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
Citation	Pedobiologia, 91-92, 150807 https://doi.org/10.1016/j.pedobi.2022.150807
Issue Date	2022-06
Doc URL	http://hdl.handle.net/2115/89383
Rights	© 2022. This manuscript version is made available under the CC-BY-NC-ND 4.0 license http://creativecommons.org/licenses/by-nc-nd/4.0/
Type	article (author version)
File Information	TH -2022-Pedob.pdf

Title: Negative effects of brown bear digging on soil nitrogen availability and production in the larch plantations in northern Japan: their role as an agent of bioturbation

K. Tomita, and T. Hiura

Author names and affiliations

Kanji Tomita , Graduate School of Environmental Science, Hokkaido University, N10 W5 Sapporo, Hokkaido 060-0810, Japan, e-mail: ktomita38@gmail.com

Tsutom Hiura, Department of Ecosystem Studies, The University of Tokyo, Yayoi 1-1-1, Bunkyo-ku, Tokyo, 113-8657 Japan, e-mail: hiura@g.ecc.u-tokyo.ac.jp

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

Abstract

Digging mammals displace a large amount of soil, thereby strongly altering soil ecosystem processes such as nitrogen cycling through bioturbation. Although it is well known that bears displace a large amount of soil by digging for food and denning, there is negligible empirical evidence of the effects on soil properties. In the Shiretoko World Heritage site, we investigated the effects of brown bear digging for cicada nymphs on soil properties, such as soil water content, organic and inorganic nitrogen concentrations, and nitrogen mineralization rate that are important components of soil ecosystem function and are essential for plant growth. We compared the properties of soil recently dug by brown bears with undisturbed soil in larch plantations. We found that brown bear digging decreased soil water content, organic matter, inorganic nitrogen concentration, net mineralization rates. Our results suggest that soil digging by brown bear may reduce plant growth by decreasing soil nutrient availability, thereby diminishing the net primary production of the larch plantation at the study site.

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;

Fleming et al., 2014; Mallen-Cooper et al., 2019). Although larger mammals tend to displace a larger volume of soil per one digging pit for food (Haussmann, 2017), there are relatively few studies on the digging impacts of large mammals except for studies that focus on wild boars on soil ecosystem processes (Barrios-Garcia and Ballari, 2012). The brown bear (*Ursus arctos*) displaces a large amount of soil (Butler, 1992; Haussmann, 2017; Platt et al., 2016) because it forages on a wide variety of belowground resources, such as subterranean animals and plant roots, in large quantities (Butler, 1995; Mattson, 1997; Tardiff and Stanford, 1998; Tomita and Hiura, 2020). However, there is only one study showing the effect of brown bear digging on soil properties (Tardiff and Stanford, 1998), and there are no studies from forest ecosystems where brown bears generally dig for food (Munro et al., 2006; Tomita and Hiura, 2020). Tardiff and Stanford (1998) found that brown bear digging for the bulbs of glacier lilies (*Erythronium grandiflorum*) enhanced seed production by increasing soil inorganic nitrogen production in an alpine meadow of Glacier National Park, USA. The effects of digging on soil properties vary among ecosystem types even within the same species due to the differences in environmental conditions, such as ground solar radiation and vegetation composition (Davies et al., 2019; Yurkewycz et al., 2014). Therefore, testing their digging impacts on soil properties in forests are important for deepening our understandings of their ecological role as agents of bioturbation.

In the Shiretoko World Heritage site (hereafter; SWH), Hokkaido, northern Japan, where has one of the highest densities of brown bears in the world (Shimozuru et al., 2020), they have been reported to dig for final instar nymphs of cicadas (*Lyristes bihamatus*) in the summer since 2000 (Fig. 1), suggesting that brown bears have caused novel bioturbation through behavioral changes since 2000 (Tomita and Hiura, 2020). In this area, brown bear digging for cicadas occurred in conifer plantations but not in natural mixed forests (Tomita and Hiura, 2021a). In the larch (*Larix kaempferi*) plantations, bears dug up almost all the areas, and the area of a dug patch was often more than 100 m^2 (Tomita and Hiura, 2020, 2021a). Larch plantations at the study site are expected to facilitate natural forest regeneration because many native saplings occur within the plantation (Suzuki et al., 2021). Accordingly, we evaluated the effects of brown bear digging on the soil properties to develop understanding of the contribution of bears to natural forest regeneration in the larch plantations.

A recent meta- analysis study found that vertebrate digging significantly increased soil nitrogen and decreased water run-off (Mallen-Cooper et al., 2019). Tardiff and Stanford (1998) showed a positive effect of brown bear digging on nitrogen production. Hence, we hypothesized that brown bear digging for cicada nymphs would increase soil water content, inorganic nitrogen availability, 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, and three females with cub(s)) and 11 bears (one adult male, one sub-adult, two solitary adult females, and three females with cub(s)) dug for cicada nymphs in 2018 and 2019, respectively (Tomita, 2021; Tomita and Hiura, 2020). Two cicada species *Lyristes bihamatus* and *Yezoterpnosia nigricosta*, occur at the study site, but bears forage on the final instar nymphs of *L. bihamatus* (Tomita and Hiura, 2020). The reason behind bears only digging for cicadas within conifer plantations is that the density of *L. bihamatus* is several times higher in conifer plantations than in natural forests (Tomita and Hiura, 2021a). Based on our field observations, brown bear digging for cicada nymphs does not create pits and mounds, but rather is similar to rooting by wild boars (Fig. 1). This is because brown bears mainly consume final-instar cicada nymphs, which stay in surface soil (~ 15 cm depth) (Tomita and Hiura, 2020). Brown bears continued digging for cicada nymphs until early August, when cicada emergence was completed (Tomita, 2021).

Soil sampling

In September 2018, we found the highest frequency of brown bear digging for cicada nymphs in larch plantations (Tomita and Hiura, 2021a). Based on this finding, we chose 14 independent larch plantations as soil sampling points in October 2018 (Fig.2) when brown bear digging had ended about two months ago. To maintain independence among the sampling points, each point was spaced at least 100 m apart. At each sampling point, surface soil (0-10 cm) was collected from both dug and adjacent undisturbed soil using a 100-ml soil core sampler. To make up the paired-sample design, we collected undisturbed soil that was completely covered by pasture grass without any presence of overturned soil and apart 1 m from dug areas. To ensure that the undisturbed soil was not dug by brown bears, we also observed the accumulation of larch litter in the undisturbed soil. The dug soil were exposed to bare soil without a litter layer owing to soil disturbance in the sampling year. The collected soil was sieved a 2 mm to remove roots and coarse gravel, and mixed well for homogenization. The soil was kept at 6 °C prior to chemical analysis and laboratory incubation.

Evaluation of soil properties

Soil moisture was measured by drying the soil at 105 °C for 24 h. For total nitrogen and carbon concentrations, approximately 20 mg of dry soil was analyzed using a CN analyzer (NC- 900; Sumitomo, Osaka, Japan). For inorganic nitrogen availability, 6 g of fresh soil was weighed into plastic bottles and extracted with 27.5 mL 1 M KCl with shaking for 1 h. By using an auto-analyzer (AACS-4, BL-TEC, Inc., Japan), ammonium and nitrate nitrogen was analyzed by indophenol blue absorptiometry and naphthyl ethylenediamine dihydrochloride spectrophotometry, respectively. The total concentration of nitrogen in nitrate and ammonium was regarded as the total nitrogen availability.

For net nitrogen mineralization rate, 6 g of fresh soil adjusted to 60 % of water-holding capacity (field capacity) was placed in a 50 mL glass vials and incubated at 25 °C for 30 days. The net mineralization rate was determined from the difference in the total inorganic nitrogen concentration (ammonia + nitrate-nitrogen concentration) before and after incubation. The nitrification rate was determined from the difference in nitrate nitrogen concentration before and after incubation. The units for both rates were converted to 1 kg of dry soil per day. After checking the normal distribution of the data using the Shapiro-Wilk test, we conducted Welch's t-test. The data that did not have a normal distribution and was fitted to a normal distribution by log10-transformation followed by analysis using t-test. All statistical analyses were conducted using R version 3.5.1 (R Core Team, 2018).

Results

Soil water content, organic nitrogen and carbon contents, carbon nitrogen ratio, ammonium nitrogen concentration, and net mineralization rates in dug soil were significantly lower than those in undisturbed soil ($P < 0.05$, Table S1, Figs. 1a, c, d, f, h, and i). Nitrate nitrogen concentration and, nitrification rate in the dug soil was not significantly lower than that in undisturbed soil (nitrate nitrogen [$P = 0.379$, Fig. 1g], nitrification rate [$P=0.342$, Fig. 1j]. Carbon nitrogen ratio was marginally significantly higher in dug soil than in undisturbed soil (Fig.1e, $P = 0.079$) Bulk density in dug areas was significantly higher than that in undisturbed areas (Fig.1b, $P < 0.01$). Percentage differences in soil properties between dug and undisturbed soil are shown in Table S1.

Discussion

Contrary to our hypothesis, brown bear digging negatively affected soil water and nitrogen availability in the larch plantations. To our knowledge, this is the first study showing the effects of digging on soil properties in forest ecosystems, where bear digging normally occurs (Munro et al. 2006). Given that soil water and nitrogen availability are positively correlated with net primary production in temperate forests (Pastor et al., 1984; Tateno et al., 2004), brown bear digging may decrease net primary production in the larch plantation of the study site through changes at soil nutrient dynamics.

Interestingly, in contrast with our results, Tardiff and Stanford (1998) found that brown bear digging increased soil inorganic nitrogen availability in an alpine meadow. A possible reason for this is the differences in the light environment on the surface ground between meadows and forests. In open habitat with strong ground solar radiation, such as meadows and grasslands, digging by mammals increases soil albedo due to the exposure of the darker mineral soil by the removal of plants and litter, thereby increasing soil temperature (Canals et al., 2003; Yurkewycz et al., 2014). Given that soil temperature positively affects the nitrogen mineralization rate (Guntiñas et al., 2012; Knoepp and Swank, 2002), the positive effect of digging on inorganic nitrogen production in open habitats would be yielded by an increase in soil temperature by digging (Tardiff and Stanford, 1998).

As digging does not affect soil temperature in forests with weak ground solar radiation (Barrios-Garcia et al., 2014; Risch et al., 2010), the positive effects of digging on soil inorganic nitrogen would be subtle in forests. Rather, soil mixing by digging is one of the possible mechanisms for the reduction in organic nitrogen content and thereby inorganic nitrogen concentration (Kurek et al., 2014; Wirthner et al., 2012), because it is usually the highest in the surface organic layer (Persson and Wirén, 1995). This is supported by the result that the net mineralization rate of the dug soil was lower than that of the undisturbed soil, even under the same water and temperature conditions (Fig. 3i). Brown bear digging would also negatively affect inorganic nitrogen production through reduction in soil water contents (Fig. 3a). These implies that brown bear digging for cicadas might negatively affect soil inorganic nitrogen by not only altering the soil water availability as well as the mixture of organic and mineral soil.

Digging can increase inorganic nitrogen availability through the removal of plant root (Canals et al., 2003). However, our results did not support this mechanism, even though the dug soil was removed understory cover by brown bear digging. This suggests that the negative effect of soil mixing obscures the positive effect of root removal. Note that this difference may be due to methodological differences between this study and that of Tardiff and Stanford (1998), who evaluated the net mineralization rate by field nitrogen incubation using resin bags. Although bears could enhance soil nitrogen availability by depositing dung and urine when digging for cicada nymphs (Tardiff and Stanford, 1998), our results suggest that their excrement seems to have a weak effect on soil nitrogen, or that the negative effect of digging exceeded its effects.

While digging by pocket gophers (*Thomomys bottae*) can accelerate the soil nitrification rate through promoting soil aeration during the gopher activity season (Canals et al., 2003), our results showed that nitrification rate of the dug soil did not significantly differ from that of undisturbed soil. The positive effect of digging on nitrate nitrogen through soil aeration may be weak because our soil sampling was conducted in October, approximately 2 months after the bear diggings occurred, by which time the soil is likely to have been redistributed (e.g., by rainfall) among the pores created by the initial digging event. The reduction in soil water content through digging may be caused by litter removal because the litter layer can prevent water evaporation from the surface soil (Sayer, 2006). Their digging may also decrease soil water content by exposing the soil to the air, thereby facilitating the direct evaporation of soil water (Bueno et al., 2013). The consumption of cicada nymphs may be a possible mechanism for the negative effects of brown bear digging on soil water and nitrogen, given that the nymphs can release a large amount of water and nitrogen from tree roots into the soil through xylem feeding activity (Hunter, 2016).

Although the ecosystem roles of brown bears are well known (García-Rodríguez et al., 2021; Helfield and Naiman, 2006), little attention has been paid to their ecosystem role as digging mammals (Tardiff and Stanford, 1998). Deepening the understanding of the ecological roles of wildlife is important for justifying conservation and management policy making (Somaweera et al., 2020). We hope that this study provides ecological insights for their conservation and management by evaluating the role of bears as agents of bioturbation in a landscape composed of natural forests and plantations. However, we should carefully consider whether our finding are applicable to other ecosystem types, because the direction and magnitude of digging impacts vary with local and regional environmental conditions, even in the same species (Yurkewycz et al., 2014).

Our previous study suggested that brown bears have caused novel bioturbation since 2000 when they started digging for cicada nymphs (Tomita and Hiura, 2020). This study speculated an ecological consequence of this emerging behavior, in which their digging negatively affected soil water and nitrogen availability in larch plantations. Given that brown bear digging for cicada nymphs occurred extensively in the larch plantations (Tomita and Hiura, 2021b, 2021a), their digging may have strongly affected tree growth and regeneration in the plantations. Since xylem feeding by cicada nymphs can negatively affect tree growth occasionally (Karban, 1980), there may be both negative and positive effects on brown bear digging for cicadas via soil disturbance and trophic cascade by reducing cicada density, respectively. This hypothesis is worth testing in the future study for examining ecological consequences when simultaneously occurring trophic and non-trophic effects of apex predators.

A recent study showed that many native tree saplings established in larch plantations at the study site, and thus proposed their potential role on the establishment of naturally regenerating forests (Suzuki et al., 2021). Brown bears may hinder natural forest regeneration in larch plantations by overturning seedlings and limiting water and nitrogen uptake by these saplings. Additionally, brown bears may also affect forest regeneration in plantations in other ways we did not address in this study. For example, bears may disperse seeds of wild cherry, which is an important summer food for bears (Koike et al., 2008), into the plantation if they deposit scats containing the seeds while digging for cicada nymphs. Further investigation of their roles on tree growth and establishment through limiting soil nutrient availability and cicada density is required to develop the understanding of their contribution to natural forest regeneration in the plantations.

Acknowledgements

We thank members of Shiretoko Nature Foundation for providing information on the study site and Drs. K. Makoto and S. Niwa for advising measurements of soil properties. We also thank three anonymous reviewers for their very helpful comments on the manuscript.

References

Barrios-Garcia, M.N., Ballari, S.A., 2012. Impact of wild boar (Sus scrofa) in its introduced and native range: a review. Biol Invasions 14, 2283–2300. https://doi.org/10.1007/s10530-012-0229-6

Barrios-Garcia, M.N., Classen, A.T., Simberloff, D., 2014. Disparate responses of above- and belowground properties to soil disturbance by an invasive mammal. Ecosphere 5, art44. https://doi.org/10.1890/ES13-00290.1

Bétard, F., 2021. Insects as zoogeomorphic agents: an extended review. Earth Surf Process Landf 46, 89–109. https://doi.org/10.1002/esp.4944

Bueno, C.G., Azorín, J., Gómez-García, D., Alados, C.L., Badía, D., 2013. Occurrence and intensity of wild boar disturbances, effects on the physical and chemical soil properties of alpine grasslands. Plant Soil 373, 243–256. https://doi.org/10.1007/s11104-013-1784-z

Butler, D.R., 1995. Zoogeomorphology: Animals as Geomorphic Agents. Cambridge University Press.

Butler, D.R., 1992. The grizzly bear as an erosional agent in mountainous terrain. Zeitschrift für Geomorphologie 36, 179–189.

Canals, R.M., Herman, D.J., Firestone, M.K., 2003. How Disturbance by Fossorial Mammals Alters N Cycling in a California Annual Grassland. Ecology 84, 875–881. https://doi.org/10.1890/0012-9658(2003)084[0875:HDBFMA]2.0.CO;2

Coggan, N.V., Hayward, M.W., Gibb, H., 2018. A global database and "state of the field" review of research into ecosystem engineering by land animals. J Anim Ecol 87, 974–994. https://doi.org/10.1111/1365-2656.12819

Davidson, A.D., Detling, J.K., Brown, J.H., 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. Front Ecol Environ 10, 477–486. https://doi.org/10.1890/110054

Davies, G.T.O., Kirkpatrick, J.B., Cameron, E.Z., Carver, S., Johnson, C.N., 2019. Ecosystem engineering by digging mammals: effects on soil fertility and condition in Tasmanian temperate woodland. R Soc Open Sci 6, 180621. https://doi.org/10.1098/rsos.180621

Fleming, P.A., Anderson, H., Prendergast, A.S., Bretz, M.R., Valentine, L.E., Hardy, G.E.StJ., 2014. Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? Mamm Rev 44, 94–108. https://doi.org/10.1111/mam.12014

Gabet, E.J., Reichman, O.J., Seabloom, E.W., 2003. The Effects of Bioturbation on Soil Processes and Sediment Transport. Annu Rev Earth Planet Sci 31, 249–273. https://doi.org/10.1146/annurev.earth.31.100901.141314

García-Rodríguez, A., Albrecht, J., Szczutkowska, S., Valido, A., Farwig, N., Selva, N., 2021. The role of the brown bear Ursus arctos as a legitimate megafaunal seed disperser. Sci Rep 11, 1282. https://doi.org/10.1038/s41598-020-80440-9

Guntiñas, M.E., Leirós, M.C., Trasar-Cepeda, C., Gil-Sotres, F., 2012. Effects of moisture and temperature on net soil nitrogen mineralization: A laboratory study. Eur J Soil Biol 48, 73–80. https://doi.org/10.1016/j.ejsobi.2011.07.015

Haussmann, N.S., 2017. Soil movement by burrowing mammals: A review comparing excavation size and rate to body mass of excavators. Prog Phys Geogr 41, 29–45. https://doi.org/10.1177/0309133316662569

Helfield, J.M., Naiman, R.J., 2006. Keystone Interactions: Salmon and Bear in Riparian Forests of Alaska. Ecosystems 9, 167–180. https://doi.org/10.1007/s10021-004-0063-5

Hunter, M.D., 2016. The Phytochemical Landscape: Linking Trophic Interactions and Nutrient Dynamics, The Phytochemical Landscape. Princeton University Press. https://doi.org/10.1515/9781400881208

Karban, R., 1980. Periodical cicada nymphs impose periodical oak tree wood accumulation. Nature 287, 326–327. https://doi.org/10.1038/287326a0

Knoepp, J.D., Swank, W.T., 2002. Using soil temperature and moisture to predict forest soil nitrogen mineralization. Biol Fertil Soils 36, 177–182. https://doi.org/10.1007/s00374-002-0536-7

Koike, S., Kasai, S., Yamazaki, K., Furubayashi, K., 2008. Fruit phenology of Prunus jamasakura and the feeding habit of the Asiatic black bear as a seed disperser. Ecol Res 23, 385–392. https://doi.org/10.1007/s11284-007-0399-3

Kurek, P., Kapusta, P., Holeksa, J., 2014. Burrowing by badgers (Meles meles) and foxes (Vulpes vulpes) changes soil conditions and vegetation in a European temperate forest. Ecol Res 29, 1–11. https://doi.org/10.1007/s11284-013-1094-1

Maisey, A.C., Haslem, A., Leonard, S.W.J., Bennett, A.F., 2021. Foraging by an avian ecosystem engineer extensively modifies the litter and soil layer in forest ecosystems. Ecol Appl 31, e02219. https://doi.org/10.1002/eap.2219

Mallen-Cooper, M., Nakagawa, S., Eldridge, D.J., 2019. Global meta-analysis of soil-disturbing vertebrates reveals strong effects on ecosystem patterns and processes. Glob Ecol Biogeogr 28, 661–679. https://doi.org/10.1111/geb.12877

Mattson, D.J., 1997. Selection of Microsites by Grizzly Bears to Excavate Biscuitroots. J Mamm 78, 228–238. https://doi.org/10.2307/1382656

Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin’s last idea. Trends Ecol Evol 21, 688–695. https://doi.org/10.1016/j.tree.2006.08.002

Munro, R.H.M., Nielsen, S.E., Price, M.H., Stenhouse, G.B., Boyce, M.S., 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. J Mamm 87, 1112–1121. https://doi.org/10.1644/05-MAMM-A-410R3.1

Pastor, J., Aber, J.D., McClaugherty, C.A., Melillo, J.M., 1984. Aboveground Production and N and P Cycling Along a Nitrogen Mineralization Gradient on Blackhawk Island, Wisconsin. Ecology 65, 256–268. https://doi.org/10.2307/1939478

Persson, T., Wirén, A., 1995. Nitrogen mineralization and potential nitrification at different depths in acid forest soils. Plant Soil 168/169, 55–65.

Platt, B.F., Kolb, D.J., Kunhardt, C.G., Milo, S.P., New, L.G., 2016. Burrowing Through the Literature: The Impact of Soil-Disturbing Vertebrates on Physical and Chemical Properties of Soil. Soil Sci 181, 175–191. https://doi.org/10.1097/SS.0000000000000150

R Core Team, 2018. R: A language and environment for statistical computing.

Risch, A.C., Wirthner, S., Busse, M.D., Page-Dumroese, D.S., Schütz, M., 2010. Grubbing by wild boars (Sus scrofa L.) and its impact on hardwood forest soil carbon dioxide emissions in Switzerland. Oecologia 164, 773–784. https://doi.org/10.1007/s00442-010-1665-6

Sayer, E.J., 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol Rev 81, 1–31. https://doi.org/10.1017/S1464793105006846

Shimozuru, M., Shirane, Y., Jimbo, M., Yamanaka, M., Nakanishi, M., Ishinazaka, T., Kasai, S., Nose, T., Fujimoto, Y., Tsuruga, H., Mano, T., Tsubota, T., 2020. Male reproductive input, breeding tenure, and turnover in high-density brown bear (Ursus arctos yesoensis) populations on the Shiretoko Peninsula, Hokkaido, Japan. Can. J. Zool. 98, 175–185. https://doi.org/10.1139/cjz-2019-0061

Shoyama, K., 2008. Reforestation of abandoned pasture on Hokkaido, northern Japan: effect of plantations on the recovery of conifer-broadleaved mixed forest. Landscape Ecol Eng 4, 11–23. https://doi.org/10.1007/s11355-008-0034-7

Somaweera, R., Nifong, J., Rosenblatt, A., Brien, M.L., Combrink, X., Elsey, R.M., Grigg, G., Magnusson, W.E., Mazzotti, F.J., Pearcy, A., Platt, S.G., Shirley, M.H., Tellez, M., van der Ploeg, J., Webb, G., Whitaker, R., Webber, B.L., 2020. The ecological importance of crocodylians: towards evidence-based justification for their conservation. Biol Rev 95, 936–959. https://doi.org/10.1111/brv.12594

Suzuki, K.F., Kobayashi, Y., Seidl, R., Senf, C., Tatsumi, S., Koide, D., Azuma, W.A., Higa, M., Koyanagi, T.F., Qian, S., Kusano, Y., Matsubayashi, R., Mori, A.S., 2021. The potential role of an alien tree species in supporting forest restoration: Lessons from Shiretoko National Park, Japan. For Ecol Manag 493, 119253. https://doi.org/10.1016/j.foreco.2021.119253

Tardiff, S.E., Stanford, J.A., 1998. Grizzly Bear Digging: Effects on Subalpine Meadow Plants in Relation to Mineral Nitrogen Availability. Ecology 79, 2219–2228. https://doi.org/10.1890/0012-9658(1998)079[2219:GBDEOS]2.0.CO;2

Tateno, R., Hishi, T., Takeda, H., 2004. Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. For Ecol Manag 193, 297–306. https://doi.org/10.1016/j.foreco.2003.11.011

Tomita, K., 2021. Camera traps reveal interspecific differences in the diel and seasonal patterns of cicada nymph predation. Sci Nat 108, 52. https://doi.org/10.1007/s00114-021-01762-w

Tomita, K., Hiura, T., 2021a. Reforestation provides a foraging habitat for brown bears (Ursus arctos) by increasing cicada Lyristes bihamatus density in the Shiretoko World Heritage site. Can J Zool 99, 205–212. https://doi.org/10.1139/cjz-2020-0222

Tomita, K., Hiura, T., 2021b. Disentangling the direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of the brown bear Ursus arctos. Wildl Biol 2021, wlb.00886. https://doi.org/10.2981/wlb.00886

Tomita, K., Hiura, T., 2020. Brown bear digging for cicada nymphs: a novel interaction in a forest ecosystem. Ecology 101, e02899. https://doi.org/10.1002/ecy.2899

Wirthner, S., Schütz, M., Page-Dumroese, D.S., Busse, M.D., Kirchner, J.W., Risch, A.C., 2012. Do changes in soil properties after rooting by wild boars (Sus scrofa) affect understory vegetation in Swiss hardwood forests? Can J For Res 42, 585–592. https://doi.org/10.1139/x2012-013

Yurkewycz, R.P., Bishop, J.G., Crisafulli, C.M., Harrison, J.A., Gill, R.A., 2014. Gopher mounds decrease nutrient cycling rates and increase adjacent vegetation in volcanic primary succession. Oecologia 176, 1135–1150. https://doi.org/10.1007/s00442-014-3075-7

Figure legend

Figure 1 (a) Trace of brown bear digging for cicada nymphs within a larch plantation. This picture shows the representative soil sampling point. We collected the disturbed and undisturbed soil samples within and without the dug area, respectively. (b) A bear scat containing the fragments of cicada nymphs (c) A female brown bear with two cubs dig for cicada nymphs in a larch plantation. Photo credit: (a) and (c) Shiretoko Nature Foundation, (b) Kanji Tomita

Figure 2 Location of the soil sampling points superimposed on a vegetation map of the study site. This vegetation map is reprinted from Tomita and Hiura (2021a) and created by Shiretoko Nature Foundation (unpublished information). This figure was created using QGIS 3.14.0.

Figure 3 Comparisons of soil water content (a), bulk density (b), total carbon (c), total nitrogen (d), C:N ratio (e), ammonium nitrogen (f), nitrate nitrogen (g), total inorganic nitrogen (h), net mineralization rate (i), and nitrification rate (j) between dug (Grey color) and undisturbed (Black color) soil. *P*-values in each boxplot were the results of analysis of variance.

Figure 1

Figure 2

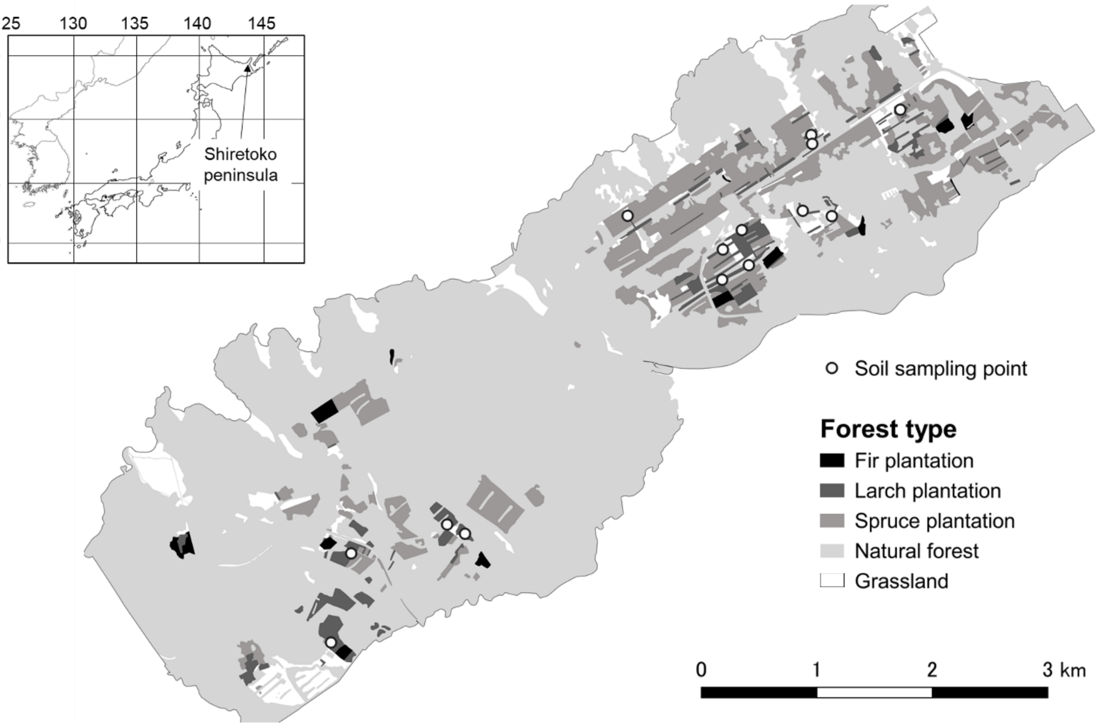
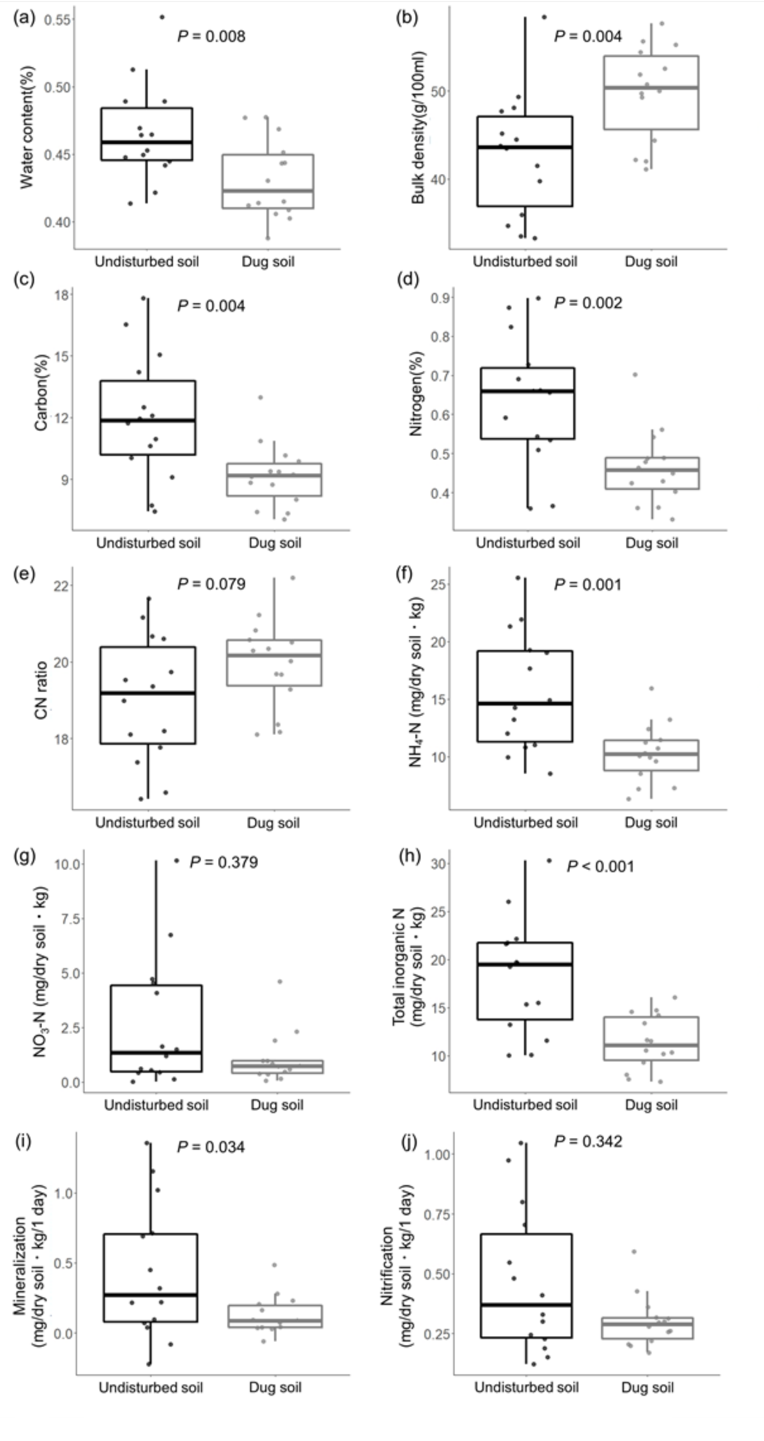

125
130
135
140
145
45
40
35
30
Shiretoko peninsula
Soil sampling point
Forest type
Fir plantation
Larch plantation
Spruce plantation
Natural forest
Grassland
0
1
2
3 km

Figure 3


(a)
P = 0.008
Water content(%)
0.55
0.50
0.45
0.40
Undisturbed soil
Dug soil
(b)
P = 0.004
Bulk density(g/100ml)
50
40
Undisturbed soil
Dug soil
(c)
P = 0.004
Carbon(%)
18
15
12
9
Undisturbed soil
Dug soil
(d)
P = 0.002
Nitrogen(%)
0.9
0.8
0.7
0.6
0.5
0.4
Undisturbed soil
Dug soil
(e)
P = 0.079
CN ratio
22
20
18
Undisturbed soil
Dug soil
(f)
P = 0.001
NH_4-N (mg/dry soil · kg)
25
20
15
10
Undisturbed soil
Dug soil
(g)
P = 0.379
NO_3-N (mg/dry soil · kg)
10.0
7.5
5.0
2.5
0.0
Undisturbed soil
Dug soil
(h)
P < 0.001
Total inorganic N (mg/dry soil · kg)
30
25
20
15
10
Undisturbed soil
Dug soil
(i)
P = 0.034
Mineralization (mg/dry soil · kg/1 day)
1.0
0.5
0.0
Undisturbed soil
Dug soil
(j)
P = 0.342
Nitrification (mg/dry soil · kg/1 day)
1.00
0.75
0.50
0.25
Undisturbed soil
Dug soil