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Title	Negative effects of brown bear digging on soil nitrogen availability and production in larch plantations in northern Japan : Their potential role as an agent of bioturbation
Author(s)	Tomita, Kanji; Hiura, Tsutom
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1   Title: Negative effects of brown bear digging on soil nitrogen availability and production in the larch

2   plantations in northern Japan: their role as an agent of bioturbation

3   K. Tomita, and T. Hiura

4   **Author names and affiliations**

5   Kanji Tomita , Graduate School of Environmental Science, Hokkaido University, N10 W5 Sapporo,

6   Hokkaido 060-0810, Japan, e-mail: ktomita38@gmail.com

7   Tsutom Hiura, Department of Ecosystem Studies, The University of Tokyo, Yayoi 1-1-1, Bunkyo-ku,

8   Tokyo, 113-8657 Japan, e-mail: hiura@g.ecc.u-tokyo.ac.jp

9   **Corresponding author**, Kanji Tomita (e-mail: ktomita38@gmail.com)

10

11   **Abstract**

12   Digging mammals displace a large amount of soil, thereby strongly altering soil ecosystem

13   processes such as nitrogen cycling through bioturbation. Although it is well known that bears

14   displace a large amount of soil by digging for food and denning, there is negligible empirical

15   evidence of the effects on soil properties. In the Shiretoko World Heritage site, we investigated the

16   effects of brown bear digging for cicada nymphs on soil properties, such as soil water content,

17   organic and inorganic nitrogen concentrations, and nitrogen mineralization rate that are important

18   components of soil ecosystem function and are essential for plant growth. We compared the

19   properties of soil recently dug by brown bears with undisturbed soil in larch plantations. We found

20   that brown bear digging decreased soil water content, organic matter, inorganic nitrogen

21   concentration, net mineralization rates. Our results suggest that soil digging by brown bear may

22   reduce plant growth by decreasing soil nutrient availability, thereby diminishing the net primary

23   production of the larch plantation at the study site.

24

25   **Keywords**: bioturbation, nitrogen mineralization, soil disturbance, *Ursus arctos*

Introduction

Soil bioturbation is the process of physical displacement of soil by organisms, such as plants, insects, birds, and mammals (Bétard, 2021; Fleming et al., 2014; Gabet et al., 2003; Maisey et al., 2021). It is an important biotic factor affecting many soil ecosystem functions (Meysman et al., 2006; Platt et al., 2016). Mammals that regularly dig for food and nest building are among the most extensive agents of bioturbation around the world (Coggan et al., 2018; Davidson et al., 2012; Mallen-Cooper et al., 2019; Platt et al., 2016). Mammalian digging for acquiring belowground food resources can directly and indirectly affect soil ecosystem processes through soil turnover and consumption of soil organisms, respectively, which significantly affects soil quality (Barrios-Garcia et al. 2014). Digging mammals displace a large amount of soil, thereby strongly altering soil ecosystem processes such as carbon dioxide emission and inorganic nitrogen production through bioturbation (Barrios-Garcia and Ballari, 2012; Mallen-Cooper et al., 2019; Platt et al., 2016; Risch et al., 2010). For instance, digging activity by wild boar (*Sus scrofa*) disturbed 27−54 % of the forest floor, decreased soil nitrogen availability and increased carbon dioxide emissions in a Switzerland woodland (Risch et al., 2010).

Previous studies on the effects of digging by mammals on soil ecosystem processes have mainly focused on small mammals such as social rodents and Australian marsupials (Davidson et al., 2012;

3

43   Fleming et al., 2014; Mallen-Cooper et al., 2019). Although larger mammals tend to displace a larger

44   volume of soil per one digging pit for food (Haussmann, 2017), there are relatively few studies on

45   the digging impacts of large mammals except for studies that focus on wild boars on soil ecosystem

46   processes (Barrios-Garcia and Ballari, 2012). The brown bear (*Ursus arctos*) displaces a large

47   amount of soil (Butler, 1992; Haussmann, 2017; Platt et al., 2016) because it forages on a wide

48   variety of belowground resources, such as subterranean animals and plant roots, in large quantities

49   (Butler, 1995; Mattson, 1997; Tardiff and Stanford, 1998; Tomita and Hiura, 2020). However, there

50   is only one study showing the effect of brown bear digging on soil properties (Tardiff and Stanford,

51   1998), and there are no studies from forest ecosystems where brown bears generally dig for food

52   (Munro et al., 2006; Tomita and Hiura, 2020). Tardiff and Stanford (1998) found that brown bear

53   digging for the bulbs of glacier lilies (*Erythronium grandiflorum*) enhanced seed production by

54   increasing soil inorganic nitrogen production in an alpine meadow of Glacier National Park, USA.

55   The effects of digging on soil properties vary among ecosystem types even within the same species

56   due to the differences in environmental conditions, such as ground solar radiation and vegetation

57   composition (Davies et al., 2019; Yurkewycz et al., 2014). Therefore, testing their digging impacts

58   on soil properties in forests are important for deepening our understandings of their ecological role

59   as agents of bioturbation.

60   In the Shiretoko World Heritage site (hereafter; SWH), Hokkaido, northern Japan, where has one

61   of the highest densities of brown bears in the world (Shimozuru et al., 2020), they have been

62   reported to dig for final instar nymphs of cicadas (*Lyristes bihamatus*) in the summer since 2000

63   (Fig. 1), suggesting that brown bears have caused novel bioturbation through behavioral changes

64   since 2000 (Tomita and Hiura, 2020). In this area, brown bear digging for cicadas occurred in

65   conifer plantations but not in natural mixed forests (Tomita and Hiura, 2021a). In the larch (*Larix*

66   *kaempferi*) plantations, bears dug up almost all the areas, and the area of a dug patch was often more

67   than 100 m^2 (Tomita and Hiura, 2020, 2021a). Larch plantations at the study site are expected to

68   facilitate natural forest regeneration because many native saplings occur within the plantation

69   (Suzuki et al., 2021). Accordingly, we evaluated the effects of brown bear digging on the soil

70   properties to develop understanding of the contribution of bears to natural forest regeneration in the

71   larch plantations.

72   A recent meta- analysis study found that vertebrate digging significantly increased soil nitrogen

73   and decreased water run-off (Mallen-Cooper et al., 2019). Tardiff and Stanford (1998) showed a

74   positive effect of brown bear digging on nitrogen production. Hence, we hypothesized that brown

75   bear digging for cicada nymphs would increase soil water content, inorganic nitrogen availability,

76   and nitrogen mineralization rate.

Material and methods

Study site

The present study was conducted in the Horobetsu-Iwaobetsu area (44°09 'N, 145°02 'E;

altitude, 120-220 m) located in the western parts of the SWH. The soil type at the study site is low-

humic allophanic Andosols (https://soil-inventory.dc.affrc.go.jp/). This area is certified as a

UNESCO World Natural Heritage site, as it represents one of the richest northern temperate

ecosystems globally. Natural forests are typical conifer–broadleaved mixed forests dominated by

Sakhalin firs (*Abies sachalinensis*) and Mongolian oaks (*Quercus crispula*) (Tatewaki 1958). Natural

forests accounted for 82 % , and plantations accounted for the remaining 18 % of the total forested

area at the study site. Sakhalin spruce (*Picea glehnii*), Japanese larch, and Sakhalin fir plantations

account for 13%, 4%, and 1% of the total forested area, respectively (Tomita and Hiura 2021). Soil

sampling was conducted in larch plantations with an understory dominated by pasture grass species

such as Chinese silvergrass (*Miscanthus sinensis*) and sweet vernalgrass (*Anthoxanthum odoratum*).

These grass species were introduced for cattle breeding during the cultivation period from 1930s to

1970s. Most larch and fir plantations were established in 1970s, whereas spruce plantations were

established in the early 1990s (Shoyama, 2008).

Camera traps in larch plantations found that 11 bears (two sub-adults, two solitary female adults,

94   and three females with cub(s)) and 11 bears (one adult male, one sub-adult, two solitary adult

95   females, and three females with cub(s)) dug for cicada nymphs in 2018 and 2019, respectively

96   (Tomita, 2021; Tomita and Hiura, 2020). Two cicada species *Lyristes bihamatus* and *Yezoterpnosia*

97   *nigricosta*, occur at the study site, but bears forage on the final instar nymphs of *L. bihamatus*

98   (Tomita and Hiura, 2020). The reason behind bears only digging for cicadas within conifer

99   plantations is that the density of *L. bihamatus* is several times higher in conifer plantations than in

100   natural forests (Tomita and Hiura, 2021a). Based on our field observations, brown bear digging for

101   cicada nymphs does not create pits and mounds, but rather is similar to rooting by wild boars (Fig.

102   1). This is because brown bears mainly consume final-instar cicada nymphs, which stay in surface

103   soil (~ 15 cm depth) (Tomita and Hiura, 2020). Brown bears continued digging for cicada nymphs

104   until early August, when cicada emergence was completed (Tomita, 2021).

105   **Soil sampling**

106   In September 2018, we found the highest frequency of brown bear digging for cicada nymphs in

107   larch plantations (Tomita and Hiura, 2021a). Based on this finding, we chose 14 independent larch

108   plantations as soil sampling points in October 2018 (Fig.2) when brown bear digging had ended

109   about two months ago. To maintain independence among the sampling points, each point was spaced

110   at least 100 m apart. At each sampling point, surface soil (0-10 cm) was collected from both dug and

111   adjacent undisturbed soil using a 100-ml soil core sampler. To make up the paired-sample design, we

112   collected undisturbed soil that was completely covered by pasture grass without any presence of

113   overturned soil and apart 1 m from dug areas. To ensure that the undisturbed soil was not dug by

114   brown bears, we also observed the accumulation of larch litter in the undisturbed soil. The dug soil

115   were exposed to bare soil without a litter layer owing to soil disturbance in the sampling year. The

116   collected soil was sieved a 2 mm to remove roots and coarse gravel, and mixed well for

117   homogenization. The soil was kept at 6 °C prior to chemical analysis and laboratory incubation.

118   **Evaluation of soil properties**

119   Soil moisture was measured by drying the soil at 105 °C for 24 h. For total nitrogen and carbon

120   concentrations, approximately 20 mg of dry soil was analyzed using a CN analyzer (NC- 900;

121   Sumitomo, Osaka, Japan). For inorganic nitrogen availability, 6 g of fresh soil was weighed into

122   plastic bottles and extracted with 27.5 mL 1 M KCl with shaking for 1 h. By using an auto-analyzer

123   (AACS-4, BL-TEC, Inc., Japan), ammonium and nitrate nitrogen was analyzed by indophenol blue

124   absorptiometry and naphthyl ethylenediamine dihydrochloride spectrophotometry, respectively. The

125   total concentration of nitrogen in nitrate and ammonium was regarded as the total nitrogen

126   availability.

127   For net nitrogen mineralization rate, 6 g of fresh soil adjusted to 60 % of water-holding capacity

128   (field capacity) was placed in a 50 mL glass vials and incubated at 25 °C for 30 days. The net

129   mineralization rate was determined from the difference in the total inorganic nitrogen concentration

130   (ammonia + nitrate-nitrogen concentration) before and after incubation. The nitrification rate was

131   determined from the difference in nitrate nitrogen concentration before and after incubation. The

132   units for both rates were converted to 1 kg of dry soil per day. After checking the normal distribution

133   of the data using the Shapiro-Wilk test, we conducted Welch's t-test. The data that did not have a

134   normal distribution and was fitted to a normal distribution by log10-transformation followed by

135   analysis using t-test. All statistical analyses were conducted using R version 3.5.1 (R Core Team,

136   2018).

Results

137

138   Soil water content, organic nitrogen and carbon contents, carbon nitrogen ratio, ammonium

139   nitrogen concentration, and net mineralization rates in dug soil were significantly lower than those in

140   undisturbed soil ($P < 0.05$, Table S1, Figs. 1a, c, d, f, h, and i). Nitrate nitrogen concentration and,

141   nitrification rate in the dug soil was not significantly lower than that in undisturbed soil (nitrate

142   nitrogen [$P = 0.379$, Fig. 1g], nitrification rate [$P=0.342$, Fig. 1j]. Carbon nitrogen ratio was

143   marginally significantly higher in dug soil than in undisturbed soil (Fig.1e, $P = 0.079$) Bulk density

144   in dug areas was significantly higher than that in undisturbed areas (Fig.1b, $P < 0.01$). Percentage

145   differences in soil properties between dug and undisturbed soil are shown in Table S1.

146

147 **Discussion**

148   Contrary to our hypothesis, brown bear digging negatively affected soil water and nitrogen

149 availability in the larch plantations. To our knowledge, this is the first study showing the effects of

150 digging on soil properties in forest ecosystems, where bear digging normally occurs (Munro et al.

151 2006). Given that soil water and nitrogen availability are positively correlated with net primary

152 production in temperate forests (Pastor et al., 1984; Tateno et al., 2004), brown bear digging may

153 decrease net primary production in the larch plantation of the study site through changes at soil

154 nutrient dynamics.

155   Interestingly, in contrast with our results, Tardiff and Stanford (1998) found that brown bear

156 digging increased soil inorganic nitrogen availability in an alpine meadow. A possible reason for this

157 is the differences in the light environment on the surface ground between meadows and forests. In

158 open habitat with strong ground solar radiation, such as meadows and grasslands, digging by

159 mammals increases soil albedo due to the exposure of the darker mineral soil by the removal of

160 plants and litter, thereby increasing soil temperature (Canals et al., 2003; Yurkewycz et al., 2014).

161 Given that soil temperature positively affects the nitrogen mineralization rate (Guntiñas et al., 2012;

162 Knoepp and Swank, 2002), the positive effect of digging on inorganic nitrogen production in open

163 habitats would be yielded by an increase in soil temperature by digging (Tardiff and Stanford, 1998).

164   As digging does not affect soil temperature in forests with weak ground solar radiation (Barrios-

165   Garcia et al., 2014; Risch et al., 2010), the positive effects of digging on soil inorganic nitrogen

166   would be subtle in forests. Rather, soil mixing by digging is one of the possible mechanisms for the

167   reduction in organic nitrogen content and thereby inorganic nitrogen concentration (Kurek et al.,

168   2014; Wirthner et al., 2012), because it is usually the highest in the surface organic layer (Persson

169   and Wirén, 1995). This is supported by the result that the net mineralization rate of the dug soil was

170   lower than that of the undisturbed soil, even under the same water and temperature conditions (Fig.

171   3i). Brown bear digging would also negatively affect inorganic nitrogen production through

172   reduction in soil water contents (Fig. 3a). These implies that brown bear digging for cicadas might

173   negatively affect soil inorganic nitrogen by not only altering the soil water availability as well as the

174   mixture of organic and mineral soil.

175   Digging can increase inorganic nitrogen availability through the removal of plant root (Canals et

176   al., 2003). However, our results did not support this mechanism, even though the dug soil was

177   removed understory cover by brown bear digging. This suggests that the negative effect of soil

178   mixing obscures the positive effect of root removal. Note that this difference may be due to

179   methodological differences between this study and that of Tardiff and Stanford (1998), who

180   evaluated the net mineralization rate by field nitrogen incubation using resin bags. Although bears

181 could enhance soil nitrogen availability by depositing dung and urine when digging for cicada

182 nymphs (Tardiff and Stanford, 1998), our results suggest that their excrement seems to have a weak

183 effect on soil nitrogen, or that the negative effect of digging exceeded its effects.

184   While digging by pocket gophers (*Thomomys bottae*) can accelerate the soil nitrification rate

185 through promoting soil aeration during the gopher activity season (Canals et al., 2003), our results

186 showed that nitrification rate of the dug soil did not significantly differ from that of undisturbed soil.

187 The positive effect of digging on nitrate nitrogen through soil aeration may be weak because our soil

188 sampling was conducted in October, approximately 2 months after the bear diggings occurred, by

189 which time the soil is likely to have been redistributed (e.g., by rainfall) among the pores created by

190 the initial digging event. The reduction in soil water content through digging may be caused by litter

191 removal because the litter layer can prevent water evaporation from the surface soil (Sayer, 2006).

192 Their digging may also decrease soil water content by exposing the soil to the air, thereby facilitating

193 the direct evaporation of soil water (Bueno et al., 2013). The consumption of cicada nymphs may be

194 a possible mechanism for the negative effects of brown bear digging on soil water and nitrogen,

195 given that the nymphs can release a large amount of water and nitrogen from tree roots into the soil

196 through xylem feeding activity (Hunter, 2016).

197   Although the ecosystem roles of brown bears are well known (García-Rodríguez et al., 2021;

198   Helfield and Naiman, 2006), little attention has been paid to their ecosystem role as digging

199   mammals (Tardiff and Stanford, 1998). Deepening the understanding of the ecological roles of

200   wildlife is important for justifying conservation and management policy making (Somaweera et al.,

201   2020). We hope that this study provides ecological insights for their conservation and management

202   by evaluating the role of bears as agents of bioturbation in a landscape composed of natural forests

203   and plantations. However, we should carefully consider whether our finding are applicable to other

204   ecosystem types, because the direction and magnitude of digging impacts vary with local and

205   regional environmental conditions, even in the same species (Yurkewycz et al., 2014).

206   Our previous study suggested that brown bears have caused novel bioturbation since 2000 when

207   they started digging for cicada nymphs (Tomita and Hiura, 2020). This study speculated an

208   ecological consequence of this emerging behavior, in which their digging negatively affected soil

209   water and nitrogen availability in larch plantations. Given that brown bear digging for cicada

210   nymphs occurred extensively in the larch plantations (Tomita and Hiura, 2021b, 2021a), their

211   digging may have strongly affected tree growth and regeneration in the plantations. Since xylem

212   feeding by cicada nymphs can negatively affect tree growth occasionally (Karban, 1980), there may

213   be both negative and positive effects on brown bear digging for cicadas via soil disturbance and

214 trophic cascade by reducing cicada density, respectively. This hypothesis is worth testing in the

215 future study for examining ecological consequences when simultaneously occurring trophic and non-

216 trophic effects of apex predators.

217   A recent study showed that many native tree saplings established in larch plantations at the study

218 site, and thus proposed their potential role on the establishment of naturally regenerating forests

219 (Suzuki et al., 2021). Brown bears may hinder natural forest regeneration in larch plantations by

220 overturning seedlings and limiting water and nitrogen uptake by these saplings. Additionally, brown

221 bears may also affect forest regeneration in plantations in other ways we did not address in this

222 study. For example, bears may disperse seeds of wild cherry, which is an important summer food for

223 bears (Koike et al., 2008), into the plantation if they deposit scats containing the seeds while digging

224 for cicada nymphs. Further investigation of their roles on tree growth and establishment through

225 limiting soil nutrient availability and cicada density is required to develop the understanding of their

226 contribution to natural forest regeneration in the plantations.

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15

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362 **Figure legend**

363 Figure 1 (a) Trace of brown bear digging for cicada nymphs within a larch plantation. This picture

364 shows the representative soil sampling point. We collected the disturbed and undisturbed soil

365 samples within and without the dug area, respectively. (b) A bear scat containing the fragments of

366 cicada nymphs (c) A female brown bear with two cubs dig for cicada nymphs in a larch plantation.

367 Photo credit: (a) and (c) Shiretoko Nature Foundation, (b) Kanji Tomita
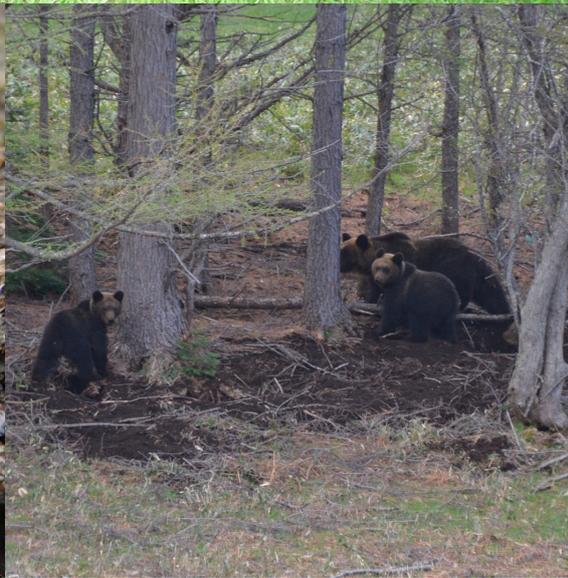
368 Figure 2 Location of the soil sampling points superimposed on a vegetation map of the study site.

369 This vegetation map is reprinted from Tomita and Hiura (2021a) and created by Shiretoko Nature

370 Foundation (unpublished information). This figure was created using QGIS 3.14.0.

371 Figure 3 Comparisons of soil water content (a), bulk density (b), total carbon (c), total nitrogen (d),

372 C:N ratio (e), ammonium nitrogen (f), nitrate nitrogen (g), total inorganic nitrogen (h), net

373 mineralization rate (i), and nitrification rate (j) between dug (Grey color) and undisturbed (Black

374 color) soil. *P*-values in each boxplot were the results of analysis of variance.

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376 **Figure 1**

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379 **Figure 2**

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381   **Figure 3**

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