Biological Conservation 159 (2013) 206–213

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Differential responses of scavenging arthropods and vertebrates to forest loss maintain ecosystem function in a heterogeneous landscape

Shinji Sugiura *, Ryusei Tanaka, Hisatomo Taki, Natsumi Kanzaki

Forestry and Forest Products Research Institute (FFPRI), 1 Matsunosato, Tsukuba, Ibaraki 305–8687, Japan

ARTICLE INFO

Article history:
Received 3 July 2012
Received in revised form 3 November 2012
Accepted 5 November 2012
Available online 23 January 2013

Keywords:
Burying beetles
Decomposition
Ecosystem function
Functional redundancy
Nicrophorus
Resource competition
Response diversity
Scavenging mammals

ABSTRACT

Forest loss and degradation can impact on ecosystem functions. Decomposition of vertebrate carcasses is an important ecosystem function in forests, and burying beetles and scavenging vertebrates is known to contribute to the provision of this function in forests. However, the relative importance of burying beetles and scavenging vertebrates in the removal of vertebrate carcasses has rarely been explored in terms of the impact of forest loss and degradation. Here, we experimentally placed mouse carcasses on forest floors to investigate burial and removal rates by forest animals during a 7-day period at 31 sites (natural broad-leaved forests and conifer plantations in an urban/agricultural matrix) in central Japan. Ninety-six percent of dead mice disappeared with 7 days of being placed on the forest floor. Rates of carcass disappearance increased with forest area surrounding the study sites. Field observations and camera trapping showed that two species of *Nicrophorus* burying beetles and six species of scavenging vertebrates contributed to the carcass burial and removal. Burial rates by beetles increased with forest area, while removal rates by vertebrates decreased with forest area. Model comparisons showed that the area of both natural forests and plantations surrounding the study sites influenced burial and removal rates. Therefore, forest loss influenced the disappearance rates of vertebrate carcasses. Different responses to forest loss between burying beetles and scavenging vertebrates could maintain the carcass burying/removing function at a landscape level.

1. Introduction

Habitat loss and degradation have important effects on biodiversity (e.g. Fahrig, 2003). Among the many human activities that cause habitat loss, urban development can lead to local extinction and decline of many species (McKinney, 2002). Furthermore, conversion from natural habitats to plantations or agricultural fields causes habitat degradation, resulting in the decline of species (Dunn, 2004; Koh and Wilcover, 2008). Habitat loss and degradation can also reduce ecosystem functions such as pollination (e.g. Aizen and Feinsinger, 1994), decomposition (e.g. Didham, 1998), herbivory (Valladares et al., 2006), predation (Small and Hunter, 1988) and parasitism (Valladares et al., 2006). Understanding the mechanisms of how habitat loss and degradation affect ecosystem functions requires an understanding of how ecosystem functions can be stabilised. The biological insurance hypothesis, which states that ecosystem functioning is more stable in more species-rich communities, has been considered important for understanding the stabilising mechanisms of ecosystem functions (Winfree and Kremen, 2009). According to the hypothesis, the redundancy of species contributing to the same function (functional redundancy) reduces fluctuations in the function over space or time (Naeem, 1998). Functional redundancy is based on the observation that some species perform similar roles in communities, and can therefore be substituted with little impact on ecosystem processes (Rosenfeld, 2002). However, apparently redundant species may have different environmental optima. This does not represent functional redundancy because their functional niches do not overlap when environmental axes are included (Rosenfeld, 2002). The diversity of responses to environmental change among species contributing to the same ecosystem function (i.e. response diversity) has also been considered an important stabilising mechanism (Elmqvist et al., 2003; Leary and Petchey, 2009; Winfree and Kremen, 2009). Response diversity occurs when populations of some species increase and others decrease following the same environmental change (Winfree and Kremen, 2009).

Decomposition of vertebrate carcasses is an important ecosystem function in terrestrial environments (Carter et al., 2007; Parmenter and MacMahon, 2009). Arthropods such as burying beetles (Silphidae), dung beetles (Scarabaeoidea), and ants (Formicidae) greatly contribute to the rapid decomposition processes by scavenging in both temperate and tropical forests (Klein, 1989; Scott, 1998). Vertebrates such as raccoons and rat snakes are also known as important scavengers of carcasses in temperate and

* Corresponding author.
E-mail address: sugiura.shinji@gmail.com (S. Sugiura).

0006-3207/$ - see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.biocon.2012.11.003

tropical forests (DeVault et al., 2003, 2004). *Nicrophorus* beetles, which bury carcasses that their larvae consume, frequently contribute to burial of small-sized vertebrate carcasses in temperate forests (Scott, 1998). Trumbo and Bloch (2000) indicated that burial rates of carcasses by *Nicrophorus* beetles and removal rates by scavenging vertebrates were higher and lower in large forests than small forests, respectively. This suggests that responses to environmental factors (e.g. forest loss) may be different between beetles and vertebrates (i.e. response diversity). Previous studies have investigated either beetles or vertebrates but not both simultaneously (Klein, 1989; Trumbo and Bloch, 2000; DeVault et al., 2003, 2004, 2011; Wolf and Gibbs, 2004). Therefore, the relative importance of different animal groups in the carcass burying/removing function is unclear.

Ecosystem functions are frequently provided by mobile species that live in different habitats than where they provide functions (Steffan-Dewenter et al., 2002; Chaplin-Kramer et al., 2011). Therefore, each species may operate at different scales, reinforcing the overall ecosystem functions across scales (Kremen et al., 2007). Although Klein (1989) investigated the effects of different sizes of forest fragment on the removal of vertebrate carcasses, many studies have used single spatial scales to investigate the carcass removal process (Trumbo and Bloch, 2000; Wolf and Gibbs, 2004; Olson et al., 2012). Therefore, how different spatial scales affect the function is unknown. Furthermore, intense interspecific competition is known to be important for structuring communities on animal carcasses (Janzen, 1977; Scott, 1998; DeVault et al., 2003), suggesting overlap of this ecosystem function among species (i.e. functional redundancy). Functional redundancy or different responses to the same environmental change among species (i.e. response diversity) can be considered important mechanisms for stabilising the function. However, the methods by which response diversity and functional redundancy stabilise this carcass burying/removing function have never been explored.

To elucidate the effects of forest loss and degradation on the ecosystem function provided by burying beetles and scavenging vertebrates, we experimentally placed mouse carcasses in forest sites (natural broad-leaved forests and conifer plantations in an urban/agricultural matrix) in central Japan. Japan has a moderate proportion of forest coverage (67% of land area) and high proportions of conifer plantations (41% of total forest area; Forestry Agency Japan, 2010; Yamaura et al., 2012). Urbanisation and conversion to conifer plantations have reduced the area of natural forests, resulting in biodiversity loss (Yamaura et al., 2011). Therefore, Japanese forests are suitable for clarifying the impacts of forest loss and degradation on ecosystem functions.

The main goals of this study were to test the following hypotheses: (1) forest loss (decrease in forest area surrounding study sites) reduces burial or removal rates of carcasses at particular spatial scales, (2) forest degradation (conversion from natural broad-leaved forests to conifer plantations) reduces burial or removal rates of carcasses at particular spatial scales and (3) responses to forest loss and degradation and the important spatial scales are different between burying beetles and vertebrates. These tests allowed us to consider the impacts of forest loss and degradation on the relative importance of the function of burying beetles and scavenging vertebrates.

2. Materials and methods

2.1. Study sites and landscape structure

To clarify effects of forest loss and degradation on the removal rates of vertebrate carcasses, we conducted field experiments in Kitaibaraki City and Takahagi City, Ibaraki Prefecture, central Japan (Fig. 1; Table S1; 36°70′N–36°91′N, 140°55′E–140°74′E; altitude, 0–774 m above sea level). Average monthly temperatures ranged from 2.1 °C to 23.9 °C, and total annual precipitation was 1548 mm in 2011 (Kitaibaraki Meteorological Station). We established 31 study sites in the area, with a mean distance to the nearest site of 2455 m, and a range of 1707–3618 m (Fig. 1; Table S1). Areas in this region consist of natural forests (26.1%), conifer plantations (55.8%), grasslands (2.8%), agricultural fields (7.4%) and residences (7.9%). The age class of most forest stands in the study region ranged from 40 to 70 years old. To accommodate the high demand for timber and due to the decline of agricultural practices after the Second World War, broad-leaved forests were converted to coniferous forests until the late 1970s. Natural forest was composed mainly of broad-leaved tree species such as *Quercus* spp., *Acer* spp. and *Carpinus* spp., while conifer plantations were composed of *Cryptomeria japonica* Don and *Chamaecyparis obtusa* Endl.

The location of the study sites was mapped using a global positioning system (GPS) device (GPS map 60CSx; Garmin, Olathe, Kansas, USA) and ArcGIS 9.2 software (ESRI, St. Charles, Missouri, USA). Thirty-one geographical points that fell within the polygons in the study region were chosen. The criteria for accepting a selected point within a forest included it being <30 m from roads and having a minimum separation distance of 1500 m from any other chosen forest points (Fig. 1). Sites where no trees grew were not selected. Although the number of forested sites ($N = 25$) was much larger than the number of deforested sites ($N = 6$), the proportion of forested sites ($25/31 \times 100 = 80.6\%$) was similar to that of the total forest area in this region (81.9%).

To investigate effects of forest loss on removal rates of vertebrate carcasses, we measured the amount of forest (forest area) surrounding the study sites at radii of 100, 200, 300, 400, 500, 600, 700, 800, 900, 1000, 1100 and 1200 m from the mapped points. These radii were selected based on the foraging area of silphid beetles including *Nicrophorus* (100 ha, i.e. at 560 m radii; Wolf and Gibbs, 2004) and medium-sized mammals such as the racoon dog (23–228 ha, i.e. 270–851 m radii; Saeki et al., 2007). Forested area was determined from digital vegetation maps delineated by Yamaura et al. (2009) and the digital vegetation map published by the Ministry of the Environment of Japan. Forested area was categorised into natural broad-leaved forest or conifer plantation based on the digital maps. Because the local environment of each study area can influence carcass burial and removal, we characterised the local environment for each $10 \times 10\text{-m}^2$ study area (Table S1). Organic debris (leaf and twig litters) of conifer plantations is twice thicker than that of broad-leaved forest floors in the study areas (Hasegawa et al., 2009), suggesting the local environment at study sites may affect the abundance or behaviour of scavenging invertebrates. Therefore, conifer plantation floors or broad-leaved forest floors were recorded as local environmental factors at all the study sites (Table S1). We measured soil hardness (kg/cm^2) under the leaf litter using a penetrometer (DIK-5553; Daiki, Saitama, Japan) at all the sites, and found it was not different between plantation floors (0.7–4.7 kg/cm^2) and broad-leaved forest floors (1.9–4.2 kg/cm^2).

2.2. Field experiment

We experimentally placed carcasses of the house mouse *Mus musculus* L. (Muridae) on the forest floor to investigate the burial and removal rates of vertebrate carcasses under field conditions. The different biotic and abiotic factors between forest edges and inner forests are well known (e.g. Murcia, 1995). Therefore, to control variations of the edge effects, the dead mice placed in the inner forests were set <20 m from the forest edge (or roads) at all study sites. Dead mice have been frequently used for estimating burial or removal rates of vertebrate carcasses (Ohkawara et al., 1998;