. Ironically, however, these recoveries have not always received a favorable reception, because these mammals can also be agricultural pests. To open public debate on the recoveries, based on a thorough understanding of their multifaceted roles in sustaining the local ecosystem, we evaluated the initial stage ripple effects caused by the mammalian population recovery on the community assembly of dung beetles, which are keystone decomposer organisms in terrestrial ecosystems. For the evaluation, we conducted manipulative snapshot experiments, using camera and pitfall traps, for mammal and dung beetle assemblages, respectively, in four different mountain ranges within the heavy snow areas of northern Japan, where the recovery of three mammal populations was at an early stage. The current findings implied that, although the feces of every recovering mammal species could provide valuable resources for most beetles, the ripple effects from the mammal population recoveries were subject to hysteresis of the local ecosystem, i.e., catastrophic shifts in ecosystems originating from the historical background of regional mammal defaunation. In particular, the abundance of tunnelers that could benefit from positive ripple effects decreased with an increase in past disturbances, which resulted in *emptier forests*, i.e., an ecosystem with fewer large mammals. The findings suggested that recovering populations of large mammals do not always contribute to the restoration of the original dung beetle communities, at least initially.

1. Introduction

As part of the recently growing trend for biodiversity conservation, there are several cases where the recovery of vulnerable or extinct mammal populations in their native ranges has been a success of ecological conservation or restoration initiatives (Morrison, 2009; Steinmetz et al., 2010). However, the recovery of populations could also lead to discord among various stakeholders, if the species also functions as an agricultural pest, or ecosystem engineer, that creates irreversible environmental changes inconsistent with our modern way of life (Augustine and Frelich, 1998; Morzillo et al., 2007; Olson et al., 2015). Japan is a typical country facing such a dilemma. In addition to past conservation initiatives, the rapidly declining human population throughout the country has become a strong driving force for recovering various native large mammals that were once threatened with extinction owing to massive human disturbances (i.e., excessive hunting and forest exploitation); as a result of those recoveries, unprecedented human-wildlife conflicts have begun to occur in recent years (Enari and Suzuki, 2010; Sakurai et al., 2013; Ohashi et al., 2016). In particular, in cool-temperate forests with heavy snow in northern mainland Japan, the recent population recovery of Sika deer (*Cervus nippon*), wild boar (*Sus scrofa*), and Japanese macaque (*Macaca fuscata*) (Fig. 1) represents a prime example of this; the agricultural damage by these recovering populations has continued to spread. As a result, many local governments have now adopted an official policy to prevent these populations from further recovery.

It is possible that these three mammals also fulfill some positive roles within the original ecosystem functions, but these have not previously been carefully validated, with very few exceptions (for boars, Barrios-Garcia and Ballari, 2012; for macaques, Enari and Sakamaki-

* Corresponding author.
E-mail address: h_enari@hotmail.com (H. Enari).

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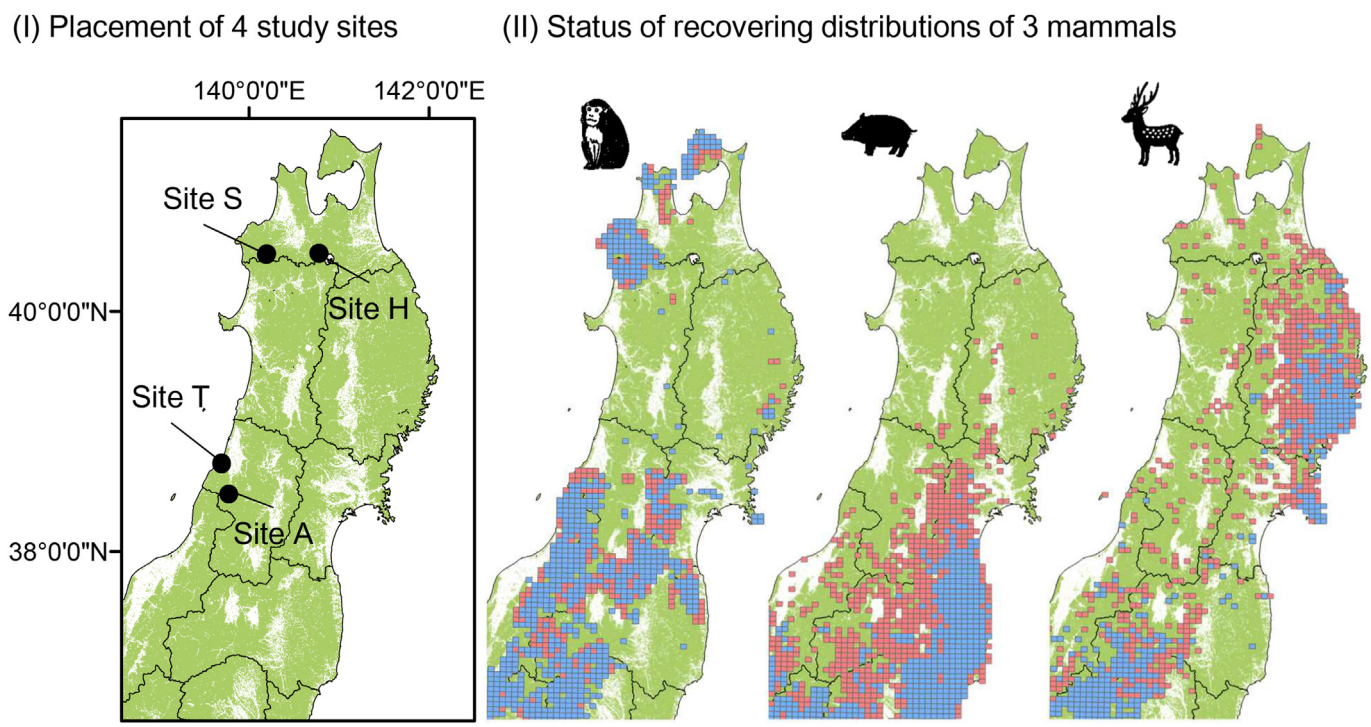

Fig. 1. Map of the study area (I) and current distribution of recovering populations of Japanese macaques, wild boar, and Sika deer (II) according to the Ministry of the Environment (unpublished data). Green-colored areas show the distribution of forests. Blue and red grids (5 km resolution) in (II) indicate each mammal's distribution as of 2003, and their recovery areas by 2015, respectively.

Enari, 2014). In this context, the present study focused on interspecies relationships between recovering mammal populations, and dung beetle assemblages; we treated beetles belonging to the families Scarabaeidae, Geotrupidae, and Trogidae as dung beetles in a broad sense owing to their shared role, i.e., dung decomposition. Dung beetles are organisms that draw widespread attention because of their multiple key roles in sustaining regional ecology, with functions ranging from secondary seed dispersal and nutrient cycling, to parasite suppression (Nichols et al., 2008). Moreover, dung beetles are often considered as ecological indicators because of their short life cycle, broad distribution, high abundance, and rapid response to environmental fluctuations (Davis et al., 2001; McGeoch et al., 2002; Nichols et al., 2007; Viegas et al., 2014). In fact, the abundance and richness of dung beetles is highly sensitive to the distribution of mammals, which leave excrement on which the beetles feed or oviposit (Fincher et al., 1970; Hanski and Cambefort, 1991b; Nichols et al., 2007; Culot et al., 2013; Bogoni et al., 2016). Therefore, when environmental disturbances lead to the defaunation of native mammals—i.e., the nonrandom loss of medium-to large-bodied vertebrates (Redford, 1992)—the abundance and richness of dung beetles are often severely disrupted; this is widely described as an ecological cascade of downstream extinctions (Nichols et al., 2009; Culot et al., 2013). However, less attention has been paid to the opposite effects of the ecological cascade, i.e., whether mammal population recovery has some positive ripple effects to benefit the abundance and richness of dung beetles. Here, we aimed to validate our hypothesis concerning the existence of such ripple effects caused by mammal population recovery, by establishing a study area within cool-temperate forests with heavy snowfall. Such high-latitude forests can potentially support a limited biomass of mammals, resulting in a corresponding limited abundance and diversity of dung beetles, when compared to those in warmer forests (Hanski and Cambefort, 1991b; Davis et al., 2002; Enari et al., 2011, 2013). Thus, the recovery from defaunation might be more strongly expected to restore the self-sustaining ecosystem, owing to lower initial functional redundancy in the forests.

As with the above three mammal species, it is possible that most other mammals have also been affected by the overexploitation of natural resources and, therefore, their abundance and distribution varies greatly among different mountain ranges. Allowing for the possibility that native species pools of beetle fauna were already missing because of past mammal defaunation, we designed verification experiments for the hypothesis, concerning positive ripple effects in four different mountain ranges with similar physical environments (Fig. 1) based on the following three steps: (1) evaluating the influences of the different mammal community compositions observed in each mountain range on the composition of dung beetles; (2) predicting ecological outcomes caused by the new resource supply produced by recovering populations of deer, boar, and macaques, by quantifying the feces preference of existing beetles; and (3) discussing regional differences between potential ripple effects, in terms of hysteresis (i.e., catastrophic shifts in ecosystems; Scheffer et al., 2001; Mayer and Rietkerk, 2004) originating from the historical background of regional mammal defaunation, which potentially determines the differentiation of the native species pool of the dung beetle community.

2. Materials and methods

2.1. Study area and subject species

We set four study sites—S (40° 30′ N, 140° 12′ E; 250 m above sea level, ASL), H (40° 30′ N, 140° 46'; 450 m ASL), A (38° 30′ N, 139° 49′ E; 670 m ASL), and T (38° 45′ N, 139° 44′ E; 270 m ASL)—within different mountain ranges of Shirakami, Hakkoda, Asahi, and Takadate, respectively, located in northeastern Japan (Fig. 1). Each mountain range is a designated nature reserve—UNESCO World Nature Heritage site (Shirakami), National parks (Hakkoda and Asahi), prefectural natural park (Takadate)—with undisturbed natural broad-leaved forests, mainly composed of beech (*Fagus crenata*) and oak (*Quercus crispula*). Annual mean air temperature and total precipitation in 2015 ranged from 9.0 °C (Site A) to 13.6 °C (Site T), and from 1519.5 mm (Site H) to 2282.0 mm (Site A). Snowfall was observed from December to March in