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Title	Causes and consequences of animal behavior changes in a human-modified world : A case study of brown bear digging for cicada nymphs
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Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	甲第14768号
Issue Date	2022-03-24
DOI	https://doi.org/10.14943/doctoral.k14768
Doc URL	https://hdl.handle.net/2115/85780
Type	doctoral thesis
File Information	TOMITA_Kanji.pdf

Causes and consequences of animal behavior changes

in a human-modified world:

A case study of brown bear digging for cicada nymphs

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A dissertation submitted to Division of Biosphere Science of

Doctor of Philosophy in Graduate School of

Environmental Science, Hokkaido University, Japan

March 2022, Sapporo

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Chapter 1 General introduction

Ecological consequences of animal behavior change in the Anthropocene

Human activities have now reached to everywhere on our planet and, therefore, most living organisms spend their lives in anthropogenically impacted habitat (Hobbs et al. 2009, Barnosky et al. 2012). Environmental change has been a universal phenomenon during the life of earth, but the rate and magnitude have been exceedingly accelerated in the Anthropocene. It is urgent to understand how wildlife respond to human activities and its ecological and evolutionary consequences at population, community, and ecosystem levels (Sih et al. 2011, Johnson et al. 2017).

The initial animal response to human activities is a behavioral change, including foraging, movement, or diel activity (Wong and Candolin 2015, Fleming and Bateman 2018), and then cascade to population level effects, such as population decline. Behavioral changes also affect many higher-level ecological phenomena directly or indirectly, such as community changes and nutrient cycling (Palkovacs and Dalton 2012, Wilson et al. 2020). However, most past studies have investigated anthroponotic effects on either one of the behavioral changes or population/ community/ ecosystem patterns and there is a critical gap linking animal behavior to higher-

17   order ecological processes (Wilson et al. 2020). Clarifying causes and consequences of animal

18   behavior changes is particularly useful to conservation biologists and ecosystem managers for

19   predicting the anthropogenetic impacts on entire ecosystems (Candolin and Wong 2012, Wilson

20   et al. 2020).

21   One key challenge for hindering our understanding of ecological consequences of animal

22   behavior changes is that altered behavior does not always lead to substantial ecological

23   outcomes. Therefore, we should focus on specific species with or behavior underlying

24   ecologically important functions when detecting the ecological consequences of behavior

25   change (Wilson et al. 2020). Keystone species or ecosystem engineers have far more important

26   effects than others for overall ecosystem function. For instance, mammalian ecosystem

27   engineers such as beavers (*Castor canadensi*s) and digging mammals (e.g. wild boar *Sus scrofa*

28   and prairie bogs Cynomys spp.) have disproportionately large impacts on community structure

29   and ecosystem processes at landscape level (Jones et al. 1997, Power et al. 1996, Davidson et al.

30   2012).

31   Ecosystem effects through animal behavior are generally divided into two groups; that is,

32   trophic and non-trophic effects (Jones et al. 1997, Wilby et al. 2001, Schmitz et al. 2004, Kefi et

33   al. 2012). Trophic effects are defined as the influences from consumers at higher trophic level to

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34   those at lower trophic level through direct consumption such as herbivory and predation and

35   non-consumptive pathways such as fear effects (Wooton 1994, Schmitz et al. 2004, Hawlena et

36   al. 2012). Non-trophic effects exert without trophic pathway from consumers to organisms at

37   lower trophic levels (Wooton 1994, Kefi et al. 2012). One of the most representative examples

38   of agents of non-trophic effects is ecosystem engineers defined as organisms that directly or

39   indirectly modulate the availability of resources (other than themselves) to other species by

40   causing physical (and chemical) state changes in biotic or abiotic materials (Jones et al. 1997,

41   chemical engineers are defined by Berke 2010). For ecosystem engineers, trophic and non-

42   trophic effects often co-occur with different direction and magnitude (Jones et al. 1997, Keri et

43   al. 2012). For example, digging for plants by mammalian ecosystem engineers such as

44   porcupine (*Hystrix indica*), bilbies (*Macrotis lagotis*) and grizzly bear (*Ursus arctos horribilis*)

45   has simultaneously trophic and non-trophic effects on plants via plant consumption (negative)

46   and soil modification (positive) (Jones et al. 1997, Tardiff and Stanford 1998, Wilby et al. 2001,

47   Verdon et al. 2016). Soil modification through their digging activities also affect growth and

48   establishment of other plant species that were not directly consumed by these mammals.

49   Therefore, elucidating ecosystem consequences of animal behavior changes should separately

50   evaluate trophic and non-trophic effects, not only net effects of them.

3

Forest plantations as human-modified ecosystems

51

52   The most drastic change by human activity is the landscape modification. Human-

53   modified ecosystems have generally emerged within the natural landscapes and thereby, most of

54   the current landscapes represent mosaic structures consisting of natural and human-modified

55   ecosystems (Shoyama and Braimoh 2012, Heikkinen et al. 2004, Umetsu &Pardini 2007). Many

56   wildlife species increasingly live in such mixed ecosystems. For instance, in a large part of the

57   world, large carnivores are returning to human-modified ecosystems due to development of land

58   abandonment (Kuiper et al. 2016). Thus, elucidating ecological consequences of animal

59   behavior changes may contribute to our understanding of the ecological role of wildlife that are

60   recolonizing to human- modified ecosystems (Kuiper et al. 2016). Furthermore, such mixed

61   ecosystems should be considered for elucidating ecological consequences of animal behavior

62   changes caused by anthropogenic environmental alterations because the ecological effects of

63   behavior changes induced by the alterations can affect population, community and ecosystem

64   functions in natural ecosystems (Kuiper et al. 2016, Manlick and Newsome 2021).

65   Forests in the world form the mosaic landscapes of human-modified ecosystem (e.g.

66   plantations), natural primary and secondary forests and many animals use each component

67   properly (Mazzolli 2010). Understanding behavior changes in mixed landscapes can help for

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68   solving wildlife management issues such as human wildlife conflicts because mosaic landscape

69   can enhance wildlife appearance from natural areas to human- inhabited areas (Siljander et al.

70   2020). Plantation is a representative example of the human-modified ecosystems in forest

71   landscapes (Stephens & Wagner 2007). Plantations have been often called as "green desert"

72   because of poor biodiversity (Brockerhoff et al. 2008). However, there is an increasing evidence

73   on animals that ingeniously utilize plantations (Brockerhoff et al. 2008, Stock et al. 2013,

74   Tomita 2021). Given that the creation of plantations is among the most important factors

75   causing changes in animal behavior such as foraging, roosting and habitat selection in forest

76   landscapes (Nielsen et al. 2004, Stewart et al. 2021), investigating animal behavior change

77   associated with the creation of plantations can help in-depth understanding of causes and

78   consequences of changes in animal behavior.

79   **Brown bear as target species**

80   The brown bear (*Ursus arctos*), which is one of the most widespread and largest carnivores

81   in terrestrial ecosystems, is an appropriate species for linking altered behaviors to ecological

82   consequences in the human-modified ecosystems. They play numerous crucial ecological roles

83   as an apex predator, a long-distance seed disperser, nutrient vectors, and ecosystem engineers

84   (Tardiff and Stanford 1998, Reimchen 2000, Helfield and Naiman 2006, Ripple et al. 2014,

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85   Steyaert et al. 2019). Brown bears utilize a wide variety of foods and exhibit a high degree of

86   behavioral flexibility through individual and social learning (Bojanska and Selva 2012,

87   Morehouse et al. 2016, Gilbert et al. 1999). Accordingly, brown bears sensitively respond to

88   anthropogenic habitat changes due to forestry (e.g., afforestation), agricultural cultivation, and

89   industrial development (Cristescu et al. 2015; Frank et al. 2015; Sorensen et al. 2015; Penteriani

90   et al. 2018). In fact, woodland conversion to cropland may lead to an increased attraction of

91   bears to agricultural areas for crop raiding, and consequently, increases their human-caused

92   mortality (Hata et al. 2017; Penteriani et al. 2018). In forest ecosystems, clearcuts temporarily

93   change in resource availability for bears via increasing light environment and biomass of coarse

94   woody debris, and influence their habitat selection (Nielsen et al. 2004; Frank et al. 2015). For

95   example, in west-central Alberta, Canada, grizzly bears select clearcut sites, which provide

96   some foraging resources such as ants, plants, and berries, during summer (Nielsen et al. 2004).

97   Furthermore, population status of brown bear is stable (Ripple et al. 2014), even though they

98   normally live in human-modified ecosystems while changing their behaviors such as diel

99   activity and habitat selection (Sorensen et al. 2015, Ordiz et al. 2012). This fact implies that the

100 relative ecological importance of behaviorally mediated effects is larger than that of density-

101 mediated effects for brown bears. Therefore, setting brown bears as target species expects to

102 overcome the above-mentioned hurdles for linking behavior change to cascading ecological

103   effects.

104   In my doctor thesis, I investigated brown bear digging behavior to forage on nymphs of a

105   cicada species (*Lyristes bihamatus*) in the Shiretoko World Heritage site (hereafter: SWH),

106   northern Japan. In SWH, a reforestation project started in the 1970s was led by the local

107   government and residents to recover forest landscape from abandoned farmland. As a result, the

108   SWH forests currently form a mosaic landscape of natural forests and human- created

109   plantations. Through the findings of Chapters 2~4 that bears only dug for cicada nymphs within

110   the restored plantations, I regarded brown bear digging for cicada nymphs as a form of animal

111   behavior change due to anthropogenic ecosystem modification. In Chapter 5~6, I investigated

112   ecological effects of brown bear digging on soil nitrogen dynamics and canopy tree growth as

113   the consequences of animal behavior change. Soil digging is among the most representative

114   form of animal ecosystem engineers through soil modification (Coggan et al. 2018, Mallen-

115   Cooper et al. 2019). In my general discussion, I discussed the behavior change in brown bears.

116   Finally, I evaluated two ecological consequences of the behavior change in brown bears, (1)

117   how many cicada nymphs were prey upon by brown bears, thereby how much nitrogen flux was

118   decreased through cicada predation (trophic effect); (2) how much inorganic nitrogen

119   production was changed by soil disturbance through digging activity by brown bears (non-

120   trophic effects).

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Study site: Shiretoko World Heritage site

This study was conducted in the Horobetsu-Iwaobetsu area (44°09=N, 145°02=E) located

in the western parts of the SWH (Fig. 1). The elevation ranges from 120 to 220 m. The annual

mean temperature at the study site is 6.2 °C. and monthly mean temperature ranged from –

10.4 °C in February to 15.1 °C in August (1981–2010). The annual mean precipitation is 1,149

mm (1981–2010). UNESCO certified this area as a World Natural Heritage site because it

represents one of the richest northern temperate ecosystems in the world

(http://whc.unesco.org/en/list/1193). In the study area, approximately 40% of the conifer-

broadleaved mixed forests were converted to farmland for grazing by cattle during the post-war

period from the 1940s to the 1960s (Shoyama 2008). Agricultural crops such as corn and sugar

beet were rarely cultivated in this area. During the period of high economic growth in Japan,

from the late 1960s to the 1970s, all the farmland was abandoned because farmers immigrated

to urban areas. Since 1977, reforestation of the abandoned farmland has been conducted by the

local government and residents through a national trust movement. Coniferous trees such as

Japanese larch, Sakhalin spruce (*Picea glehnii*) and Sakhalin fir (*Abies sachalinensis*), have

been planted on the abandoned farmland for the purpose of reforestation. Most of the larch and

fir plantations were established during the 1970s, whereas the spruce plantations were

established during the early 1990s. The restored plantations accounted for 18 % of the total

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140   forest area (Shoyama 2008), with Sakhalin spruce, Japanese larch and Sakhalin fir plantations

141   account for 13 %, 4 %, and 1 %, respectively. The natural forests are conifer-broadleaved mixed

142   forests, mainly consisting of Sakhalin fir and Mongolian oak (*Quercus crispula*) and maple

143   (*Acer mono* Maxim.), and account for 82 % of the forest area in the study site. On the

144   abandoned farmland, pasture grass such as *Miscanthus sinensis* and *Anthoxanthum odoratum*

145   are dominant and soft mast species such as *Rubus* spp., which are a common food for bears in

146   summer, rarely grow (Ministry of the Environment, the Government of Japan 2017).

147   The SWH has one of the highest densities of brown bears in the world (Shimozuru et al.

148   2020). In the study area, food items of the brown bears change across the seasons, depending on

149   resource availability. Herbaceous plants are consumed in spring, and herbaceous plants, ants and

150   cicada nymphs in summer, from June to August. *Q. crispula* acorns, *Vitis coignetiae* berries, and

151   anadromous salmons (*Oncorhynchus gorbuscha*) are consumed in autumn, from September to

152   November (Ohdachi and Aoi 1987; Matsubayashi et al. 2014). Home range size of adult female

153   bears is estimated at 26.5 km^2 in the study area (Kohira et al. 2009). Bear viewing is a major

154   tourism activity in this region which generates an estimate 3 million dollars in revenue (Kubo

155   and Shoji 2014). Camera traps revealed that eleven bears (two sub-adults, two solitary female

156   adults, and three females accompanied by cub(s)) and eleven bears (one adult male, one sub-

10

157   adult, two solitary adult females, and three females with cub(s)) were observed digging for

158   cicada nymphs in 2018 and 2019, respectively (Tomita, 2021; Chapter 2). Individual

159   identification and age classes were determined based on color, marks, body size, and family

160   structure of bears. Two native cicada species, *L. bihamatus* and *Yezoterpnosia nigricosta*, only

161   occur in forest of the SWH and emerge during late summer and spring to early summer,

162   respectively. In the study site, brown bear preys on the final instar nymphs of *L. bihamatus*, but

163   not *Y. nigricosta*. Hence, this study focuses on the final instar nymph of *L. bihamatus* as a prey

164   of bears; the term "cicada" represents *L. bihamatus*.

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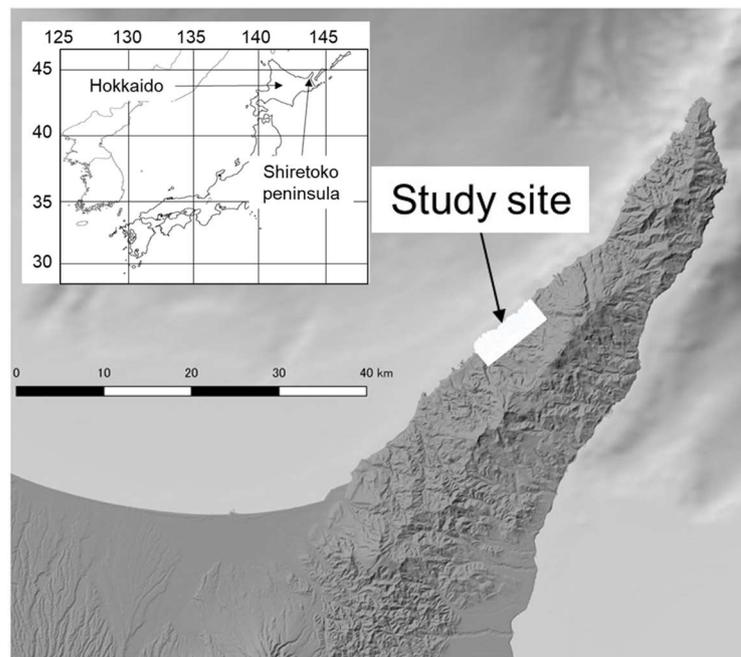
Figure 1 Location of study site

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Chapter 2 Brown bear digging for cicadas:

a novel interaction in a forest ecosystem

Main text

The brown bear (*Ursus arctos*) is one of the most widespread large carnivores in the northern hemisphere. Their diets are highly diverse and depend on resource availabilities across regions and seasons (Bojarska and Selva 2012). Brown bears often consume starchy plant roots and insects by digging into the soil (Mattson et al. 1991, Tardiff and Stanford 1998). In the Shiretoko World Heritage, Hokkaido, northern Japan (44° N, 145° E), where the density of brown bears is high (Kohira et al. 2009), these animals have recently been observed digging for cicada nymphs (*Lyristes bihamatus*) during summer (Fig. 1a,b). This behavior has not been previously reported, even though some other mammalian species forage for cicada nymphs (Hahus and Smith 1990). In this article, I show some preliminary results of my field survey on this novel interaction between brown bear and cicada. I then discuss the reasons why brown bears forage on cicada nymphs and the possible ecological consequences of their digging in the forest ecosystem.

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Figure 1 (a) Female brown bear with two cubs dig for cicada nymphs in a larch plantation. (b) Brown bear scat containing final instar *Lyristes bihamatus* nymphs. Scale bar: 50 mm (photo credit: Shiretoko Nature Foundation).

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185   Wildlife managers first observed brown bears digging for cicada nymphs in 2000 in the

186   study area. Cicada nymphs were not reported in scats of brown bears collected in the summers

187   of the mid-1980s in the study area (Fig. 2; Yamanaka and Aoi 1988). This earlier study, along

188   with ours, allows us to determine whether the proportion of cicadas and other foods in the diet

189   has changed during the past 30 yr. In 2018, I evaluated the composition of brown bear scats

190   collected in the same season and region as the earlier study. By comparing scat compositions

191   between the mid-1980s and 2018, I determined the changes in brown bears diets in the study

192   area during the past 30 yr. The proportion of cicada nymphs was estimated at 14.3%, suggesting

193   that brown bears consume cicada nymphs at a certain rate in summer. Final instar nymphs are

194   highly nutritious and finish their development until emergence in shallow soil during summer,

195   and so bears can easily dig for them (Hayashi and Saisho 2011). Although herbaceous plants

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196   comprised the highest proportion in scats from both periods, I found that the proportion of

197   herbaceous plants in scats in 2018 is one-half that recorded in mid-1980s (Fig. 2).
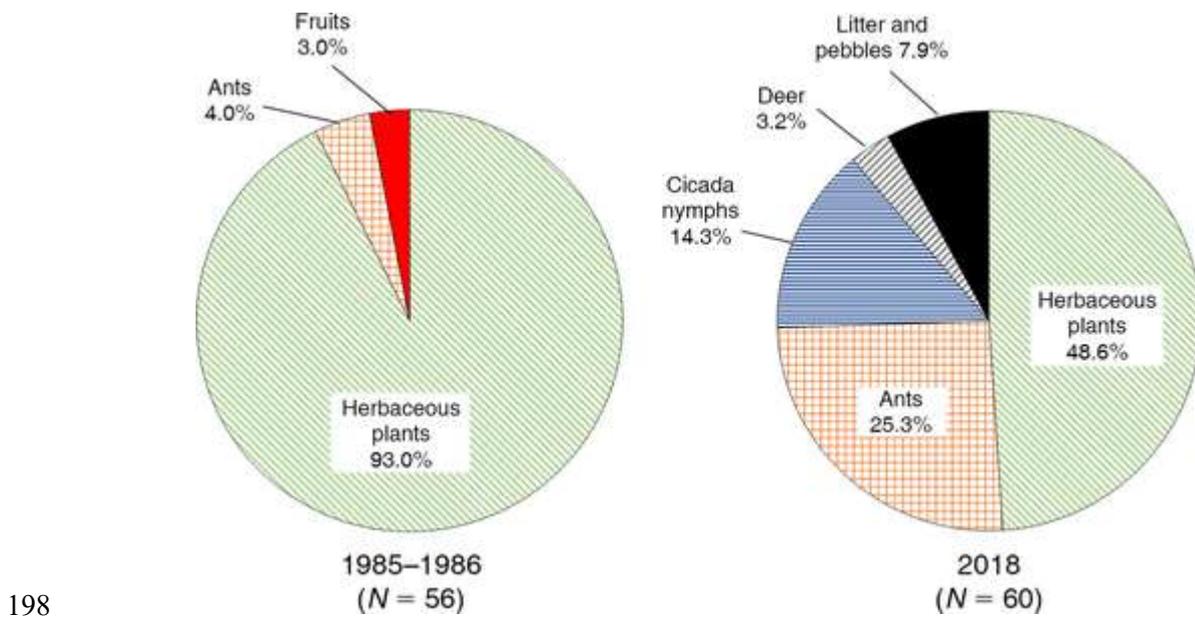
198

Figure 2 Scat composition of brown bears in visually estimated percent
volumes for major categories, in 1985–1986 (left) and 2018 (right). Data of the
scat composition in 1985–1986.

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200   Evidence of brown bear digging was frequently observed in the larch (*Larix kaempferi*)

201   plantations, whereas I could not find evidence of digging in the Sakhalin spruce (*Picea glehnii*)

202   plantations and the natural mixed forests. In August 2017, when final instar cicada nymphs

203   completed emergence, I created 10 survey plots of 100 m2 area in each forest type and counted

204   the number of exuviae of L. bihamatus nymphs as a proxy of their abundance in each plot. The

205   largest number of the L. bihamatus exuviae occurred in the larch plantations (153.9 ± 15.6

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206   exuviae/100 m2 [mean ± SE]). The number of *L. bihamatus* exuviae in the Sakhalin spruce

207   plantations and the natural mixed forests was 8.7 ± 3.0 and 4.5 ± 2.3, respectively. These data

208   indicate that brown bears can most efficiently forage on cicada nymphs by searching intensively

209   in the larch plantation where the nymphs aggregate at high density.

210   I set up eight camera traps in the larch plantations where brown bears dug the previous year

211   to evaluate how many brown bears dug for cicada nymphs, by counting the minimum number of

212   brown bears based on useful features for individual identification (e.g., color, body size, and

213   family structure). As a result, I captured 112 videos wherein bears were recorded to be digging

214   and detected a minimum number of 11 individuals; three adult bears were females with cub(s),

215   two were solitary adult female bears, and two were subadult bears. (See Videos S1 and S2 for

216   two examples.)

217   Why have brown bears begun foraging on cicada nymphs since 2000? One possible reason

218   may be that overgrazing by sika deer (Cervus nippon yesoensis) has altered the diet of brown

219   bears by reducing the available herbaceous plants for bears. An index of population density of

220   sika deer by spotlight surveys has revealed a remarkable increase from 1 deer/km in the late

221   1980s to 20 deer/km in the early 2000s in the study area (Kaji et al. 2006). Because herbaceous

222   plant species preferred by sika deer were partially in common with the species upon which

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223 brown bears foraged in summer during the 1980s (Kaji 1988), the availability of herbaceous

224 plants for bears during summer may have decreased in the study area. This is also supported by

225 the results of my scat analysis (Fig. 2). Therefore, brown bears may have foraged on cicada

226 nymphs as an alternative food resource to herbaceous plants.

227 Our camera traps revealed that three female brown bears with cub(s) dug for cicada

228 nymphs in the study area. Possibly, the digging behavior of brown bears will propagate through

229 the bear population via social learning from mother bear to cub, because bears likely acquire

230 foraging behavior through learning from their mothers during at least the first year of their life

231 (Gilbert 1999, Hopkins 2013). Moreover, because home ranges of female brown bears tend to

232 be fixed in proximity to that of their mother's (Zedrosser et al. 2007), female bears acquiring the

233 digging behavior will remain in the same population. Thus, in the future, the number of brown

234 bears that dig for cicada nymphs will probably increase via social learning in the study area.

235 Bioturbation by digging mammals is a well-studied example of ecosystem engineering that

236 alters habitat structure for other species and soil nutrient dynamics (Tardiff and Stanford 1998,

237 Meysman et al. 2006, Mallen-Cooper et al. 2019). I observed the area of a dug patch was often

238 over 100 m2, and there were at least several dozen of the patches. Furthermore, an individual

239 bear apparently dug up a large amount of soil, according to observation by my camera traps.

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240   Thus, bioturbation by brown bear digging may have significant engineering effects in the forest

241   ecosystem. Additionally, in the study area, brown bears may have exerted these effects since

242   2000 when they started digging for cicada nymphs. In other words, the novel interaction

243   between native species may have generated novel bioturbation in the forest ecosystem.

244   As the number of brown bears that dig for cicada nymphs increases, the ecological

245   importance of the brown bear as an ecosystem engineer will increase in the forest ecosystem.

246   Finally, I propose a hypothesis that propagation of the digging behavior via social learning

247   might strengthen their ecological effects of bioturbation. This hypothesis may shed light on

248   linkage between social learning and ecosystem engineering (i.e., bioturbation). Testing this

249   hypothesis requires data on (1) population trends of digging bears; (2) their kinship based on

250   fecal DNA, which can evaluate the relationship between kinship and diet; (3) temporal

251   dynamics in spatial patterns of brown bear digging; and (4) engineering effects of the digging

252   on other organisms and soil nutrient dynamics.

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Chapter 3 The creation of plantations provides a foraging habitat for brown bears by increasing cicada density

Abstract

Reforestation, which converts abandoned farmland back into forestland by planting woody species, can provide habitat for wildlife, including the brown bear (*Ursus arctos*). In the Shiretoko World Heritage site, northern Japan, where brown bears occur at high density, conifers have been planted since the 1970s to reforest abandoned farmland. In this area, brown bears were first observed digging for cicada nymphs (*Lyristes bihamatus*) from 2000. An observations by Chapter 2 suggested the emergence of digging behavior might be associated with reforestation. I examined whether reforestation provided a foraging habitat for brown bears. I found that digging occurred only within the restored conifer forests, but not within the natural forest. The densities of cicada nymphs in the restored forests were higher than in the natural forest. These results indicate that the reforestation of abandoned farmland provides a habitat for brown bears by increasing the availability of cicada nymphs in the study site.

18

Introduction

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271   Forests, which occupy one third of terrestrial ecosystems, harbor the highest biodiversity in

272   the world (Millenium Ecosystem Assessment 2005). From the 1700s to the 1990s,

273   approximately 20 % of forests were converted to farmland, and consequently a wide range of

274   forest habitat was lost around the world (Goldewijk 2001). Since the 1900s, large areas of

275   farmland have also been abandoned in developed countries because of declines in human

276   population in agricultural areas as a result of aging populations and migration to urban areas

277   (Ramankutty and Foley 1999). Reforestation, which is a major ecological restoration action in

278   forest ecosystems, aims to convert abandoned farmland to forestland by planting woody species

279   (Chazdon 2008; Aerts and Honnay 2011). The goals of reforestation are not only re-

280   establishment of forest cover, but also the enhancement of forest ecosystem functions such as

281   carbon sequestration, biodiversity conservation and wildlife habitat (Block et al. 2001; Le et al.

282   2012; Cunningham et al. 2015; Derhé et al. 2016). Because reforestation cannot fully restore the

283   original forest ecosystem, it does not necessarily succeed in recovering forest ecosystem

284   functions. Therefore, it is important for the evaluation of reforestation success to understand the

285   ecological functions of the restored forest (Le et al. 2012).

286   The direction and magnitude of reforestation's influence on wildlife, differs among species

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287 and taxonomic groups depending on their ecology such as habitat requirements (Law et al.

288 2017; Whytock et al. 2018; Fuentes-Montemayor et al. 2020). Thus, it is important for

289 deepening the understanding of a function of reforestation as wildlife habitat to clarify the

290 response per each species and taxonomic groups.

291   The brown bear (*Ursus arctos*), which is one of the most widespread and largest carnivores

292 in terrestrial ecosystems, plays important ecological roles as an apex predator and long-distance

293 seed disperser, and transport of marine-derived nutrients (Reimchen 2000; Helfield and Naiman

294 2006; Ripple et al. 2014; Steyaert et al. 2019). Brown bears sensitively respond to

295 anthropogenic habitat changes due to forestry (e.g. afforestation and deforestation), cultivation

296 and industrial development (Cristescu et al. 2015; Frank et al. 2015; Sorensen et al. 2015;

297 Penteriani et al. 2018). In fact, woodland conversion to cropland leads to an increased attraction

298 of bears to human settlements for crop raiding, and consequently increases their human-caused

299 mortality (Hata et al. 2017; Penteriani et al. 2018). In forest ecosystems, clearcuts temporarily

300 change in resource availability for bears via increasing light environment and biomass of coarse

301 woody debris, and influence their habitat selection (Nielsen et al. 2004, Frank et al. 2015). For

302 example, in west-central Alberta, Canada, grizzly bears select clearcut sites, which provide

303 some foraging resources such as ants, herbaceous plants and berries, during summer (Nielsen et

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304   al. 2004). On the other hand, it is unknown how brown bears respond to reforestation, which

305   significantly alters the habitat from farmland to forest.

306   In the Shiretoko World Heritage site (hereafter; SWH), Hokkaido, northern Japan, a

307   reforestation project started in the 1970s was led by the local government and residents to

308   recover forest landscape from abandoned farmland. In the reforested sites of the SWH, brown

309   bears have been observed digging for cicada nymphs during the summer season since 2000

310   (Chapter 2). Chapter 2 showed some preliminary observations that this behavior was frequently

311   found in reforested larch plantations (*Larix kaempferi*) , and that the density of cicada nymphs

312   in the plantations was over 30-fold higher than in natural forests. These preliminary results

313   suggest that reforestation has increased the availability of cicadas for brown bears. However,

314   there is no quantitative data on this behavior, information such as the frequency of this digging

315   behavior between the restored forests and natural forest has yet to be studied. Because cicada

316   emergence density usually fluctuates between years (Sato and Sato 2015), to elucidate if

317   reforestation has provided a foraging habitat for bears, I should examine whether cicada

318   emergence density in the plantations is higher than in natural forests across years.

319   I compared the frequency of this digging behavior and the density of cicada nymphs

320   between the natural forest and plantations. Based on my findings from Chapter 2, I made the

321   following predictions: (1) brown bears digging for cicada nymphs occurs more frequent in the

322   restored plantations than in the natural forests, (2) the density of cicada nymphs is higher in the

323   plantations than in the natural forests, (3) there is a positive relationship between digging

324   frequency and the density of cicada nymphs.

325   **Material and Methods**

326   *Field Survey*

327   I conducted field surveys in two successive years. From late August to September 2018 and

328   2019, 100 m^2 survey plots were set on the following forest types: larch plantations ($n = 15$), fir

329   plantations ($n = 12$), spruce plantations ($n = 15$), and natural forests ($n= 30$). Since bears dig for

330   cicada nymphs until the end of July when the final instar nymphs fully emerge (Chapter 2), this

331   survey's duration is appropriate for the evaluation of this behavior and cicada emergence

332   density. The locations of the survey plots are shown in Fig. 1. I set more plots in the natural

333   forest because it made up the highest proportion of all forest types. The availability of cicada

334   nymphs was determined by the density of cicada exuviae collected from all trees (diameter

335   breast height, DBH > 2 cm) within the plots, since brown bears forage on only the nymphs in

336   their final instar (Chapter 2). Cicada exuviae attached to trees were collected from trunks and

337   branches under 3 m from the ground, as most exuviae on trees can be observed under this

338   height. I also collected the exuviae on the ground within 1 m from the trunk of a tree, because

339   most exuviae falling from the tree were found within 1 m of the trunk. Since final instar cicada

340   nymphs usually attach to the tree trunk when they emerge, the exuviae density in a survey plot

341   can be regarded as the total emergence density from a given plot. Although exuviae could move

342   a short distance due to the wind, the plot size (i.e. 100 m^2) is large enough to cover for passive

343   movement of the exuviae after emergence. Digging marks were regarded as evidence of brown

344   bears foraging on cicada nymphs. According to my preliminary observations using 8 camera

345   traps set in larch plantations where brown bears dug the previous year, brown bears usually dig

346   for cicada nymphs near tree trunks. Thus, I evaluated the digging frequency per plot as the

347   proportion of trees which had the digging traces within 50 cm diameter from the base of a tree,

348   to all trees (DBH > 2 cm) in the plot.
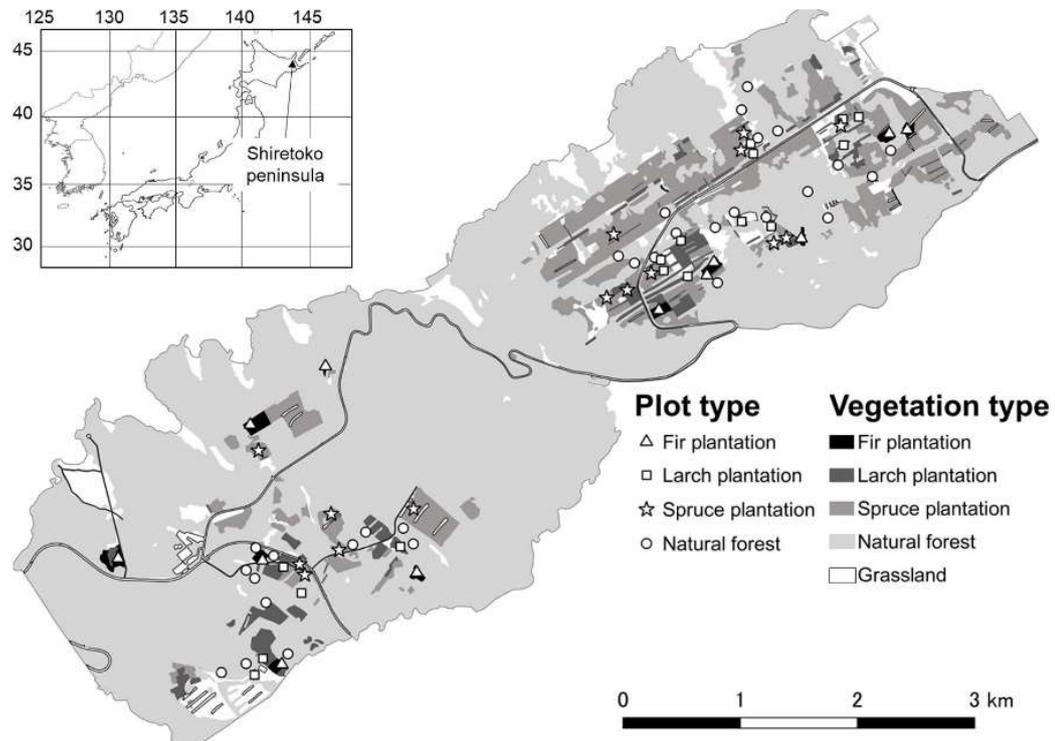
349

Figure 1 Location of the survey plots in vegetation map of the study site. Black lines indicate roads. This vegetation map was created by Shiretoko Nature Foundation (Shiretoko Nature Foundation unpublished information). This figure was created using QGIS version 3.14.0

350

351 *Statistical Analysis*

352   Generalized linear models (GLMs) with log link, Poisson error distribution and Tukey post

353 hoc test were used to examine the differences in the digging frequencies and the densities of

354 cicada nymphs among the forest types. When the GLMs indicated a significant difference (*p-*

355 *value* < 0.05) of one forest type from others, I performed multiple comparisons among the forest

356 types. The GLMs were used to compare the digging frequency and the density of cicada nymphs

24

357   between 2018 and 2019. In GLMs for digging frequency, I introduced an offset term as the log-

358   transformed number of trees to adjust for differences in the number of trees among the survey

359   plots. To examine the effects of the density of cicada nymphs on the digging frequency, I

360   performed GLMs for each forest type. All statistical analyses were conducted in R version 3.5.1

361   (R Core Team 2018).

362   *Biomass measurement of cicada nymphs*

363   In mid-June 2019, I collected 10 cicada final instar nymphs from the larch plantation. In

364   the laboratory, these nymphs were measured individual using dry mass after a 48 hour at 60 ℃

365   drying period. The biomass of cicada final instar nymphs per 100 m^2 were calculated by

366   multiplying individual dry mass of the nymph by the density of cicada exuviae.

367   **Results**

368   Across all survey plots, I collected a total of 629 and 3344 cicada exuviae in 2018 and

369   2019, respectively and recorded a total of 2176 trees with or without digging traces. The GLMs

370   found a significant effect of forest type on digging frequency and the density of cicada nymphs.

371   Bears only dug for cicada nymphs in the restored plantation plots, even when the natural forest

372   plots were mainly composed of fir species (Fig. 2). Digging frequency in the larch plantations

373   was highest in all forest types in both years, but significantly differed between years.
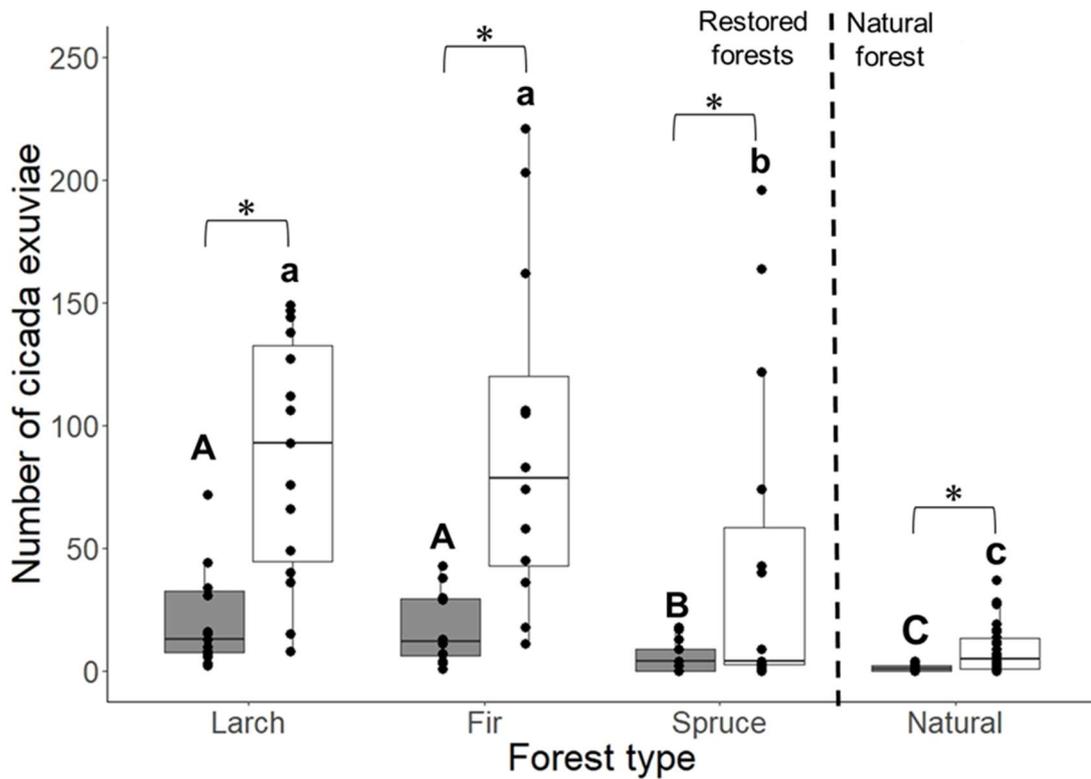
25
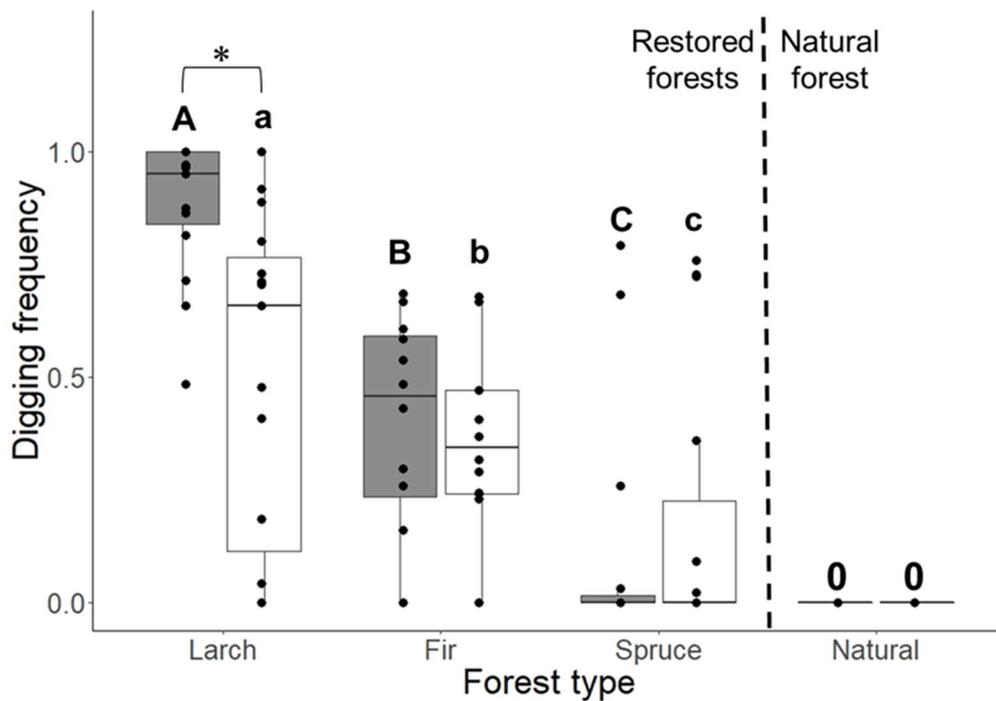
Figure 2 The digging frequencies of brown bear *Ursus arctos* across all forest types in 2018 (dark grey) and 2019 (white). Upper case and lower letters indicate significant differences among forest types in 2018 and 2019 according to post-hoc Tukey's test, respectively ($p < 0.05$). Single asterisk indicates significant differences in the digging frequency between 2 years by generalized linear model ($p < 0.001$).

374

375

376   The density of cicada nymphs in the larch plantations did not differ from the fir plantations,

377   which had a lower digging frequency (Fig. 3). The density of cicada nymphs was lowest in the

378   natural forest (Fig. 3). The spruce plantation plots had a lower digging frequency and density of

379   cicada nymphs than other types of plantation plots (Fig. 2, 3). Cicada nymph density across all

380   forest types in 2019 were significantly higher than in 2018 ($p < 0.001$, Fig. 3).

26

Figure 3 The digging frequencies of brown bear *Ursus arctos* across all forest types in 2018 (dark grey) and 2019 (white). Upper case and lower letters indicate significant differences among forest types in 2018 and 2019 according to post-hoc Tukey's test, respectively ($p < 0.05$). Single asterisk indicates significant differences in the digging frequency between 2 years by generalized linear model ($p < 0.001$).

The density of cicada nymphs positively correlated to the digging frequencies in fir and spruce plantations ($p < 0.001$), but not in larch plantations in 2018 ($p = 0.19$) (Fig. 4). Individual dry mass of the final instar nymphs was evaluated at 1.12 ± 0.20 g (mean ± SD), and the biomass density of nymphs in each forest type is shown in Table 1.

27

Table 2 The density and estimated biomass of final instar nymphs of cicada *Lyristes bihamatus* in the plot (100 m²) across forest types. Biomass of the nymphs was calculated as multiplying mean individual dry mass of the nymph (=1.12 g) by their density. Mean ± SD

Forest type	Density of the nymphs in 2018 (/100 m²)	Density of the nymphs in 2019 (/100 m²)	Biomass of the nymphs in 2018 (g/100 m²)	Biomass of the nymphs in 2019 (g/100 m²)
Larch plantation	20.20 ± 18.71	87.07 ± 47.72	22.62 ± 20.96	97.52 ± 53.44
Fir plantation	16.92 ± 13.71	93.50 ± 66.55	18.95 ± 15.36	104.72 ± 74.54
Spruce plantation	5.67 ± 6.22	44.40 ± 63.08	6.35 ± 6.96	49.73 ± 70.65
Natural forest	1.27 ± 1.41	8.33 ± 9.44	1.42 ± 1.58	9.33 ± 10.57

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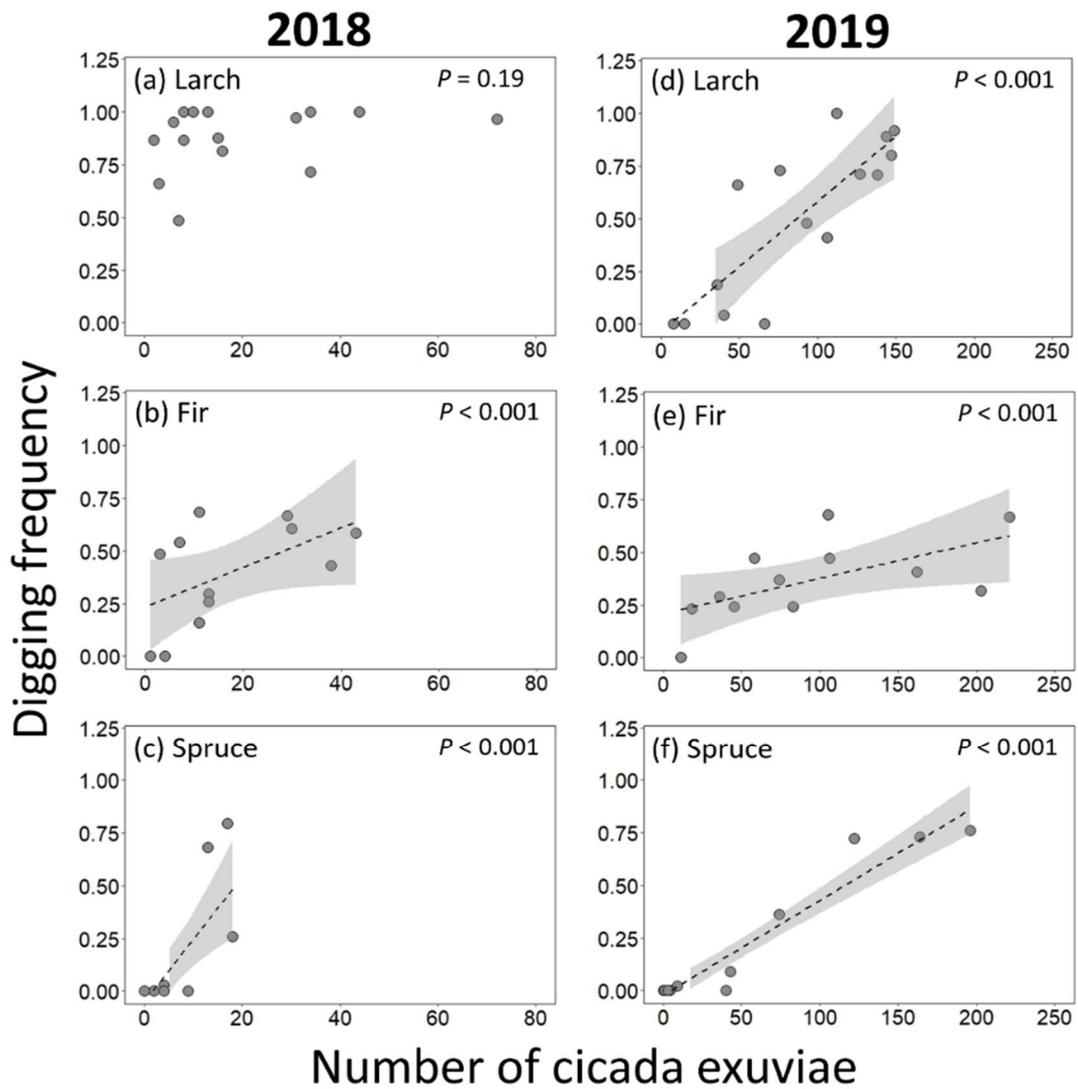
391

Figure 4 Relationships between the digging frequencies of brown bear Ursus arctos and the densities of cicada Lyristes bihamatus nymphs in the restored forests; (A) larch and (B) fir, (C) spruce in 2018, (D) larch and (E) fir, (F) spruce in 2019. Dashed lines show the linear model predictions with shaded areas indicating the 95% CI.

392

393 **Discussion**

394   The results of this study generally supported my predictions.   In particular, brown bears

395 foraged on cicada nymphs only in plantations, not in natural forests (Fig. 2). This clearly

396 indicates that reforestation provided a foraging habitat for brown bears by increasing the

397 availability of cicada nymphs. To my knowledge, this is the first study showing that

398 reforestation provides a foraging habitat for brown bears.

399   Our results indicate that the difference in the digging frequency among forest types can

400 generally be explained by the density of cicada nymphs (Figs. 2, 3, 4). The digging frequency

401 showed that brown bears preferentially dug for cicada nymphs in the larch plantations, although

402 there were no differences in the density of cicada nymphs between larch and fir plantations

403 (Figs. 2, 3). Brown bears might indirectly search for the nymphs by using larch trees as an

404 aboveground landmark for detecting the location of underground cicada nymphs. In the study

405 site, larch trees do not occur in the natural forest because larches are an introduced plantation

406 species. Thus, brown bears may have learned to associate nymphs with larch trees. This

407 potential explanation is supported by my finding that a lower density of cicada nymphs did not

408 affect digging frequency in larch plantations during 2018 (Fig. 4A). Another possible

409 explanation is that brown bears have fewer chances of encountering fir plantations than larch

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410   plantations, because the total area of larch plantations is larger than that of fir plantations in the

411   study site.

412   Within the same forest type, digging frequencies were positively affected by the density of

413   cicada nymphs (Fig. 4B-F). This indicates that brown bears can accurately detect the location of

414   the cicada nymphs within a certain distance, perhaps using their remarkable olfactory senses

415   (Gittleman 1991; Rosell et al. 2011). Other fossorial mammals can use the smell of volatile

416   signals from unseen belowground resources to detect food (Sörensen et al. 2019; Stephens et al.

417   2020). Thus, bears may identify locations where there are high densities of cicada nymphs by

418   smelling the volatile signals. I note that it is unclear yet whether cicada nymphs emit volatile

419   signals to the surface.

420   If bears rely on olfaction while searching for cicada nymphs, the relationship between

421   digging frequency and cicada density should be significantly positive in the larch plantations.

422   The possible reason is that the searching tactics of bears are different among individuals; some

423   bears rely on spatial learning, associating cicada with larches, while others use olfactory cues.

424   Behavioral differences among individuals are common in bears (Leclerc et al. 2016; Lesmerises

425   and St-Laurent 2017). Data based on the digging behavior of individuals is required to deepen

426   our understanding of how bears search for cicada nymphs.

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427   Across all forest types, the density of cicada nymphs in 2019 were significantly higher than

428   that of 2018 (Fig.2), suggesting that emergence density of *L. bihamatus* varies among years.

429   Emergence densities of annual cicada vary among years because of the age structure in the

430   nymphal stage (Sato and Sato 2015), so this inter-annual difference is probably a general pattern

431   for cicada species. Importantly, the emergence densities of cicadas in the restored forests were

432   significantly higher than in the natural forest, despite the different density of cicadas over the

433   study period. Given that the plantations are located proximate to the natural forests in the study

434   site (see Fig.1) and dispersal distance in adult cicadas is estimated at about 100-250 m (Andrade

435   et al. 2020), adult cicadas can easily come and go between the plantations and the natural forest.

436   Since emergence schedule in cicada is usually homogeneous within same population (e.g.

437   periodical cicadas (Dybas and Lloyd 1974)), periodicity of cicada emergence doesn't differ

438   between the plantations and natural forests. These strongly indicate that the restored forests play

439   a role as foraging habitat for brown bears across years.

440   I speculate that the reason for high densities of cicada nymphs in the conifer plantations is

441   because adult cicadas intensively oviposit on coniferous species. The spatial distribution of

442   cicada nymphs is determined by the oviposition preference of adult cicadas because the nymphs

443   cannot move a long distance in the soil (Oberdörster and Grant 2006). A study showed that

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444   oviposition density of the periodical cicada (*Magicicada sp.*) increased with increasing canopy

445   openness (Yang 2006). Although the canopy openness of larch plantations was higher than

446   natural forests, fir and spruce plantations were similar to the natural forests (Table 1), suggesting

447   that variations in light among forest types was insufficient for explaining the difference in

448   cicada density. Another possible factor is the host tree architecture (Mattingly and Flory 2011).

449   Several annual cicada species in Japan lay their eggs on dead branches attached to living trees

450   (e.g. *Cryptotympana facialis*), Moriyama et al. (2016)). In the study site, oviposition scars by *L.*

451   *bihamatus* were frequently observed on dead branches of the living larch trees (K. Tomita

452   *personal observation*), suggesting that this species also deposits its eggs on the dead branches of

453   living trees. Since conifer plantations usually have a larger number of attached dead branches

454   than natural forests (Yoshida and Hijii 2006) , the former would have a higher availability of

455   oviposition sites for cicadas than the latter.

456   Our previous study showed that the proportion of cicada nymphs in bear scats was

457   estimated at 14.3% (Chapter 2). Given that brown bears forage on cicada nymphs only in the

458   restored plantations (Fig.2), the plantation could contribute to the bears' summer diet to some

459   extent, even though it only accounts for 18% of the total forest area. Insects such as ants

460   (Formicidae) and the army cutworm moth (*Euxoa auxiliaris* Grote, 1873) are some of the most

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461   important summer foods for brown bears around the world (Mattson et al. 1991; Elgmork and

462   Kaasa 1992; Sato et al. 2005; Bojarska and Selva 2012). Mattson et al. (1991) estimated the

463   proportion of army cutworm moths in bear scats during summer was at 42-77% in alpine areas

464   of the Yellowstone National Park, North America. The proportions of ants, the most common

465   insect prey for bears across their distributional range, in Sweden, North America, Slovenia and

466   Japan was reported at 16%, <5%, 25% and 18%, respectively (Swenson et al. 1999; Mattson

467   2001; Große et al. 2003; Sato et al. 2005). These suggest that the dependency of brown bears on

468   cicada nymphs in this area seems to be to the same extent as ants in other regions, though not as

469   significant as army cutworm moths in Yellowstone National Park.

470   The dry biomass of the final instar nymphs of cicada in the larch plantation was estimated

471   at 22.62 and 97.51 g/100 m^2 in 2018 and 2019, respectively (Table 2). In Sweden, Slovenia and

472   Japan, the dry biomass of ants was estimated at 96, 1.35 and 0.59 g/100 m^2, respectively

473   (Swenson et al. 1999; Große et al. 2003; Yamazaki et al. 2012). This indicates that the biomass

474   density of the nymphs in the plantations is more or equal than that of ants, which is a major

475   summer food for bears. Nevertheless, this does not mean that the total biomass of cicada

476   nymphs in the whole forest is higher than that of ants or other food sources, because a large

477   biomass of cicada nymphs only occurs in the restored plantations, accounting for a small

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478   proportion (ca. 18%) of the study site. Further data on the foraging ecology, such as the

479   nutrients provided by the nymphs and energetic cost of the digging behavior, are required to

480   deepen our understanding of the value of cicadas as a food resource for bears.

481   In the SWH, the body condition of brown bears declines from June to August (Shirane et

482   al. 2020), suggesting that their nutritional status is lowest in summer. Because their body

483   condition rapidly increases during autumn, from September to November (Shirane et al. 2020),

484   how bears overcome poor nutrition in the summer might be important for their fitness. The

485   restored plantations, in which bears dig for cicada nymphs, might play a role in mitigating the

486   poor nutrition in summer, to some extent, via food supplementation in summer (i.e. cicada

487   nymphs).

488   **Management implications**

489   The primary goal of the reforestation program in the SWH to recover the forest landscape

490   from abandoned farmland has already been achieved (Shoyama 2008), but its ecological

491   functions remain largely unknown (but see Fujii et al. (2017)). My findings shed light on an

492   ecological function of the restored forests for brown bears via providing a food resource (i.e.

493   cicadas). In the SWH, brown bears play important roles in ecological and economical services,

494   such as the transporting of salmon-derived nutrients and nature tourism (Koshino et al. 2013;

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495   Kubo and Shoji 2014). However, bear appearances along the roads have often occurred in the

496   study site (Shimozuru et al. 2020), and this is a potential cause for increasing human-bear

497   conflicts like "bear jams" (Herrero et al. 2005). Because large areas of the restored plantations

498   located near the roads are frequently used by tourists (Fig.1), bears would need to approach the

499   roads to forage on cicada nymphs. In fact, wildlife managers often observed bears digging for

500   the nymphs within the plantations adjacent roads (Shiretoko Nature Foundation *personal*

501   *communication*). Perhaps, the plantations might not only provide a foraging habitat for bears,

502   but also intensify human-bear conflict by attracting bears towards the roads. Of course, it is also

503   possible that human-habituated bears mainly dig for the nymphs in the plantations. Testing this

504   hypothesis requires more data on space use by bears.

505   I found that brown bears foraged on cicada nymphs only in the monoculture plantations,

506   but not the natural forests with higher tree diversity. Nevertheless, it doesn't mean that

507   monocultures are an overall more valuable habitat for bears than natural forests because tree

508   diversity assumes to enhance the ecological value of forests as wildlife habitat (Stephens and

509   Wagner 2007). Recently, there is growing evidence indicating that monoculture plantations are

510   more valuable as wildlife habitat than previously thought (Brockerhoff et al. 2008; Sakamaki

511   and Enari 2012). Given this evidence, including our finding, monocultures might be regarded as

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512 distinct habitat compared with mixed forests, not as less valuable habitat for wildlife. Especially,

513 larch, one of the typical pioneer tree species, can rapidly recover forest canopy. Moreover, due

514 to high light availability on the forest floor of larch plantations, biomass of herbaceous species

515 on the plantation have same extent as natural forests and deciduous broadleaved trees can easily

516 invade into the plantation (Kitaoka and Koike 2004; Takafumi and Hiura 2009). Larch

517 plantations with high availability of cicadas are the potential foraging habitat for predators

518 consuming cicadas (e.g. birds (Pons 2020), mammals (Lovari et al. 1994; Way 2008)).

519 Therefore, larch may be a candidate species for tentative reforestation on abandoned land

520 although it should consider that in the Hokkaido island, larch is now an alien species but had

521 distributed during the last glacial period (Ooi et al. 1997). When selecting tree species for

522 reforestation, we, wildlife ecologists, need to consider the ecological functions of the species,

523 not only following an assumption that the value of restored forests increases as tree diversity

524 increases.

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Chapter 4 Disentangling the direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of the brown bear

Abstract

Elucidating the factors affecting the foraging habitat selection of wildlife can further our understanding of the animal–habitat relationships and inform wildlife conservation and management. Canopy and understory vegetation may directly or indirectly affect the foraging habitat selection of carnivores through changes in habitat structure and prey availability, respectively; however, the relative importance of these two effects remains largely unknown. Dwarf bamboo *Sasa kurilensis* is a predominant understory plant that suppresses regeneration in the forests of northern Japan. The purpose of this Chapter was to disentangle the direct and indirect effects of canopy forest type *Larix kaempferi* plantation vs. natural mixed forest) and dwarf bamboo on foraging habitat selection of a large carnivore, the brown bear *Ursus arctos*. In the Shiretoko World Heritage, brown bears dig for cicada nymphs during summer. I evaluated the frequency of brown bear foraging on cicadas by investigating traces of digging for cicada nymphs. A structural equation model was used to statistically disentangle the direct and indirect effects of vegetation. Our results demonstrated that canopy and understory vegetation directly

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544   and indirectly affected foraging habitat selection of brown bears. Dwarf bamboo negatively

545   affected cicada nymph density, which positively affected brown bear digging. This suggests that

546   dwarf bamboo also had indirect negative effects on brown bears. Forest type had significant

547   direct and indirect effects via change in cicada nymph density on foraging behavior in brown

548   bears. Forestry managers in northern Japan, including the study site, try to remove dwarf

549   bamboo for assisting natural regeneration. Removal of dwarf bamboo might not only promote

550   natural regeneration, but also provide a beneficial foraging habitat for bears.

551

Introduction

552

553   Understanding the foraging habitat selection of animals in the natural environment is a

554   major goal of animal ecology (Rosenzweig 1981, Lima and Zollner 1996, Morrison et al. 2012)

555   and can provide useful information for habitat management for conservation (Morris 2003,

556   Mayor et al. 2009). Foraging habitat selection is directly and indirectly affected by many

557   environmental factors such as vegetation biomass and structure or prey availability (Jonkel and

558   Cowan 1971, Risenhoover and Bailey 1985, Heithaus et al. 2009), because environmental

559   factors often show causal relationships among one another. For instance, vegetation can directly

560   and negatively affect carnivores by decreasing prey-searching efficiency (Gorini et al. 2012),

561   but it has indirect and positive effects on carnivores through enhancing prey availability due to

562   increase in plant biomass (Lantschner et al. 2012). Although evaluating the direct and indirect

563   effects of vegetation separately can deepen our understanding of the mechanisms of habitat

564   selection of carnivores and thereby contribute to accurately identifying habitat attributes that

565   should be protected, there is little consideration of these two effects on foraging habitat

566   selection (Eby et al. 2014, Belanger et al. 2020).

567   Canopy and understory vegetation serve important functions in forest ecosystems, such as

568   enabling nutrient cycling and providing wildlife habitat (Ellison et al. 2005, Nilsson and Wardle

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569   2005, Hagar 2007). Vegetation also influences animal behavior by serving as foraging and

570   resting habitat, or shelter from predators (Ellison et al. 2005, Royo and Carson 2006, Lone et al.

571   2014, Davies et al. 2016) and strongly influence carnivore habitat selection (Lantschner et al.

572   2012, Lone et al. 2014, Gastón et al. 2019). For instance, Lone et al. (2014) showed that

573   Eurasian lynx (*Lynx lxnx*) predation occurred more frequently in areas with dense understory

574   vegetation than in areas with sparse understory vegetation due to the increased availability of

575   ambush sites. Gaston et al. (2019) showed that the Iberian lynx (*Lynx pardinus*) preferred

576   broadleaved forests with low canopy cover, possibly due to its indirect effect on lynx through

577   increased prey density (i.e., rabbits). However, the relative importance of direct and indirect

578   effects of canopy and understory vegetation on the foraging habitat selection of carnivores

579   remains largely unknown.

580   The brown bear (*Ursus arctos*), which is one of the most widespread large carnivores in the

581   northern hemisphere, consumes a wide variety of foods from plants to animals (Mattson et al.

582   1991, Sato et al. 2005, Shirane et al. 2021). Canopy and understory vegetation provide bears

583   with foods such as herbs, nuts, and berries (Nielsen et al. 2004, Martin et al. 2010, McClelland

584   et al. 2020). Even though brown bears mainly consume plant materials, use of herbivorous

585   animals is ubiquitous in bear diets (Mattson et al. 1991, Kobayashi et al. 2012). Thus, canopy

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586   and understory vegetation may also directly and indirectly affect the foraging habitat selection

587   of brown bears. While it is well known that canopy vegetation affects the habitat selection of

588   brown bears (Martin et al. 2010, Milakovic et al. 2012), there are few studies showing the

589   effects of understory vegetation on bears (Nielsen et al. 2004, McClelland et al. 2020).

590   In the Shiretoko World Heritage (hereafter; SWH), Hokkaido, northern Japan, brown bears

591   dig for final instar nymphs of cicadas (*Lyristes bihamatus*) during summer (Chapter 2). Chapter

592   3 found that their digging for cicada nymphs only occurred in conifer plantations, but not in

593   natural mixed forest, and cicada nymph densities were higher in plantations than in the natural

594   forest. In the SWH site, the dominant understory species is dwarf bamboo (*Sasa kurilensis*) with

595   tough and dense rhizomes, and thus understory vegetation may negatively affect foraging

596   habitat selection of bears for cicadas through increase in the energy required for digging. Dwarf

597   bamboo may also indirectly affect foraging habitat selection through changes in cicada nymph

598   density because the density of cicada nymphs, which feed on xylem sap, is affected by biomass

599   and composition of understory vegetation (Smith et al. 2006). Accordingly, I predicted that

600   forest type and the presence or absence of understory vegetation might directly or indirectly

601   affect foraging habitat selection of brown bears for cicada nymphs through changes in habitat

602   structure and prey availability (i.e., cicada density), respectively. To independently evaluate the

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603   direct and indirect effects of forest type and dwarf bamboo, I used structural equation modelling

604   (SEM), which is a powerful statistical framework to develop causal understanding (Grace

605   2006).

Materials and Methods

Field survey

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607

608   In larch plantations without understory dwarf bamboo where the bears frequently dug for

609   *L. bihamatus* nymphs, the emergence density of cicadas in 2018 (20.20 ± 18.71) was lower than

610   that in 2019 (87.07 ± 47.72) (Chapter 3). Thus, I conducted field surveys in these two years to

611   consider the influence of the annual difference in cicada emergence density on the foraging

612   habitat selection of brown bears. From late August to September, survey plots (100 m^2) were set

613   in the larch plantations and natural forests with and without understory dwarf bamboo (N = 15

614   for each type). I maintained spatial separation among survey plots with the same vegetation type

615   to avoid spatial autocorrelation (Fig. 1). Because bears dig for cicada nymphs from mid-May to

616   the end of July, during which the final instar nymphs fully emerge (Chapter 2), the chosen

617   survey duration was appropriate for evaluating the foraging behavior of bears and the

618   emergence density of cicadas. Although brown bears dig for cicada nymphs in the spruce and fir

619   plantations (Chapter 3), I did not use the data collected from these plantations because dwarf

620   bamboo is absent in these forest types. According to my preliminary observations using eight

621   camera traps set in larch plantations where brown bears dug the previous year, bears usually dig

622   for cicada nymphs near tree trunks. Thus, I evaluated the digging frequency per plot as the

623   proportion of all trees (DBH > 2 cm) that had digging traces within 50 cm diameter from the

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624   base of a tree. Freshness of digging traces was visually determined, as traces scratched in the

625   current year had no fresh leaf litter on the ground and fluffy soil. The density of cicada nymphs

626   was measured as the density of cicada exuviae collected from all trees (DBH > 2 cm) within the

627   plots. The sampling height of trees was below 3 m, because most exuviae on trees are observed

628   at this height (Chapter 3). Exuviae on the ground were collected within 1 m of the tree trunk,

629   because most exuviae falling from the tree are found at this distance. I only collected exuviae

630   associated with trees, not dwarf bamboo because *L. bihamatus* use dead branches on tree trunk

631   for oviposition (Chapter 3) and cicada exuviae were never found on stems and leaves of dwarf

632   bamboo. Cicada exuviae were generally used as an index of cicada nymph density because they

633   empirically reflect the density of underground nymphs (Lee et al. 2010, Pons 2015, Moriyama

634   and Numata 2015). All trees with DBH > 2 cm within the survey plot were measured for

635   quantifying the stand basal area and number of trees per plot in 2018.
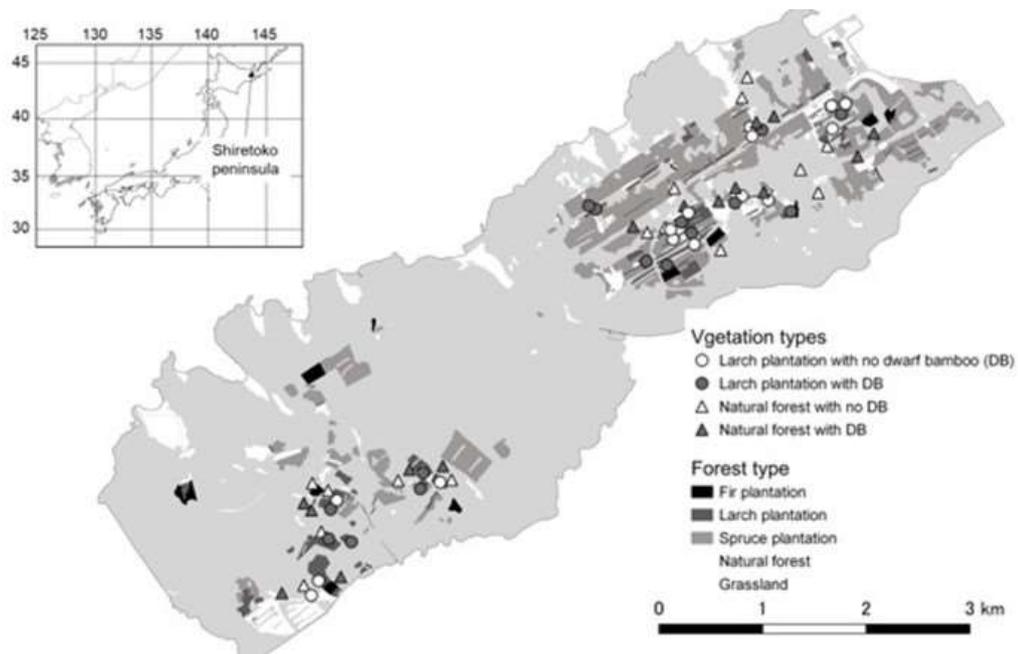
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Figure 1 Location of the survey plots in the vegetation map of the study site. This vegetation map is reprinted from Chapter 3 and created by Shiretoko Nature Foundation (Shiretoko Nature Foundation unpubl. information). This figure was created using QGIS 3.14.0.

637

638   *Statistical analysis*

639   Generalized linear models (GLMs) with log link and Poisson error distribution were used

640   to test the differences in digging frequencies and cicada nymph densities among vegetation

641   types (i.e., larch plantation and natural forest with and without dwarf bamboo). For digging

642   frequencies, I constrained GLMs only on larch plantations due to no occurrence in natural

643   forests. For GLMs of digging frequency, I introduced an offset term as the log-transformed

644   number of trees to adjust for differences in the number of trees among the survey plots.

645   In the field of ecology, SEM has recently been used to disentangle the causal relationships

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646   among biotic and abiotic factors and independently evaluate the strength of direct and indirect

647   effects based on observational data (Grace 2006, Eisenhauer et al. 2015). In SEMs, an a priori

648   hypothetical model is built following ecologically realistic assumptions and then the path

649   coefficients are estimated (Eisenhauer et al. 2015). Accordingly, a hypothetical path model was

650   constructed for applying SEM to the observational data (Fig.2), based on the following

651   assumptions. The foraging behavior of brown bears may be affected by the density of cicada

652   nymphs and the presence of dwarf bamboo. Furthermore, brown bears may directly detect the

653   location of belowground cicada nymphs, or indirectly search for them by associating the

654   location with the aboveground landmarks such as forest type (e.g. natural forest vs. larch

655   plantation) and stand characteristics (e.g. stand basal area and number of trees) (Chapter 3).

656   These forest characteristics would also indirectly affect the foraging habitat selection of bears

657   through changes in the density of cicadas, whose life cycle depends on the forest trees. Thus, I

658   assumed that forest characteristics directly and indirectly affect the foraging habitat selection of

659   brown bears for cicada nymphs. To test the effect of forest type in the model, larch plantation

660   and natural forest were converted to dummy variables (i.e., larch plantation = "1", and natural

661   forest = "0"). Thus, the target variables showing higher values in the larch plantation than in the

662   natural forest indicated the positive effects of forest type. I assumed that the density of cicada

663   nymphs is affected by dwarf bamboo and forest characteristics, such as forest type, stand basal

664   area, and number of trees, because cicadas depend on forest plants for their life cycle. All count

665   data (i.e. the number of trees and cicada nymphs) were log 10 (n+1) transformed. The strength

666   of indirect effects was calculated by multiplying the path coefficients of the mediated variables

667   by those of the associated variables. Since the effect size of each variable could be regarded as

668   absolute values of standardized path coefficients (Grace et al. 2010, Ando et al. 2017), I

669   compared the values to evaluate the relative importance of each variable on the foraging habitat

670   selection of bears.

671   To test the goodness of model fit, I used the Root Mean Square Error of Approximation

672   (RMSEA) (Steiger 1990) and the Comparative Fit Index (CFI) (Bentler 1990), which examine

673   the absolute fit of the model to the observational data. Values of CFI $\geq$ 0.95 and RMSEA $\leq$ 0.06

674   suggest an appropriate model fit (Hu and Bentler 1999). Use of multiple measures for testing

675   model fit is recommended to build a highly robust model (Hu and Bentler 1999). All analyses

676   were performed using the lavaan package (Rosseel 2012) of R version 3.5.1.
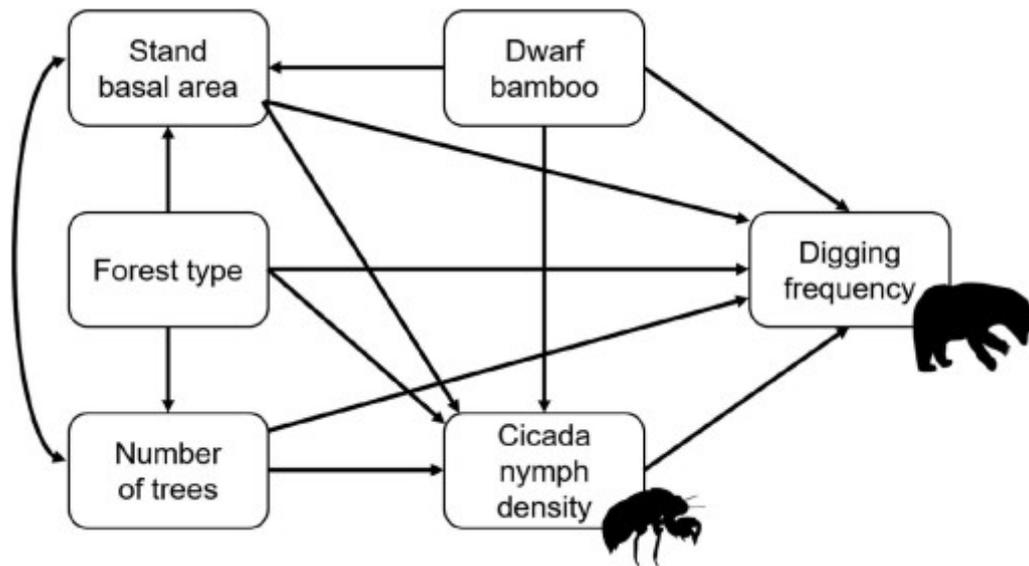
Figure 2 Hypothetical path model to represent the causal relationships among forest characteristics, cicada nymph density and frequency of brown bear digging for cicada nymphs. Cicada nymph density was measured as the number of cicada exuviae within a survey plot. Digging frequency indicates the proportion of trees with digging traces at their base among all trees (diameter at breast height > 2 cm) in the plot

678

Results

679 **Results**

680   In both years, dwarf bamboo had a significant negative effect on digging frequency, and

681 forest type had a significant positive effect on cicada nymph density (Table 1). For SEMs in

682 both years, the RMSEA and CFI values were 0.000 (90 % CI: 0.000 - 0.305) and 1.000

683 respectively, indicating that the model adequately fit the data. The SEM results (i.e. R^2 values,

684 standardized path coefficients, and standard error of each variable) in 2018 and 2019 are

685 summarized in Table 1, and the detailed information is presented in Tables S1 and S2 (*see*

686 Supplementary material). In both years, the frequency of brown bear diggings for cicada

687 nymphs was positively affected by the density of cicada nymphs and negatively by the presence

688 of dwarf bamboo. Forest type had the largest positive effect on digging frequency (Table 1).

689 Digging frequencies, including densities of cicada exuviae, were greatest in larch forests

690 without a dwarf bamboo understory. The direct effect of dwarf bamboo presence on digging

691 frequency (2018: -0.22, 2019: -0.12) was stronger than the indirect effect via cicada nymph

692 density (2018: -0.61 × 0.14 = -0.08; 2019: -1.03×0.09 = -0.09) (Fig. 3). The direct effect of

693 forest type on digging frequency (0.38) was stronger than the indirect effect via cicada nymph

694 density (1.44×0.14 = 0.20) in 2018, whereas the direct effect (0.14) was same as or slightly

695 weaker than the indirect effect (1.75×0.09 = 0.16) in 2019. In both years, cicada nymph density

696 was positively affected by forest type (2018: 1.44; 2019: 1.75) but negatively affected by dwarf

50

697   bamboo presence (2018: -0.61; 2019: -1.03), respectively (Fig. 3). No significant effects of

698   stand basal area and number of trees were observed, indicating that these factors did not affect

699   cicada nymph density. The presence of dwarf bamboo negatively affected stand basal area (-

700   0.24). Forest type positively affected stand basal area, indicating stand basal area in larch

701   plantations was higher than in natural forests.

(a) 2018
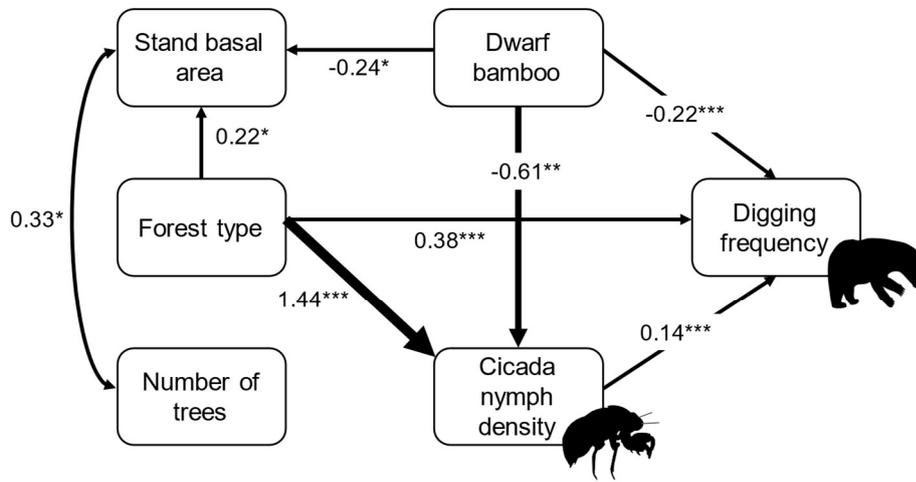
(b) 2019
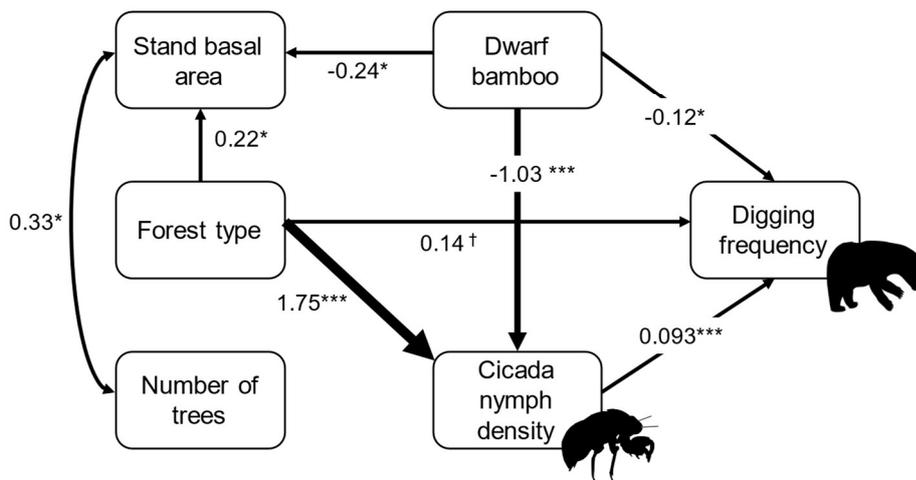
Figure 3 Structural equation model showing the causal relationships among forest characteristics, cicada *Lyristes bihamatus* nymph density, and frequency of brown bear digging for cicada nymphs in (a) 2018 and (b) 2019. All paths described in the figure are statistically significant ($P < 0.05$). Numbers next to the arrows indicate standardized path coefficients significant at ***$P < 0.001$, **$P < 0.01$, and *$P < 0.05$. Arrow width is proportional to the strength of the standardized path coefficients. R^2 is the coefficient of determination, indicating the variability explained for each dependent variable.

704 **Table 1** Summary of the structural equation model showing standardized path coefficients and

705 standard errors (SE) in 2018 and 2019. R^2 show the coefficient of determination indicating the

706 variability explained for each variable. Underlined places indicate the pathways directly

707 associated with my predictions

Pathway			2018		2019	
			Standardized path coefficient	SE	Standardized path coefficient	SE
<u>Digging frequency</u>	←	<u>Cicada nymph density</u>	0.136^{***}	0.031	0.093^{***}	0.026
<u>(2018: R^2 = 0.783)</u> <u>(2019: R^2 = 0.514)</u>	←	<u>Dwarf bamboo</u>	-0.219^{***}	0.052	-0.120^{*}	0.059
	←	Forest type	0.384^{***}	0.066	$0.135^{†}$	0.070
	←	Stand basal area	-0.026	0.059	-0.074	0.065
	←	Number of trees	-0.077	0.081	-0.003	0.088
Cicada nymph density (exuviae 100m^{-2})	←	Dwarf bamboo	-0.610^{**}	0.203	-1.026^{***}	0.260
(2018: R^2 = 0.542) (2019: R^2 = 0.580)	←	Forest type	1.442^{***}	0.202	1.750^{***}	0.258
	←	Stand basal area	0.139	0.248	0.455	0.317
	←	Number of trees	0.383	0.335	0.618	0.428
Stand basal area (m^2 100 m^{-2})	←	Dwarf bamboo	-0.240^{*}	0.101	-0.240^{*}	0.101
R^2 = 0.195 (2018 & 2019)	←	Forest type	0.220^{*}	0.101	0.220^{*}	0.101
	↔	Number of trees	0.334^{*}	0.077	0.334^{*}	0.077
Number of trees (trees 100 m^{-2}) R^2 = 0.002 (2018 & 2019)	←	Forest type	0.024	0.016	0.024	0.016

708

709 *Note: Significant at ***P < 0.001, ** P < 0.01, *P < 0.05, and †P = 0.054.*

710   **Discussion**

711   In the present study, I evaluated the direct and indirect effects of canopy and understory

712   vegetation on the foraging habitat selection of brown bears. Although there were differences in

713   direct and indirect effect sizes, these two effects of forest type and dwarf bamboo were

714   significantly positive and negative, respectively. To the best of my knowledge, this is the first

715   study to independently evaluate the direct and indirect effects of vegetation on the foraging

716   habitat selection of carnivores.

717   *Factors affecting the foraging habitat selection of brown bears*

718   The direct effect of dwarf bamboo on the digging frequency was stronger than the indirect

719   effect through decrease in the density of cicada nymphs (Fig. 3), indicating that dwarf bamboo

720   physically interferes with digging behavior of brown bears. Our results demonstrate that

721   understory vegetation such as dwarf bamboo may obstruct foraging behavior in brown bears.

722   The selection of digging site by brown bears is determined by the balance between the energy

723   for excavating soil and energy gain from food (Mattson 1997). It may be energetically costly to

724   dig up the surface ground covered with dwarf bamboo because bear claws get caught in their

725   tough and dense rhizomes. Likewise, dwarf bamboo would interfere with the digging behavior

726   of other wildlife in natural environments.

54

727   Although the reason bears intensively dig for cicada nymphs in the larch plantations may

728   be the higher cicada availability in plantations than in natural forests, they also directly selected

729   the plantations regardless of the density of cicada nymphs (direct effect of forest type on

730   digging in 2018, *see* Fig.3a). Moreover, the absolute values of direct effect of forest type on

731   brown bears were stronger than that of dwarf bamboo, indicating that canopy vegetation has a

732   larger effect on bears than understory dwarf bamboo. Brown bears may have learned to

733   associate nymphs with larch trees, because these trees are an introduced species, and cicada

734   nymphs occur within the larch plantations at the study site. Learning which is an important

735   process determining the behavior of bears (Mazur and Seher 2008), may yield a strong and

736   direct association between their foraging behavior and forest type.

737   *Factors affecting cicada nymph density*

738   A possible reason for the positive effect of the larch plantations on cicada nymph density

739   might be the fact that larches harbor more oviposition sites for cicadas than broadleaved trees.

740   Cicada species in Japan usually lay eggs on dead branches attached to living trees (Moriyama et

741   al. 2016). Conifer plantations usually have more attached dead branches than natural forests

742   (Yoshida and Hijii 2006). Another possible reason is that the nutrient content of the xylem sap

743   of larches is higher than that of the xylem sap of broadleaved trees in natural forests.

744   Consequently, adult cicadas would intensively oviposit on larches because the oviposition

745   preference of herbivorous insects is typically positively correlated with larval performance

746   (Thompson 1988, Yang and Karban 2009).

747   A possible mechanism underlying the negative effect of dwarf bamboo on cicada nymph

748   density is the decrease in the nutrient content of tree xylem sap, which is a food source for

749   cicada nymphs, due to competition with dwarf bamboo for resource such as soil nutrients (e.g.,

750   inorganic nitrogen) and water (Ishii et al. 2008). The belowground competition between dwarf

751   bamboo and trees is supported by the negative effect of bamboo on stand basal area (Fig. 3). I

752   observed no consistent effect of stand basal area on cicada nymph density. Although cicada

753   nymph density may have been positively correlated with root biomass, resource quality (e.g.,

754   nutrient content of xylem sap) rather than quantity (i.e., root biomass) would be a more

755   important factor affecting viability of cicada nymphs. Even if cicada nymphs can forage on the

756   xylem sap of dwarf bamboo, its nutrient content would not be higher than that of the xylem sap

757   of trees occurring in forests without dwarf bamboo due to belowground competition.

758   *Differences in SEM results between 2018 and 2019*

759   Even though the emergence density of cicadas in 2018 was lower than that in 2019

760   (Chapter 3), the direction of the effect of cicada nymph density and dwarf bamboo presence on

761   brown bear digging was consistent between both years, indicating that my SEM results provide

762   robust estimation of the foraging habitat selection of brown bears for cicada nymphs.

763   Conversely, the indirect effect of forest type via cicada nymph density was weaker and stronger

764   (or the same) than the direct effect in 2018 and 2019, respectively. This difference suggests that

765   in 2018, brown bears directly searched for the nymphs associated with the larch plantations

766   regardless of cicada nymph density. It may be more difficult for brown bears to find cicada

767   nymphs in years with a low emergence density of cicadas than with a high emergence density,

768   because foraging efficiency usually decreases with decrease in prey availability (Bell 1991). In

769   such years, bears might be more dependent on larch trees as aboveground landmarks to search

770   cicada nymphs.

771   **Management implications**

772   We separately evaluated the direct and indirect effects of vegetation on carnivores. Our

773   study can provide important implications for wildlife management. Understanding the

774   mechanisms of wildlife resource use can help to solve problems in wildlife habitat management

775   (Morris 2003, Hebblewhite et al. 2005). The indirect effect of vegetation via changes in prey

776   availability is an overlooked pathway affecting the foraging behavior of carnivores. Given their

777   foraging habitat selection is strongly affected by the distribution patterns of herbivorous animals

57

778   that are determined by the distribution of vegetation, the indirect effect may be important for

779   shaping their foraging habitat. Therefore, considering the indirect effects of vegetation would be

780   able to help us to understand how the foraging habitat of carnivores determines and possibly

781   improves their habitat conservation.

782   Because dwarf bamboo suppress natural regeneration due to its dense cover, forestry

783   managers in northern Japan, including the study site, try to remove dwarf bamboo for assisting

784   natural regeneration (Yamazaki and Yoshida 2020). Given the negative effects of dwarf bamboo

785   on brown bear foraging as shown by this study, bamboo scarification might have a positive

786   effect on bears through reducing the cost of digging for food and increasing prey availability.

787   Thus, it is possible that scarification can not only promote natural regeneration, but also provide

788   a beneficial foraging habitat for bears. Since the goal of sustainable forest management is to

789   maintain a balance between timber production and environmental values (Dennis et al. 2008),

790   scarification of dwarf bamboo may be an option for sustainable forestry in the study site.

791   However, application of scarification should be carefully considered because of unknown

792   effects on other wildlife species.

793

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Chapter 5 Negative effects of brown bear digging on soil nitrogen availability and production in the larch plantations in northern Japan

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 this Chapter, I 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. I 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. My 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.

59

Introduction

810

811   Soil bioturbation is the process of physical displacement of soil by organisms, such as

812   plants, insects, birds, and mammals (Bétard, 2021; Fleming et al., 2014; Gabet et al., 2003;

813   Maisey et al., 2021). It is an important biotic factor affecting many soil ecosystem functions

814   (Meysman et al., 2006; Platt et al., 2016). Mammals that regularly dig for food and nest building

815   are among the most extensive agents of bioturbation around the world (Coggan et al., 2018;

816   Davidson et al., 2012; Mallen-Cooper et al., 2019; Platt et al., 2016). Mammalian digging for

817   acquiring belowground food resources can directly and indirectly affect soil ecosystem

818   processes through soil turnover and consumption of soil organisms, respectively, which

819   significantly affects soil quality (Barrios-Garcia et al. 2014). Digging mammals displace a large

820   amount of soil, thereby strongly altering soil ecosystem processes such as carbon dioxide

821   emission and inorganic nitrogen production through bioturbation (Barrios-Garcia and Ballari,

822   2012; Mallen-Cooper et al., 2019; Platt et al., 2016; Risch et al., 2010). For instance, digging

823   activity by wild boar (*Sus scrofa*) disturbed 27–54 % of the forest floor, decreased soil nitrogen

824   availability and increased carbon dioxide emissions in a Switzerland woodland (Risch et al.,

825   2010).

826   Previous studies on the effects of digging by mammals on soil ecosystem processes have

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827   mainly focused on small mammals such as social rodents and Australian marsupials (Davidson

828   et al., 2012; Fleming et al., 2014; Mallen-Cooper et al., 2019). Although larger mammals tend to

829   displace a larger volume of soil per one digging pit for food (Haussmann, 2017), there are

830   relatively few studies on the digging impacts of large mammals except for studies that focus on

831   wild boars on soil ecosystem processes (Barrios-Garcia and Ballari, 2012). The brown bear

832   (*Ursus arctos*) displaces a large amount of soil (Butler, 1992; Haussmann, 2017; Platt et al.,

833   2016) because it forages on a wide variety of belowground resources, such as subterranean

834   animals and plant roots, in large quantities (Mattson, 1997; Tardiff and Stanford, 1998).

835   However, there is only one study showing the effect of brown bear digging on soil properties

836   (Tardiff and Stanford, 1998), and there are no studies from forest ecosystems where brown bears

837   generally dig for food (Munro et al., 2006). Tardiff and Stanford (1998) found that brown bear

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

839   increasing soil inorganic nitrogen production in an alpine meadow of Glacier National Park,

840   USA. The effects of digging on soil properties vary among ecosystem types even within the

841   same species due to the differences in environmental conditions, such as ground solar radiation

842   and vegetation composition (Davies et al., 2019; Yurkewycz et al., 2014). Therefore, testing

843   their digging impacts on soil properties in forests are important for deepening our

844   understandings of their ecological role as agents of bioturbation.

61

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

846　　　has one of the highest densities of brown bears in the world (Shimozuru et al., 2020), they have

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

848　　　2000 (Fig. 1), suggesting that brown bears have caused novel bioturbation through behavioral

849　　　changes since 2000 (Chapter 2). In this area, brown bear digging for cicadas occurred in conifer

850　　　plantations but not in natural mixed forests (Chapter 3). In the larch (*Larix kaempferi*)

851　　　plantations, bears dug up almost all the areas, and the area of a dug patch was often more than

852　　　100 m^2 (Chapter 2 and 3). Larch plantations at the study site are expected to facilitate natural

853　　　forest regeneration because many native saplings occur within the plantation (Suzuki et al.,

854　　　2021). Accordingly, I evaluated the effects of brown bear digging on the soil properties to

855　　　develop understanding of the contribution of bears to natural forest regeneration in the larch

856　　　plantations.

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

858　　　nitrogen and decreased water run-off (Mallen-Cooper et al., 2019). Tardiff and Stanford (1998)

859　　　showed a positive effect of brown bear digging on nitrogen production. Hence, I hypothesized

860　　　that brown bear digging for cicada nymphs would increase soil water content, inorganic

861　　　nitrogen availability, and nitrogen mineralization rate.

862   Material and methods

863   *Soil sampling*

864   Brown bears continued digging for cicada nymphs until early August, when cicada

865   emergence was completed (Tomita, 2021). In September 2018, I found the highest frequency of

866   brown bear digging for cicada nymphs in larch plantations (Chapter 3). Based on this finding, I

867   chose 14 larch plantations as soil sampling points in October 2018 when brown bear digging

868   had ended about two months ago. To maintain independence among the sampling points, each

869   point was spaced at least 100 m apart. At each sampling point, surface soil (0-10 cm) was

870   collected from both dug and adjacent undisturbed soil using a 100-ml soil core sampler. To

871   make up the paired-sample design, I collected undisturbed soil that was completely covered by

872   pasture grass without any presence of overturned soil and apart 1 m from dug areas. To ensure

873   that the undisturbed soil was not dug by brown bears, I also observed the accumulation of larch

874   litter in the undisturbed soil. The dug soil were exposed to bare soil without a litter layer owing

875   to soil disturbance in the sampling year. The collected soil was sieved a 2 mm to remove roots

876   and coarse gravel, and mixed well for homogenization. The soil was kept at 6 °C prior to

877   chemical analysis and laboratory incubation.

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

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-

64

883   900; Sumitomo, Osaka, Japan). For inorganic nitrogen availability, 6 g of fresh soil was

884   weighed into plastic bottles and extracted with 27.5 mL 1 M KCl with shaking for 1 h. By using

885   an auto-analyzer (AACS-4, BL-TEC, Inc., Japan), ammonium and nitrate nitrogen was analyzed

886   by indophenol blue absorptiometry and naphthyl ethylenediamine dihydrochloride

887   spectrophotometry, respectively. The total concentration of nitrogen in nitrate and ammonium

888   was regarded as the total nitrogen availability.

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

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

891   The net mineralization rate was determined from the difference in the total inorganic nitrogen

892   concentration (ammonia + nitrate-nitrogen concentration) before and after incubation. The

893   nitrification rate was determined from the difference in nitrate nitrogen concentration before and

894   after incubation. The units for both rates were converted to 1 kg of dry soil per day. After

895   checking the normal distribution of the data using the Shapiro-Wilk test, I conducted a one-way

896   analysis of variance (ANOVA). The data that did not have a normal distribution and was fitted

897   to a normal distribution by log10-transformation followed by analysis using ANOVA. All

898   statistical analyses were conducted using R version 3.5.1 (R Core Team, 2018).

65

Results

900   Soil moisture content, organic nitrogen and carbon contents, carbon nitrogen ratio,

901   ammonium nitrogen concentration, and net mineralization rates in dug soil were significantly

902   lower than those in undisturbed soil ($P < 0.05$, Table 1, Figs. 2a, c, d, f, h, and i). Nitrate

903   nitrogen concentration and, nitrification rate in the dug soil was not significantly lower than that

904   in undisturbed soil (nitrate nitrogen [$P = 0.369$, Fig. 2g], nitrification rate [$P=0.241$, Fig. 2j].

905   Carbon nitrogen ratio was marginally significantly higher in dug soil than in undisturbed soil

906   (Fig.2e, $P = 0.098$) Bulk density in dug areas was significantly higher than that in undisturbed

907   areas (Fig.2b, $P < 0.01$). Percentage differences in soil properties between dug and undisturbed

908   soil are shown in Table 1.
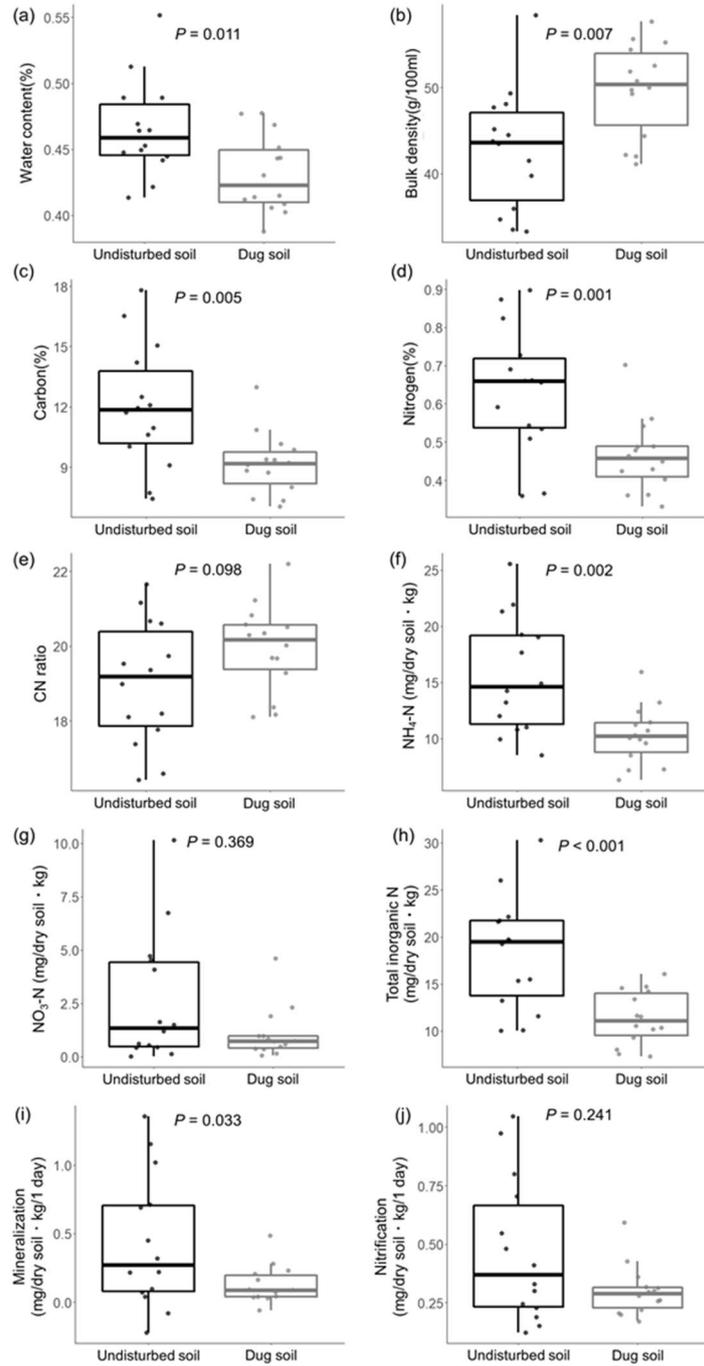
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Figure 2 Comparisons of soil water content (a), bulk density (b), total carbon (c), total nitrogen (d), C:N ratio (e), ammonium nitrogen (f), nitrate nitrogen (g), total inorganic nitrogen (h), net mineralization rate (i), and nitrification rate (j) between dug (Grey color) and undisturbed (Black color) soil. P-values in each boxplot were the results of ANOVA.

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Table 1 Mean ± SD, percentage difference, and *P* value from ANOVA of each soil property between soil dug by brown bears and undisturbed soil.

Soil property	Dug	Undisturbed	Difference (%)	*P* value
Water content(%)	43.13 ± 2.93	46.52 ± 3.63	-7.29	**0.011**
Bulk density(g/100 ml)	49.76 ± 5.43	42.78 ± 7.07	16.31	**0.007**
Total carbon (%)	9.17 ± 1.56	12.0 ± 3.08	-23.51	**0.005**
Total nitrogen (%)	0.46 ± 0.10	0.64 ± 0.17	-27.11	**0.001**
CN ratio	19.95 ± 1.18	19.01 ± 1.67	4.92	0.098
Ammonium nitrogen (mg/dry soil · kg)	10.30 ± 2.56	15.68 ± 5.17	-34.24	**0.002**
Nitrate nitrogen (mg/dry soil · kg)	1.07 ± 1.19	2.62 ± 3.03	-59.07	0.369
Total inorganic nitrogen (mg/dry soil · kg)	11.38 ± 2.85	18.30 ± 6.00	-37.8	**< 0.001**
Net mineralization rate (mg/dry soil · kg/1 day)	0.13 ± 0.14	0.43 ± 0.48	-70.18	**0.033**
Nitrification rate (mg/dry soil · kg/1 day)	0.30 ± 0.11	0.47 ± 0.31	-35.72	0.241

Discussion

915

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

917   availability in the larch plantations. To my knowledge, this is the first study showing the effects

918   of digging on soil properties in forest ecosystems, where bear digging normally occurs (Munro

919   et al. 2006). Given that soil water and nitrogen availability are positively correlated with net

920   primary production in temperate forests (Pastor et al., 1984; Tateno et al., 2004), brown bear

921   digging may decrease net primary production in the larch plantation of the study site through

922   changes at soil nutrient dynamics.

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

924   bear digging increased soil inorganic nitrogen availability in an alpine meadow. A possible

925   reason for this is the differences in the light environment on the surface ground between

926   meadows and forests. In open habitat with strong ground solar radiation, such as meadows and

927   grasslands, digging by mammals increases soil albedo due to the exposure of the darker mineral

928   soil by the removal of plants and litter, thereby increasing soil temperature (Canals et al., 2003;

929   Yurkewycz et al., 2014). Given that soil temperature positively affects the nitrogen

930   mineralization rate (Guntiñas et al., 2012; Knoepp and Swank, 2002), the positive effect of

931   digging on inorganic nitrogen production in open habitats would be yielded by an increase in

69

932   soil temperature by digging (Tardiff and Stanford, 1998).

933   As digging does not affect soil temperature in forests with weak ground solar radiation

934   (Barrios-Garcia et al., 2014; Risch et al., 2010), the positive effects of digging on soil inorganic

935   nitrogen would be subtle in forests. Rather, soil mixing by digging is one of the possible

936   mechanisms for the reduction in organic nitrogen content and thereby inorganic nitrogen

937   concentration (Kurek et al., 2014; Wirthner et al., 2012), because it is usually the highest in the

938   surface organic layer (Persson and Wirén, 1995). This is supported by the result that the net

939   mineralization rate of the dug soil was lower than that of the undisturbed soil, even under the

940   same water and temperature conditions (Fig. 2i). Brown bear digging would also negatively

941   affect inorganic nitrogen production through reduction in soil water contents (Fig. 2a). These

942   implies that brown bear digging for cicadas might negatively affect soil inorganic nitrogen by

943   not only altering the soil water availability as well as the mixture of organic and mineral soil.

944   Digging can increase inorganic nitrogen availability through the removal of plant root

945   (Canals et al., 2003). However, our results did not support this mechanism, even though the dug

946   soil was removed understory cover by brown bear digging. This suggests that the negative effect

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

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

70

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

950 bears could enhance soil nitrogen availability by depositing dung and urine when digging for

951 cicada nymphs (Tardiff and Stanford, 1998), my results suggest that their excrement seems to

952 have a weak effect on soil nitrogen, or that the negative effect of digging exceeded its effects.

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

954 rate through promoting soil aeration during the gopher activity season (Canals et al., 2003), my

955 results showed that nitrification rate of the dug soil did not significantly differ from that of

956 undisturbed soil. The positive effect of digging on nitrate nitrogen through soil aeration may be

957 weak because my soil sampling was conducted in October, in which brown bear digging had

958 ended approximately 2 months ago. The reduction in soil water content through digging may be

959 caused by litter removal because the litter layer can prevent water evaporation from the surface

960 soil (Sayer, 2006). Their digging may also decrease soil water content by exposing the soil to

961 the ground, thereby facilitating the direct evaporation of soil water (Bueno et al., 2013). The

962 consumption of cicada nymphs may be a possible mechanism for the negative effects of brown

963 bear digging on soil water and nitrogen, given that the nymphs can release a large amount of

964 water and nitrogen from tree roots into the soil through xylem feeding activity (Hunter, 2016).

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

966   2021; Helfield and Naiman, 2006), little attention has been paid to their ecosystem role as

967   digging mammals (Tardiff and Stanford, 1998). Deepening the understanding of the ecological

968   roles of wildlife is important for justifying conservation and management policy making

969   (Somaweera et al., 2020). I hope that this study provides ecological insights for their

970   conservation and management by evaluating the role of bears as agents of bioturbation in a

971   landscape composed of natural forests and plantations. However, I should carefully consider

972   whether our finding are applicable to other ecosystem types, because the direction and

973   magnitude of digging impacts vary with local and regional environmental conditions, even in

974   the same species (Yurkewycz et al., 2014).

975   My Chapter 2 suggested that brown bears have caused novel bioturbation since 2000 when

976   they started digging for cicada nymphs. This study showed an ecological consequence of this

977   emerging behavior, in which their digging negatively affected soil water and nitrogen

978   availability in larch plantations. Given that brown bear digging for cicada nymphs occurred

979   extensively in the larch plantations (Chapter 2 and 3), their digging may have strongly affected

980   tree growth and regeneration in the plantations. A recent study showed that many native tree

981   saplings established in larch plantations at the study site, and thus proposed their potential role

982   on the establishment of naturally regenerating forests (Suzuki et al., 2021). Brown bears may

983 hinder natural forest regeneration in larch plantations by overturning seedlings and limiting

984 water and nitrogen uptake by these saplings. Additionally, brown bears may also affect forest

985 regeneration in plantations in other ways I did not address in this study. For example, bears may

986 disperse seeds of wild cherry, which is an important summer food for bears (Koike et al., 2008),

987 into the plantation if they deposit scats containing the seeds while digging for cicada nymphs.

988 Further investigation of their roles on tree growth and establishment is required to develop the

989 understanding of their contribution to natural forest regeneration in the plantations.

990

Chapter 6 Brown bear digging decreases radial growth of canopy trees: an ecological consequence of animal behavior change in a human- modified ecosystem

Abstract

A large number of studies has revealed loss of ecological functions of animals on human-modified ecosystems through population decline. However, there is little attention to ecological consequences of animal behavior changes in the human- modified ecosystems even though behaviourally mediated effects can modulate numerous ecosystem function as well as density-mediated effects. In the SWH, cicada emergence density was significantly higher in conifer plantations than in natural mixed forests, implying that the creation of forest plantations was a driver generating a novel behavior of brown bears via increase in local densities of cicadas. In this chapter, I tested the effects of brown bear digging on radial growth of Japanese larches (*Larix kaempferi*) via changes in soil nutrient conditions. I found their digging decreased fine root biomass of larch soil water and nitrogen availability. Tree ring data suggested digging negatively affected radial growth of larches and the effect became larger with tree diameter. Brown bear digging negatively affected needle nitrogen content, but not carbon isotope ratios ($\delta^{13}C$), an index of water stress of trees. The results indicated brown bear digging decreased

74

1008   radial growth of larch trees through reduction in photosynthetic ability due to limiting soil

1009   nitrogen uptake. This digging effect is a novel ecosystem function of brown bears in the study

1010   area through their behavior change due to the creation of plantation (Chapter 3). Animals that

1011   persist, with changing in behavior themselves, under human- modified world no longer play the

1012   same ecological roles on the pristine ecosystems. We may need to give more consideration to

1013   behavior change for understanding of the ecological role of animals in human-modified

1014   ecosystem.

1015

Introduction

1016

1017   Human activities have now reached to everywhere on our planet and, therefore, most living

1018   organisms spend their lives in human- dominated ecosystems (Hobbs et al. 2009; Barnosky et

1019   al. 2012). Although environmental change has been a universal phenomenon during the life of

1020   earth, the rate and magnitude have been exceedingly accelerated in the Anthropocene. It is

1021   emergent to understand how wildlife respond to human activities and its ecological

1022   consequences at population, community, and ecosystem levels (Sih et al. 2011, Johnson et al.

1023   2017).

1024   There is a growing body of literature documenting changes in animal behavior and

1025   population density (Estes et al., 2011; Tucker et al., 2018; Wilson et al., 2020; Wong &

1026   Candolin, 2015), and consequently species interaction and ecosystem functions in human-

1027   modified ecosystems. A large number of studies has revealed loss of functions of ecologically

1028   important species such as apex predators on human- dominated ecosystems through population

1029   decline (Estes et al., 2011; Estes & Duggins, 1995). For example, extirpation and population

1030   decline of apex predators in anthropogenically transformed ecosystems have caused functional

1031   loss of trophic cascades that modulate ecosystem functions such as primary productivity, food

1032   web dynamics, and nutrient cycling (Dirzo et al., 2014; Estes et al., 2011; Ripple et al., 2014).

76

1033   However, there is little attention to ecological consequences of animal behavior changes in the

1034   human- modified ecosystems (Wilson et al. 2020) even though behaviourally mediated effects

1035   can modulate numerous ecosystem function as well as density- mediated effects (Schmitz et al.

1036   2004, Trussell et al. 2006, Kujiper et al. 2016). Elucidating ecosystem consequences of animal

1037   behavior changes is particularly useful to conservation biologists and ecosystem managers for

1038   predicting the anthropogenetic impacts on entire ecosystems (Candolin and Wong 2012, Wilson

1039   et al. 2020).

1040   Despite the magnitude of behavior changes, the cascading ecological effects will finally

1041   depend on the ecological importance of a focal behavior. Behavior of some important groups

1042   such as ecosystem engineers or keystone species may be remarkable for this research field

1043   because they have more crucial roles for ecosystem functions than other species (Jones et al.

1044   1997, Power et al. 1996). Therefore, we should focus on specific species with or behavior

1045   underlying ecologically important functions when detecting the ecological consequences of

1046   behavior change (Wilson et al. 2020).

1047   Large mammals such as the brown bear (*Ursus arctos*), which have strong impacts on

1048   ecosystem functions, including ecosystem engineering (Barry et al., 2019; Ripple et al., 2014;

1049   Tardiff & Stanford, 1998; Villar & Medici, 2021), have often innovated novel food resources in

1050   human- modified landscapes (Fleming & Bateman, 2018; Moss et al., 2016; Penteriani et al.,

1051   2018). The exploitation of novel foods may result in novel ecological functions of large

1052   mammals via change in foraging behavior. For example, in the Shiretoko world heritage

1053   (hereafter: SWH) site, northern Japan, brown bears have recently dug for cicada nymphs

1054   (*Lyristes bihamatus*) in plantations of Japanese larches (*Larix kaempferi*) (Chapter 2). Plantation

1055   is a typical human- modified ecosystem in forests (Lindenmayer et al., 2008). In the SWH,

1056   cicada emergence density was significantly higher in conifer plantations than in natural mixed

1057   forests, implying that the creation of forest plantations was a driver generating a novel behavior

1058   of brown bears via increase in local densities of cicadas (Chapter 2 and 3). Given that soil

1059   disturbance by mammalian digging is assumed to be among the most widespread and important

1060   ecosystem engineering (Coggan et al., 2018; Mallen-Cooper et al., 2019; Reichman &

1061   Seabloom, 2002), this behavioral change may lead to emergence of a novel ecological effect

1062   through soil disturbance. Here, I show empirical evidence on emergence of an ecosystem

1063   engineering effect caused by a novel behavior of brown bears on a plantation forest.

1064   In this study, I tested the effects of brown bear digging on canopy tree growth. Canopy

1065   trees are a sort of the foundation species, which is defined as organisms that control biodiversity

1066   of associated species and modulate important ecosystem processes in forest ecosystems (Ellison

1067 et al., 2005; Enquist et al., 2020). Elucidating the factors affecting canopy tree growth can gain

1068 an insight into management of ecosystem services. Moreover, tree growth plays a key role in

1069 forest ecosystem services such as net primary production, wood production, and carbon fixation

1070 (Bennett et al., 2009; Blattert et al., 2017; Lasky et al., 2014). Therefore, testing the effects of

1071 brown bear digging on canopy tree growth is important for in-depth understanding of ecosystem

1072 consequence of the behavior change on human- modified ecosystems.

1073 Brown bear digging may affect nutrient status of canopy trees via a direct and an indirect

1074 pathways: soil disturbance by digging can (1) decrease root biomass and nutrient uptake by

1075 mechanical root damage [direct effect], (2) decrease soil nutrients such as water contents and

1076 inorganic nitrogen concentration (Chapter 5) [indirect effect]. Since inorganic nitrogen

1077 concentration is usually the highest in the surface organic layer (Laverman et al., 2000), mixing

1078 of soil by digging is a possible mechanism decreasing organic nitrogen contents and thereby

1079 inorganic nitrogen concentration (Kurek et al., 2014). Nutrient deficiency of trees due to brown

1080 bear digging may subsequently decrease foliar photosynthesis rate, which is strongly

1081 determined by soil nutrient availability (Watanabe et al., 2011), and thereby their growth (Shen

1082 et al., 2014). Thus, I predicted brown bear digging decreased canopy tree growth by nutrient

1083 deficiency due to reduction in nutrient uptake from soil.

1084 **Materials and methods**

1085 *Plot preparation*

1086   In June 2019, I selected 100 m^2 five larch stands that have been extensively dug by bears

1087 since 2000, based on field records by wildlife managers. I checked fresh trace of bear digging

1088 and distinct bare soil in the dug plots. 100m^2 five larch stands covered with dense dwarf

1089 bamboo nearby each dug plot were selected as the undug plots. I checked the presence of thick

1090 litter and humus layer at the surface soil in the undug plots to confirm no occurrence of digging

1091 activity. Based on the field record, I determined the beginning year of occurrence of brown bear

1092 digging in the dug plots. I measured diameter at breast height (DBH > 2 cm) of all trees

1093 emerging within each plot. I then calculated basal area density as the sum of the basal areas of

1094 all trees within the plot divided by the plot area (100m^2). Basal area of each tree was calculated

1095 using DBH data (i.e., basal area (m^2/ 100m^2) = $\pi \times$ (DBH/2)^2). Detailed plot information was

1096 shown in Table 1.

1097

1098 *Data collection*

1099   I compared soil nutrients, several physiological traits of larch needles with regard to

1100 photosynthesis rate and water stress levels, and radial tree growth patterns between the dug and

1101 undug plots. For mid-August 2019, four pits with 45 cm depth were excavated in each plot to

1102 collect soil samples from various depth levels. I regarded four depth classes of the soil as 0-10,

1103 10-20, 20-30, and 30-40 cm depth. Using a soil core sampler, I collected three soil samples at

1104 each soil depth level from the side of the pit after removal of the litter layer. The reason why I

1105 collected three soil samples with the same depth level from pit is minimization of variation in

1106 soil properties among each sidewall of a pit. The soil samples were sieved with a 2 mm sieve to

1107 homogenize the soil and remove gravel, fine roots and coarse woody debris. Soil moisture

1108 contents were measured drying soil after sieving at 105 °C for 24 h. For total nitrogen and

1109 carbon concentrations, approximately 20 mg of dry soil was analyzed by a CN analyzer (NC-

1110 900; Sumitomo, Osaka, Japan). For inorganic nitrogen availability, 6 g of fresh soil was

1111 weighed into plastic bottles and extracted with 27.5 ml 1 M KCl for 1 h. Using an auto-analyzer

1112 (AACS-4, BL-TEC, Inc., Japan), ammonium and nitrate nitrogen was analyzed by indophenol

1113 blue absorptiometry and naphthyl ethylenediamine dihydrochloride spectrophotometry,

1114 respectively. The total values of the nitrogen concentration in nitrate and ammonium nitrogen

1115 were regarded as the total nitrogen availability. Dry biomass of fine root was evaluated as dry

1116 weight of fine root (diameter < 2 mm) separated through sieving process. I determined fine root

1117 with light color and high elasticity as living root. Because fine roots of larches show darker than

1118 those of dwarf bamboo, species identification of fine roots could be easily conducted. I

81

1119   separately measured fine root biomass of both species.

1120   For August 2019, ten canopy larch trees ranging of DBH from 20 cm to 40 cm were

1121   selected from each survey plots. The reason for size variations in target trees is to test size

1122   dependent effects of brown bear digging on tree growth. I visually confirmed that the selected

1123   trees had no serious damage from other animals such as bark stripping by voles (*Clethrionomys*

1124   *rufocanus*) and sika deer (*Cervus nippon*), and wood and leaf damages by insect herbivores. To

1125   quantify annual growth rates of larch trees, I collected increment core samples from all selected

1126   trees (N=50 from both dug and undug plots). A core sample was taken at breast height from the

1127   trunk of each tree using an increment borer (5 mm diameter). After polishing the surface of

1128   cores using sandpapers, ring widths were visually measured to the nearest 0.5 mm. To

1129   standardize the ring width values, I multiplied each ring width by a ratio of tree radius to core

1130   length.

1131   By using a pole with 15 m height on 3 m ladder, one canopy branch from each tree at about

1132   15 m height, which were shined on a strong sunlight, were collected from five of the ten

1133   selected trees (N=30 with 24 < DBH < 35 cm). The reason for the difference in range of tree

1134   diameter between core and needle samples is that I determined trees with DBH < 24 cm as

1135   shaded individuals based on visually checking from the ground and trees with DBH > 35 cm

82

1136 couldn't be reached until canopy branches that shined on enough sunlight. As needle traits are

1137 strongly affected by light intensity (Barnosky et al., 2012; Liu et al., 2020), I measured needle

1138 traits from trees that can be assumed to grow under the same light environment among them.

1139 Since larch has two branch types, that is long shoot and fascicle, with different leaf traits (e.g.

1140 needle leaves on long shoot have higher nitrogen and toxic diterpenoid acid contents) (Johns et

1141 al., 2012), I collected 50 needles, without attack of pests, attaching on each long shoot and

1142 fascicle from each sampled branch. Needles were immediately placed into plastic bag, frozen

1143 within 8 hours after collection, and kept frozen until laboratory processing. I scanned 50 fresh

1144 needles of each tree and measured surface leaf area using LIA 32 software

1145 (https://www.agr.nagoya-u.ac.jp/~shinkan/LIA32/). These needles were dried at 60 ℃ for

1146 48 h and weighed to calculate leaf mass per area (LMA), which is often used as an index of

1147 water stress of plants and has a negative correlation with soil water availability (de la Riva et al.,

1148 2016). The dried needles were smashed to prepare for subsequent chemical analysis. About 2

1149 mg smashed needle samples were wrapped in tin capsules to analyze carbon and nitrogen

1150 contents and carbon isotopic ratios. Leaf nitrogen content represents leaf photosynthesis

1151 capacity because having a positive correlation with photosynthesis rate (Reich et al., 1995).

1152 Stable carbon isotope ratio of leaf is an index of tree water stress because as water stress levels

1153 increase, trees must increase water use efficiency to more efficiently use water resource (Hanba

83

1154 et al., 1999). Chemical analysis was conducted at the Faculty of Environmental Earth Science,

1155 Hokkaido University, Japan, using a continuous-flow carrier-gas system (ConFlo) with an

1156 isotope ratio mass spectrometer (Delta V, Thermo Finnigan, Bremen, Germany) and an

1157 elemental analyzer (Flash EA 1112). Carbon isotope ratios (δ^{13}C) were expressed as:

1158
$$\delta^{13}C = \left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \times 1000 \ (‰)$$

1159 where R_{sample} and R_{standard} are the molar ratios of heavy to light isotopes (^{13}C/^{12}C) of the samples

1160 and standards, respectively. The standards were Vienna PeeDee Belemnite (V-PDB). Needle

1161 nitrogen per area [(Narea (g/m^2)] was calculated by multiplying LMA by Nmass (mg/g).

1162 Nitrogen content per one needle (N-needle) was calculated by multiplying Narea by needle area.

1163 *Data analysis*

1164 　　Linear mixed models (LMMs) with plot as a random factor were performed to compare

1165 soil properties between the dug and undug soil per each soil depth. Given that dwarf bamboo

1166 might affect canopy tree growth through belowground competition for soil available nitrogen, I

1167 should consider the effects of this understory plant on soil nitrogen availability. Accordingly, I

1168 tested the relative importance of fine root biomass of these two species and brown bear digging

1169 for soil nitrogen availability (i.e. inorganic nitrogen concentration) and water content using a

1170 piecewise structural equation model with plot as a random factor (Lefcheck, 2016). SEM was

1171   conducted soil samples at 0-10 cm depth because fine root of both species concentrate in the

1172   surface soil. For piecewise SEM, the goodness-of-fit of the causal model was tested using

1173   Fisher's C and the model is determined an appropriate fit when this value has $p > 0.05$

1174   (Lefcheck, 2016). I built two hypothetical SEM model for soil nitrogen and water availabilities

1175   as follows. Inorganic nitrogen concentration is affected by organic nitrogen content, bear

1176   digging, fine root biomass of dwarf bamboos and larches. Inorganic nitrogen is produced from

1177   organic nitrogen via mineralization. Bear digging affects fine root biomass of larches and

1178   organic nitrogen content (Chapter 5). Bear digging affects fine root biomass of larches. If there

1179   is no significant effect of fine root biomass of dwarf bamboo on soil nitrogen and water

1180   availabilities in the path model, belowground competition with dwarf bamboo for soil nutrients

1181   is thought to be ignored in my study because this plant can only affect canopy tree growth via

1182   changes in soil nutrient availability (Takahashi et al., 2003). All statistical analyses for soil

1183   properties were conducted in R version 3.5.1 (RCore Team2018).

1184   LMMs with plot as a random factor were used to analyze needle traits. Each needle trait

1185   was regarded as a response variable. Tree diameter, brown bear digging (binary), and these

1186   interaction term were regarded as explanatory variables because needle traits generally have a

1187   strong correlation with tree diameter (Liu et al., 2020). I separately analyzed needle traits on

1188 long shoots and fascicles.

1189   Based on the evidence that brown bear have been observed digging for cicada nymphs

1190 since 2000 in the study site (Chapter 2), first, I defined annual tree rings before (1980~ 1999)

1191 and after (2000 ~ 2018) the beginning of brown bear digging. Next, I divided the data before the

1192 beginning of brown bear digging into 1980~1989 (period I) and 1990~1999 (period II) because

1193 the former was the initial growth stage for larches and thus radial growth rate at this period was

1194 significantly higher than the latter. To align the same number of annual ring width data among

1195 the periods, I also categorized the data after the beginning of brown bear digging into

1196 2000~2009 (period III) and 2010~2018 (period IV). I separately analyzed tree ring widths per

1197 each period and compared between trees in the dug and undug plots using LMMs with tree

1198 individual as a random factor. Response variable was defined as annual ring width (mm). Tree

1199 diameter and brown bear digging were included in the model as explanatory variables because

1200 radial growth rates are higher in large trees than those in small trees. To test size-dependent

1201 digging effects on tree growth, I introduced an interaction term of diameter and digging into the

1202 model. I predicted that annual ring widths of larches in the dug plots are lower than those in the

1203 undug plots during period III and IV whereas there is no significant difference in annual ring

1204 widths of trees between the dug and undug plots during period I and II. All statistical analysis

1205   for needle traits and annual ring width were performed in JMP Pro ver. 16 (SAS Institute).

1206

1207   *Brown bear digging for cicada nymphs*

1208   The SWH site has one of the highest densities of brown bears in the world (Shimozuru et

1209   al., 2020). Since about 2000, brown bears have been observed digging for cicada nymphs in the

1210   study site (Chapter 2). Bears exclusively feed on the final instar nymphs that stay in shallow soil

1211   because the nymphs are highly nutritious, and bears can easily dig for them. Brown bears have

1212   dug for the final instar nymphs until the end of cicada emergence, from late May to late July

1213   (Tomita, 2021). The proportion of cicada nymphs in bear diet during summer was estimated at

1214   14.3 % (Chapter 2). Camera traps revealed that eleven bears (two sub-adults, two solitary

1215   female adults, and three females accompanied by cub(s)) and eleven bears (one adult male, one

1216   sub-adult, two solitary adult females, and three females with cub(s)) were observed digging for

1217   cicada nymphs in 2018 and 2019, respectively (Tomita, 2021; Chapter 2). Because the

1218   occurrence frequency of the digging is the highest in larch plantations across other plantation

1219   forests (Chapter 3), I tested the effects of brown bear digging on growth of canopy larch trees.

1220   Brown bears digging for cicada nymphs occur in the larch plantations covered with understory

1221   dwarf bamboo (*Sasa kurilensis*) more extensive that in those not covered with dwarf bamboo

1222   (Chapter 4). Understory dwarf bamboo could reduce their digging activity by interfering with

1223   digging behavior due to their hard and dense rhizomes at surface soil, and decreasing cicada

1224   density (Chapter 4). Thus, I set the survey plots that were dug and undug by brown bears as the

1225 larch plantations covered with no dwarf bamboo and dwarf bamboo, respectively. The dug plots

1226 were confirmed not only the absence of dwarf bamboo, but also the evidence of digging by

1227 bears .

1228 **Results**

1229 *Soil properties*

1230 In 0-10 cm, water contents, organic carbon and nitrogen contents, ammonium and total

1231 inorganic nitrogen concentrations and fine root biomass density in soil samples from the dug

1232 plots were significantly lower than those from the undug plots (LMM, $p < 0.01$; Fig. 1). In 10-

1233 20 cm soil layer, fine root biomass density in the dug soil was marginally significantly lower

1234 than that in the undug soil (LMM, $p = 0.06$, Fig.1A). In 10-20, 20-30 and 30-40 cm, nitrate

1235 nitrogen concentration in the dug soil was significantly higher than that in the undug soil

1236 (LMM, $p < 0.01$; Fig. 1F) while there was no significant difference in nitrate nitrogen

1237 concentration between dug and undug soil in 0-10 cm layer (LMM. $p = 0.61$; Fig. 1F). The

1238 causal network by SEM (Fig.2) was satisfied by the goodness-of-fit criteria (Fisher's C = 11.143

1239 $p = 0.084$). Digging have an indirect negative effect on soil inorganic nitrogen concentration via

1240 reduction in organic nitrogen contents (Fig.2). Fine root biomass of dwarf bamboo didn't affect

1241 soil inorganic nitrogen concentration (Fig.2), indicating belowground competition with dwarf

89

1242   bamboo for soil nutrients is assumed to be ignored in this study because understory dwarf

1243   bamboo can only affect canopy tree growth via changes in soil properties. In the undug plots

1244   that were covered with dense dwarf bamboo, there were no significant correlation between fine

1245   root biomass of this plant and soil inorganic nitrogen concentration (LMMs, $p > 0.2$).
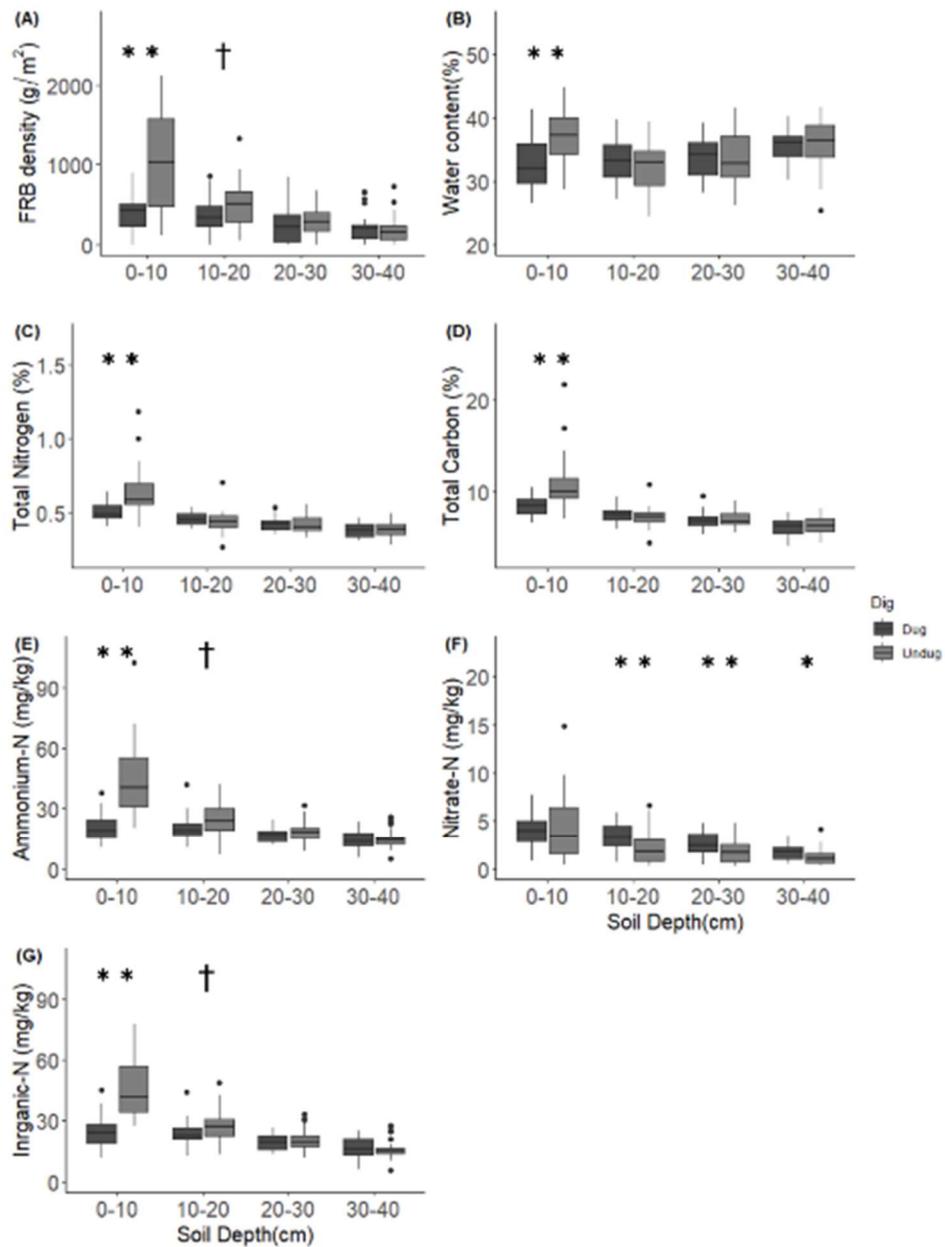
1246

Figure 1 Comparison of fine root biomass (A) and soil properties (B- G) between the undug (dark grey) and undug plots (light grey) by each soil layer (0- 10, 10-20, 20-30, and 30- 40 cm). (B) water contents, (C) total organic nitrogen (%), (D) total organic carbon (%), (E) ammonium (NH_4^+), (F) nitrate (NO_3^-), (G) inorganic nitrogen (= $NH_4^+ + NO_3^-$). †, *, and ** indicate p = 0.06, p < 0.05, and p < 0.01.

1247
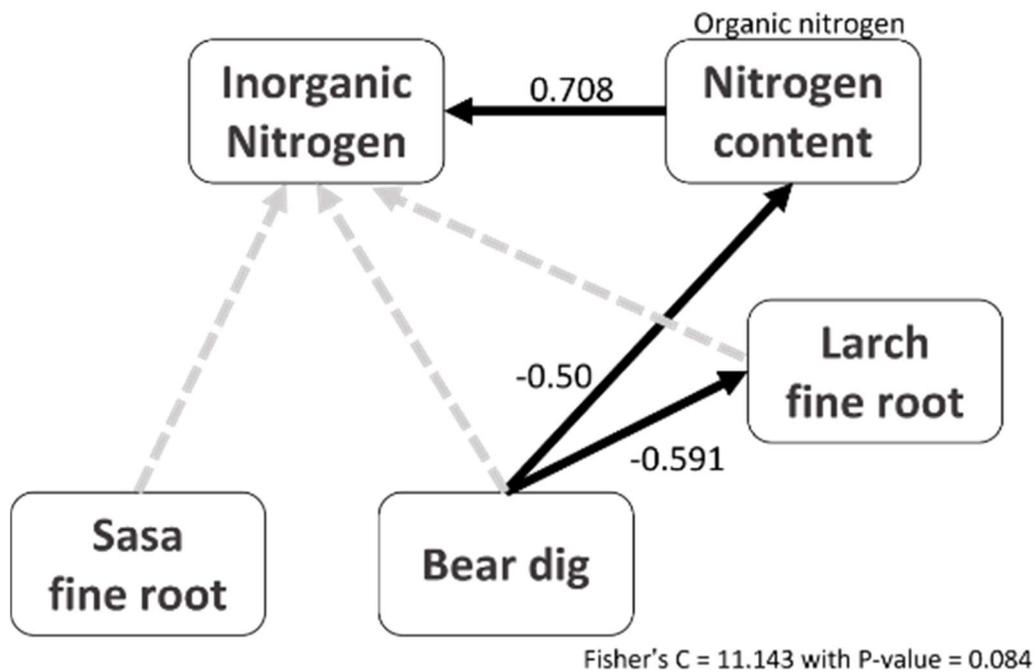
Figure 2 A piecewise structural equation model showing the causal relationships among brown bear digging, fine root biomass of larches *Larix kaempferi* and dwarf bamboo Sasa kurilensis, soil organic nitrogen, soil inorganic nitrogen (= NH4 + + NO3 −). Black solid lines are significant pathways (p < 0.05). Dashed grey lines are no significant pathways (p > 0.05).

1249

1250 *Needle traits*

1251   Tree diameter had a significant positive effect on LMA of fascicle needles and $\delta^{13}C$

1252 (Fig.3A, H). There were no significant effects of digging on all needle traits of long shoots

1253 (Table 2). However, for long shoot needles, the estimated coefficients of interaction between

1254 tree diameter and brown bear digging were significant negative values for needle area, Nmass,

1255 N-needle, and CN ratio (LMMs, p<0.05, Fig.3 C, D, F, G). For fascicle needles, brown bear

1256 digging negatively affected needle mass and area, Narea and N-needle (LMM, p<0.05, Fig.3 B,

1257 C, E, F). The estimated coefficients of interaction between tree diameter and digging were

1258 significant negative values for Nmass and CN ratio (LMMs, p<0.05, Fig.3 G, D). For both

1259 needle types, the interaction had marginally a negative effect on Narea (LMMs, p<0.06, Fig. 3).

92
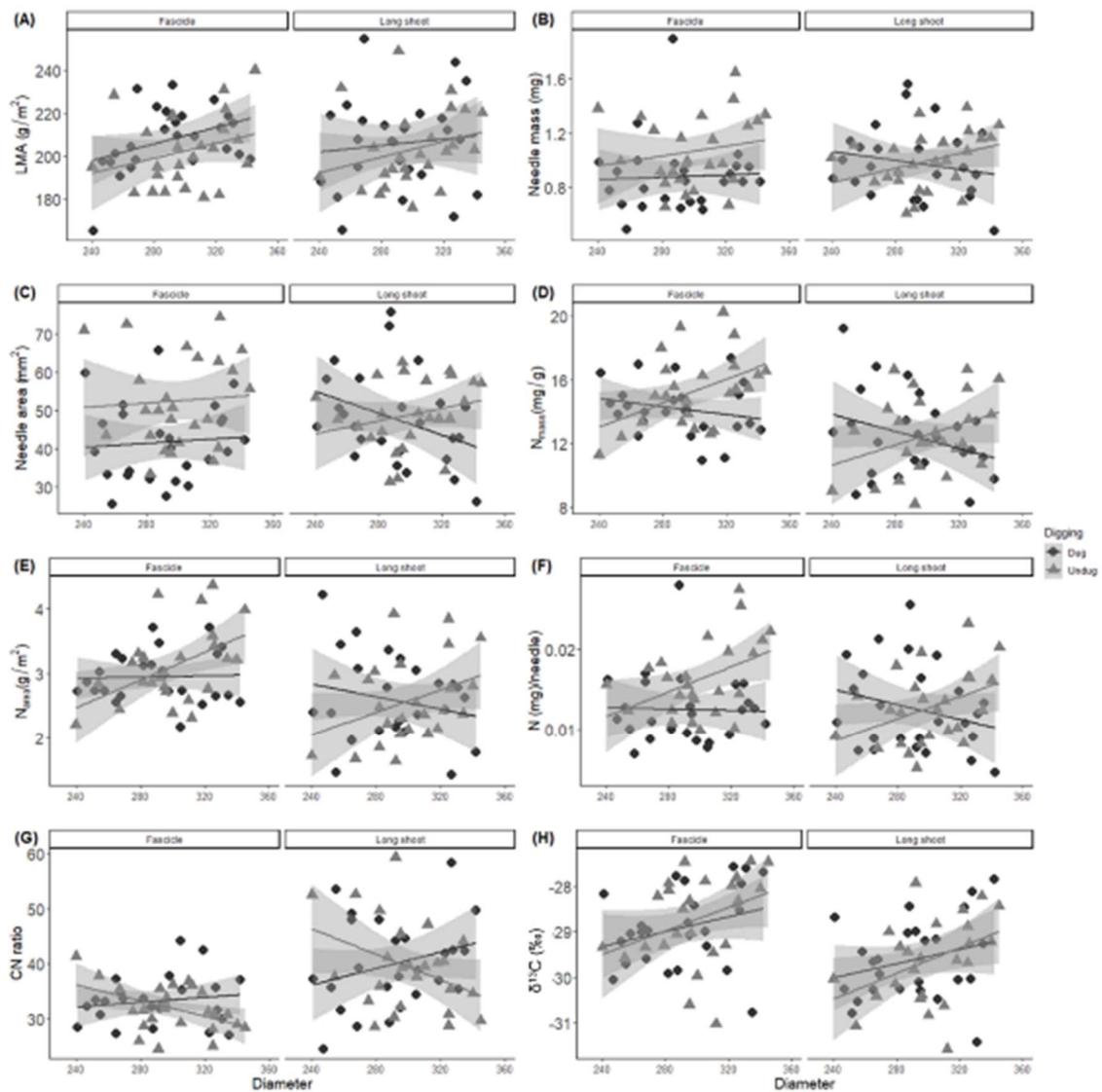
1260

Figure 3 The relationships between tree diameter (mm) and needle traits of larches *Larix kaempferi* by individuals from the dug (black circles, black lines) and undug (grey circles, grey lines) plots. Lines indicate predicted slope from linear models with 95 % CI shaded. Left and right panels are fascicle and long shoot needles, respectively. (A) leaf mass per area (mg/ cm^2), (B) dry mass per unit needle (mg), (C) Surface area per unit needle (mm^2), (D) needle nitrogen content per unit dry weight (mg/ g), (E) needle nitrogen content per unit surface area (g/m^2), (F) nitrogen content (mg) per unit needle, (G) the ratio of carbon to nitrogen per unit needle, (H) delta ^{13}C values (‰) of needle.

1261

1262 *Tree radial growth*

1263 In period I (1980~1989) and II (1990~1999), there were no significant effects of brown bear

1264 digging on annual ring width of larches (LMMs, p>0.05, Table 3, Fig.4 A, B). On the other

1265 hand, there were the negative effects of their digging on annual ring width in period III

1266 (2000~2009) and IV (2010~ 2018) (LMMs, p<0.01, Fig.4 C, D). In period II, III and IV, there

1267 were the positive effects of tree diameter on annual ring width (LMMs, p<0.01, Fig.4 B, C, D).

1268 Across all periods, there was no significant interaction effect on annual ring width (Table 3).

1269

94
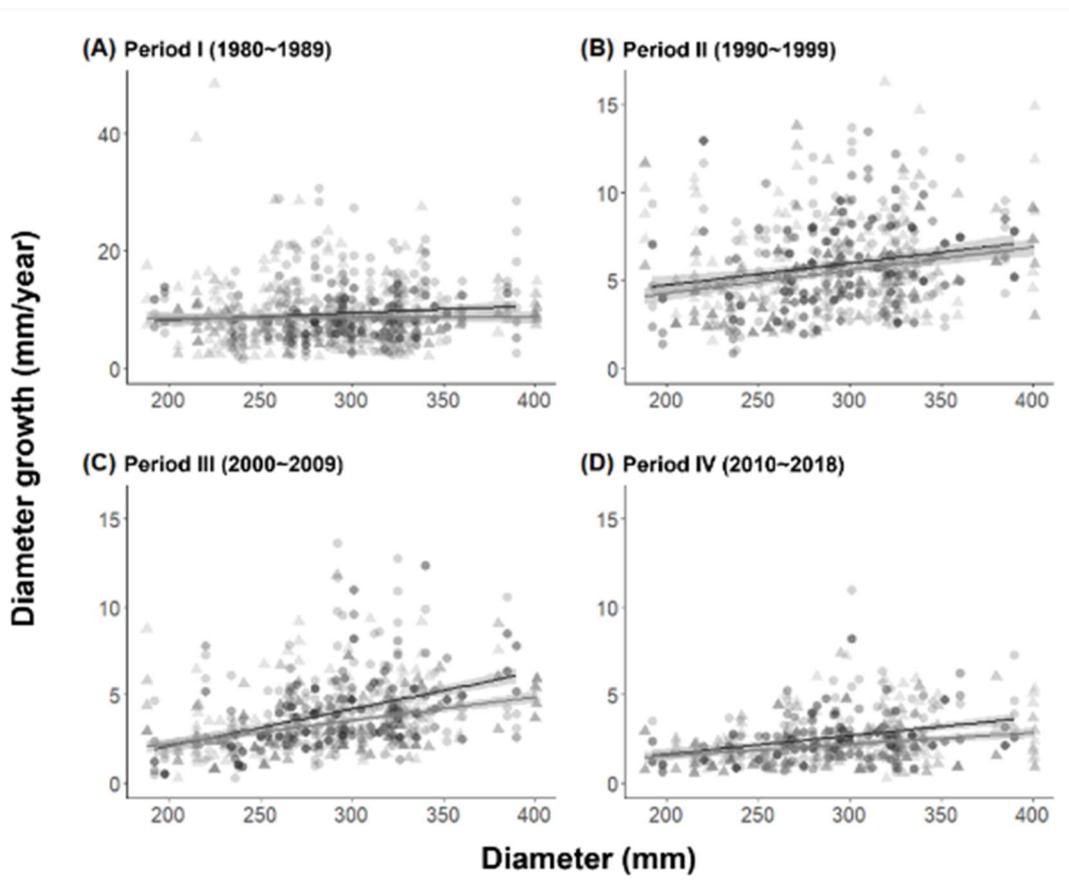
Figure 5 (one page back) The relationships between tree diameter (mm) and annual ring width (mm / year) of larches *Larix kaempferi* by individuals from the dug (black circles, black lines) and undug (grey circles, grey lines) plots. Lines indicate predicted slope from linear models with 95 % CI shaded. (A) period I (1980~1989) and (B) period II (1990~1999) show the radial growth of larches before the beginning of brown bear digging for cicada nymphs. (C) period III (2000~2009) and (D) period IV (2010~2018) show the radial growth after the beginning of brown bear digging.

1270

1271 **Discussion**

1272   My results indicate brown bear digging decreased radial growth of larch trees possibly

1273 most probably through reduction in photosynthetic ability due to limiting soil nutrient

1274 availability and nutrient uptake (i.e. decreasing fine root biomass). Radial growth and fine root

1275 biomass of trees occupy aboveground and belowground net primary productivity in forests,

1276 respectively. Thus, brown bear digging is likely to contribute to decreasing net primary

1277 productivity in the plantation forest of the study site. Importantly, this is a novel ecosystem

1278 function of brown bears in the study area through their behavior change due to the creation of

1279 plantation (Chapter 3). Animal behavior changes in the human- modified ecosystems have been

1280 well documented; however, their ecosystem consequences are less unknown (Wilson et al.,

1281 2020). This study also emphasizes the importance of the behavior underlying ecosystem

1282 engineering, such as digging behavior for understanding ecosystem consequences of animal

1283 behavior changes in the human- modified ecosystems.

95

1284   I found that brown bear digging can affect soil properties and fine root biomass only at the

1285   surface ground (0 ~ 10 cm). The reason is that bears just need to dig up the shallow soil to

1286   acquire cicada nymphs because they dig for only the final instar nymphs of cicadas which stay

1287   at shallow soil for the emergence (Chapter 2). Chapter 5 proposed a potential mechanism of the

1288   negative effect of digging on nitrogen availability at surface soil that mixing of organic and

1289   mineral soil by digging decreases organic nitrogen content and thereby inorganic nitrogen

1290   concentration. If this mechanism dominates, nitrogen concentrations at mineral soil (e.g. 10 ~

1291   20 cm) in the dug plots is higher than those in the undug plots. Two possible mechanisms

1292   without soil mixing are thought to explain this pattern. First, the negative effect of organic

1293   nitrogen content at surface soil may be able to be explained by removal of organic layer through

1294   accidental ingestion of soil when bears dig for cicadas. Materials that were assumed to derive

1295   from organic soil layer, including litter and soil were contained about 8 % in bear's scat contents

1296   in the study area (Chapter 2). Second, destruction of organic soil layer due to bear's digging

1297   might reduce microbial and soil micro-invertebrate (e.g. Oribatid mites and Collembolas)

1298   activities associating with nitrogen mineralization. Since their activities for soil nitrogen

1299   mineralization are the most efficient in organic soil layer (Persson & Wirén, 1995), brown bear

1300   digging may decrease inorganic nitrogen concentration via reduction in their activities in surface

1301   soil. In fact, the surface soil dug by bears have lower nitrogen mineralization rate under

1302 laboratory incubation than soil that wasn't dug, indicating that microbial activity itself declined

1303 by brown bear digging (Chapter 5). Although brown bears may increase nitrogen availability in

1304 the surface soil by depositing dung and urine during digging for cicada nymphs (Tardiff &

1305 Stanford, 1998), my results suggest that their excrements seem to have no effects on soil

1306 nutrient, or digging effects exceeded these effects.

1307 My results indicate that brown digging decreased nitrogen content per needle area (Narea)

1308 through reduction in root nitrogen uptake by negative effects on fine root biomass and soil

1309 nitrogen availability, and consequently negatively affected radial growth of larches. Whereas

1310 brown bear digging negatively affected Narea of fascicle needles that were strongly associated

1311 with photosynthetic ability, such needle traits of long shoots were not affected by their digging

1312 itself and rather likely to be affected interactively by digging and tree diameter. Importantly,

1313 larch has much more fascicle than long shoot needles (Fellner et al., 2016), indicating that the

1314 former play more important role in term of photosynthesis than the latter. However, the results

1315 of LMA and $\delta^{13}C$ values indicate that they did not suffer from drought stress by brown bear

1316 digging through limiting water use despite reduction in fine root biomass and soil water

1317 availability by digging. The negative effect of brown bear digging on larch growth via decrease

1318 in soil water availability may be weaker than this effect via decrease in soil nitrogen availability.

1319　Whereas soil nitrogen availability was the highest in the surface soil (i.e. 0-10 cm depth) where

1320　is the most susceptible soil layer against digging, water availability in the deeper soil (i.e. 30-40

1321　cm) did not differ from that in the shallow soil (Fig. 1 C, D). Larches may be able to

1322　compensate water depletion in the surface soil by enhancing root water uptake in the deep soil

1323　even though there is lower fine root biomass in the deep soil than that in the surface soil. In fact,

1324　other conifer species, including *P. massoniana, P. elliottii and Cunninghamia lanceolata*,

1325　consumed deeper soil water during dry season than during wet season (Yang et al., 2015). Thus,

1326　it is also possible that soil water below 40 cm depth that I failed to evaluate play an important

1327　role as water reservoir for larches under water stress condition.

1328　　　Interestingly, in term of needle traits, trees with large DBH were likely to be more

1329　susceptible to brown bear digging than those with small DBH (Fig. 3), even though the sampled

1330　needles were assumed to be exposed by the same light environment across all diameter range of

1331　the selected trees. Tree responses to soil disturbance by brown bear digging may vary depending

1332　on tree diameter. Since larger trees need to utilize a larger amount of soil nitrogen for

1333　maintaining photosynthetic activities than smaller trees, larger trees may be more susceptible to

1334　nitrogen deficiency due to soil disturbance by digging than smaller ones. Under an assumption

1335　that needle biomass did not differ among larches in the dug and undug plots, larger trees allocate

1336   a few amount of nitrogen to each needle (Fig.3 F). However, for radial growth, there was no

1337   significant interaction effect of brown bear digging and tree diameter. Since photosynthetic

1338   nitrogen-use efficiency, the rate of photosynthesis per unit leaf nitrogen content, decrease as tree

1339   diameter become larger (Nabeshima & Hiura, 2004), the decreasing rate of photosynthesis may

1340   be lower in large trees than in small trees as needle nitrogen content decreases. Therefore, I

1341   speculate brown bear digging negatively affected needle nitrogen content of large trees more

1342   than that of small trees, but its cascading effect on photosynthesis was dampened due to size

1343   dependency of photosynthetic nitrogen-use efficiency.

1344   Taking together with my previous studies, brown bears innovated a novel food resource

1345   (i.e. cicadas) as a response to the creation of plantation (Chapter 2 and 3), and thereby have had

1346   a novel functional role as ecosystem engineer in the plantations. In human- modified

1347   landscapes, animals have increasingly made innovation to exploit novel resources as behavioral

1348   adaptation on the novel environments (Fehlmann et al., 2020; Klump et al., 2021; Valentine et

1349   al., 2018). If the innovated behavior was a mediator of important ecological functions such as

1350   ecosystem engineering and seed dispersal, behavior innovation may cause cascading ecosystem

1351   impacts, as is the case of brown bear digging for cicada nymphs in my study site. Large-bodied,

1352   long-lived mammals, including bears tend to be more innovative due to larger brain size

1353 (Deecke, 2012; Lefebvre et al., 2004; Roth & Dicke, 2005). Such animals often play important

1354 ecosystem roles such as predators and ecosystem engineers (Barry et al., 2019; Davies & Asner,

1355 2019; Hyvarinen et al., 2021; Ripple et al., 2014). Therefore, large- bodied mammals may be an

1356 important mediator linking behavior change and its ecosystem consequences under a human-

1357 modified world.

1358 **Conclusions**

1359 　　In the Anthropocene, almost all of animals are facing ongoing rapid environmental changes

1360 and thereby behavior changes as a response to environmental changes have been increasingly

1361 given much attention from basic and applied ecologists (Candolin & Wong, 2012). As

1362 anthropogenic ecosystem modifications will have growing impacts on animal behavior, the

1363 likelihood of cascading ecosystem consequences and the necessity for its understandings and

1364 predictions will increase despite a lack of such evidence (Palkovacs & Dalton, 2012; Wilson et

1365 al., 2020). Moreover, given elucidating the ecosystem roles of animals is important for

1366 justification for their conservation and management strategies (Somaweera et al., 2020), we

1367 would need to reconsider ecological roles of wildlife in human-modified ecosystems. In my

1368 case that brown bear digging decreased tree growth rate, they might have had a negative impact

1369 on wood production in the plantation. Accordingly, animal behavior changes due to

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1370   anthropogenic habitat changes could yield their novel ecosystem services or disservices.

1371   Animals that persist, with changing in behavior themselves, under human- modified world no

1372   longer play the same ecological roles on the pristine ecosystems. We may need to give more

1373   consideration to behavior change for understanding of the ecological role of animals in human-

1374   modified ecosystem.

1375

1376 **Table 1** Stand information of the dug and undug plots

Plot type	Tree density (trees per 100 m^2 plot)	Average diameter at breast height (mm)	Basal area (m^2 per 100 m^2 plot)	Understory
Dug (N=5)	23.60±2.41	286.74±13.90	0.160±0.029	No
Undug (N=5)	24.00±2.24	284.69±8.71	0.158±0.017	Dwarf bamboo

1377

Table 2 Summary of linear mixed models for each needle traits of fascicles and long shoots.

Tree size indicates diameter at breast height of larch trees (unit: mm)

Needle trait (response variable)	Needle part	Factors	Coefficient	Standard error	t value	p value
LMA (mg/cm^2)	Fascicles	Digging (D)	0.070	0.044	1.600	0.118
		Tree size (T)	0.002	0.001	2.260	**0.029***
		D*T	0.000	0.002	0.130	0.897
	Long shoots	D	0.035	0.056	0.620	0.537
		T	0.001	0.001	1.020	0.312
		D*T	-0.001	0.002	-0.370	0.712
Needle mass (mg)	Fascicles	D	-20.130	6.484	-3.100	**0.003****
		T	0.155	0.121	1.280	0.206
		D*T	-0.137	0.239	-0.580	0.568
	Long shoots	D	-0.985	6.849	-0.140	0.886
		T	0.053	0.127	0.420	0.677
		D*T	-0.432	0.251	-1.720	0.092
Needle area (mm^2)	Fascicles	D	-10.409	3.099	-3.360	**0.002****
		T	0.042	0.058	0.730	0.472
		D*T	-0.029	0.114	-0.260	0.798
	Long shoots	D	-1.393	2.899	-0.480	0.633
		T	-0.028	0.054	-0.530	0.601
		D*T	-0.233	0.107	-2.180	**0.034***
Nmass (mg/g)	Fascicles	D	-0.008	0.005	-1.610	0.115
		T	0.000	0.000	0.700	0.487
		D*T	0.000	0.000	-2.090	**0.042***
	Long shoots	D	-0.001	0.007	-0.160	0.877
		T	0.000	0.000	-0.120	0.901
		D*T	-0.001	0.000	-2.190	**0.034***
Narea (g/m^2)	Fascicles	D	-0.065	0.028	-2.330	**0.025***
		T	0.000	0.001	-0.860	0.397
		D*T	-0.002	0.001	-1.960	0.057
	Long shoots	D	-0.018	0.030	-0.590	0.561
		T	0.000	0.001	-0.510	0.612

		D*T	-0.002	0.001	-1.950	0.057
N-needle	Fascicles	D	-0.009	0.003	-3.160	**0.003****
		T	0.000	0.000	0.100	0.924
		D*T	0.000	0.000	-1.030	0.308
	Long shoots	D	-0.002	0.003	-0.520	0.605
		T	0.000	0.000	-0.500	0.622
		D*T	0.000	0.000	-2.270	**0.028***
CN ratio	Fascicles	D	1.190	1.134	1.050	0.300
		T	-0.020	0.021	-0.940	0.355
		D*T	0.085	0.042	2.030	**0.048***
	Long shoots	D	0.449	2.136	0.210	0.834
		T	-0.009	0.040	-0.230	0.819
		D*T	0.173	0.079	2.200	**0.033***
$\delta\ ^{13}C$	Fascicles	D	-0.086	0.261	-0.330	0.744
		T	0.012	0.005	2.420	**0.020***
		D*T	-0.007	0.010	-0.750	0.456
	Long shoots	D	0.115	0.252	0.460	0.651
		T	0.011	0.005	2.400	**0.021***
		D*T	-0.007	0.009	-0.710	0.483

1380   *: $p < 0.05$, **: $p < 0.01$ Supplement??

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1382 **Table 3** Summary of linear mixed models to test effects of brown bear digging and tree
1383 diameter on radial growth of larches (*Larix kaempferi*). Tree size indicates diameter at breast
1384 height of larch trees (unit: mm)

Period	Factors	Coefficient	Standard error	t value	p value
I (1980~1989)	Digging (D)	-1.004	0.567	-1.770	0.080
	Tree size (T)	0.006	0.006	0.970	0.337
	D*T	-0.018	0.013	-1.440	0.152
II (1990~1999)	D	-0.554	0.351	-1.580	0.118
	T	0.013	0.004	3.350	**0.001****
	D*T	-0.003	0.008	-0.330	0.743
III (2000~2009)	D	-0.620	0.234	-2.650	**0.001****
	T	0.017	0.003	6.700	**<0.0001*****
	D*T	-0.009	0.005	-1.700	0.092
IV (2010~2018)	D	-0.485	0.166	-2.920	**0.0043****
	T	0.009	0.002	5.060	**<0.0001*****
	D*T	-0.005	0.004	-1.310	0.193

1385 **:$p<0.01$, ***: $p<0.001$

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Chapter 7 General discussion

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1388   Most wildlife are living in the ecosystems that have been dramatically altered by human

1389   activities (Hobbs et al., 2009). The initial animal response to human activities is a behavior

1390   change prior to population level change (Wong and Candolin 2015). Although behavior changes

1391   may also have cascading effects to higher-level ecological processes such as species

1392   interactions, community assembly and nutrient cycling (Palkovacs and Dalton 2012, Wilson et

1393   al. 2020), there is a critical gap linking animal behavior changes to higher-order ecological

1394   processes (Wilson et al. 2020). To fill this knowledge gap, brown bear is thought to be an

1395   appropriate species for linking altered behaviors to ecological consequences in the human-

1396   modified ecosystems. In the SWH site, brown bears have been observed digging for cicada

1397   nymphs since about 2000. In this thesis, I examined the causes (Chapter 2~4) and ecosystem

1398   consequences (Chapter 5~6) of this behavior change. My general discussion consists of 3

1399   sections: (1) The causes of this behavior change, (2) An extension to ecosystem-level

1400   consequences of the behavior change, (3) Factors affecting the strength of ecosystem

1401   consequences of animal behavior change: lesson from brown bear digging for cicada nymphs.

1402

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Causes of the behavior change in brown bears

1403

1404   In my Chapter 2 and 3, I detected brown bear digging behavior toward cicada nymphs has

1405   been observed since about 2000. One possible factor causing the emergence of this behavior

1406   may be that grazing by sika deer has altered the diet of brown bears by reducing the available

1407   herbaceous plants for bears because population density of sika deer dramatically increased from

1408   the late 1980s to the early 2000s in the study area (Chapter 2). Another possible factor is the

1409   creation of conifer plantations by a reforestation project named as "*100 Square-Meter Forest*

1410   *Movement Trust*". The results in Chapter 3 showed that brown bear digging for cicadas occurred

1411   only in the restored plantations. Cicada density survey using cicada exuviae revealed about 10

1412   times higher exuviae density in the plantations than in natural forests (Chapter 3). In Chapter 4,

1413   I found digging behavior of brown bears was negatively affected by understory dwarf bamboo

1414   by using structural equation modeling. Given that dwarf bamboo population in SWH site

1415   declined from 1980s to 2000 due to deer grazing (Yabe 1995), sika deer might enhance bear

1416   foraging on cicada nymphs by increasing the areas without dwarf bamboo. Together with

1417   Chapter 2~4, the reasons why brown bears have dug for cicada nymphs were caused by changes

1418   in their foraging environment: (1) increase in cicada densities by the creation of conifer

1419   plantations; (2) vegetation changes due to deer overgrazing.

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1420   Cicada predation by brown bears have been only known in Hokkaido even though the

1421   creation of plantations and deer overgrazing were widespread factors modifying their foraging

1422   environment (Cote et al. 2004, Le et al. 2012). Why is this behavior so rare ? A plausible reason

1423   is that distributional area of brown bears does not so much overlap with that of cicadas. At least

1424   3000 cicada species distribute worldwide, with the majority being in tropical regions (Sanborn

1425   and Phillips 2013). Periodical cicadas Magicicada spp., which is the highest population density

1426   around all of cicada species, distributes southeastern part of United States out of the

1427   distributional range of brown bears. Although over 10 cicada species (genera: *Okanagana*)

1428   occur in British Columbia, western Canada, where a large grizzly bear population live, their

1429   cicada consumption have not been found (McLeland and Hovey 1995). Given that grizzlies in

1430   this region mainly consume plant materials such as berries *Vaccinium* spp., graminoids, and

1431   herbs during summer (McLellan and Hovey 1995), they may not so actively exploit animal prey

1432   in summer. We should further consider the causes of this foraging behavior for understanding

1433   the rarity of this behavior.

1434   Behavioral causes must be considered for deepening our understandings why bears start

1435   digging for cicada nymphs because they are strongly constrained by behavioral mechanisms, not

1436   only environmental factors (Steyaert et al. 2016, Mazur and Seher 2008). Next, I discuss the

1437   potential roles of cognition, sex differences in use of human-dominated habitat, and social

1438   learning.

1439   *Cognitive ability for use of novel resources*

1440   Whether wildlife can utilize novel resources or not is associated with their cognition such

1441   as innovation and neophilia (Barrett et al. 2019). Owing to a high cognitive ability (Gilbert

1442   1999), brown bears might be able to exploit novel resources. Likewise bears, red foxes and

1443   jungle crows use the plantation to forage on cicada nymphs (Tomita 2021). Given that these

1444   species can often use anthropogenic resources due to high cognitive ability (Gittleman

1445   1986,1991, Bogale et al. 2014), use of plantations indicates the importance of cognitive ability

1446   for utilizing novel resources. However, Tomita (2021) did not find use of plantation by raccoon

1447   dogs and Japanese martens in the study site, even though they have been reported consumption

1448   of cicada nymphs in other regions (Adachi et al. 2016, Sako et al. 2008). These species have

1449   lower cognitive ability than brown bears, red foxes, jungle clows. This interspecific difference

1450   in use of plantations also explain the importance of cognitive ability for utilizing novel

1451   resources.

1452   *Sex differences*

1453   The result of Chapter 2 that cicada predation by bears is female -bias behavior also suggest

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1454 sex differences in the likelihood of behavior that utilizes human modified environment. In the

1455 study site, brown bears would need to approach the roads to forage on cicada nymphs because

1456 large areas of the larch plantations are located near the roads (Chapter 3). One possible

1457 mechanism for this sex difference is sexual conflict in brown bears. Female brown bears,

1458 especially female with cubs, prefer to human modified environment such as human habitation,

1459 road and clearcut forests during breeding season (May ~July) to avoid infanticide (Steyaert et al.

1460 2016, Elfstrom et al. 2014). The adaptive significance of infanticide by male bears is generally

1461 explained by sexually selected infanticide, a male reproductive strategy in which perpetrators

1462 kill unrelated dependent cubs to create mating opportunities with the victimized females

1463 (Bellemain et al. 2006). Because adult males avoid to anthropogenic habitat, females use

1464 "human shields" to avoid infanticide (Steyaert et al. 2016). Therefore, behavioral responses of

1465 brown bears to anthropogenic environmental modification would differ between female and

1466 male bears because of sexual conflict, that is, females is more exploiters to use anthropogenic

1467 resources than males. In contrast, livestock depredation by coyotes (*Canis latrans*) is biased to

1468 males during breeding season, due to large body size (Blejwas et al. 2006). Sex of carnivores,

1469 including brown and black bears (*U. americanus*), cougars (*Puma concolor*), and lions

1470 (*Panthera leo*), shot of trapped for depredation control is skewed to male, which in turn,

1471 produces sex biased conflict (Linnell et al. 1999). Male- biased natal dispersal may lead to bear

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1472   intrusion into anthropogenic habitat, thereby intensifying human -bear conflict (Linnell et al.

1473   1999). Sex differences in the likelihood of use of anthropogenic resources among carnivore

1474   species would be determined by many behavioral factors such as avoidance of sexual conflict,

1475   hunting ability, and sex- biased natal dispersal. In brown bears, while sexual conflict and sex

1476   differences in dispersal strategies can explain use of anthropogenic resources by females and

1477   males, respectively. Understanding its mechanisms may help for predicting and mitigating

1478   human- carnivore conflicts.

1479   *Social learning*

1480   Vertical social learning is one possible behavioral mechanism for persisting and

1481   transmitting digging behavior toward cicada nymphs within bear population at the study site.

1482   The Chapter 2 and Tomtia (2021) found that brown bears that dig for cicada nymphs mainly

1483   consist of female adult and sub adult bears. Since socially learned foraging behaviors in bears

1484   are expected to be biased on female (Mazur and Seher 2008, Hopkins 2013), this behavior

1485   might propagate through the brown bear population via social learning. Actually, my

1486   preliminary result found that most bears (6/7 individuals) that have been confirmed digging for

1487   cicada nymphs belong to the same pedigree (Tomita, Shimozuru, and Hiura *unpublished data*).

1488   Moreover, female bears socially learning this behavior may stay the study site because brown

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1489   bears in the SNH show female-biased philopatry (Shirane et al. 2019), suggesting that bears

1490   acquiring this behavior through social learning remain in the population.

1491   Social transmission of information that cicada nymphs are abundant in the plantations from

1492   mother bear to their cubs might facilitate the use of plantation as foraging habitats by bears in

1493   the study area. Thus, social learning from mother to cubs may contribute to transmission of

1494   foraging behavior for coping with anthropogenic habitat within brown bear population facing to

1495   human- induced rapid environmental change. However, vertical social learning can also help to

1496   transmit conflict behavior from mother to offspring for brown bears (Morehouse et al. 2016).

1497   For example, Morehouse et al. (2016) showed that conflict behaviour in grizzly bears such as

1498   crop raiding and livestock killing were socially learned from mother bears, rather than

1499   genetically inherited from parents.

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Ecosystem-level effects of the behavior change in brown bears

In this section, I try to extend the interpretation of the results to ecosystem level consequences

of the behavior change. In line with a concept provided by Jones et al. (1997) that ecosystem

engineers have direct and indirect ecosystem effects via trophic and non-trophic effects,

respectively, I assume two ecosystem effects as ecological consequences of the behavior

changes in brown bears. First, cicada consumption by bears can affect other predators on

cicadas and N flux from belowground to aboveground subsystem through decreasing cicada

emergence density. I estimated how many cicada nymphs were prey upon by brown bears,

thereby how much nitrogen flux was decreased through cicada predation at the study site.

Second, non-trophic effects of brown bears through digging for cicada nymphs (i.e. soil

bioturbation) is assumed as the negative effects of inorganic nitrogen production (Chapter 5). I

also estimated the spatial extent of brown bear digging for cicadas and the reduced amount of

inorganic nitrogen concentration in the plantations at the study site.

Trophic effects of brown bears

  Cicada consumption by brown bears

    At first, I estimated the number and biomass of cicadas emerging in 2018 and 2019 based

on the data on cicada exuviae densities from Chapter 3 and 4. The proportion of larch plantation

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1518 and natural forest covered by dwarf bamboo is assumed as 50 % of the area of each forest type.

1519 Notably, the number of cicadas emerging from the plantation (2018: 117,013 cicadas, 2019:

1520 752,052 cicadas) was higher than that from natural forest (2018: 84,625 cicadas, 2019: 555,394

1521 cicadas), even though plantation only account for a small proportion (ca. 18%) of the study

1522 forest.

1523   At this moment, the influences of brown bear digging for cicada nymphs is able to directly

1524 exert within the plantations, but not natural forests, given the findings from Chapter 2 and 3.

1525 However, they may be able to affect other organisms, especially free -living cicada predators,

1526 which do not restrict within plantations, via limiting cicada resource pulse from plantations.

1527 Since many birds regularly prey upon adult cicadas (Pons 2020) and jungle crows prey on

1528 cicadas at the study site (Tomita 2021), cicada predation by brown bears might decrease cicada

1529 availability for birds. Moreover, given that cicada emergence can strongly contribute to nitrogen

1530 flux from belowground to aboveground subsystem (Callaham et al. 2000, Yang 2004), cicada

1531 predation may affect nitrogen flux from belowground. Importantly, N flux associated with

1532 cicada emergence is assumed to be a factor accelerating forest nitrogen cycling (Hunter 2016).

1533   To examine these ecological effects of cicada consumption by bears I estimate how many

1534 cicada nymphs were prey upon by brown bears, thereby how much nitrogen flux was decreased

1535   through cicada predation at the study site by calculating the following equations

1536
$$CQ_{scat} = \frac{MSW \times P}{CW}$$

1537   where CQ_{scat} is the number of cicada nymphs contained in one scat, MSW is mean dry weight of

1538   one bear scat (221.2 ± 137.4 g) given by Murray et al. (2017), CW is dry weigt of final instar

1539   cicada nymphs (1.12 ± 0.20 g) given by Chapter 3, P is the proportion of cicada nymphs in bear

1540   scats containing cicada nymphs at the study site (0.367) after corrected by Hewitt and Robbins

1541   (1996)'s correction factor.

1542
$$CQ_{indiv} = CQ_{scat} \times DR \times F \times Days \times Time$$

1543   where CQ_{indiv} is the number of cicada nymphs consumed by one bear, DR is adult brown bear's

1544   defecation rate for mammalian carcass in summer with no sex difference (4 defecations / 24

1545   hours) given by Elfstrom et al. (2013) and Roth (1980), F is the occurrence frequency of cicada

1546   nymphs in bear scats (0.527) given by Chapter 2, $Days$ is the number of days during which

1547   bears dig for cicadas [56 days (May 25 ~ July 20)] by camera trap data (Tomita *unpublished*

1548   *data*), $Time$ is the proportion of bear activity time consuming cicada predation [14 hours

1549   (5:00~18:00)] in one day (24 hours) at the study site (0.583) given by Tomita (2021). CQ_{indiv} was

1550   estimated at 4,988.39 nymphs.

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1551
$$TCQ = CQ_{indiv} \times N_{bears}$$

1552   where *TCQ* is the number of cicadas consumed by brown bears at the study site annually, N_{bears}

1553   is the minimum number of adult brown bear digging for cicada nymphs (5 female adult bears)

1554   given by Chapter 2. As a result, I estimated brown bears consumed 24,941.95 cicada nymphs

1555   annually. Given that the number of emerging cicadas in the study population in 2018 was

1556   estimated at 201,638.57 individuals, it was estimated that brown bears prey upon as much as

1557   12.4 % of cicada nymphs emerging in 2018. Although this is just a preliminary estimation,

1558   impacts of brown bears to the cicada population and other animals preying upon the cicada

1559   should be significant.

1560

1561   *Non-trophic effects through brown bear digging for cicada nymphs*

1562   Estimation of amount of soil displacement by brown bear digging

1563   I estimated the spatial extent of brown bear digging at the study site by considering the

1564   occurrence frequency of digging and the forest area per each forest type. The area dug by bears

1565   was estimated at 35.27 ha (4.2 % of total forest area) and 33.72 ha (4.0 % of total forest area) in

1566   2018 and 2019, respectively (Table 1). Chapter 6 indicated that depth of the diggings was about

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1567   10 cm. Thus, soil volume displaced by bears in the total area of plantations was estimated at

1568   231.55 m^3 ha^{-1} yr^{-1} in 2018 and 221.38 m^3 ha^{-1} yr^{-1} in 2019. Soil volume displaced by bears in

1569   the total forest area was estimated at 43.19 m^3 ha^{-1} yr^{-1} in 2018 and 41.29 m^3 ha^{-1} yr^{-1} in 2019

1570   (Table 1). I compared the excavation rate with those by other digging mammals in Table 2.

1571   Brown bears at the study site is likely to displace much more soil than other digging mammals.

1572   Given that these diggings were created by five female adult bears (Chapter 2 and Tomita

1573   2021), soil area and volume displaced by one bear was estimated at 7.05 ha and 8.64 m^3 ha^{-1} yr^{-1}

1574   in 2018 and 6.74 ha and 8.26 m^3 ha^{-1} yr^{-1} in 2019, respectively. The estimated dug area in 2019

1575   do not indicate that emergence of new digging area was 33.72 ha in 2019 because I observed

1576   brown bear have repeatedly dug up the same area across years.

1577

1578   **Table 1** Forest area, occurrence frequency of brown bear digging, and estimated dug area

1579   among forest types (larch, fir, spruce plantations, and natural forest)

Year	Tree species	Understory type	Area (ha)[*1]	Proportion (%)	Mean Digging frequency[*2]	SD	Estimated dug area (ha)[*3]
2018	Larch	No cover	16.87	2.06	0.88	0.15	14.81
2018	Larch	Dwarf bamboo	16.87	2.06	0.28	0.26	4.72
2018	Fir	No cover	0.64	0.78	0.39	0.24	0.25
2018	Spruce	No cover	112.23	13.71	0.12	0.25	13.24
2018	Natural	No cover	333.17	40.70	0	NA	0
2018	Natural	Dwarf bamboo	333.17	40.70	0	NA	0
2019	Larch	No cover	16.87	2.06	0.50	0.36	8.47
2019	Larch	Dwarf bamboo	16.87	2.06	0.08	0.13	1.41
2019	Fir	No cover	0.64	0.78	0.37	0.18	0.23
2019	Spruce	No cover	112.23	13.71	0.19	0.29	2.16
2019	Natural	No cover	333.17	40.70	0	NA	0
2019	Natural	Dwarf bamboo	333.17	40.70	0	NA	0

1580   *1: The proportion of larch plantation and natural forest covered by dwarf bamboo is assumed as 50 % of
1581   the area of each forest type.

1582   *2: These data are estimated by chapter 3 and 4.

1583   *3: Calculated as multiplying *"Area (ha)"* by *"Mean digging frequency"*.

1584

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1585   **Table 2** Excavation rates of digging mammals resulting from the literature search

Species	Study area	Ecosystem	Weight (kg)	Behavior	Mean displaced volume (m³ ha-1 yr-1)	Reference
Brown bear (*Ursus arctos*)	**Japan**	**Forest**	**100~400**	**F**	**43.19**	**This thesis**
Brown bear (*Ursus arctos*)	**Japan**	**Forest**	**100~400**	**F**	**41.29**	**This thesis**
Grizzly bear (*Ursus arctos horribilis*)	Canada	Grassland	100~400	F	4.66	Hall & Lamont (2003)*
American badger (*Taxidea taxus*)	USA	Shrubland	8.6	F	3.9	Eldridge (2004)*
Europian rabbit (*Oryctolagus cuniculus*)	Australia	Grassland	1.6	F	3.28	James et al. (2011)*
Marsupial community	Tasmania	Forest	0.035~5.5	F	12.2	Davies et al. (2019)
House mouse (*Mus musculus*)	Marion Island	Tundra	0.02	N	20.6	Eriksson & Eldridge (2014)*
Botta's pocket gopher (*Thomomys bottae*)	USA	Grassland	0.12	N	40	Gabet (2000)*
Mountain pocket gopher (*Thomomys monticola*)	USA	Grassland	0.07	N	14.42	Ingles (1952)*
Northern pocket gopher (*Thomomys talpoides*)	USA	Grassland	0.13	N	9.6	Ellison (1946)*
European badger (*Meles meles*)	UK	Forest	9.9	N	0.03	Coombes & Viles (2015)*
Arctic ground squirrel (*Spermophilus saturatus*)	Canada	Grassland	0.22	N	15.4	Price (1971)*

1586

1587   F: foraging, N: nesting

1588   References with asterisk were cited from Haussmann (2015)

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Factors affecting the strength of ecosystem consequences of animal behavior change: lesson from brown bear digging for cicada nymphs

Anthropogenic environmental modifications can have the potential to modulate multiple ecosystem functions through behaviorally mediated pathways. These pathways may not be substantial enough to affect ecosystem functions even if human activities alter animal behavior. Thus, detecting factors controlling the strength of behaviorally mediated pathways is important for developing our predictability of ecological consequences of human- induced animal behavior change (Wilson et al. 2020). Wilson et al. (2020) proposed three factors influencing the strength of pathways linking from animal behavior changes to ecosystem consequences: (1) ecological importance of a given behavior, (2) population impacts of behavior change, (3) the magnitude and persistence of behavior change. However, they provided only a theoretical framework, but not practical cases due to a lack of such evidence. Finally, I discuss factors influencing the strength of behaviorally mediated pathways based on the findings of my doctor thesis.

(1) Ecological importance of impacted behavior

I examined ecosystem effects of soil disturbance through brown bear digging and trophic cascade to N flux and other cicada predators through cicada predation as the consequences of animal behavior change. Digging mammal is a representative form of ecosystem engineers

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1607   (Mallen-Cooper et al. 2019), and cicadas have numerous ecological roles such as prey and

1608   nutrient vector enhancing above- and belowground linkage (Yang 2006, Pons 2020). Thus,

1609   behavior change can lead to substantial ecosystem consequences when behavior underlying

1610   ecosystem engineering effects (e.g. digging and nest building) and predatory behavior on

1611   ecologically important prey (e.g. keystone predation) change due to anthropogenic

1612   environmental modifications.

1613   *(2) Population impacts of behaviour change*

1614   Bears would need to approach the roads to forage on cicada nymphs because large areas of

1615   the plantations located near the roads that have been frequently used by tourists (Chapter 3). In

1616   fact, wildlife managers often observed bears digging for the nymphs within the adjacent roads

1617   of plantations (Shiretoko Nature Foundation, *personal communication*). A female bear which

1618   frequently dug for cicada nymphs in the plantations was killed preventively for mitigating

1619   human–bear conflict. Accordingly, this behavior change might increase human-caused mortality

1620   due to human–bear conflict, thereby dampening of the bear population. In places where human-

1621   induced behavior change lead to substantial ecological consequences, human-wildlife conflicts

1622   may be intense, because the degree of behavior change become greater with the place close to

1623   human settlements. In such case, the pathways linking animal behavior change to ecosystem

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1624   consequences may weaken due to decreasing population size.

1625   **Concluding remarks**

1626   Throughout my thesis, I found some novel species interactions such as bear- cicada

1627   (Chapter 2-3), bear- dwarf bamboo (Chapter 4), bear- tree (Chapter 6), and possibly bear-

1628   cicada-insectivorous birds (General discussion), induced by behavior change of brown bears.

1629   This suggests that behavior shifts following environmental changes may increase the number

1630   and type of interactions around brown bears at the study site. The reason is that brown bears

1631   inherently link to a wide variety of species across taxa through foraging. Thus, behavior changes

1632   in ecologically important species such as brown bears may make more complex ecological

1633   networks and ultimately result in change in food web stability.

1634   In the Anthropocene, many ecologists are concerning about ecosystem consequences of

1635   population declining and extirpation such as trophic downgrading and meso predator release

1636   (Ripple et al. 2014, Estes et al. 2012). Behavior change have tended to be ignored as a driver of

1637   cascading ecosystem effects but recently gained a growing attention (Wilson et al. 2020). Some

1638   challenges, such as difficulty of separating behaviorally- mediated from density- mediated

1639   effects, hinder our understanding of cascading effects of altered behavior to ecosystem function.

1640   In the future, many large carnivores, including brown bears will increasingly recolonize to a

1641 large area of developed countries following to land abandonment (Kujiper et al. 2016). Because

1642 recolonizing carnivores will have to live in human- modified ecosystems, their behavioral

1643 differences between anthropogenic and natural landscapes will be significantly large. Thus,

1644 elucidating behaviorally mediated effects on community structure and ecosystem processes in

1645 human- modified landscapes will be increasingly important for wildlife conservation and

1646 management. However, the scientific support for understanding behaviorally mediated effects of

1647 human impacts on ecosystems is currently limited (Kujiper et al. 2016). As I showed throughout

1648 my Ph. D thesis, brown bear is worth to be a target species for filling this gap, given their high

1649 degree of behavioral flexibility and numerous ecological functions. Moreover, their population

1650 is globally stable (Ripple et al. 2014), suggesting that the relative ecological importance of

1651 behaviorally mediated effects is larger than that of density-mediated effects. Thus,

1652 understanding ecosystem effects of altered behavior of bears would provide new insights into

1653 management practice for anthropogenic landscapes composed of natural and human- modified

1654 ecosystems.

Acknowledgements

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