

# Catchment-scale deer exclusion changes longitudinal patterns of macroinvertebrate communities through soil runoff mitigation

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## ABSTRACT

Deer overpopulation is occurring worldwide, and deer-induced soil runoff into streams increases levels of suspended sediment and fine sedimentation. While deer-induced fine sedimentation in depositional habitats including first- and fourth-order streams is known to alter macroinvertebrate communities, effects of drifting suspended sediment in erosional habitats between the stream orders are poorly understood. Here, habitat and macroinvertebrate community structures in first- to third-order streams were compared between deer-excluded and grazed catchments of a Japanese headwater system. Fine sediment cover on the streambed was significantly greater in the grazed catchments than the deer-excluded catchment only for first-order streams, while macroinvertebrate community structure differed distinctly between the deer-excluded and grazed catchments at all stream orders. Burrowing collector-gatherers, which inhabit fine streambed sediments, were less abundant in first-order streams in the deer-excluded catchment than the grazed catchments, while clinging collector-filterers, which are vulnerable to suspended sediment inputs, were more abundant in second- and third-order streams of the deer-excluded catchment than the grazed catchments. These results suggest that the effect of deer exclusion on stream ecosystems varies with longitudinal changes in sediment deposition and transport capacity. Hydrogeomorphological processes are thus fundamental to assessing the restoration of forest-stream ecosystems, particularly in spatiotemporally dynamic headwater systems.

## 1. Introduction

Deer overpopulation is occurring worldwide due to various factors, including extinction of predators, decreased hunting pressure, and climate change (Côté et al., 2004; Takatsuki, 2009). Deer over-browsing and grazing have resulted in a dramatic reduction of forest vegetation (Côté et al., 2004; Takatsuki, 2009), and the indirect impacts include not only alteration of terrestrial animal communities (Kato and Okuyama, 2004; Sakata and Yamasaki, 2015) but also soil erosion and subsequent sediment input into streams (Sakai et al., 2012, 2013, 2022). These deer-induced sediment inputs alter stream animal communities, especially in depositional habitats (Sakai et al., 2012, 2013, 2022; Nakagawa, 2019, 2021). Mitigating the impairment of forest-stream ecosystems caused by deer overgrazing is thus of great importance for global biodiversity conservation.

Headwater stream systems (~1 km<sup>2</sup>) occupy 70–80% of total river catchment areas (Sidle et al., 2000) and represent a nexus of biodiversity, with disproportionate numbers of species using the terrestrial-aquatic interface zone (Olson et al., 2007). Streams show

characteristic changes in channel morphology along their length due to changes in stream hydraulics (Church, 2002) often starting with colluvial valleys in their steepest headwaters and transitioning through step-pool, plane-bed, and pool-riffle morphologies in a downstream direction (Montgomery and Buffington, 1997). This heterogeneity leads to longitudinal changes in macroinvertebrate communities with stream order (Grubaugh et al., 1996; Miserendino, 2001; Heino et al., 2004), and thus sediment inputs into such systems may have different effects on animal communities in each geomorphological zone, with fine sedimentation in depositional habitats (Wood and Armitage, 1997; Rabení et al., 2005) and increased suspended sediment concentrations in erosional habitats (Grubaugh and Wallace, 1995; Jones et al., 2012).

Sakai et al. (2012, 2013) reported that sediment input due to deer overgrazing alters macroinvertebrate communities in first-order streams but not in second-order streams, defined based on Strahler (1957). Studies have suggested that the greater hydraulics of second-order streams hamper settling of fine sediments, as well as their impacts on macroinvertebrate communities. Meanwhile, Nakagawa (2019, 2021) reported that fine sediment due to recent deer overgrazing impacted fish

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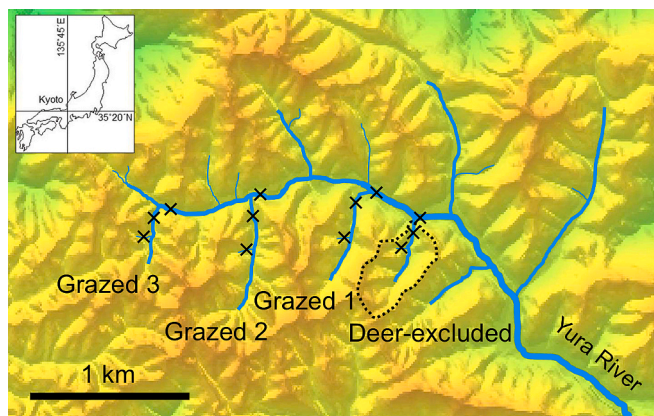
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and macroinvertebrate communities in a fourth-order stream connected to the streams studied by Sakai et al. (2012, 2013). These studies suggest that fine sediment occurring in depositional habitats is the primary impact of deer overgrazing on stream ecosystems. However, increased concentrations of suspended sediment can also impair food quality and availability for collector-filterers and grazers (Grubaugh and Wallace, 1995; Jones et al., 2012). As the intermediate section between the streams assessed by Sakai et al. (2012, 2013) and Nakagawa (2019, 2021) (second- and third-order streams) receives substantial amounts of suspended sediment (Sakai et al., 2022), continual input of suspended sediment may diminish abundances of intolerant species. In contrast to fine sedimentation, which alters both food resources and habitats, suspended sediment primarily affect food resources and may require more time to impact the animal community. Nevertheless, the possible time lag has been overlooked, even though evaluating the propagation of deer impacts is one of urgent missions to conserve the integrity of headwater systems.

Here, this study hypothesized that impacts of suspended sediment addition due to deer overgrazing on macroinvertebrate communities would occur later than those of fine sedimentation. To test the hypothesis, additional investigations were conducted in first- to third-order streams including the same streams studied by Sakai et al. (2012, 2013). The previous studies conducted manipulative comparisons between deer-excluded and grazed catchments 2–4 years after the deer exclusion, while the present study was conducted 6–8 years after the exclusion. To test which macroinvertebrate groups are impacted by deer overgrazing, macroinvertebrate community structures were compared between deer-excluded and grazed catchments in each stream order. Although a variety of terrestrial alterations, including deer overgrazing, fire, and forest logging have been reported to increase soil runoffs (e.g., Minshall, 2003; Zhang et al., 2009; Sakai et al., 2022), the time lags between the impact of fine sedimentation and suspended sediment addition on animal communities is largely unexplored. As fine sediment addition has induced a variety of detrimental effects on aquatic taxa including hyporheic macroinvertebrates (Geist and Auerswald, 2007), fishes (Mueller et al., 2020) as well as fish egg developments (Sternecker et al., 2013; Nagel et al., 2020), elucidating the spatiotemporal propagation of impacts of soil runoffs on heterogeneous headwater systems would provide important clues for adequate watershed managements against such impacts.



**Fig. 1.** Map showing the studied stream reaches in the deer-excluded and grazed catchments. Cross marks indicate the locations of studied stream reaches. Broken line along the ridgeline of the deer-excluded catchment indicates the deer-proof fence.

## 2. Materials and methods

### 2.1. Study site

This study was conducted at the Ashiu Research Forest Station of the Field Science Education and Research Center, Kyoto University, Japan (Fig. 1). The study site is located in a cool-temperate zone, and the geological setting of the area includes the sandstone, mudstone, and shale of the Mesozoic Tanba Belt. Mean annual precipitation and temperature were 2298 mm and 11.9 °C, respectively (Sakai et al., 2012, 2013). The study site is a portion of the headwaters of the Yura River, and is covered with primeval deciduous forest dominated by *Fagus crenata*, *Acer mono*, and *Carpinus tschonoskii* (Sakai et al., 2013).

Since the 1990s, grazing by sika deer (*Cervus nippon*) has dramatically altered floral, and thus faunal structures (Kato and Okuyama, 2004; Sakata and Yamasaki, 2015). The dramatic reduction in understory vegetation has increased overland flow and soil runoff into streams, thereby altering macroinvertebrate communities in first-order streams (Sakai et al., 2012, 2013). Data for population estimates over the previous decade (2007–2018) suggest that deer density peaked at 71 individuals/km<sup>2</sup> in 2010 and has since decreased by at least 10 individuals/km<sup>2</sup> (Mizuki et al., 2020). However, deer grazing pressure still has maintained a bare soil surface, even at low population densities (Nakagawa, 2019), and patches of plant species that are unpalatable to deer are gradually expanding (Nakahama et al., 2016).

To mitigate the extensive impacts of deer overgrazing on biodiversity and maintain the integrity of forest-stream ecosystems, a deer-excluded catchment (13.5 ha) draining a second-order stream was established by members of the Ashiu Biological Conservation Project in June 2006 (Fig. 1). A 2.5-m-high fence was constructed of poles and nets along the ridgeline of the entire deer-excluded catchment (Sakai et al., 2012, 2013). The cost for this fence construction was approximately \$21 per meter that was much cheaper than that for metal fence construction (Takayanagi, 2013). Understory vegetation has been dramatically restored inside the catchment, whereas the soil surface outside the catchment has remained bare (Sakai et al., 2012, 2013, 2022). In this study, three neighboring second-order grazed catchments were selected to compare habitat and stream macroinvertebrate community structure with the deer-excluded catchment (Fig. 1).

Twelve 30-m-long study reaches were established in the deer-excluded catchment and each grazed catchment (first- to third-order streams in each catchment) to assess habitat characteristics and sample macroinvertebrates (Fig. 1). The third-order stream reaches were set in the same channel (Fig. 1), and each reach was positioned slightly downstream of a confluence point of second-order streams, where water and sediment flow from the catchments are expected to influence habitat and community structure (Rice et al., 2001; Katano et al., 2009). The channel morphology of all first- and second-order streams was colluvial, whereas the third-order streams had riffle-pool morphology according to the classification of Montgomery and Buffington (1997). In the third-order stream reaches, the measurement of habitat characteristics and macroinvertebrate sampling were performed in riffles randomly. Representative points containing similar habitats in the first- and second-order stream reaches were selected for these surveys. All studied streams had permanent water flows.

### 2.2. Habitat characteristic measurements

Three points along each study reach were measured, at 10-m intervals, to determine both wetted width and canopy openness. To estimate canopy openness, hemispherical photographs were taken with a digital camera (D40, Nikon, Tokyo, Japan) equipped with a fisheye lens (4.5 mm F2.8 EX DC Circular Fisheye HSM, Sigma, Kanagawa, Japan) that was fixed horizontally 1 m above the streambed. Canopy openness (%) was estimated for each study reach using CanopOn 2 software (Takenaka, 2009).

Water depth, current velocity, and fine sediment deposition on the streambed were measured at 10-m intervals in each study reach (four points per reach). Repeated 5-s measurements of current velocity were taken with an electromagnetic current meter (VE10, Kenek, Tokyo, Japan) at each point. The methods described by Sakai et al. (2013) were employed to visually estimate the percent of fine sediment (< 2 mm) cover on the streambed within quadrats (25 × 25 cm). Measurement of all habitat characteristics (wetted width, canopy openness, water depth, current velocity, and fine sediment deposition) was conducted under base flow conditions in November 2014.

### 2.3. Macroinvertebrates

Surber nets (25 × 25 cm, 0.5-mm mesh) were used to sample macroinvertebrates in four randomly placed quadrats per reach. Sample collection was performed on November 26–29, 2014. This time was selected as the optimal season for sampling most macroinvertebrate taxa inhabiting the study site before snow accumulation impeded access to the study reaches (M. Sakai, unpublished data). However, an intense rainfall event occurred on November 29, 2014, precluding sampling in second- and third-order stream reaches of the deer-excluded catchment. Therefore, I supplemented the missing data with macroinvertebrate samples collected previously at those two study reaches on November 28, 2012. All macroinvertebrates were preserved in 70% ethanol and identified to the lowest possible taxonomic level. In addition, macroinvertebrates were classified by life-form type and functional feeding group (shredders, grazers, collector-gatherers, collector-filterers, and predators) based on information published by Takemon (2005), Merritt et al. (2008), Kawai and Tanida (2018), and my own unpublished data.

### 2.4. Statistical analysis

First, to test for the presence of significant spatial autocorrelation patterns in the macroinvertebrate communities among study reaches, I generated spatial eigenvectors using Moran's eigenvector maps (MEM; Dray et al., 2006), a powerful multivariate approach allowing the detection of multiscale spatial structures in ecological data. To obtain the spatial eigenvectors, a spatial weighting matrix based on a Gabriel graph weighted with a decreasing linear function of distance among stream reaches was used (details in Bauman et al., 2018a, 2018b, Sakai et al., 2021). A redundancy analysis (RDA) of the reach-scale community matrix was performed against the whole set of spatial eigenvectors associated with positive spatial autocorrelation patterns for each spatial weighting matrix and was tested using 9999 permutations. If a significant spatial autocorrelation pattern was detected, the pattern should be considered to adequately evaluate focal fixed effects on community assembly in further statistical analyses (e.g., variation partitioning) (Borcard et al., 2018). However, the MEM analysis did not show any significant patterns of spatial autocorrelation in macroinvertebrate community composition ( $p = 0.833$ ), indicating spatial independence among the sampled communities. Therefore, in further analyses, effects of geometrical spatial autocorrelation on macroinvertebrate communities were discarded.

Second, to test for differences in macroinvertebrate variables between presence and absence of deer, generalized linear mixed models (GLMMs) were separately constructed for each stream order. The response variables were total abundance, taxa richness, and abundances of each functional feeding group which are expected to respond to fine sedimentation and suspended sediment addition. The explanatory variable was presence/absence of deer. Deer-absent category was assigned for the third-order stream reach positioned slightly downstream of the confluence point of the EC stream, whereas deer-present category for the other third-order stream reaches. For the GLMMs, identifiers for each study reach were included in the models as a random intercept, as the community is likely to be more similar within a reach than among reaches. The sampling year (2012 or 2014) were also included as a

random intercept in the models to consider potential temporal variability of the community structures. A Poisson error structure was used for response variables with a log link function. Then, full and null models were compared to select models that yielded the lowest Akaike information criterion (AIC) to grasp whether deer influenced each variable in each stream order.

Third, an RDA was performed to visualize the relationships between environmental variables and macroinvertebrate community structure. To avoid multicollinearity in the RDA, the correlations between each possible pair of environmental variables were examined in a correlation matrix built using Spearman's rank correlation. For any pair of highly correlated environmental variables ( $\rho > 0.70$ ,  $p < 0.05$ ), one of the variables was excluded and the variable expectable to be more closely related to macroinvertebrate community structure was retained. The RDA was followed by permutational multivariate analysis of variance (PERMANOVA) based on the Chao index (Chao et al., 2005), testing for significant differences in macroinvertebrate community structure between the presence and absence of deer and among stream orders. PERMANOVA was conducted using 9999 permutations. I further tested whether any macroinvertebrate taxa were significant indicators of stream characteristics, displaying both high fidelity and specificity to one habitat type. The *IndVal* index was calculated for all taxa in the six stream groups (first-, second-, and third-order streams in the deer-excluded catchment, and those in the grazed catchments) (Dufrene and Legendre, 1997) and tested using 10,000 Monte Carlo permutations. Macroinvertebrate abundance data were transformed using the Hellinger transformation method before conducting RDA. All statistical analyses were performed in R 3.6.3 (R Core Team, 2021) using the packages *adespatial* (Dray et al., 2021) for the MEM analysis, *lme4* (Bates et al., 2022) for the GLMMs, *MuMIn* (Barton, 2022) for the AIC-based model selections, *vegan* (Oksanen et al., 2020) for the RDA and PERMANOVA, and *indicspecies* (Cáceres et al., 2020) for the indicator species analysis.

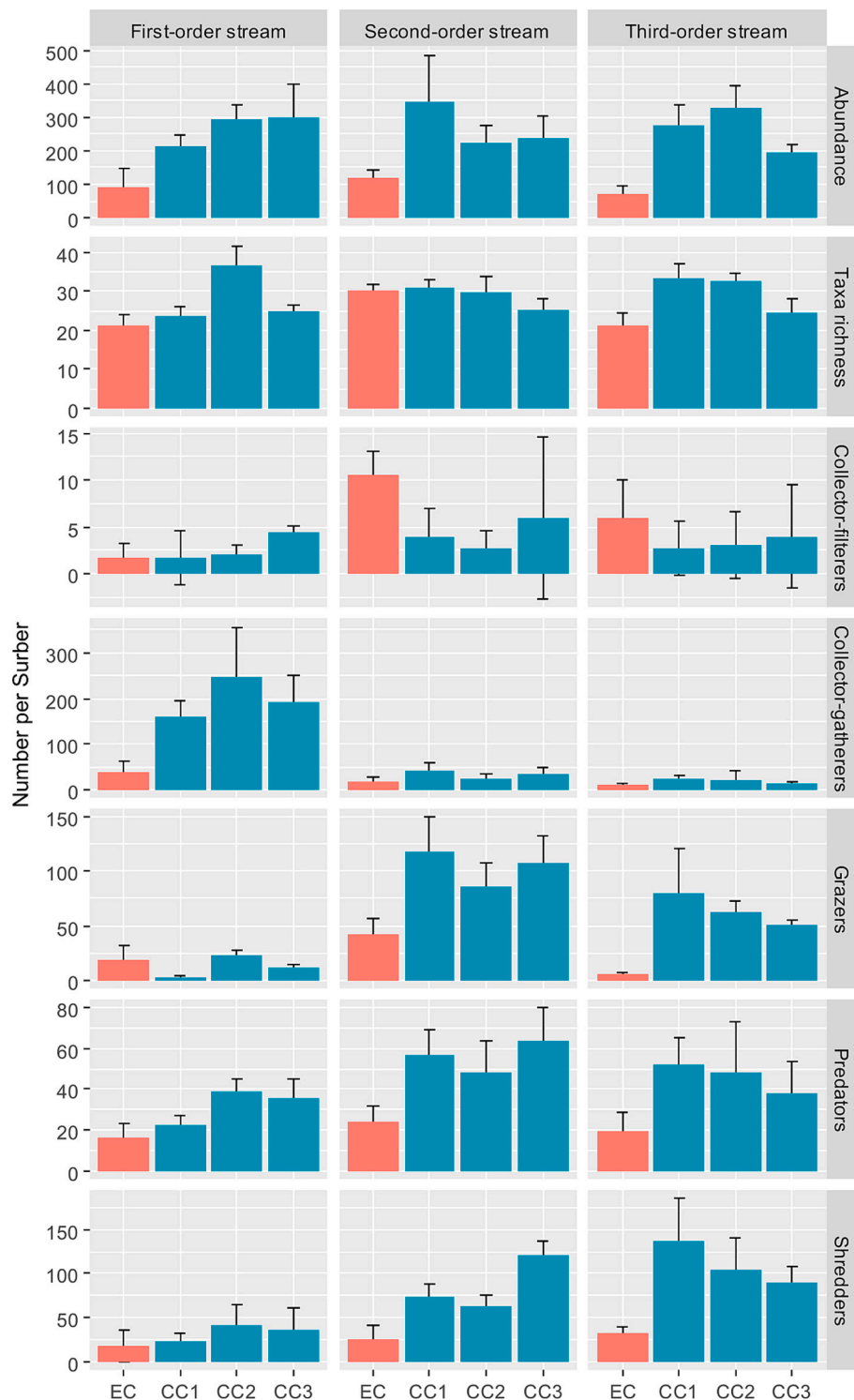
## 3. Results

In the first-order streams, total abundance, and abundances of collector-gatherers, predators, and shredders of macroinvertebrates were greater in the grazed catchments than in the deer-excluded catchment (Table 1, Fig. 2). In the second-order streams, total abundance, and abundances of collector-gatherers, grazers, predators, and shredders were greater in the grazed catchments than in the deer-excluded catchment, whereas abundance of collector-filterers was greater in the deer-excluded catchment than in the grazed catchments (Table 1, Fig. 2). In the third-order streams, total abundance, taxa richness, and abundances of collector-gatherers, grazers, predators, and shredders were greater in the grazed catchments than in the deer-excluded catchment, whereas abundance of collector-filterers was greater in the deer-excluded catchment than in the grazed catchments (Table 1, Fig. 2). Overall, total abundance and abundances of collector-

**Table 1**

Results of the model selections based on Akaike information criterion for each response variable in first-, second-, and third-order streams. Asterisks denote selected effects of deer presence on macroinvertebrate communities in the best generalized linear mixed models.

	First-order stream	Second-order stream	Third-order stream
Total abundance	*	*	*
Taxa richness			*
Collector-filterers		*	*
Collector-gatherers	*	*	*
Grazers		*	*
Predators	*	*	*
Shredders	*	*	*



**Fig. 2.** Means and 1 standard deviations for each macroinvertebrate variable (abundance, taxa richness, abundances of collector-filterers, collector-gatherers, grazers, predators, and shredders) in the study reaches of deer-excluded and grazed catchments.

gatherers, shredders, and predators were greater in the grazed catchments, but in the second- and third-order streams, collector-filterers had greater numbers in the deer-excluded catchment than in the grazed catchments.

The first two axes of the RDA captured 89.9% of the total variation (Fig. 3), and PERMANOVA indicated that macroinvertebrate community structure differed significantly between reaches with and without deer and among stream orders (deer:  $F = 148$ ,  $R^2 = 0.379$ ,  $p < 0.001$ , stream

order:  $F = 128$ ,  $R^2 = 0.655$ ,  $p < 0.001$ ). The first RDA axis indicated that the second- and third-order streams had greater wetted width, water depth, and canopy openness than first-order streams (Fig. 3). The second RDA axis separated first-order streams in the grazed catchments from those in the deer-excluded catchment, indicating differences in community structure and fine sediment deposition (Fig. 3).

Indicator species analysis identified several significant indicator taxa for first-, second-, and third-order streams in the deer-excluded



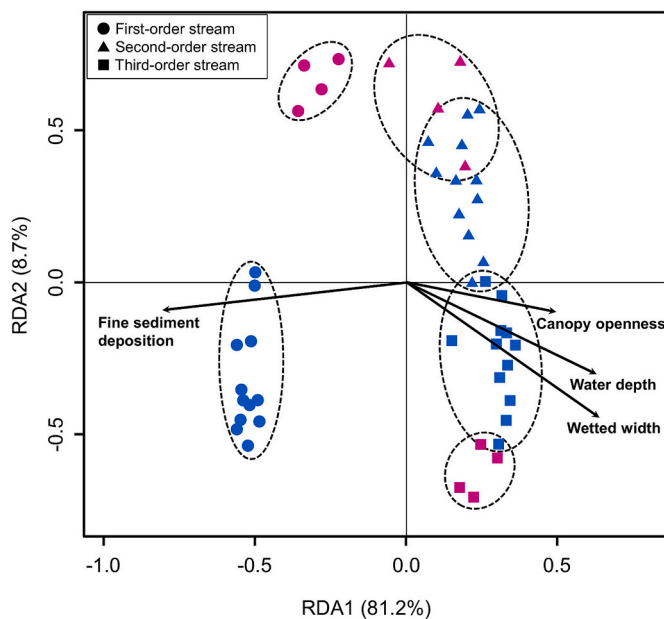


Fig. 3. Results of redundancy analysis based on the abundances of all macroinvertebrate taxa and selected environmental variables. Pink plots indicate macroinvertebrate communities in the deer-excluded catchment whereas blue plots indicate those in the grazed catchments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

catchment and the first-order streams in the grazed catchments, as well as for several combinations of study reaches (Table 2). The indicator taxa for first-order streams in the deer-excluded catchment were sprawling or swimming shredders (*Lepidostoma crassicornis* and *Sternomoera japonica*). Indicators of second-order streams in the EC were trichopterans, a clinging collector-filterer (*Melanotrichia* sp.) and a sprawling predator (*Apsilochorema sutshanum*), while third-order streams in the deer-excluded catchment were represented by a clinging collector-filterer trichopteran (*Dolophilodes japonica*) (Table 2). The indicator taxa of first-order streams in the grazed catchments were collector-gather ephemeropterans (*Kageronia kihada* and *Baetis* sp.) and

predatory odonates (*Planaeschna milnei* and *Anotogaster sieboldii*) (Table 2). For first-order streams in the deer-excluded and grazed catchments, as well as second-order streams in the grazed catchments, collector-gatherer dipterans that burrow into fine sediments (Tanypodinae spp., Chironominae spp., Ceratopogonidae spp.) and a shredder plecopteran (*Protonemura* sp.) were selected as indicator taxa, whereas the macroinvertebrate communities of third-order streams in the deer-excluded and grazed catchments were characterized by a sprawling predatory plecopteran (*Gibosia* sp.). The indicator taxa for first-order streams in the deer-excluded and grazed catchments were sprawling plecopterans (*Nemoura* spp. and *Niponiella limbatella*) and a burrowing dipteran (*Microtendipes* sp.), while first- and second-order streams in the deer-excluded catchment were represented by a sprawling decapod (*Geothelphusa dehaani*), and second- and third-order streams in the grazed catchments by a sprawling trichopteran (*Lepidostoma* spp.) and a clinging trichopteran (*Hydroptila* sp.) (Table 2).

#### 4. Discussion

This study demonstrated that fine sediment cover and macroinvertebrate community structure differ in first-order streams between the deer-excluded and grazed catchments, in accordance with previous studies (Sakai et al., 2013, 2021). Meanwhile, irrespective of similar fine sediment cover (Fig. S1), compositions of macroinvertebrate community differed also in second- and third-order streams between the deer-excluded and grazed catchments, in contrast to previous studies. In particular, abundances of most functional feeding groups and resultant total abundance were greater in the grazed catchments, while the abundance of collector-filterers was greater in the deer-excluded catchment than in the grazed catchments. The inconsistency in the results of comparison between stream substrate and macroinvertebrate communities suggests that deer-induced sediment runoff can influence communities not only through fine sedimentation in first-order streams but also through other processes affecting second- and third-order streams. In particular, the spatial independence of macroinvertebrate communities among the third-order stream reaches observed here implies potential effects of material transports from adjacent tributaries on the communities (e.g., Rice et al., 2001; Katano et al., 2009).

Previous studies at the same study site reported that overland flow into the stream was greater for one of the grazed catchments than the

Table 2

Significant indicator taxa for each stream type ( $p < 0.05$ ; adjusted  $p$  for multiple tests). DEC and GC indicate deer-excluded and grazed catchments, respectively. For life-form types (LFT), Sp, Sw, C, and B denote sprawler, swimmer, clinger, and burrower, respectively. For functional feeding groups (FFG), S, C/G, C/F, P, S, and G denote shredder, collector-gatherer, collector-filterer, predator, and grazer, respectively.

Family	Taxon	LFT	FFG	Stream group	IndVal	P
Lepidostomatidae	<i>Lepidostoma crassicornis</i>	Sp	S	DEC 1st	0.688	0.009
Pontogeneiidae	<i>Sternomoera japonica</i>	Sw	C/G, S	DEC 1st	0.685	0.031
Xiphocentronidae	<i>Melanotrichia</i> sp.	C	C/F	DEC 2nd	0.986	<0.001
Hydrobiosidae	<i>Apsilochorema sutshanum</i>	Sp	P	DEC 2nd	0.640	0.047
Philopotamidae	<i>Dolophilodes japonica</i>	C	C/F	DEC 3rd	0.723	0.007
Heptageniidae	<i>Kageronia kihada</i>	Sp	C/G	GC 1st	0.989	<0.001
Baetidae	<i>Baetis</i> sp.	Sw	C/G	GC 1st	0.957	<0.001
Aeshnidae	<i>Planaeschna milnei</i>	Sp	P	GC 1st	0.764	0.002
Cordulegastridae	<i>Anotogaster sieboldii</i>	B	P	GC 1st	0.707	0.006
Nemouridae	<i>Nemoura</i> sp.	Sp	S	GC 1st, DEC 1st	0.941	<0.001
Perlidae	<i>Niponiella limbatella</i>	Sp	P	GC 1st, DEC 1st	0.926	<0.001
Chironomidae	<i>Microtendipes</i> sp.	B	C/G	GC 1st, DEC 1st	0.705	0.020
Lepidostomatidae	<i>Lepidostoma</i> spp.	Sp	S	GC 2nd, GC 3rd	0.902	<0.001
Hydroptilidae	<i>Hydroptila</i> sp.	C	G	GC 2nd, GC 3rd	0.707	0.012
Perlidae	<i>Gibosia</i> sp.	Sp	P	GC 3rd, DEC 3rd	0.791	0.001
Potamidae	<i>Geothelphusa dehaani</i>	Sp	C/G	DEC 1st, DEC 2nd	0.658	0.026
Hydropsychidae	<i>Hydropsyche orientalis</i>	C	C/F	DEC 2nd, DEC 3rd	0.720	0.008
–	<i>Hydrachnellae</i> spp.	Sp	P	GC 1st, GC 2nd, GC 3rd	0.866	<0.001
Chironomidae	Tanypodinae spp.	B	P	GC 1st, GC 2nd, DEC 1st	0.898	<0.001
Chironomidae	Chironominae spp.	B	C/G	GC 1st, GC 2nd, DEC 1st	0.895	<0.001
Ceratopogonidae	Ceratopogonidae spp.	B	C/G	GC 1st, GC 2nd, DEC 1st	0.863	<0.001
Nemouridae	<i>Protonemura</i> sp.	Sp	S	GC 1st, GC 2nd, DEC 1st	0.855	<0.001

deer-excluded catchment due to deer overgrazing (Table 3, Sakai et al., 2012, 2013). Decreased overland flow by deer exclusion lowered suspended sediment concentration especially during large rainfall events (Table 3, Sakai et al., 2022), and then fine sedimentation was pronounced in first-order streams of grazed catchments (Sakai et al., 2013). The previous study was conducted within 4 years after the deer exclusion, and the same pattern was observed in this study (6–8 years after deer exclusion). This similarity indicates that deer overgrazing continues to cause deposition and storage of fine sediments in first-order streams, but not second- and third-order streams. As the current velocity becomes faster at higher stream order (Fig. S1), fine sediment cover decreases independent of the presence or absence of deer and this basal longitudinal change in stream hydraulics controls sediment transport and deposition.

Meanwhile, transported fine sediments can settle in stagnant downstream habitats (Montgomery and Buffington, 1997; Church, 2002), inducing expansion of fine sediment cover and associated alteration of stream communities. For example, in a fourth-order stream connected to our study streams, both macroinvertebrate and fish communities changed with the expansion of fine sediment deposition in recent years (Nakagawa, 2019, 2021). Thus, in the study area, deer-induced fine sedimentation is pronounced in first- and fourth-order streams, whereas intermediate streams (i.e., second- and third-order streams) receive their main inputs of suspended sediments during rainfall events (Sakai et al., 2022).

Suspended sediments are fatal stressors for specific macroinvertebrate groups such as collector-filterers and grazers due to impairment of the quality and quantity of their food (Grubaugh and Wallace, 1995; Jones et al., 2012). In second- and third-order streams, collector-filterer abundance was greater in the deer-excluded catchment than the grazed catchments. This result suggests that sediment input associated with deer overgrazing can impact species that are vulnerable to suspended sediments in second- and third-order streams without altering streambed conditions. Communities in the deer-excluded catchment were characterized by several trichopterans that inhabit erosional gravel beds (Merritt et al., 2008; Kawai and Tanida, 2018), some of which were collector-filterers. In contrast, one of the selected indicator taxa of communities in the grazed catchments (*Lepidostoma* spp.) was a detritivorous trichopteran that prefers depositional habitats (Merritt et al., 2008; Kawai and Tanida, 2018). These results suggest that catchment-scale deer exclusion restored habitat for taxa that preferentially inhabit erosional environments and consume suspended particulate organic matter in second- and third-order streams. Because collector-filterers have the potential to themselves govern the suspended sediments through water filtration, their declines may thus be indicative of problems with fine sediments that following their declines

then has further impacts on other macroinvertebrates (Lummer et al., 2016).

The findings of this study provide new insights into the impacts of deer on stream ecosystems that were not observed 4 years after deer exclusion (Sakai et al., 2013). Even if deer-induced fine sediment inputs do not settle on the streambeds of second- and third-order streams, species vulnerable to suspended sediments (i.e., collector-filterers) may gradually diminish due to deer overgrazing. Meanwhile, grazers, which are intolerant to reduced algal productivity driven by suspended sediment discharge (Grubaugh and Wallace, 1995), were more abundant in the grazed catchments than the deer-excluded catchment. Primary productivity is generally controlled by factors such as turbidity, nutrients, salinity, and light intensity (Larned, 2010; Costello et al., 2018). Among factors, the effects of turbid water on periphyton and grazers are generally known from streams impacted by anthropogenic land modification (Wood and Armitage, 1997; Yamada and Nakamura, 2002), and are even lower in streams impacted by natural increases of ungulates. Thus, sediment inputs from deer overgrazing may not be fatal to grazers. Meanwhile, nitrate inputs from deer-grazed catchments may enhance the growth of periphyton and negate the impacts of suspended sediments (cf. Costello et al., 2018), as the demise of understory vegetation increases the nitrate concentration in stream water (Table 3, Sakai et al., 2022). The effects of deer overgrazing on water chemistry and associated aquatic organisms remain unclear, but may be as important as the impacts of suspended sediment on macroinvertebrate communities.

In first-order streams, the abundance of burrowing collector-gatherers that inhabit fine sediments was significantly greater in the grazed catchments compared to the deer-excluded catchment, corresponding to greater cover of fine sediments. Meanwhile, indicator species analysis showed that macroinvertebrate communities in both catchment types are characterized by multiple detritivores inhabiting depositional habitats. These results suggest that first-order streams are essentially depositional, but the additional fine sediment provided by deer due to overgrazing may provide further suitable habitats for burrowers, leading to their predominance. Interestingly, the indicator taxa of first-order streams in the deer-excluded catchment included a detritivorous amphipod that uses interstitial habitats in headwaters (Sakai et al., 2013; Vadher et al., 2015). Because amphipod species are intolerant of fast currents (Barquín and Death, 2004; Meyer et al., 2007), the predominance of this species implies the presence of interstitial spaces in which amphipods can seek protection in first-order streams of the deer-excluded catchment.

The macroinvertebrate communities of first-order streams in the grazed catchments were characterized by odonate carnivores. Because the abundance of macroinvertebrates was significantly greater in the grazed catchments than the deer-excluded catchment, carnivorous taxa

**Table 3**

Comparisons of overland flow discharge, overland flow contribution to stream, and flow-weighted mean concentrations of suspended sediment and  $\text{NO}_3^-$  in between the deer-excluded and grazed catchments, from Sakai et al. (2012, 2013, 2022).

Variable	Monitoring period	Total precipitation (mm)	Deer-excluded catchment	Grazed catchment	Reference
Overland flow discharge/precipitation (%)	Jun. to Nov. 2009	1472	1.55%	4.10%	Sakai et al. (2012)
Component index of overland flow in stream water	Apr. to Nov. 2010	1200	393	546	Sakai et al. (2013)
Flow-weighted mean suspended sediment concentration (mg/L)	7 Sep. 2010	61.5	21.5	37.8	Sakai et al. (2022)
	22 Nov. 2010	37.0	1.8	2.8	
	10 Jun. 2011	40.5	6.4	4.7	
	24 Jun. 2011	28.0	6.8	3.7	
	18 Jul. 2011	314.5	61.9	72.1	
	19 Aug. 2011	18.0	18.3	25	
	1 Sep. 2011	340.0	95.6	113.3	
	7 Sep. 2010	61.5	0.45	0.77	
	22 Nov. 2010	37.0	0.28	0.36	
	10 Jun. 2011	40.5	0.18	0.25	
Flow-weighted mean $\text{NO}_3^-$ concentration (mg N/L)	24 Jun. 2011	28.0	0.18	0.23	Sakai et al. (2022)
	18 Jul. 2011	314.5	0.32	0.46	
	19 Aug. 2011	18.0	0.21	0.25	
	1 Sep. 2011	340.0	0.37	0.54	

may predominate due to high food availability (Richardson and Neill, 1991; Kobayashi and Kagaya, 2004). The contrast in communities between the deer-excluded and grazed catchments suggests that deer-induced sediment inputs can increase the abundance of detritivores, and thus that of carnivores. This process may also plausibly occur in larger streams, as the abundance of predators was significantly greater in the grazed catchments than the deer-excluded catchment across all stream orders. For instance, deposited sediment in pools may supplement food resources for predators in riffles (Finlay et al., 2002). Meanwhile, an omnivorous freshwater crab characterized the communities of first- and second-order streams in the deer-excluded catchment. This species is amphibious (Okano et al., 2000), and lush understory vegetation within the catchment may provide suitable terrestrial habitat and food resources for this species.

Overall, the results of RDA indicated that the macroinvertebrate communities differed among stream orders in both the deer-excluded and grazed catchments, and the communities in second-order streams were intermediate between those of first- and third-order streams. While the impacts of deer overgrazing on these communities are attributable to fine sediment deposition in first-order streams, increased concentration of suspended sediments (and perhaps nitrate) can have impacts in second- and third-order streams. Nevertheless, the clear patterns of longitudinal changes in macroinvertebrate communities suggested that the basal relationship between the macroinvertebrate community and fluvial geomorphology was not deteriorated due to overgrazing by deer.

Sediment addition through soil erosion has been one of the most potent factors impairing riverine biodiversity (Wood and Armitage, 1997; Jones et al., 2012). While terrestrial alteration of soil conditions can be a primal factor influencing input fluxes of sediments (García-Ruiz et al., 2015), structural properties of the stream itself (Braun et al., 2012) and its flow regime (Auerswald and Geist, 2018) affect the settlement of fine sediments. Also, anthropogenic impacts including climate change can alter the magnitude of these factors (Hoess and Geist, 2020). Therefore, elucidating spatiotemporal propagation of impacts of fine sedimentation and increased concentration of suspended sediments on riverine biodiversity, as reported here is important for exploring adequate sediment managements. Although feasible and sustainable measures for stream substratum restoration still remain elusive (Pander et al., 2015), the measure and associated responses of macroinvertebrate communities might suggest that the catchment-scale deer exclusion is of feasible and low-cost solutions to sediment addition by deer overgrazing.

## 5. Conclusions

The present study demonstrated that sediment runoff due to deer overgrazing alters streambed cover in first-order streams but not in second- or third-order streams in the grazed catchments after 6–8 years of deer exclusion in the deer-excluded catchment. However, the macroinvertebrate communities indicated that deer overgrazing can alter community structures across stream orders. The propagation of deer impacts on first- to third-order stream ecosystems proposed here highlights the importance of investigating the long-term dynamics of fine particles in lotic systems. Elucidating underlying geomorphological conditions is crucial to assessing the effects of soil runoff of terrestrial alterations such as increased populations of ungulates (Sakai et al., 2013), farmland reclamation (Harden, 2006; Von Bertrab et al., 2013), forest logging (Angradi, 1999; Zhang et al., 2009), and fire (Minshall, 2003) on benthic environments. Further studies on sediment dynamics and associated responses of biota in heterogeneous headwater systems in various locations can facilitate successful conservation and restoration of the integrity of forest-stream ecosystems.

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## CRedit authorship contribution statement

**Masaru Sakai:** Conceptualization, Investigation, Resources, Writing – original draft, Visualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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