Forest Ecology and Management 314 (2014) 166–171

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Parasites and forest chronosequence: Long-term recovery of nematomorph parasites after clear-cut logging

Takuya Sato [a,c,*], Katsutoshi Watanabe [b], Keitaro Fukushima [c], Naoko Tokuchi [c]

[a] The Hakubi Center for Advanced Research, Kyoto University, Yoshida-Ushinomiya-cho, Sakyo-ku, Kyoto 606-8302, Japan
[b] Department of Zoology, Division of Biological Science, Graduate School of Science, Kyoto University, Kitashirakawa-Oiwakecho, Sakyo-ku, Kyoto 606-8502, Japan
[c] Field Science Education and Research Center, Kyoto University, Kitashirakawa-Oiwakecho, Sakyo-ku, Kyoto 606-8502, Japan

A R T I C L E I N F O

Article history:
Received 15 July 2013
Received in revised form 5 December 2013
Accepted 7 December 2013
Available online 3 January 2014

Keywords:
Allochthonous input
Ecosystem succession
Forest management
Manipulative parasite
Riparian ecosystem
Nematomorpha

A B S T R A C T

Temporal scales at which anthropogenic disturbances affect ecosystem linkages are often unclear. The nematomorph parasites tightly link forests to stream ecosystems via manipulation of their terrestrial hosts. We examined the abundance and species/genetic diversities of nematomorphs with their terrestrial hosts along a forest-recovery gradient after clear-cut logging, using a chronosequence. Only one nematomorph species was found from eight watersheds with different forest ages (3–48 years). The nematomorphs suffered local extinction immediately after logging and then increased linearly with forest age. Their relative abundances were highest in September in older forests, but in October in younger forests, suggesting clear-cut logging can cause not only long-term (>50 years) disruption of the magnitude but also timing of the forest–stream linkage mediated by the nematomorphs. Camel crickets (*Diestrammena tsushimensis* and *D. elegantissima*), dominant definitive hosts of the nematomorphs, recovered with a peak at around 30-year-old forests, which was insufficient to explain the long-term recovery of the nematomorphs. This study provided an empirical example of the time-scale (>50 years) at which forests and streams should be managed as integrated systems.

1. Introduction

Predicting spatial and temporal scales at which anthropogenic disturbances affect ecosystems is a challenging task in conservation and management (Odum, 1969; Likens and Bormann, 1974). Clear-cut logging, a common forest management practice, most seriously affects not only forests but also stream ecosystems by disrupting the movement of consumers, materials and nutrients that link those systems (Naiman et al., 2005). Increasing literature has suggested that a riparian reserve and buffer zone can be a useful tool for protecting stream ecosystems from forest logging (Naiman et al., 2000; Richardson and Danehy, 2007; Marczak et al., 2010). In contrast, temporal aspects have not been well considered in many cases (Vitousek and Reiners, 1975; Valett et al., 2002), while the rates and processes of the forest–stream linkage can change through successional time after the disturbances (Milner et al., 2007). Given the potential shift from physical to biotic controls in ecosystem linkages through succession (Milner et al., 2007), the knowledge gap between spatial and temporal scales will make it difficult to provide appropriate time scales for forest management plans.

Here, we first demonstrate a parasite that mediates cross-ecosystem energy flow shows slowest recovery after clear-cut logging of a forest in Japan. Parasitic nematomorphs (Nematomorpha: Gordioidea), or hairworms, manipulate their terrestrial invertebrate hosts, such as orthopterans, to seek and jump into water where the adult hairworms must reproduce (Thomas et al., 2002). These terrestrial hosts become an important seasonal energy subsidy for aquatic predators such as stream salmonids (Sato et al., 2011a,b); accounting for 60% of the annual energy intake of an endangered Kirikuchi char population (*Salvelinus leucomaenis japanicas*) in a temperate Japanese stream (Sato et al., 2011a). The energy flow mediated by the nematomorphs can indirectly alter the whole stream communities and even an ecosystem function, i.e., leaf break-down rate, in the streams (Sato et al., 2012a).

Intensive conifer plantation was negatively associated with the abundance of the adult nematomorphs, which resulted in sharp declines in seasonal prey consumption of stream salmonids in those managed streams (Sato et al., 2011b). However, a temporal association between the nematomorphs and forest management remains unclear. Due to their complex life cycle (Hanelt et al., 2005), the nematomorphs may take a much longer time to recover from forest disturbances compared to their hosts or other elemental resources that link forest and stream systems. Consequently,

* Corresponding author. Present address: Department of Biology, Graduate School of Science, Kobe University, 1-1 Rokkodai, Nada-ku, Kobe 657-8501, Japan. Tel./fax: +81 78 803 5707.
E-mail address: takuya@species.jp (T. Sato).

0378-1127/$ - see front matter
http://dx.doi.org/10.1016/j.foreco.2013.12.004

forest–stream linkages might be disrupted for much longer than previously thought. Here, we examined the abundance and species/genetic diversities of nematomorphs with their terrestrial hosts along a forest recovery gradient after clear-cut logging.

2. Study sites

The study was conducted at Mt. Gomadan Experimental Forest (GEF) (34°04′N, 135°35′E) in an upper drainage of the Totsu River system, Nara Prefecture, central Honshu, Japan (Fig. 1; see also Fukushima and Tokuchi (2009) for climatic, geologic conditions or native vegetation). The GEF catchment (≈1000 ha) consists of more than 50 adjacent small watersheds (2.14–24.16 ha) with the same underlying bedrock geology. All watersheds were clear-cut between 1912 and 1916, and Japanese cedar (*Cryptomeria japanica*), and to a lesser extent Japanese cypress (*Chamaecyparis obtusa*), were planted with a subsequent clear-cut logging (≈40 years) on a watershed basis. Most watersheds have now been planted twice, and forest ages varied among the watersheds.

2.1. Rationale for chronosequence study

We considered GEF to be appropriate for a watershed-scale chronosequence study. Despite the potential usefulness of a chronosequence, its application will be least appropriate when the different sites of same ages do not follow the same trajectory (Walker et al., 2010). However, geologic and geomorphological features are similar among the watersheds in GEF and forest age was the dominant factor controlling forest biomass accumulation, soil development, air/water temperatures and movement of resources to stream ecosystems (Fukushima and Tokuchi, 2009; Tateno et al., 2009; Tokuchi and Fukushima, 2009; Kobayashi et al., 2010; Fukushima et al., 2011). NO_3^- exports were more strongly correlated among the different watersheds covered by same-aged stands than among the repeated measures within a watershed (Tokuchi and Fukushima, 2009), which strongly supported the key assumption of the adequacy of a chronosequence study (Walker et al., 2010). Additionally, community structures of benthic invertebrates were much more similar among watersheds with similar forest ages than among watersheds with different ages, instead of the proximities between the watersheds (Kobayashi et al., 2010).

The results of the present study are from the clear-cutting of second-growth forest, as opposed to original forest, i.e., no uncut controls for comparisons. However, we still believe that our results will provide important implications for the time scale of forest management plans because conservation/management of second-growth forest is an important environmental issue for stream ecosystem management throughout the world (Swanson and Franklin, 1992; Naiman et al., 2000; Young, 2000).

3. Methods

3.1. Field survey

Field sampling was conducted both in the stream and its surrounding forest in each of the eight watersheds from June 2010 to May 2011, except for February 2011. Estimating the accurate abundances of the adult nematomorphs and camel crickets is expected to be difficult due to their widespread distributions in each site, and therefore we measured capture rates as proximate measures of their abundances in this study. To examine the seasonal changes in the capture rates of adult nematomorphs, we set five underwater traps (Sato et al., 2011b), with 15 m between individual traps, in each stream in May 2010. Then, we counted the nematomorphs captured by the traps every 30 days during the study period. Some nematomorphs ($n = 80$; 4–25 worms in each site) were preserved in 99% ethanol for subsequent DNA analysis and body length was measured to the nearest 0.1 mm in the laboratory.

The capture rates of camel crickets (Rhaphidophoridae), the dominant hosts of the nematomorphs in this region, were examined by using baited traps (Sato et al., 2011b). Five traps were set for two days, 10–20 m away from the stream, with at least 20 m between the traps. To accommodate the potential daily variation in capture efficiency, we conducted the sampling twice in July, one month before the host manipulation starts in this region (Sato et al., 2011b). We captured the crickets mainly to evaluate the temporal changes in their abundances among study sites, and did not examine the infection of the nematomorphs. However, we believe the infection status did not bias the catch per unit effort of the crickets by the following reasons: (1) the nematomorphs are known to alter their host's behavior only when they need to enter water to mate (Biron et al., 2005; Sanchez et al., 2008); (2) the growth trajectory did not differ significantly between infected and uninfected crickets (Sato, unpublished data), suggesting the foraging behavior of the crickets would not be changed largely by the nematomorph infection.

A part of specimens of nematomorphs collected in this study were deposited in the Lake Biwa Museum, Shiga Prefecture, Japan, with the catalog numbers Misc. Invert. FY2013-12-1∼21.

3.2. DNA analysis

The 18S ribosomal RNA (18S) gene (5′-half; 861 bp) and the mitochondrial cytochrome *c* oxidase subunit I (COI) gene (5′-half;

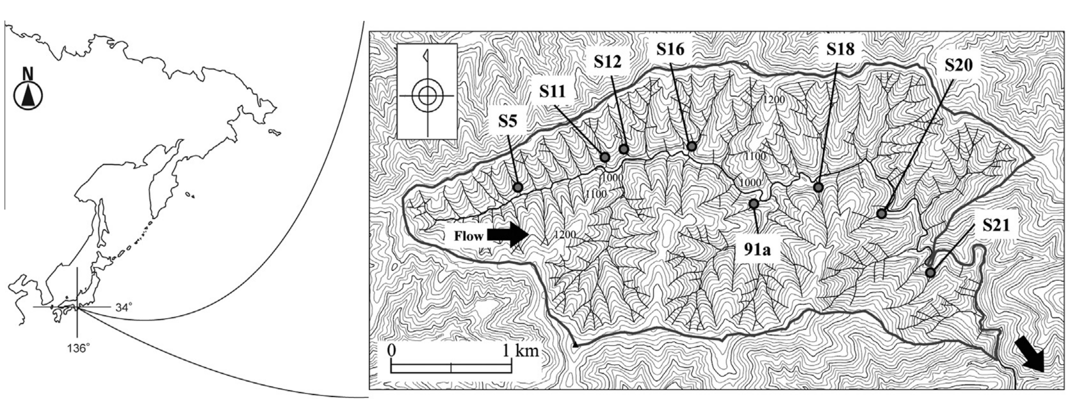

Fig. 1. Map of Mt. Gomadan Experimental Forest (GEF) and the eight sampling sites. Numbers correspond to the watershed numbers in Table 1.