



Title	Causes and consequences of animal behavior changes in a human-modified world : A case study of brown bear digging for cicada nymphs
Author(s)	富田, 幹次
Citation	北海道大学. 博士(環境科学) 甲第14768号
Issue Date	2022-03-24
DOI	10.14943/doctoral.k14768
Doc URL	<a href="http://hdl.handle.net/2115/85780">http://hdl.handle.net/2115/85780</a>
Type	theses (doctoral)
File Information	TOMITA_Kanji.pdf



[Instructions for use](#)

**Causes and consequences of animal behavior changes  
in a human-modified world:  
A case study of brown bear digging for cicada nymphs**

Kanji Tomita

A dissertation submitted to Division of Biosphere Science of  
Doctor of Philosophy in Graduate School of  
Environmental Science, Hokkaido University, Japan

March 2022, Sapporo

# Table of contents

<b>Chapter 1</b> .....	<b>1</b>
General introduction	
<b>Chapter 2</b> .....	<b>12</b>
Brown bear digging for cicadas: a novel interaction in a forest ecosystem	
<b>Chapter 3</b> .....	<b>18</b>
The creation of plantations provides a foraging habitat for brown bears by increasing cicada density	
<b>Chapter 4</b> .....	<b>38</b>
Disentangling the direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of the brown bear	
<b>Chapter 5</b> .....	<b>59</b>
Negative effects of brown bear digging on soil nitrogen availability and production in the larch plantations in northern Japan	
<b>Chapter 6</b> .....	<b>74</b>
Brown bear digging decreases radial growth of canopy trees: an ecological consequence of animal behavior change in a human- modified ecosystem	
<b>Chapter 7</b> .....	<b>106</b>
General discussion	
<b>Acknowledgements</b> .....	<b>124</b>
<b>References</b> .....	<b>126</b>

## Peer-reviewed articles

### Chapter 2

**Tomita, K., & Hiura, T.** (2020). Brown bear digging for cicada nymphs: a novel interaction in a forest ecosystem. *Ecology* 101: e02899.

### Chapter 3

**Tomita, K., & Hiura, T.** (2021). Reforestation provides a foraging habitat for brown bears (*Ursus arctos*) by increasing cicada *Lyristes bihamatus* density in the Shiretoko World Heritage site. *Canadian Journal of Zoology* 99: 205-212.

### Chapter 4

**Tomita, K., & Hiura, T.** (2021). Disentangling the direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of the brown bear *Ursus arctos*. *Wildlife Biology* 2021: wlb00886.

## In Review or Revision

### Chapter 5

**Tomita, K., & Hiura, T.** Negative effects of brown bear digging on soil nitrogen availability and production in the larch plantations in northern Japan: their role as an agent of bioturbation. *Major revision at Pedobiologia*.

### Chapter 6

**Tomita, K., & Hiura, T.** Brown bear digging decreases radial growth of canopy trees: an ecological consequence of animal behavior change in a human- modified ecosystem. *In prep*

# 1 Chapter 1 General introduction

## 2 **Ecological consequences of animal behavior change in the Anthropocene**

3 Human activities have now reached to everywhere on our planet and, therefore, most living  
4 organisms spend their lives in anthropogenically impacted habitat (Hobbs et al. 2009, Barnosky  
5 et al. 2012). Environmental change has been a universal phenomenon during the life of earth,  
6 but the rate and magnitude have been exceedingly accelerated in the Anthropocene. It is urgent  
7 to understand how wildlife respond to human activities and its ecological and evolutionary  
8 consequences at population, community, and ecosystem levels (Sih et al. 2011, Johnson et al.  
9 2017).

10 The initial animal response to human activities is a behavioral change, including foraging,  
11 movement, or diel activity (Wong and Candolin 2015, Fleming and Bateman 2018), and then  
12 cascade to population level effects, such as population decline. Behavioral changes also affect  
13 many higher-level ecological phenomena directly or indirectly, such as community changes and  
14 nutrient cycling (Palkovacs and Dalton 2012, Wilson et al. 2020). However, most past studies  
15 have investigated anthroponotic effects on either one of the behavioral changes or population/  
16 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 anthropogenic 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 canadensis*) and digging mammals (e.g. wild boar *Sus scrofa*  
28 and prairie dogs *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

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.

## 51 **Forest plantations as human-modified ecosystems**

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



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,

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).

121

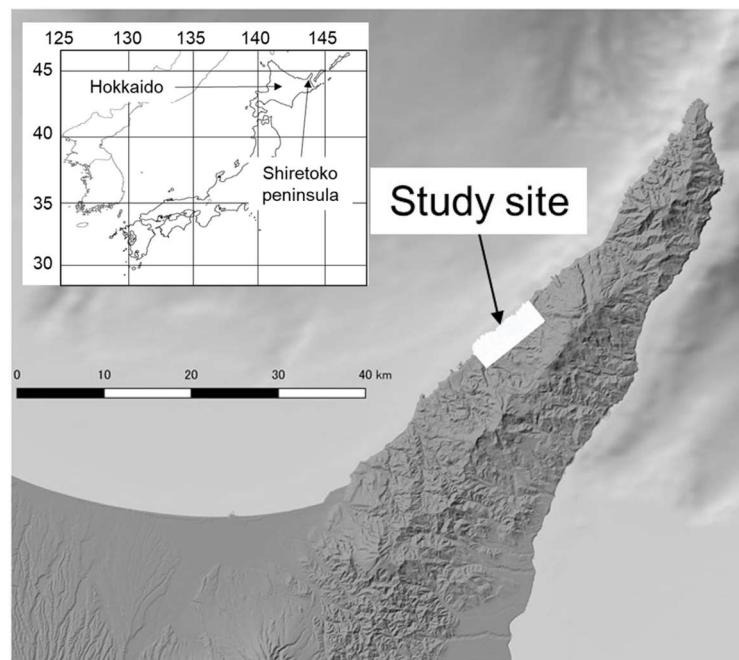
122 **Study site: Shiretoko World Heritage site**

123 This study was conducted in the Horobetsu-Iwaobetsu area (44°09=N, 145°02=E) located  
124 in the western parts of the SWH (Fig. 1). The elevation ranges from 120 to 220 m. The annual  
125 mean temperature at the study site is 6.2 °C. and monthly mean temperature ranged from –  
126 10.4 °C in February to 15.1 °C in August (1981–2010). The annual mean precipitation is 1,149  
127 mm (1981–2010). UNESCO certified this area as a World Natural Heritage site because it  
128 represents one of the richest northern temperate ecosystems in the world  
129 (<http://whc.unesco.org/en/list/1193>). In the study area, approximately 40% of the conifer-  
130 broadleaved mixed forests were converted to farmland for grazing by cattle during the post-war  
131 period from the 1940s to the 1960s (Shoyama 2008). Agricultural crops such as corn and sugar  
132 beet were rarely cultivated in this area. During the period of high economic growth in Japan,  
133 from the late 1960s to the 1970s, all the farmland was abandoned because farmers immigrated  
134 to urban areas. Since 1977, reforestation of the abandoned farmland has been conducted by the  
135 local government and residents through a national trust movement. Coniferous trees such as  
136 Japanese larch, Sakhalin spruce (*Picea glehnii*) and Sakhalin fir (*Abies sachalinensis*), have  
137 been planted on the abandoned farmland for the purpose of reforestation. Most of the larch and  
138 fir plantations were established during the 1970s, whereas the spruce plantations were  
139 established during the early 1990s. The restored plantations accounted for 18 % of the total

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<sup>2</sup> 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-

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*.



165  
166 **Figure 1** Location of study site  
167

168 Chapter 2 Brown bear digging for cicadas:

169 a novel interaction in a forest ecosystem

170 **Main text**

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





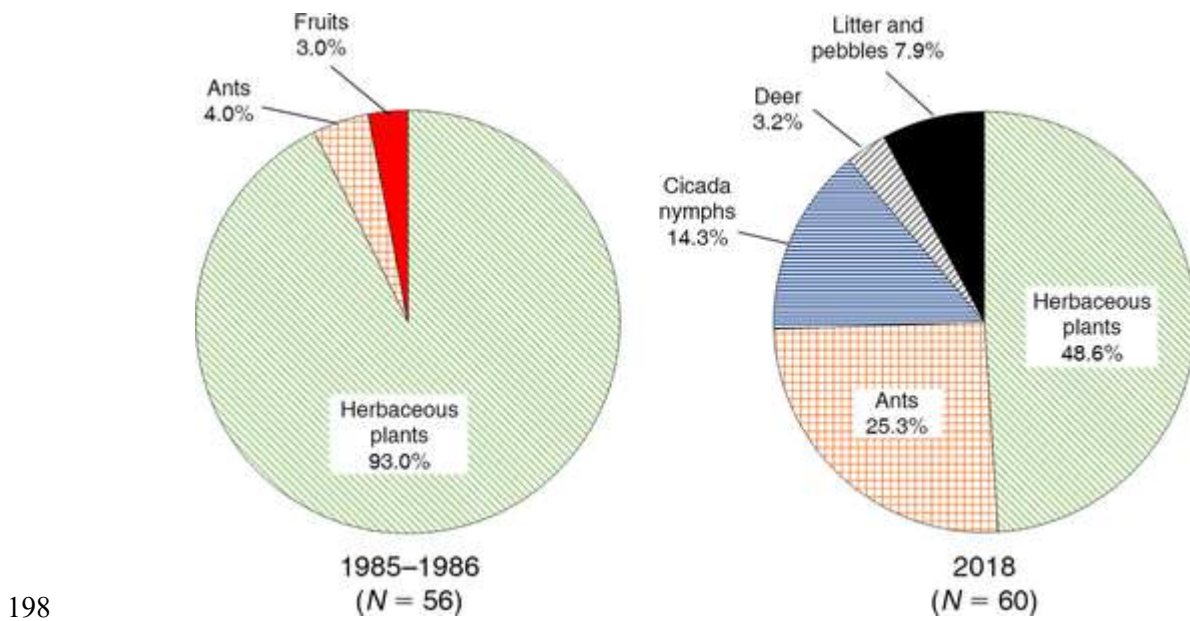
183

**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).

184

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

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.

199

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 m<sup>2</sup> 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 ( $153.9 \pm 15.6$

206 exuviae/100 m<sup>2</sup> [mean ± SE]). The number of *L. bihamatus* exuviae in the Sakhalin spruce  
207 plantations and the natural mixed forests was  $8.7 \pm 3.0$  and  $4.5 \pm 2.3$ , 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

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 m<sup>2</sup>, 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.

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.

253

254

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

257 **Abstract**

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

269

## 270 **Introduction**

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

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



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

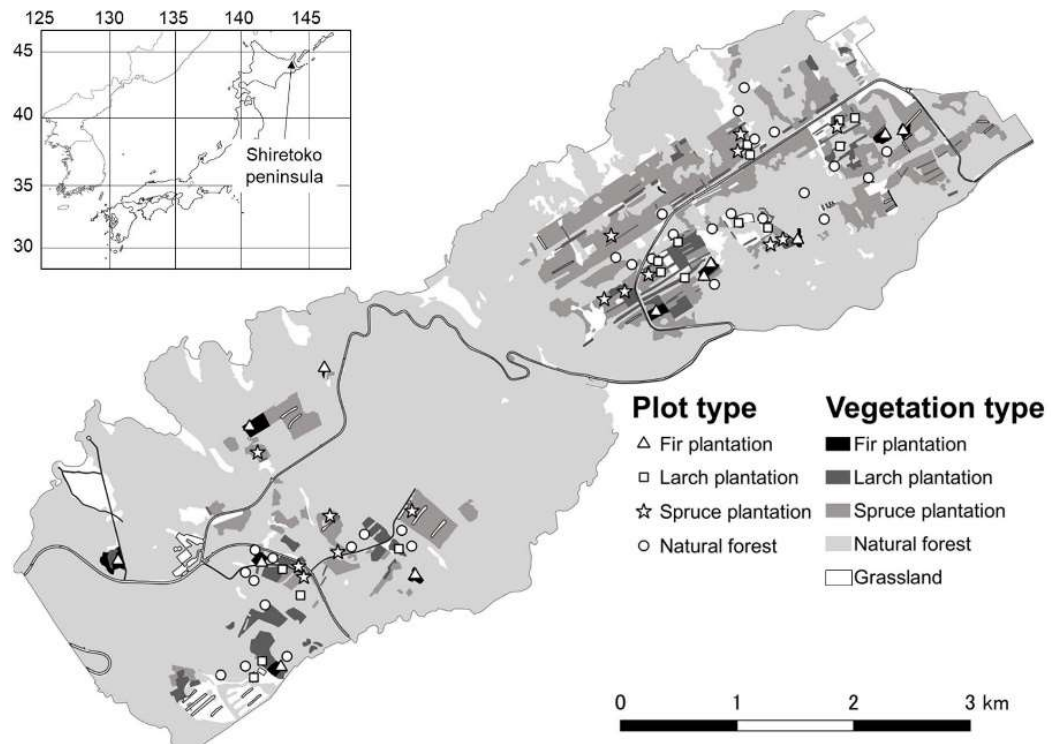
321 following predictions: (1) brown bears digging for cicada nymphs occurs more frequent in the  
322 restored plantations than in the natural forests, (2) the density of cicada nymphs is higher in the  
323 plantations than in the natural forests, (3) there is a positive relationship between digging  
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<sup>2</sup> 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<sup>2</sup>) 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

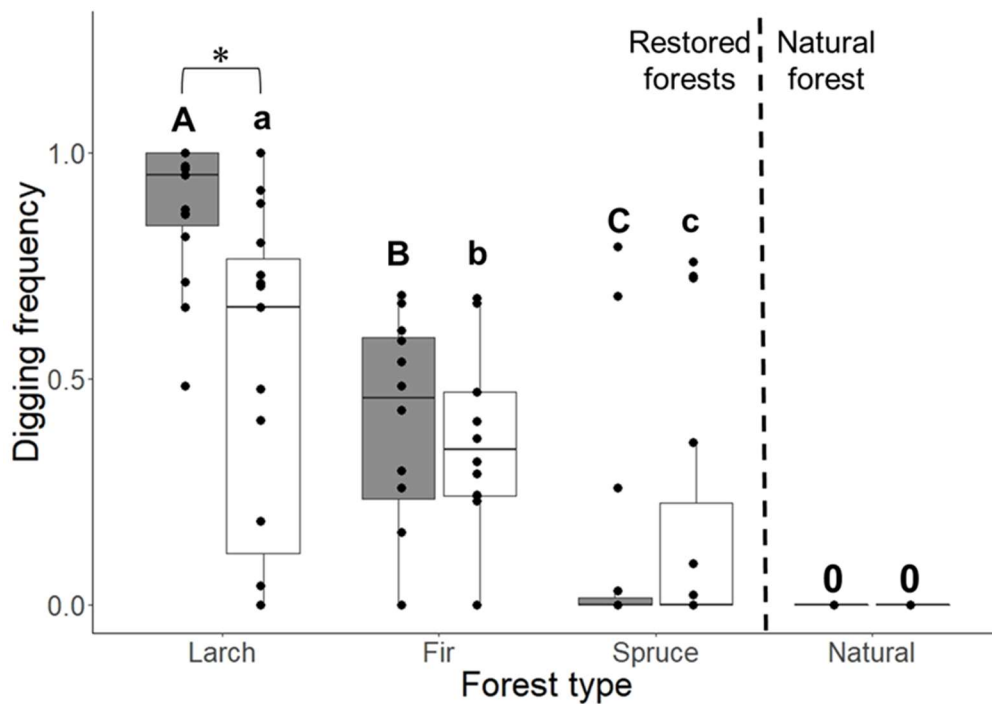
357 between 2018 and 2019. In GLMs for digging frequency, I introduced an offset term as the log-  
358 transformed number of trees to adjust for differences in the number of trees among the survey  
359 plots. To examine the effects of the density of cicada nymphs on the digging frequency, I  
360 performed 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 °C  
365 drying period. The biomass of cicada final instar nymphs per 100 m<sup>2</sup> 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.

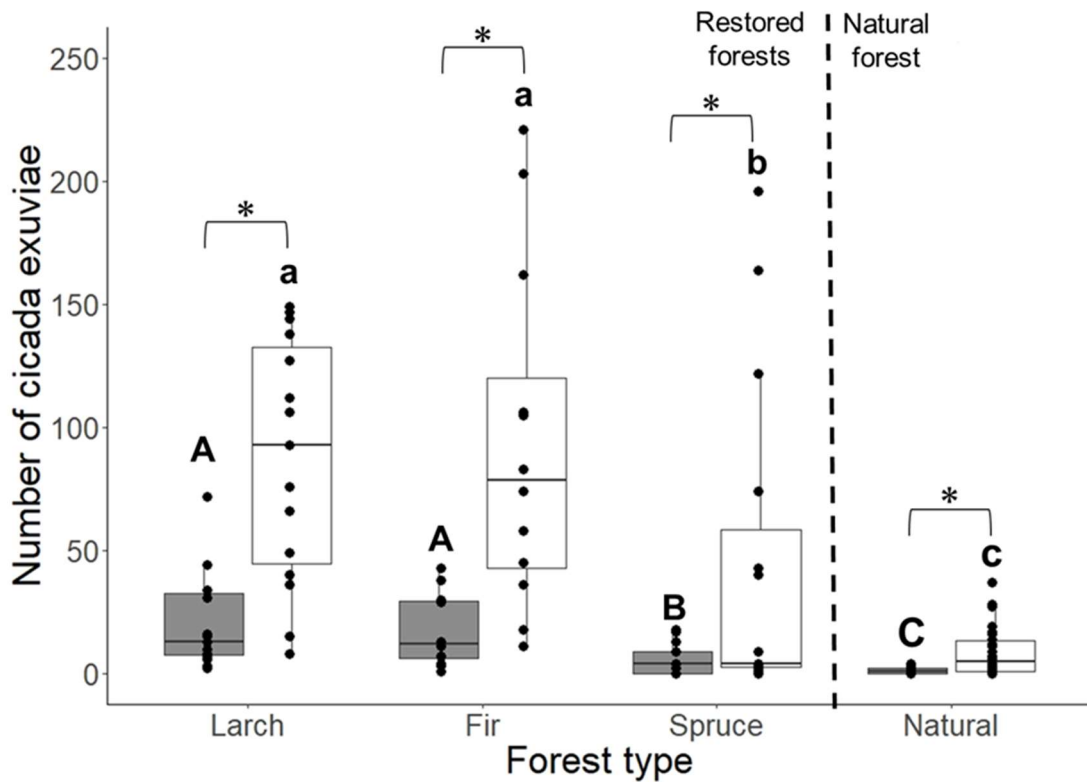


374

**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 ( $p < 0.001$ ).

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).



381

**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 ( $p < 0.001$ ).

382

383

The density of cicada nymphs positively correlated to the digging frequencies in fir and

384

spruce plantations ( $p < 0.001$ ), but not in larch plantations in 2018 ( $p = 0.19$ ) (Fig. 4). Individual

385

dry mass of the final instar nymphs was evaluated at  $1.12 \pm 0.20$  g (mean  $\pm$  SD), and the

386

biomass density of nymphs in each forest type is shown in Table 1.

387

**Table 2** The density and estimated biomass of final instar nymphs of cicada *Lyristes bihamatus* in the plot (100 m<sup>2</sup>) 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  $\pm$  SD

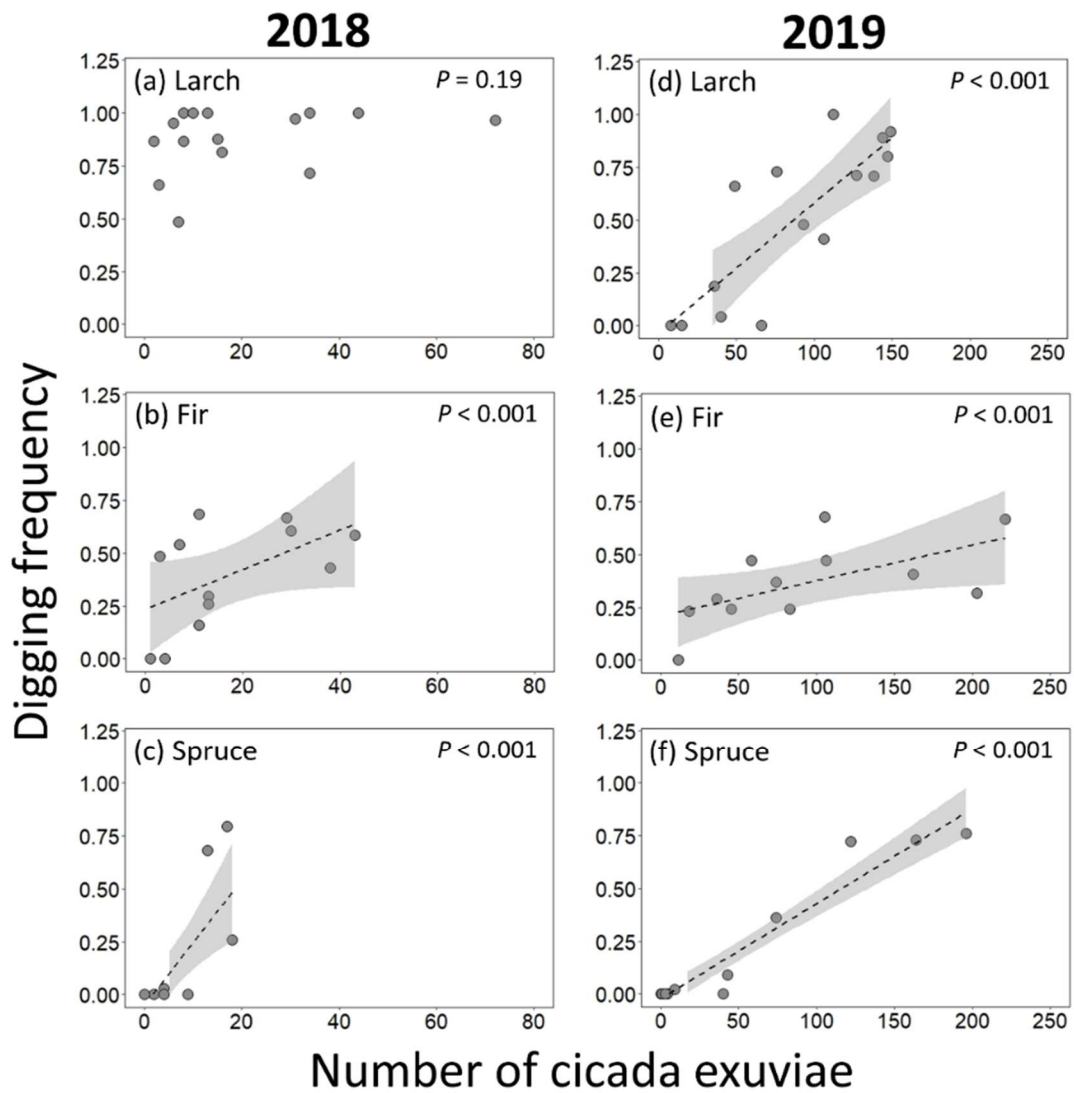
388

Forest type	Density of the nymphs in 2018 (/100 m <sup>2</sup> )	Density of the nymphs in 2019 (/100 m <sup>2</sup> )	Biomass of the nymphs in 2018 (g/100 m <sup>2</sup> )	Biomass of the nymphs in 2019 (g/100 m <sup>2</sup> )
Larch plantation	20.20 $\pm$ 18.71	87.07 $\pm$ 47.72	22.62 $\pm$ 20.96	97.52 $\pm$ 53.44
Fir plantation	16.92 $\pm$ 13.71	93.50 $\pm$ 66.55	18.95 $\pm$ 15.36	104.72 $\pm$ 74.54
Spruce plantation	5.67 $\pm$ 6.22	44.40 $\pm$ 63.08	6.35 $\pm$ 6.96	49.73 $\pm$ 70.65
Natural forest	1.27 $\pm$ 1.41	8.33 $\pm$ 9.44	1.42 $\pm$ 1.58	9.33 $\pm$ 10.57

389

390





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

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 (Sørensen 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.

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

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

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<sup>2</sup> 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<sup>2</sup>, 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

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;

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



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.

525

526

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

530 **Abstract**

531 Elucidating the factors affecting the foraging habitat selection of wildlife can further our  
532 understanding of the animal–habitat relationships and inform wildlife conservation and  
533 management. Canopy and understory vegetation may directly or indirectly affect the foraging  
534 habitat selection of carnivores through changes in habitat structure and prey availability,  
535 respectively; however, the relative importance of these two effects remains largely unknown.

536 Dwarf bamboo *Sasa kurilensis* is a predominant understory plant that suppresses regeneration in  
537 the forests of northern Japan. The purpose of this Chapter was to disentangle the direct and  
538 indirect effects of canopy forest type (*Larix kaempferi* plantation vs. natural mixed forest) and  
539 dwarf bamboo on foraging habitat selection of a large carnivore, the brown bear *Ursus arctos*.

540 In the Shiretoko World Heritage, brown bears dig for cicada nymphs during summer. I evaluated  
541 the frequency of brown bear foraging on cicadas by investigating traces of digging for cicada  
542 nymphs. A structural equation model was used to statistically disentangle the direct and indirect  
543 effects of vegetation. Our results demonstrated that canopy and understory vegetation directly

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

552 **Introduction**

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

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 lynx*) 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

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

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).

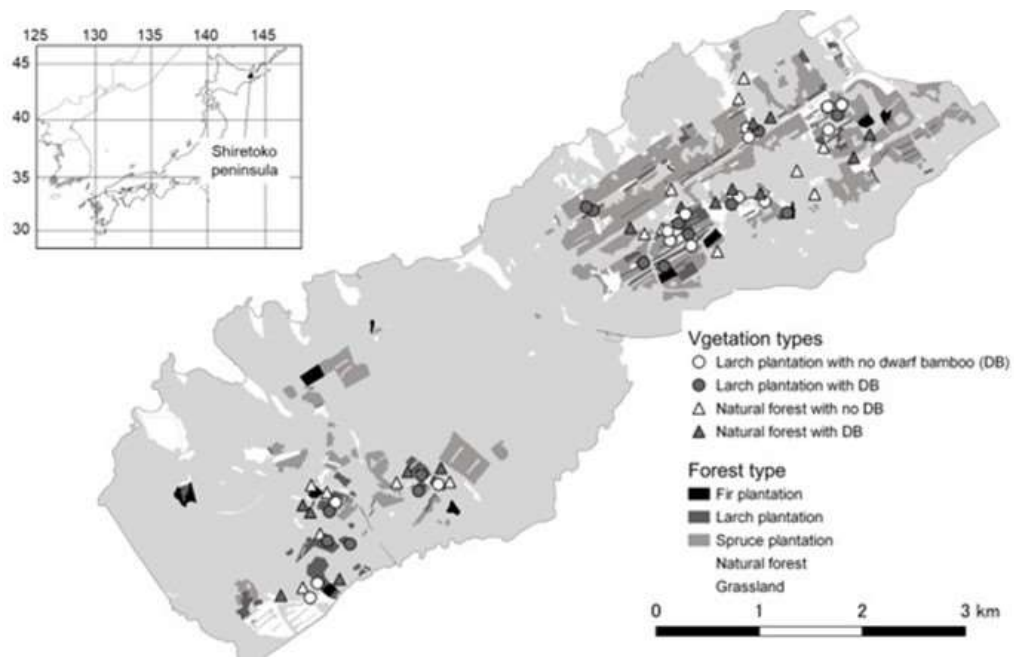
606 **Materials and Methods**

607 *Field survey*

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 ( $20.20 \pm 18.71$ ) was lower than  
610 that in 2019 ( $87.07 \pm 47.72$ ) (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<sup>2</sup>) 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



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.



636

**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

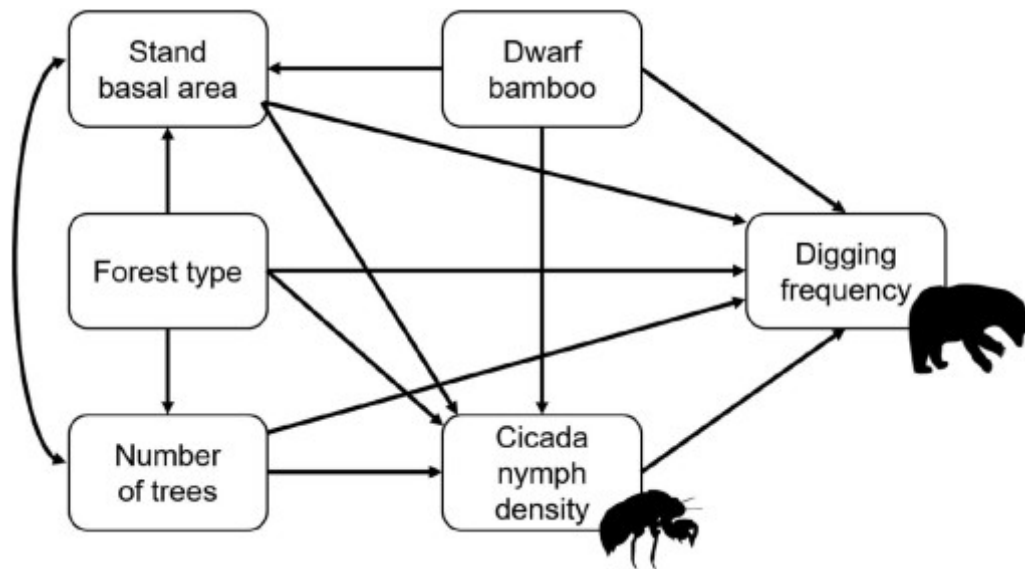
644 number of trees to adjust for differences in the number of trees among the survey plots.

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

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.



677

**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

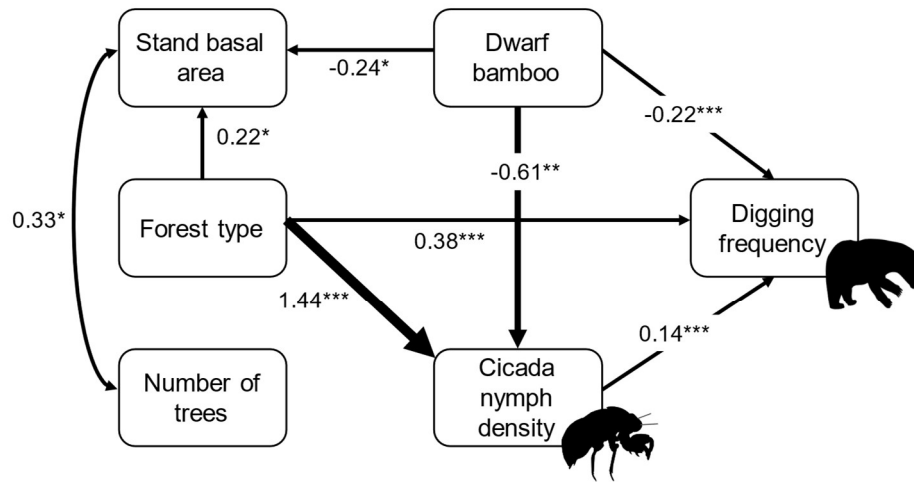
678

679 **Results**

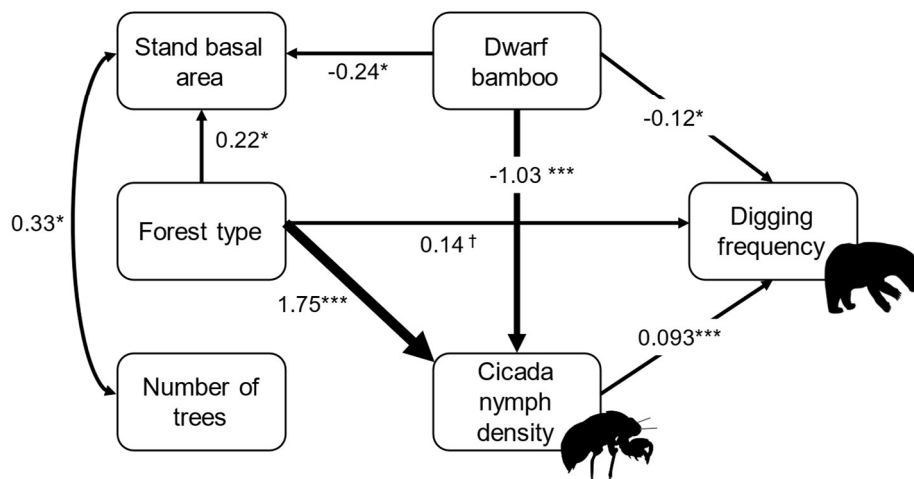
680 In both years, dwarf bamboo had a significant negative effect on digging frequency, and  
681 forest type had a significant positive effect on cicada nymph density (Table 1). For SEMs in  
682 both years, the RMSEA and CFI values were 0.000 (90 % CI: 0.000 - 0.305) and 1.000  
683 respectively, indicating 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:  $-0.61 \times 0.14 = -0.08$ ; 2019:  $-1.03 \times 0.09 = -0.09$ ) (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 ( $1.44 \times 0.14 = 0.20$ ) in 2018, whereas the direct effect (0.14) was same as or slightly  
695 weaker than the indirect effect ( $1.75 \times 0.09 = 0.16$ ) 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

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



702

**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.

703



704 **Table 1** Summary of the structural equation model showing standardized path coefficients and  
 705 standard errors (SE) in 2018 and 2019. R<sup>2</sup> 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> (2018: R <sup>2</sup> = 0.783) (2019: R <sup>2</sup> = 0.514)	<u>0.136***</u>	<u>0.031</u>	<u>0.093***</u>	<u>0.026</u>	
← Dwarf bamboo	<u>-0.219***</u>	<u>0.052</u>	<u>-0.120*</u>	<u>0.059</u>	
← Forest type	<u>0.384***</u>	<u>0.066</u>	<u>0.135†</u>	<u>0.070</u>	
← Stand basal area	<u>-0.026</u>	<u>0.059</u>	<u>-0.074</u>	<u>0.065</u>	
← Number of trees	<u>-0.077</u>	<u>0.081</u>	<u>-0.003</u>	<u>0.088</u>	
Cicada nymph density (exuviae 100m <sup>-2</sup> ) (2018: R <sup>2</sup> = 0.542) (2019: R <sup>2</sup> = 0.580)	← Dwarf bamboo	<u>-0.610**</u>	<u>0.203</u>	<u>-1.026***</u>	<u>0.260</u>
← Forest type	<u>1.442***</u>	<u>0.202</u>	<u>1.750***</u>	<u>0.258</u>	
← Stand basal area	0.139	0.248	0.455	0.317	
← Number of trees	<u>0.383</u>	<u>0.335</u>	<u>0.618</u>	<u>0.428</u>	
Stand basal area (m <sup>2</sup> 100 m <sup>-2</sup> ) R <sup>2</sup> = 0.195 (2018 & 2019)	← Dwarf bamboo	-0.240*	0.101	-0.240*	0.101
← 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 <sup>-2</sup> ) R <sup>2</sup> = 0.002 (2018 & 2019)	← Forest type	0.024	0.016	0.024	0.016

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.

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

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

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

797 **Abstract**

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

## 810 **Introduction**

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



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 (Hausmann, 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; Hausmann, 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.

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<sup>2</sup> (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.



878

**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

879

880 *Evaluation of soil properties*

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

882 carbon concentrations, approximately 20 mg of dry soil was analyzed using a CN analyzer (NC-

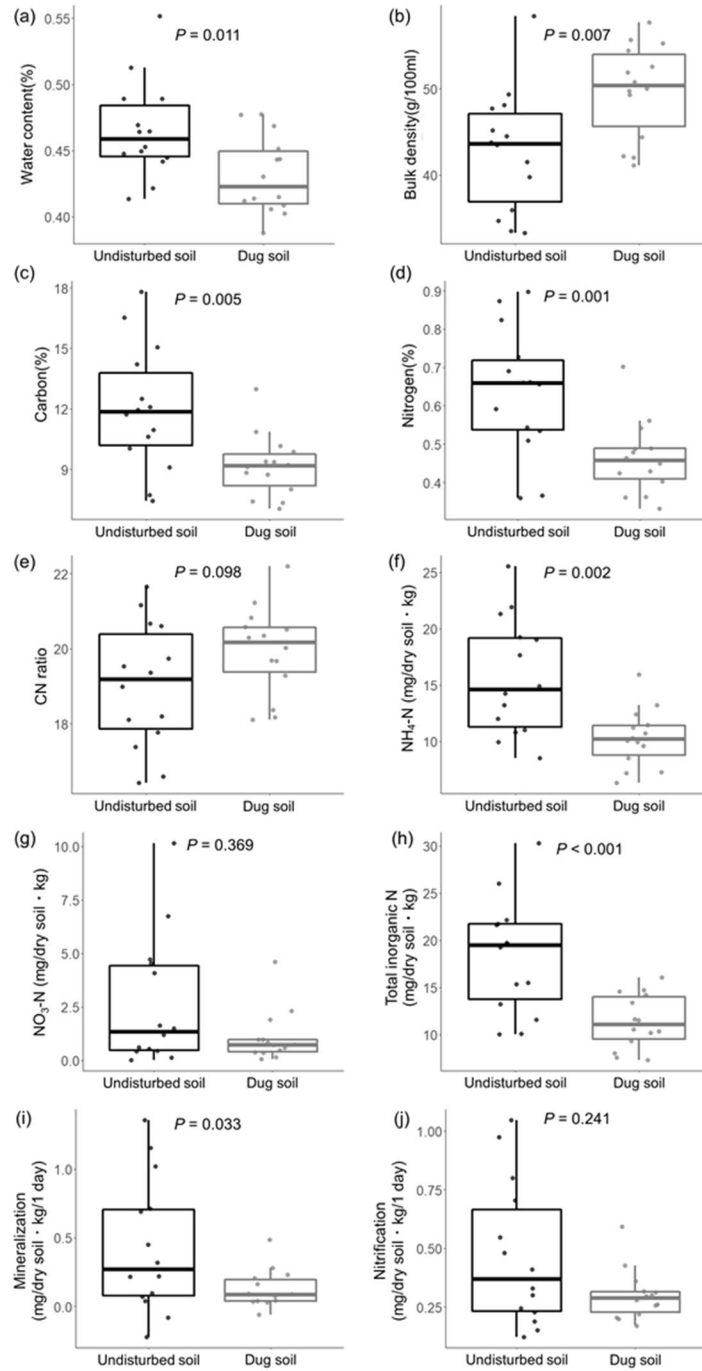
883 900; Sumitomo, Osaka, Japan). For inorganic nitrogen availability, 6 g of fresh soil was  
884 weighed into plastic bottles and extracted with 27.5 mL 1 M KCl with shaking for 1 h. By using  
885 an auto-analyzer (AACS-4, BL-TEC, Inc., Japan), ammonium and nitrate nitrogen was analyzed  
886 by indophenol 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 log<sub>10</sub>-transformation followed by analysis using ANOVA. All  
898 statistical analyses were conducted using R version 3.5.1 (R Core Team, 2018).

899 **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.

909



**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.

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

913

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

914



915 **Discussion**

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

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

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 findings 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

991 Chapter 6 Brown bear digging decreases radial growth of  
992 canopy trees: an ecological consequence of animal  
993 behavior change in a human- modified ecosystem

994 **Abstract**

995 A large number of studies has revealed loss of ecological functions of animals on human-  
996 modified ecosystems through population decline. However, there is little attention to ecological  
997 consequences of animal behavior changes in the human- modified ecosystems even though  
998 behaviourally mediated effects can modulate numerous ecosystem function as well as density-  
999 mediated effects. In the SWH, cicada emergence density was significantly higher in conifer  
1000 plantations than in natural mixed forests, implying that the creation of forest plantations was a  
1001 driver generating a novel behavior of brown bears via increase in local densities of cicadas. In  
1002 this chapter, I tested the effects of brown bear digging on radial growth of Japanese larches  
1003 (*Larix kaempferi*) via changes in soil nutrient conditions. I found their digging decreased fine  
1004 root biomass of larch soil water and nitrogen availability. Tree ring data suggested digging  
1005 negatively affected radial growth of larches and the effect became larger with tree diameter.  
1006 Brown bear digging negatively affected needle nitrogen content, but not carbon isotope ratios  
1007 ( $\delta^{13}\text{C}$ ), an index of water stress of trees. The results indicated brown bear digging decreased

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

1016 **Introduction**

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).



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 anthropogenic 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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup>). Basal area of each tree was calculated  
1095 using DBH data (i.e., basal area (m<sup>2</sup>/ 100m<sup>2</sup>) =  $\pi \times (\text{DBH}/2)^2$ ). 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

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  $24 < \text{DBH} < 35$  cm). The reason for the difference in range of tree  
1134 diameter between core and needle samples is that I determined trees with  $\text{DBH} < 24$  cm as  
1135 shaded individuals based on visually checking from the ground and trees with  $\text{DBH} > 35$  cm

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 °C 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

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 ( $\delta^{13}\text{C}$ ) were expressed as:

1158 
$$\delta^{13}\text{C} = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000 (\text{‰})$$

1159 where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the molar ratios of heavy to light isotopes ( $^{13}\text{C}/^{12}\text{C}$ ) of the samples  
1160 and standards, respectively. The standards were Vienna PeeDee Belemnite (V-PDB). Needle

1161 nitrogen per area [ (Narea ( $\text{g}/\text{m}^2$ )) ] was calculated by multiplying LMA by Nmass ( $\text{mg}/\text{g}$ ).

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 than 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

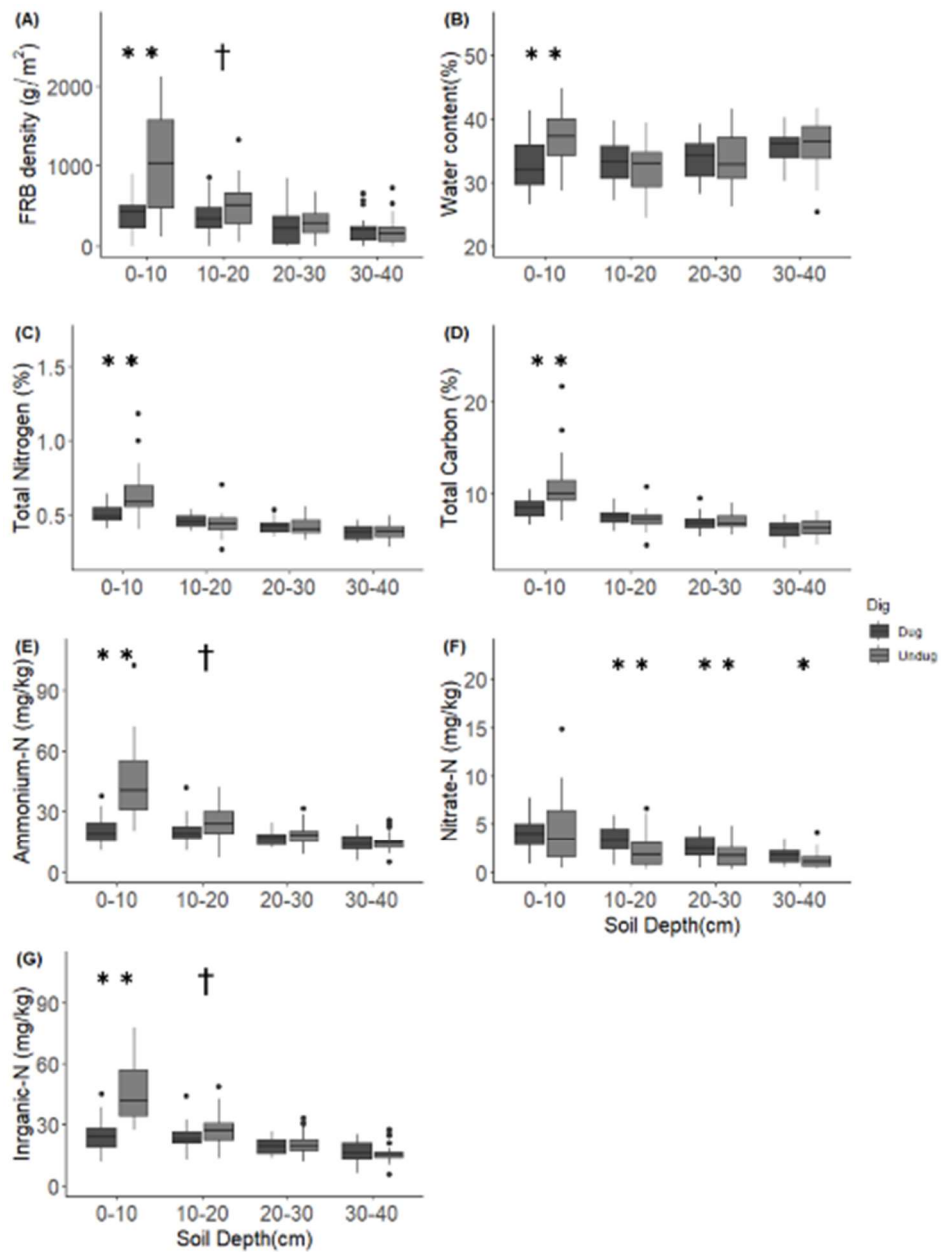
1225 larch plantations covered with no dwarf bamboo and dwarf bamboo, respectively. The dug plots  
1226 were confirmed not only the absence of dwarf bamboo, but also the evidence of digging by  
1227 bears .

## 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

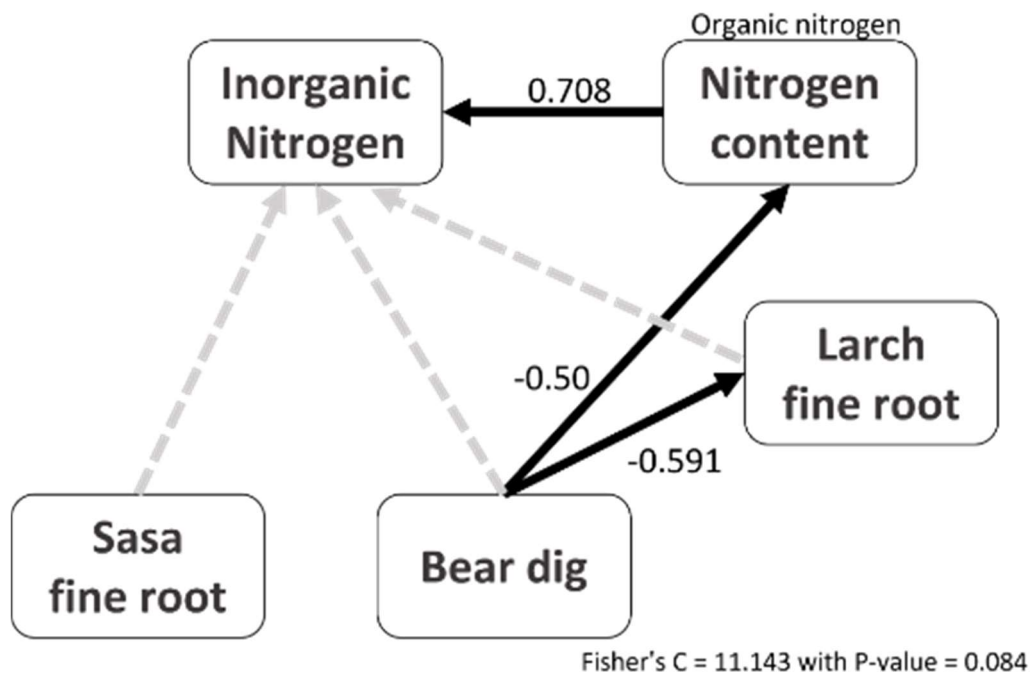
1242 bamboo for soil nutrients is assumed to be ignored in this study because understory dwarf  
1243 bamboo can only affect canopy tree growth via changes in soil properties. In the undug plots  
1244 that were covered with dense dwarf bamboo, there were no significant correlation between fine  
1245 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<sub>4</sub><sup>+</sup>), (F) nitrate (NO<sub>3</sub><sup>-</sup>), (G) inorganic nitrogen (= NH<sub>4</sub><sup>+</sup> + NO<sub>3</sub><sup>-</sup>). †, \*, and \*\* indicate p = 0.06, p < 0.05, and p < 0.01.

1247



1248

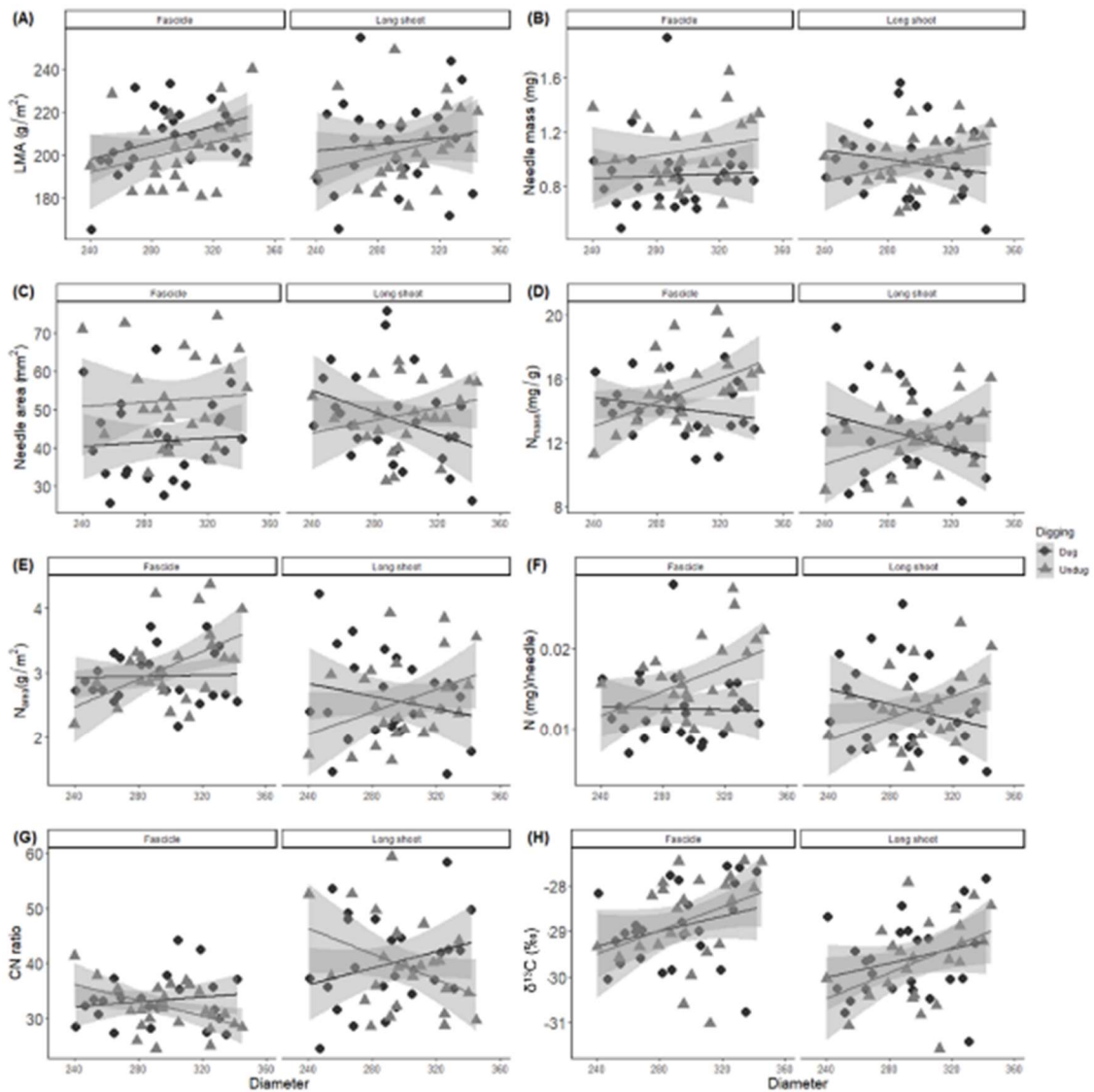
**Figure 2** A piecewise structural equation model showing the causal relationships among brown bear digging, fine root biomass of larches *Larix kaempferi* and dwarf bamboo *Sasa kurilensis*, soil organic nitrogen, soil inorganic nitrogen (=  $\text{NH}_4^+ + \text{NO}_3^-$ ). Black solid lines are 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  $\delta^{13}\text{C}$   
 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).





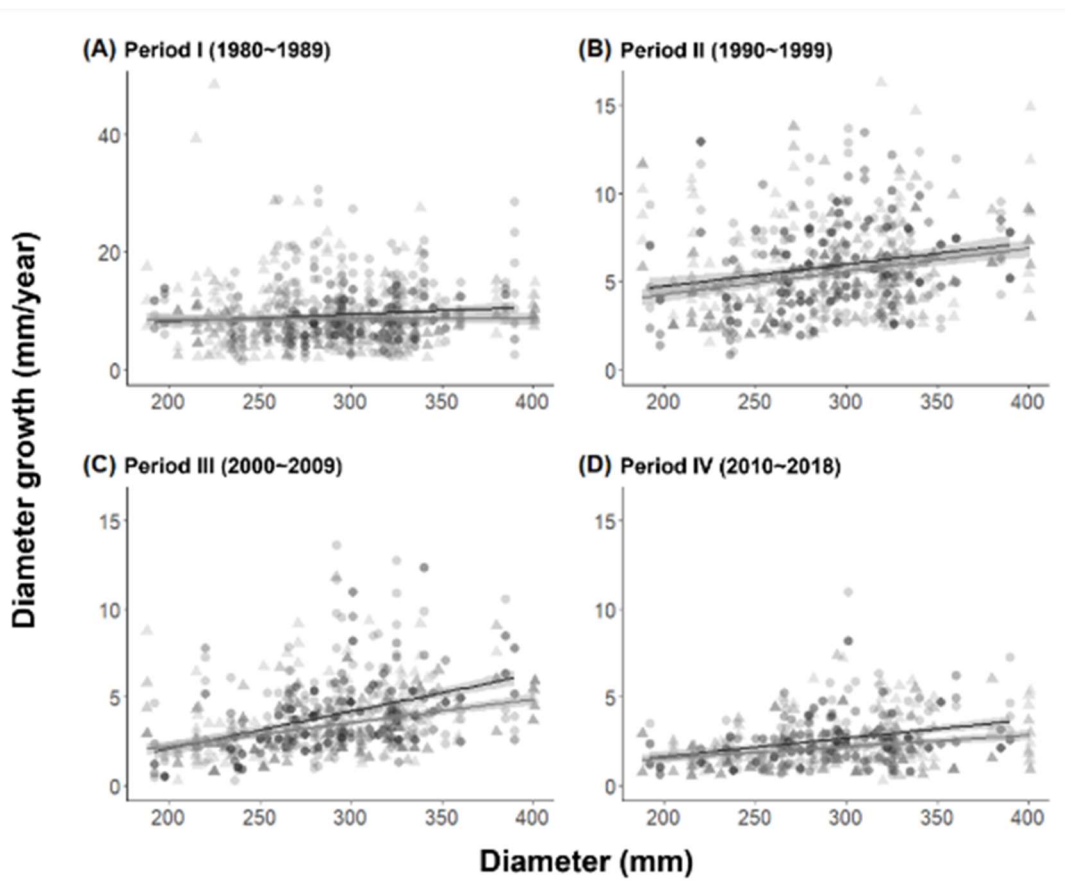
1260

**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 ( $\text{mg}/\text{cm}^2$ ), (B) dry mass per unit needle (mg), (C) Surface area per unit needle ( $\text{mm}^2$ ), (D) needle nitrogen content per unit dry weight ( $\text{mg}/\text{g}$ ), (E) needle nitrogen content per unit surface area ( $\text{g}/\text{m}^2$ ), (F) nitrogen content (mg) per unit needle, (G) the ratio of carbon to nitrogen per unit needle, (H) delta  $^{13}\text{C}$  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

**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.

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  $\delta^{13}\text{C}$  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. elliotii* 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



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 <sup>2</sup> plot)	Average diameter at breast height (mm)	Basal area (m <sup>2</sup> per 100 m <sup>2</sup> 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

1378 **Table 2** Summary of linear mixed models for each needle traits of fascicles and long shoots.

1379 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 <sup>2</sup> )	Fascicles	Digging (D)	0.070	0.044	1.600	0.118
		Tree size (T)	0.002	0.001	2.260	<b>0.029*</b>
		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	<b>0.003**</b>
		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 <sup>2</sup> )	Fascicles	D	-10.409	3.099	-3.360	<b>0.002**</b>
		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	<b>0.034*</b>
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	<b>0.042*</b>
	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	<b>0.034*</b>
Narea (g/m <sup>2</sup> )	Fascicles	D	-0.065	0.028	-2.330	<b>0.025*</b>
		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	<b>0.003**</b>
		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	<b>0.028*</b>
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	<b>0.048*</b>
	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	<b>0.033*</b>
$\delta^{13}\text{C}$	Fascicles	D	-0.086	0.261	-0.330	0.744
		T	0.012	0.005	2.420	<b>0.020*</b>
		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	<b>0.021*</b>
		D*T	-0.007	0.009	-0.710	0.483

1380

\*: p<0.05, \*\*: p<0.01 Supplement??

1381

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	<b>0.001**</b>
	D*T	-0.003	0.008	-0.330	0.743
III (2000~2009)	D	-0.620	0.234	-2.650	<b>0.001**</b>
	T	0.017	0.003	6.700	<b>&lt;0.0001***</b>
	D*T	-0.009	0.005	-1.700	0.092
IV (2010~2018)	D	-0.485	0.166	-2.920	<b>0.0043**</b>
	T	0.009	0.002	5.060	<b>&lt;0.0001***</b>
	D*T	-0.005	0.004	-1.310	0.193

1385 \*\*: $p < 0.01$ , \*\*\*:  $p < 0.001$

1386

## 1387 Chapter 7 General discussion

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

1403 **Causes of the behavior change in brown bears**

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.

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 crows. 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

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

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

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.

1500

1501 **Ecosystem-level effects of the behavior change in brown bears**

1502 In this section, I try to extend the interpretation of the results to ecosystem level consequences  
1503 of the behavior change. In line with a concept provided by Jones et al. (1997) that ecosystem  
1504 engineers have direct and indirect ecosystem effects via trophic and non-trophic effects,  
1505 respectively, I assume two ecosystem effects as ecological consequences of the behavior  
1506 changes in brown bears. First, cicada consumption by bears can affect other predators on  
1507 cicadas and N flux from belowground to aboveground subsystem through decreasing cicada  
1508 emergence density. I estimated how many cicada nymphs were prey upon by brown bears,  
1509 thereby how much nitrogen flux was decreased through cicada predation at the study site.  
1510 Second, non-trophic effects of brown bears through digging for cicada nymphs (i.e. soil  
1511 bioturbation) is assumed as the negative effects of inorganic nitrogen production (Chapter 5). I  
1512 also estimated the spatial extent of brown bear digging for cicadas and the reduced amount of  
1513 inorganic nitrogen concentration in the plantations at the study site.

1514 *Trophic effects of brown bears*

1515 Cicada consumption by brown bears

1516 At first, I estimated the number and biomass of cicadas emerging in 2018 and 2019 based  
1517 on the data on cicada exuviae densities from Chapter 3 and 4. The proportion of larch plantation

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 ( $221.2 \pm 137.4$  g) given by Murray et al. (2017),  $CW$  is dry weight of final instar  
1539 cicada nymphs ( $1.12 \pm 0.20$  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.

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



1567 10 cm. Thus, soil volume displaced by bears in the total area of plantations was estimated at  
1568  $231.55 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$  in 2018 and  $221.38 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$  in 2019. Soil volume displaced by bears in  
1569 the total forest area was estimated at  $43.19 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$  in 2018 and  $41.29 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$  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  $8.64 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$   
1574 in 2018 and 6.74 ha and  $8.26 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$  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)* <sup>1</sup>	Proportion (%)	Mean Digging frequency* <sup>2</sup>	SD	Estimated dug area (ha)* <sup>3</sup>
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

1585 **Table 2** Excavation rates of digging mammals resulting from the literature search

Species	Study area	Ecosystem	Weight (kg)	Behavior	Mean displaced volume (m <sup>3</sup> ha <sup>-1</sup> yr <sup>-1</sup> )	Reference
<b>Brown bear</b> ( <i>Ursus arctos</i> )	<b>Japan</b>	<b>Forest</b>	<b>100~400</b>	<b>F</b>	<b>43.19</b>	<b>This thesis</b>
<b>Brown bear</b> ( <i>Ursus arctos</i> )	<b>Japan</b>	<b>Forest</b>	<b>100~400</b>	<b>F</b>	<b>41.29</b>	<b>This thesis</b>
Grizzly bear ( <i>Ursus arctos horribilis</i> )	Canada	Grassland	100~400	F	4.66	Hall & Lamont (2003)*
American badger ( <i>Taxidea taxus</i> )	USA	Shrubland	8.6	F	3.9	Eldridge (2004)*
European rabbit ( <i>Oryctolagus cuniculus</i> )	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 ( <i>Mus musculus</i> )	Marion Island	Tundra	0.02	N	20.6	Eriksson & Eldridge (2014)*
Botta's pocket gopher ( <i>Thomomys bottae</i> )	USA	Grassland	0.12	N	40	Gabet (2000)*
Mountain pocket gopher ( <i>Thomomys monticola</i> )	USA	Grassland	0.07	N	14.42	Ingles (1952)*
Northern pocket gopher ( <i>Thomomys talpoides</i> )	USA	Grassland	0.13	N	9.6	Ellison (1946)*
European badger ( <i>Meles meles</i> )	UK	Forest	9.9	N	0.03	Coombes & Viles (2015)*
Arctic ground squirrel ( <i>Spermophilus saturatus</i> )	Canada	Grassland	0.22	N	15.4	Price (1971)*

1586

1587 F: foraging, N: nesting

1588 References with asterisk were cited from Haussmann (2015)

1589 **Factors affecting the strength of ecosystem consequences of animal behavior change:**  
1590 **lesson from brown bear digging for cicada nymphs**

1591 Anthropogenic environmental modifications can have the potential to modulate multiple  
1592 ecosystem functions through behaviorally mediated pathways. These pathways may not be  
1593 substantial enough to affect ecosystem functions even if human activities alter animal behavior.  
1594 Thus, detecting factors controlling the strength of behaviorally mediated pathways is important  
1595 for developing our predictability of ecological consequences of human- induced animal  
1596 behavior change (Wilson et al. 2020). Wilson et al. (2020) proposed three factors influencing the  
1597 strength of pathways linking from animal behavior changes to ecosystem consequences: (1)  
1598 ecological importance of a given behavior, (2) population impacts of behavior change, (3) the  
1599 magnitude and persistence of behavior change. However, they provided only a theoretical  
1600 framework, but not practical cases due to a lack of such evidence. Finally, I discuss factors  
1601 influencing the strength of behaviorally mediated pathways based on the findings of my doctor  
1602 thesis.

1603 *(1) Ecological importance of impacted behavior*

1604 I examined ecosystem effects of soil disturbance through brown bear digging and trophic  
1605 cascade to N flux and other cicada predators through cicada predation as the consequences of  
1606 animal behavior change. Digging mammal is a representative form of ecosystem engineers

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

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.

## 1655 Acknowledgements

1656 Firstly, I would like to thank my supervisors, Drs. Tsutom Hiura and Itsuro Koizumi, for  
1657 overall support for my research, and encouragement. Dr. Hiura taught me how scientists should  
1658 be patient during fieldwork, laboratory work, and writing scientific paper. His reminders for  
1659 submitting manuscripts allow me to write paper quickly. Even though I delayed the due date set  
1660 by myself or him every time, I am sure that a reason why now I can quickly write scientific  
1661 papers better than I used to, is his many reminders. I would like also to apologize to him about  
1662 it. He also provided the opportunity for investigating brown bear digging for cicada nymphs. Dr.  
1663 Koizumi comfortably accepted me into his laboratory when I almost lost my affiliation. He  
1664 greatly assisted development of the general introduction and discussion of this thesis. He  
1665 provide me with many broad perspectives to not only science, such as life planning. I also thank  
1666 Drs. Takashi Noda and Naoki Agetsuma for providing many valuable comments. I would like to  
1667 my parents, Yoshinori and Mari Tomita, for economically and mentally supporting from my  
1668 birth. My father said, "*The man who is the most familiar with your research field is yourself. Be*  
1669 *proud of yourself*". I thank my uncle and grandmother at Sapporo for encouraging me since my  
1670 admission to Hokkaido University and renting her house when I lost my house. I thank  
1671 members of Shiretoko Nature Foundation for providing information on brown bear digging for



1672 cicadas and supporting my long stay at study site. Especially, I thank Keita Matsubayashi for  
1673 schedule adjustment of my fieldwork. I also thank H. Maita for field survey assistance and  
1674 encouraging. Finally, I would like to celebrate an encounter between brown bears and cicadas in  
1675 the plantation, a human-created ecosystem. It is really interesting for me that this was the first  
1676 time they had met in recently created plantations even though both species have lived in the  
1677 forests of the study area since time immemorial. It always makes me fun and gives me great  
1678 motivation toward my overall academic activities.

1679

1680   **References**

- 1681   Adachi, T., Uehara, A., Kuwahara, Y., & Takatsuki, S. (2016). Seasonal food habits of the  
1682       Japanese marten (*Martes melampus melampus*) at Otome Highland, central Japan.  
1683       Honyurui Kagaku (Mammalian Science) 56: 17-25. [in Japanese with English abstract]
- 1684   Aerts, R., and Honnay, O. (2011). Forest restoration, biodiversity and ecosystem functioning.  
1685       *BMC Ecology* 11: 29.
- 1686   Ando, Y., Utsumi, S., & Ohgushi, T. (2017). Aphid as a network creator for the plant associated  
1687       arthropod community and its consequence for plant reproductive success. *Functional*  
1688       *Ecology* 31: 632-641.
- 1689   Andrade, S. C., Rossi, G. D., & Martinelli, N. M. (2020). Dispersion Pattern of Giant Cicada  
1690       (Hemiptera: Cicadidae) in a Brazilian Coffee Plantation. *Environmental Entomology* 49:  
1691       1019–1025.
- 1692   Barnosky, A. D. et al. (2012). Approaching a state shift in Earth’s biosphere. *Nature*, 486: 52–  
1693       58.
- 1694   Barrios-Garcia, M. N., Classen, A. T., & Simberloff, D. (2014). Disparate responses of above-  
1695       and belowground properties to soil disturbance by an invasive mammal. *Ecosphere* 5:1–13.
- 1696   Barrios-Garcia, M. N., and S. A. Ballari. (2012). Impact of wild boar (*Sus scrofa*) in its  
1697       introduced and native range: a review. *Biol Invasions* 14:2283–2300.
- 1698   Barry, J. M. et al. (2019). Pumas as ecosystem engineers: Ungulate carcasses support beetle  
1699       assemblages in the Greater Yellowstone Ecosystem. *Oecologia* 189: 577–586.

- 1700 Belanger, R. J., Edwards, M. A., Carbyn, L. N., & Nielsen, S. E. (2020). Evaluating trade-offs  
1701 between forage, biting flies, and footing on habitat selection by wood bison (*Bison bison*  
1702 *athabascaae*). *Canadian Journal Zoology* 98: 254–261.
- 1703 Bell, W. J. (1991). Searching behavior: the behavioral ecology of finding resources. Chapman  
1704 and Hall.
- 1705 Bellemain, E., Swenson, J. E., & Taberlet, P. (2006). Mating strategies in relation to sexually  
1706 selected infanticide in a non - social carnivore: The brown bear. *Ethology* 112: 238-246.
- 1707 Bennett, E. M., Peterson, G. D., & Gordon, L. J. (2009). Understanding relationships among  
1708 multiple ecosystem services. *Ecology Letters* 12: 1394–1404.
- 1709 Bentler, P. M. (1990). Comparative fit indexes in structural models. *Psychological Bulletin* 107:  
1710 238–246.
- 1711 Berke, S. K. (2010). Functional groups of ecosystem engineers: a proposed classification with  
1712 comments on current issues. *Integrative and Comparative Biology* 50: 147-157.
- 1713 Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial  
1714 ecosystems of the western United States. *Biological Conservation* 142: 2401-2414.
- 1715 Blattert, C., Lemm, R., Thees, O., Lexer, M. J., & Hanewinkel, M. (2017). Management of  
1716 ecosystem services in mountain forests: Review of indicators and value functions for  
1717 model based multi-criteria decision analysis. *Ecological Indicators* 79: 391–409.
- 1718 Blejwas, K. M., Williams, C. L., Shin, G. T., McCullough, D. R., & Jaeger, M. M. (2006).  
1719 Salivary DNA evidence convicts breeding male coyotes of killing sheep. *The Journal of*  
1720 *wildlife management* 70: 1087-1093.

- 1721 Block, W. M., Franklin, A. B., Ward Jr, J. P., Ganey, J. L., & White, G. C. (2001). Design and  
 1722 Implementation of Monitoring Studies to Evaluate the Success of Ecological Restoration  
 1723 on Wildlife. *Restoration Ecology* 9: 293–303.
- 1724 Bogale, B. A., Aoyama, M., & Sugita, S. (2014). Spontaneous discrimination of food quantities  
 1725 in the jungle crow, *Corvus macrorhynchos*. *Animal Behaviour* 94: 73-78.
- 1726 Bojarska, K., & N. Selva., (2012) Spatial patterns in brown bear *Ursus arctos* diet: the role of  
 1727 geographical and environmental factors. *Mammal Review* 42: 120– 143.
- 1728 Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P., & Sayer, J. (2008). Plantation forests  
 1729 and biodiversity: Oxymoron or opportunity? *Biodiversity and Conservation* 17: 925–951.
- 1730 Bueno, C. G., Azorín, J., Gómez-García, D., Alados, C. L., & Badía, D. (2013). Occurrence and  
 1731 intensity of wild boar disturbances, effects on the physical and chemical soil properties of  
 1732 alpine grasslands. *Plant and soil* 373: 243-256.
- 1733 Butler, D. R. (1992). The grizzly bear as an erosional agent in mountainous terrain;The grizzly  
 1734 bear as an erosional agent in mountainous terrain. *Zeitschrift für Geomorphologie* 36:179–  
 1735 189.
- 1736 Bétard, F. (2021). Insects as zoogeomorphic agents: an extended review. *Earth Surface*  
 1737 *Processes and Landforms* 46: 89-109.
- 1738 Canals, R. M., Herman, D. J., & Firestone, M. K. (2003). How disturbance by fossorial  
 1739 mammals alters N cycling in a California annual grassland. *Ecology* 84: 875–881.
- 1740 Candolin, U., & Wong, B. B. M. (2012). Behavioural Responses to a Changing World:  
 1741 Mechanisms and Consequences. Oxford University Press.

- 1742 Chazdon, R.L. (2008). Beyond Deforestation: Restoring Forests and Ecosystem Services on  
1743 Degraded Lands. *Science* 320: 1458–1460.
- 1744 Ciarkowska, K. and Miechówka, A. 2019. The effect of understory on cation binding reactions  
1745 and aluminium behaviour in acidic soils under spruce forest stands (Southern Poland). -  
1746 *Biogeochemistry* 143: 55–66.
- 1747 Coggan, N. V., Hayward, M. W., & Gibb, H. (2018). A global database and “state of the field”  
1748 review of research into ecosystem engineering by land animals. *Journal of Animal Ecology*  
1749 87: 974–994.
- 1750 Cristescu, B., Stenhouse, G. B., & Boyce, M. S. (2015). Grizzly bear diet shifting on reclaimed  
1751 mines. *Global Ecology and Conservation*. 4: 207–220.
- 1752 Cunningham, S. C., Mac Nally, R., Baker, P. J., Cavagnaro, T. R., Beringer, J., Thomson, J. R.,  
1753 & Thompson, R. M. (2015). Balancing the environmental benefits of reforestation in  
1754 agricultural regions. *Perspective in Plant Ecology and Evolution and Systematics* 17: 301–  
1755 317.
- 1756 Côté, S. D. (2005). Extirpation of a large black bear population by introduced white-tailed deer.  
1757 *Conservation Biology* 19: 1668-1671.
- 1758 Côté, S. D., Rooney, T. P., Tremblay, J. P., Dussault, C., & Waller, D. M. (2004). Ecological  
1759 impacts of deer overabundance. *Annu. Rev. Ecol. Evol. Syst.* 35: 113-147.
- 1760 Côté, S. D., Rooney, T. P., Tremblay, J. P., Dussault, C., & Waller, D. M. (2004). Ecological  
1761 impacts of deer overabundance. *Annual Review of Ecology, Evolution, and*  
1762 *Systematics* 35: 113-147.

- 1763 Davidson, A. D., Detling, J. K., & Brown, J. H. (2012). Ecological roles and conservation  
1764 challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers*  
1765 *in Ecology and the Environment* 10: 477-486.
- 1766 Davies, A. B., & Asner, G. P. (2019). Elephants limit aboveground carbon gains in African  
1767 savannas. *Global Change Biology*, 25(4), 1368–1382.
- 1768 Davies, A. B., Tambling, C. J., Kerley, G. I., & Asner, G. P. (2016). Effects of Vegetation  
1769 Structure on the Location of Lion Kill Sites in African Thicket. *PLOS ONE* 11: e0149098.
- 1770 Davies, G. T. O., J. B. Kirkpatrick, E. Z. Cameron, S. Carver, and C. N. Johnson. (2019).  
1771 Ecosystem engineering by digging mammals: effects on soil fertility and condition in  
1772 Tasmanian temperate woodland. *Royal Society Open Science* 6:180621.
- 1773 Deecke, V. B. (2012). Tool-use in the brown bear (*Ursus arctos*). *Animal Cognition*, 15: 725–  
1774 730.
- 1775 Dennis, R. A., Meijaard, E., Nasi, R., & Gustafsson, L. (2008). Biodiversity conservation in  
1776 Southeast Asian timber concessions: a critical evaluation of policy mechanisms and  
1777 guidelines. *Ecology and Society* 13.
- 1778 Derhé, M.A., Murphy, H., Monteith, G., and Menéndez, R. 2016. Measuring the success of  
1779 reforestation for restoring biodiversity and ecosystem functioning. *Journal of Applied*  
1780 *Ecology*. 53: 1714–1724.
- 1781 Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014).  
1782 Defaunation in the Anthropocene. *Science*, 345: 401–406.
- 1783 Dybas, H.S., and Lloyd, M. 1974. The habitats of 17-year periodical cicadas (Homoptera:  
1784 Cicadidae: *Magicicada* Spp.). *Ecological Monograph* 44: 279–324.

- 1785 Eby, S. L., Anderson, T. M., Mayemba, E. P., & Ritchie, M. E. (2014) The effect of fire on  
1786 habitat selection of mammalian herbivores: the role of body size and vegetation  
1787 characteristics. *Journal of Animal Ecology* 83: 1196–1205.
- 1788 Eisenhauer, N., Bowker, M. A., Grace, J. B., & Powell, J. R. (2015) From patterns to causal  
1789 understanding: Structural equation modeling (SEM) in soil ecology. *Pedobiologia* 58: 65–  
1790 72.
- 1791 Elfström, M., Støen, O. G., Zedrosser, A., Warrington, I., & Swenson, J. E. (2013). Gut retention  
1792 time in captive brown bears *Ursus arctos*. *Wildlife Biology* 19: 317-324.
- 1793 Elfström, M., Zedrosser, A., Støen, O. G., & Swenson, J. E. (2014). Ultimate and proximate  
1794 mechanisms underlying the occurrence of bears close to human settlements: review and  
1795 management implications. *Mammal Review* 44: 5-18.
- 1796 Elgmork, K., and Kaasa, J. 1992. Food habits and foraging of the brown bear *Ursus arctos* in  
1797 central south Norway. *Ecography* 15: 101–110.
- 1798 Ellison, A. M. et al. 2005. Loss of foundation species: consequences for the structure and  
1799 dynamics of forested ecosystems. *Frontiers in Ecology and Environment* 3: 479–486.
- 1800 Enquist, B. J., Abraham, A. J., Harfoot, M. B. J., Malhi, Y., & Doughty, C. E. (2020). The  
1801 megabiota are disproportionately important for biosphere functioning. *Nature*  
1802 *Communications* 11: 699.
- 1803 Estes, J. A., & Duggins, D. O. (1995). Sea Otters and Kelp Forests in Alaska: Generality and  
1804 Variation in a Community Ecological Paradigm. *Ecological Monographs*, 65: 75–100.
- 1805 Estes, J. A., et al (2011). Trophic Downgrading of Planet Earth. *Science* 333: 301–306.

- 1806 Fehlmann, G., O'riain, M. J., Fürtbauer, I., & King, A. J. (2020). Behavioral Causes, Ecological  
1807 Consequences, and Management Challenges Associated with Wildlife Foraging in Human-  
1808 Modified Landscapes. *BioScience* 71: biaa129.
- 1809 Fellner, H., Dirnberger, G. F., & Sterba, H. (2016). Specific leaf area of European Larch (*Larix*  
1810 *decidua* Mill.). *Trees* 30: 1237–1244.
- 1811 Fleming, P. A., & Bateman, P. W. (2018). Novel predation opportunities in anthropogenic  
1812 landscapes. *Animal Behaviour* 138: 145–155.
- 1813 Fleming, P. A., Anderson, H., Prendergast, A. S., Bretz, M. R., Valentine, L. E., & Hardy, G. E.  
1814 S. (2014). Is the loss of Australian digging mammals contributing to a deterioration in  
1815 ecosystem function?. *Mammal Review* 44: 94-108.
- 1816 Frank, S.C., Steyaert, S.M.J.G., Swenson, J.E., Storch, I., Kindberg, J., Barck, H., and  
1817 Zedrosser, A. (2015). A “clearcut” case? Brown bear selection of coarse woody debris and  
1818 carpenter ants on clearcuts. *Forest Ecology and Management*. 348: 164–173.
- 1819 Franklin, C. M., Nielsen, S. E., & Macdonald, S. E. (2019). Understory vascular plant responses  
1820 to retention harvesting with and without prescribed fire. *Canadian Journal Forest Research*  
1821 49: 1087–1100.
- 1822 Fuentes-Montemayor, E., Ferryman, M., Watts, K., Macgregor, N.A., Hambly, N., Brennan, S.,  
1823 Coxon, R., Langridge, H., and Park, K.J. (2020). Small mammal responses to long-term  
1824 large-scale woodland creation: the influence of local and landscape-level attributes.  
1825 *Ecological Applications* 30: e02028.
- 1826 Fujii, S., Mori, A.S., Koide, D., Makoto, K., Matsuoka, S., Osono, T., and Isbell, F. (2017).  
1827 Disentangling relationships between plant diversity and decomposition processes under  
1828 forest restoration. *Journal of Applied Ecology*. 54: 80–90.



- 1829 Gabet, E. J., Reichman, O. J., & Seabloom, E. W. (2003). The effects of bioturbation on soil  
1830 processes and sediment transport. *Annual Review of Earth and Planetary Sciences* 31: 249-  
1831 273.
- 1832 Gastón, A., Blázquez-Cabrera, S., Mateo-Sánchez, M. C., Simón, M. A., & Saura, S (2019). The  
1833 role of forest canopy cover in habitat selection: insights from the Iberian lynx. *European*  
1834 *Journal of Wildlife Research* 65: 1–10.
- 1835 Gil, M. A., & Hein, A. M. (2017). Social interactions among grazing reef fish drive material  
1836 flux in a coral reef ecosystem. *PNAS* 114: 4703–4708.
- 1837 Gilbert, B. K. (1999) Opportunities for social learning in bears. Pages 225– 235 in H. O. Box  
1838 and K. R. Gibson, editors. *Mammalian social learning: comparative and ecological*  
1839 *perspectives*. Cambridge University Press, Cambridge, UK.
- 1840 Gittleman, J. L. (1986). Carnivore brain size, behavioral ecology, and phylogeny. *Journal of*  
1841 *Mammalogy* 67: 23-36.
- 1842 Gittleman, J. L. (1991). Carnivore olfactory bulb size: allometry, phylogeny and  
1843 ecology. *Journal of Zoology* 225: 253-272.
- 1844 Goldewijk, K.K. (2001). Estimating global land use change over the past 300 years: The HYDE  
1845 database. *Global Biogeochemical Cycles* 15: 417–433.
- 1846 Gorini, L., Linnell, J. D., May, R., Panzacchi, M., Boitani, L., Odden, M., & Nilsen, E. B.  
1847 (2012). Habitat heterogeneity and mammalian predator-prey interactions. - *Mammal*  
1848 *Review* 42: 55–77.
- 1849 Grace, J. B. (2006). *Structural Equation Modeling and Natural Systems*. - Cambridge University  
1850 Press.

- 1851 Grace, J. B. et al. (2010). On the specification of structural equation models for ecological  
1852 systems. *Ecology Monograph* 80: 67–87.
- 1853 Große, C., Kaczensky, P., and Knauer, F. (2003). Ants: A food source sought by Slovenian  
1854 brown bears (*Ursus arctos*)? *Candian Journal of Zoology* 81: 1996–2005.
- 1855 Guntiñas, M. E., M. C. Leirós, C. Trasar-Cepeda, and F. Gil-Sotres. (2012). Effects of moisture  
1856 and temperature on net soil nitrogen mineralization: A laboratory study. *European Journal*  
1857 *of Soil Biology* 48:73–80.
- 1858 Hagar, J. C. (2007). Wildlife species associated with non-coniferous vegetation in Pacific  
1859 Northwest conifer forests: A review. *Forest Ecology and Management* 246: 108–122.
- 1860 Hahus, S. C., and K. G. Smith. (1990). Food habits of *Blarina*, *Peromyscus*, and *Microtus* in  
1861 relation to an emergence of periodical cicadas (*Magicicada*). *Journal of Mammalogy* 71:  
1862 249– 252.
- 1863 Hanba, Y. T., Miyazawa, S.-I., & Terashima, I. (1999). The influence of leaf thickness on the  
1864 CO<sub>2</sub> transfer conductance and leaf stable carbon isotope ratio for some evergreen tree  
1865 species in Japanese warm-temperate forests. *Functional Ecology* 13: 632–639.
- 1866 Hata, A., Takada, M.B., Nakashita, R., Fukasawa, K., Oshida, T., Ishibashi, Y., and Sato, Y.  
1867 (2017). Stable isotope and DNA analyses reveal the spatial distribution of crop-foraging  
1868 brown bears. *Journal of Zoology* 303: 207–217.
- 1869 Haussmann, N. S. (2017). Soil movement by burrowing mammals: a review comparing  
1870 excavation size and rate to body mass of excavators. *Progress in Physical Geography* 41:  
1871 29-45.
- 1872 Hawlena, D., Strickland, M. S., Bradford, M. A., & Schmitz, O. J. (2012). Fear of predation  
1873 slows plant-litter decomposition. *Science* 336: 1434-1438.

- 1874 Hayashi, M., and Y. Saisho. (2011) *The Cicadidae of Japan*. Seibundo-shinkosha, Tokyo, Japan.  
1875 [In Japanese.]
- 1876 Hebblewhite, M., Merrill, E. H., & McDonald, T. L. (2005). Spatial decomposition of predation  
1877 risk using resource selection functions: An example in a wolf-elk predator-prey system.  
1878 *Oikos* 111: 101–111.
- 1879 Heikkinen, R. K., Luoto, M., Virkkala, R., & Rainio, K. (2004). Effects of habitat cover,  
1880 landscape structure and spatial variables on the abundance of birds in an agricultural–forest  
1881 mosaic. *Journal of Applied Ecology* 41: 824–835.
- 1882 Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J., & Dill, L. M. (2009). Towards a  
1883 predictive framework for predator risk effects: The interaction of landscape features and  
1884 prey escape tactics. *Journal of Animal Ecology* 78: 556–562.
- 1885 Helfield, J.M., and Naiman, R.J. (2006). Keystone interactions: Salmon and bear in riparian  
1886 forests of Alaska. *Ecosystems* 9: 167–180.
- 1887 Herrero, S., Smith, T., DeBruyn, T.D., Gunther, K., and Matt, C.A. (2005). Brown bear  
1888 habituation to people—safety, risks, and benefits. *Wildlife Society Bulletin* 33: 362–373.
- 1889 Hewitt, D. G., & Robbins, C. T. (1996). Estimating grizzly bear food habits from fecal analysis.  
1890 *Wildlife Society Bulletin* 24: 547–550.
- 1891 Hiura, T. et al. 1996. Age structure and response to fine-scale disturbances of *Abies*  
1892 *sachalinensis*, *Picea jezoensis*, *Picea glehnii*, and *Betula ermanii* growing under the  
1893 influence of a dwarf bamboo understory in northern Japan. *Canadian Journal of Forest*  
1894 *Research* 26: 289–297.
- 1895 Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation  
1896 and restoration. *TREE* 24: 599–605.

- 1897 Hopkins, J. B. III. (2013) Use of genetics to investigate socially learned foraging behavior in  
1898 free-ranging black bears. *Journal of Mammalogy* 94: 1214– 1222.
- 1899 Hu, L. T. and Bentler, P. M. (1999). Cutoff criteria for fit indexes in covariance structure  
1900 analysis: Conventional criteria versus new alternatives. *Structural Equation Model* 6: 1–55.
- 1901 Hunter MD (2016). The phytochemical landscape: linking trophic interactions and nutrient  
1902 dynamics. Princeton University Press, Princeton
- 1903 Hyvarinen, O., Te Beest, M., le Roux, E., Kerley, G., de Groot, E., Vinita, R., & Cromsigt, J. P.  
1904 G. M. (2021). Megaherbivore impacts on ecosystem and Earth system functioning: The  
1905 current state of the science. *Ecography*, 44(11), 1579–1594.
- 1906 Ishii, H. T., Kobayashi, T., Uemura, S., Takahashi, K., Hanba, Y. T., Sumida, A., & Hara, T.  
1907 (2008). Removal of understory dwarf bamboo ( *Sasa kurilensis* ) induces changes in water-  
1908 relations characteristics of overstory *Betula ermanii* trees. *Journal of Forest Research* 13:  
1909 101–109.
- 1910 Johns, R., Ozaki, K., & Tobita, H. (2012). Dietary mixing within the crown of a deciduous  
1911 conifer enhances the fitness of a specialist sawfly. *Animal Behaviour* 84: 1393–1400.
- 1912 Johnson, C. N., Balmford, A., Brook, B. W., Buettel, J. C., Galetti, M., Guangchun, L., &  
1913 Wilmshurst, J. M. (2017). Biodiversity losses and conservation responses in the  
1914 Anthropocene. *Science* 356: 270-275.
- 1915 Jones, C. G., J. H. Lawton, and M. Shachak. (1994) Organisms as Ecosystem Engineers. *Oikos*  
1916 69: 373–386.
- 1917 Jones, C. G., Lawton, J. H., & Shachak, M. (1997). Positive and Negative Effects of Organisms  
1918 as Physical Ecosystem Engineers. *Ecology* 78: 1946–1957.

- 1919 Jonkel, C. J. and Cowan, I. McT. (1971). The black bear in the spruce-fir forest. *Wildlife*  
 1920 *Monograph* 27: 1–57.
- 1921 Kaji, K. (1988) Sika deer. Pages 155– 180 in N. Ohtaishi and H. Nakagawa, editors. *Animals of*  
 1922 *Shiretoko*. Hokkaido University Press, Sapporo, Japan. [In Japanese with an English  
 1923 abstract.]
- 1924 Kaji, K., H. Okada, M. Kohira, and M. Yamanaka. (2006) The Shiretoko sika deer herd. Pages  
 1925 221– 224 in D. R. McCullough, K. Kaji, and M. Yamanaka, editors. *Wildlife in Shiretoko*  
 1926 *and Yellowstone National Parks. Lessons in Wildlife Conservation from Two World*  
 1927 *Heritage Sites*. Shiretoko Nature Foundation, Syari, Japan.
- 1928 Kitaoka, S., and Koike, T. (2004). Invasion of broad-leaf tree species into a larch plantation:  
 1929 seasonal light environment, photosynthesis and nitrogen allocation. *Physiologia*  
 1930 *Plantarum*. 121: 604–611.
- 1931 Kobayashi, K. and Sato, Y (2012). Increased brown bear predation on sika deer fawns following  
 1932 a deer population irruption in eastern Hokkaido, Japan. *Ecological Research* 27: 849–855.
- 1933 Kohira, M., H. Okada, M. Nakanishi, and M. Yamanaka. (2009) Modeling the effects of human-  
 1934 caused mortality on the brown bear population on the Shiretoko Peninsula, Hokkaido,  
 1935 Japan. *Ursus* 20: 12– 22.
- 1936 Koike, S., Kasai, S., Yamazaki, K., & Furubayashi, K. (2008). Fruit phenology of *Prunus*  
 1937 *jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser. *Ecological*  
 1938 *Research* 23: 385-392.
- 1939 Koshino, Y., Kudo, H., and Kaeriyama, M. (2013). Stable isotope evidence indicates the  
 1940 incorporation into Japanese catchments of marine-derived nutrients transported by  
 1941 spawning Pacific Salmon. *Freshwater Biology* 58: 1864–1877.

- 1942 Kubo, T., and Shoji, Y. (2014). Spatial tradeoffs between residents' preferences for brown bear  
 1943 conservation and the mitigation of human-bear conflicts. *Biological Conservation*. 176:  
 1944 126–132.
- 1945 Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamailié-Jammes, S., Sand, H., Lone, K., &  
 1946 Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in  
 1947 anthropogenic landscapes. *Proceedings of the Royal Society B: Biological Sciences* 283:  
 1948 20161625.
- 1949 Kurek, P., Kapusta, P., & Holeksa, J. (2014). Burrowing by badgers (*Meles meles*) and foxes  
 1950 (*Vulpes vulpes*) changes soil conditions and vegetation in a European temperate forest.  
 1951 *Ecological Research* 29: 1–11.
- 1952 Kéfi, S., et al. (2012) More than a meal... integrating non-feeding interactions into food webs.  
 1953 *Ecology Letters* 15: 291-300.
- 1954 Lacher, T. E., et al. (2019). The functional roles of mammals in ecosystems. *Journal of*  
 1955 *Mammalogy* 100: 942–964.
- 1956 Lantschner, M. V., Rusch, V., & Hayes, J. P. (2012). Habitat use by carnivores at different  
 1957 spatial scales in a plantation forest landscape in Patagonia, Argentina. *Forest Ecology and*  
 1958 *Management* 269: 271–278.
- 1959 Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., John Kress, W., & Chazdon, R. L.  
 1960 (2014). The relationship between tree biodiversity and biomass dynamics changes with  
 1961 tropical forest succession. *Ecology Letters* 17: 1158–1167.
- 1962 Laverman, A. M., H. R. Zoomer, H. W. van Verseveld, and H. A. Verhoef. (2000). Temporal and  
 1963 spatial variation of nitrogen transformations in a coniferous forest soil. *Soil Biology and*  
 1964 *Biochemistry* 32:1661–1670.

- 1965 Law, B.S., Chidel, M., Brassil, T., Turner, G., and Gonsalves, L. (2017). Winners and losers  
 1966 among mammals and nocturnal birds over 17 years in response to large-scale eucalypt  
 1967 plantation establishment on farmland. *Forest Ecology and Management* 399: 108–119.
- 1968 Le, H. D., Smith, C., Herbohn, J., & Harrison, S. (2012). More than just trees: assessing  
 1969 reforestation success in tropical developing countries. *Journal of Rural Studies* 28: 5-19.
- 1970 LeBauer, D. S., and K. K. Treseder. (2008). Nitrogen limitation of net primary productivity in  
 1971 terrestrial ecosystems is globally distributed. *Ecology* 89: 371–379.
- 1972 Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J., and Pelletier, F. 2016.  
 1973 Quantifying consistent individual differences in habitat selection. *Oecologia*, 180: 697–  
 1974 705.
- 1975 Lee, Y. F., Lin, Y. H., & Wu, S. H. (2010). Spatiotemporal variation in cicada diversity and  
 1976 distribution, and tree use by exuviating nymphs, in east Asian Tropical Reef-Karst forests  
 1977 and forestry plantations. *Annals of the Entomological Society of America* 103: 216–226.
- 1978 Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology,  
 1979 evolution, and systematics. *Methods in Ecology and Evolution* 7: 573–579.
- 1980 Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, Innovations and Evolution in Birds and  
 1981 Primates. *Brain, Behavior and Evolution* 63: 233–246.
- 1982 Lesmerises, R., and St-Laurent, M.-H. (2017). Not accounting for interindividual variability can  
 1983 mask habitat selection patterns: a case study on black bears. *Oecologia* 185: 415–425.
- 1984 Levi, T., et al. (2020). Community ecology and conservation of bear-salmon ecosystems.  
 1985 *Frontiers in Ecology and Evolution* 8: 433.

- 1986 Lima, S. L. and Zollner, P. A. (1996). Towards a behavioral ecology of ecological landscapes. –  
1987 *TREE* 11: 131–135.
- 1988 Lindenmayer, D. B., Fischer, J., Felton, A., Crane, M., Michael, D., Macgregor, C., Montague-  
1989 Drake, R., Manning, A., & Hobbs, R. J. (2008). Novel ecosystems resulting from landscape  
1990 transformation create dilemmas for modern conservation practice. *Conservation Letters* 1:  
1991 129–135.
- 1992 Linnell, J. D., Odden, J., Smith, M. E., Aanes, R., & Swenson, J. E. (1999). Large carnivores  
1993 that kill livestock: do "problem individuals" really exist?. *Wildlife Society Bulletin* 27: 698-  
1994 705.
- 1995 Liu, Z., Hikosaka, K., Li, F., & Jin, G. (2020). Variations in leaf economics spectrum traits for  
1996 an evergreen coniferous species: Tree size dominates over environment factors. *Functional*  
1997 *Ecology* 34: 458–467.
- 1998 Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D., Odden, J., Remmen, J., & Mysterud, A.  
1999 (2014). Living and dying in a multi-predator landscape of fear: roe deer are squeezed by  
2000 contrasting pattern of predation risk imposed by lynx and humans. *Oikos* 123: 641–651.
- 2001 Long, M. S., Litton, C. M., Giardina, C. P., Deenik, J., Cole, R. J., & Sparks, J. P. (2017).  
2002 Impact of nonnative feral pig removal on soil structure and nutrient availability in  
2003 Hawaiian tropical montane wet forests. *Biological Invasions*, 19: 749–763.
- 2004 Lovari, S., Valier, P., and Lucchi, M.R. (1994). Ranging behaviour and activity of red foxes  
2005 (*Vulpes vulpes*: Mammalia) in relation to environmental variables, in a Mediterranean  
2006 mixed pinewood. *Journal of Zoology* 232: 323–339.
- 2007 Maisey, A. C., Haslem, A., Leonard, S. W., & Bennett, A. F. (2021). Foraging by an avian  
2008 ecosystem engineer extensively modifies the litter and soil layer in forest ecosystems.  
2009 *Ecological Applications* 31: e02219.



- 2010 Mallen-Cooper, M., S. Nakagawa, and D. J. Eldridge. (2019) Global meta-analysis of soil-  
 2011 disturbing vertebrates reveals strong effects on ecosystem patterns and processes. *Global*  
 2012 *Ecology and Biogeography* 28: 661–679.
- 2013 Manlick, P. J., & Newsome, S. D. (2021). Adaptive foraging in the Anthropocene: can  
 2014 individual diet specialization compensate for biotic homogenization?. *Frontiers in Ecology*  
 2015 *and the Environment* 19: 510-518.
- 2016 Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allaine, D., & Swenson, J. E. (2010).  
 2017 Coping with human disturbance: Spatial and temporal tactics of the brown bear (*Ursus*  
 2018 *arctos*). *Canadian Journal of Zoology* 88: 875–883.
- 2019 Martinuzzi, S., Vierling, L. A., Gould, W. A., Falkowski, M. J., Evans, J. S., Hudak, A. T., &  
 2020 Vierling, K. T. (2009). Mapping snags and understory shrubs for a LiDAR-based  
 2021 assessment of wildlife habitat suitability. *Remote Sensing and Environment* 113: 2533–  
 2022 2546.
- 2023 Matsubayashi, J., Morimoto, J., Mano, T., Aryal, A., and Nakamura, F. (2014). Using stable  
 2024 isotopes to understand the feeding ecology of the Hokkaido brown bear (*Ursus arctos*) in  
 2025 Japan. *Ursus* 25: 87–97.
- 2026 Mattingly, W.B., and Flory, S.L. (2011). Plant architecture affects periodical cicada oviposition  
 2027 behavior on native and non-native hosts. *Oikos* 120: 1083–1091.
- 2028 Mattson, D. J. (1997). Selection of microsites by grizzly bears to excavate biscuitroots. *Journal*  
 2029 *of Mammalogy* 78: 228–238.
- 2030 Mattson, D. J., Gillin, C. M., Benson, S. A., & Knight, R. R. (1991). Bear feeding activity at  
 2031 alpine insect aggregation sites in the Yellowstone ecosystem. *Canadian Journal of Zoology*  
 2032 69: 2430–2435.

- 2033 Mattson, D.J. (2001). Myrmecophagy by Yellowstone grizzly bears. *Canadian Journal of*  
2034 *Zoology* 79: 779–793.
- 2035 Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at  
2036 multiple scales. *Ecoscience* 16: 238–247.
- 2037 Mazur, R. and Seher, V. (2008). Socially learned foraging behaviour in wild black bears, *Ursus*  
2038 *americanus*. *Animal Behavior* 75: 1503–1508.
- 2039 Mazzolli, M. (2010). Mosaics of exotic forest plantations and native forests as habitat of  
2040 pumas. *Environmental Management* 46: 237-253.
- 2041 McClelland, C. J., Coops, N. C., Kearney, S. P., Burton, A. C., Nielsen, S. E., & Stenhouse, G.  
2042 B. (2020). Variations in grizzly bear habitat selection in relation to the daily and seasonal  
2043 availability of annual plant-food resources. *Ecological Informatics* 58: 101116.
- 2044 McLellan, B. N., & Hovey, F. W. (1995). The diet of grizzly bears in the Flathead River  
2045 drainage of southeastern British Columbia. *Canadian Journal of Zoology* 73: 704-712.
- 2046 Meysman, F. J., J. J. Middelburg, and C. H. Heip (2006) Bioturbation: a fresh look at Darwin's  
2047 last idea. *TREE* 21: 688– 695.
- 2048 Milakovic, B., Parker, K. L., Gustine, D. D., Lay, R. J., Walker, A. B., & Gillingham, M. P.  
2049 (2012). Seasonal habitat use and selection by grizzly bears in Northern British Columbia.  
2050 *Journal of Wildlife Management* 76: 170–180.
- 2051 Ministry of the Environment the Government of Japan. (2017). Report on a survey for  
2052 evaluating the impacts of deer herbivory on vegetation structure [in Japanese].
- 2053 Morehouse, A. T., Graves, T. A., Mikle, N., & Boyce, M. S. (2016). Nature vs. nurture: evidence  
2054 for social learning of conflict behaviour in grizzly bears. *PLoS One* 11: e0165425.

- 2055 Moriyama, M. and Numata, H. (2015). Urban soil compaction reduces cicada diversity.  
2056 *Zoological Letters* 1: 19.
- 2057 Moriyama, M., Matsuno, T., and Numata, H. (2016). Dead-twig discrimination for oviposition  
2058 in a cicada, *Cryptotympana facialis* (Hemiptera: Cicadidae). *Applied Entomology and*  
2059 *Zoology* 51: 615–621.
- 2060 Morris, D. W. (2003). How can I apply theories of habitat selection to wildlife conservation and  
2061 management? *Wildlife Research* 30: 303–319.
- 2062 Morrison, M. L., Marcot, B., & Mannan, W. (2012). *Wildlife-Habitat Relationships: Concepts*  
2063 *and Applications*. - Island Press.
- 2064 Moss, W. E., Alldredge, M. W., Logan, K. A., & Pauli, J. N. (2016). Human expansion  
2065 precipitates niche expansion for an opportunistic apex predator (*Puma concolor*). *Scientific*  
2066 *Reports* 6: 39639.
- 2067 Murray, M. H., Fassina, S., Hopkins III, J. B., Whittington, J., & St. Clair, C. C. (2017).  
2068 Seasonal and individual variation in the use of rail-associated food attractants by grizzly  
2069 bears (*Ursus arctos*) in a national park. *PLoS One* 12: e0175658.
- 2070 Nabeshima, E., & Hiura, T. (2004). Size dependency of photosynthetic water- and nitrogen-use  
2071 efficiency and hydraulic limitation in *Acer mono*. *Tree Physiology*, 24(7), 745–752.
- 2072 Newsome, S. D., Garbe, H. M., Wilson, E. C., & Gehrt, S. D. (2015). Individual variation in  
2073 anthropogenic resource use in an urban carnivore. *Oecologia* 178: 115–128.
- 2074 Niedziałkowska, M., M. W. Hayward, T. Borowik, W. Jędrzejewski, and B. Jędrzejewska.  
2075 (2018). A meta-analysis of ungulate predation and prey selection by the brown bear *Ursus*  
2076 *arctos* in Eurasia. *Mammal Research* 64:1–9.

- 2077 Nielsen, S.E., Boyce, M.S., and Stenhouse, G.B. (2004). Grizzly bears and forestry: I. Selection  
2078 of clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology and*  
2079 *Management* 199: 51–65.
- 2080 Nilsson, M. C. and Wardle, D. A. (2005). Understory vegetation as a forest ecosystem driver:  
2081 Evidence from the northern Swedish boreal forest. *Frontiers in Ecology and Environment*  
2082 3: 421–428.
- 2083 Northrup, J. M., Stenhouse, G. B., & Boyce, M. S. (2012). Agricultural lands as ecological traps  
2084 for grizzly bears. - *Animal Conservation* 15: 369–377.
- 2085 Oberdörster, U., and Grant, P.R. (2006). Predicting emergence, chorusing, and oviposition of  
2086 periodical cicadas. *Ecology* 87: 409–418.
- 2087 Ohdachi, S., and Aoi, T. (1987). Food Habits of Brown Bears in Hokkaido, Japan. *Bears: Their*  
2088 *Biology and Management*, 7: 215.
- 2089 Ooi, N., Tsuji, S.I., Danhara, T., Noshiro, S., Ueda, Y., and Minaki, M. (1997). Vegetation  
2090 change during the early last Glacial in Haboro and Tomamae, northwestern Hokkaido,  
2091 Japan. *Review of Palaeobotany and Palynology* 97: 79–95.
- 2092 Ordiz, A., Støen, O. G., Sæbø, S., Kindberg, J., Delibes, M., & Swenson, J. E. (2012). Do bears  
2093 know they are being hunted?. *Biological Conservation* 152: 21-28.
- 2094 O'Bryan, C. J., N. R. Patton, J. Hone, J. S. Lewis, V. Berdejo-Espinola, D. R. Risch, M. H.  
2095 Holden, and E. McDonald-Madden. (2021). Unrecognized threat to global soil carbon by a  
2096 widespread invasive species. *Global Change Biology* :gcb.15769.
- 2097 Palkovacs, E. P., & Dalton, C. M. (2012). Ecosystem consequences of behavioural plasticity and  
2098 contemporary evolution. In *Behavioural Responses to a Changing World*. Oxford  
2099 University Press.

- 2100 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts  
2101 across natural systems. *Nature* 421: 37–42.
- 2102 Pastor, J., J. D. Aber, C. A. McLaugherty, and J. M. Melillo. (1984). Aboveground Production  
2103 and N and P Cycling Along a Nitrogen Mineralization Gradient on Blackhawk Island,  
2104 Wisconsin. *Ecology* 65:256–268.
- 2105 Penteriani, V., Delgado, M. D. M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., Zarzo-Arias,  
2106 A., & Bombieri, G. (2018). Evolutionary and ecological traps for brown bears *Ursus arctos*  
2107 in human-modified landscapes. *Mammal Review* 48: 180–193.
- 2108 Persson, T., & Wirén, A. (1995). Nitrogen mineralization and potential nitrification at different  
2109 depths in acid forest soils. *Plant and Soil* 168: 55–65.
- 2110 Platt, B. F., D. J. Kolb, C. G. Kunhardt, S. P. Milo, and L. G. New. (2016). Burrowing through  
2111 the literature: The impact of soil-disturbing vertebrates on physical and chemical properties  
2112 of soil. *Soil Science* 181:175–191.
- 2113 Pons, P. (2015). Delayed effects of fire and logging on cicada nymph abundance. *Journal of*  
2114 *Insect Conservation* 19: 601–606.
- 2115 Pons, P. (2020). True cicadas (Cicadidae) as prey for the birds of the Western Palearctic: A  
2116 review. *Avian Research*. 11: 1–9.
- 2117 Power, M. E., et al. (1996). Challenges in the quest for keystones: identifying keystone species  
2118 is difficult—but essential to understanding how loss of species will affect  
2119 ecosystems. *BioScience* 46: 609-620.
- 2120 R Core Team (2018). R: A language and environment for statistical computing.

- 2121 Ramankutty, N., and Foley, J.A. (1999). Estimating historical changes in global land cover:  
2122 Croplands from 1700 to 1992. *Global Biogeochemical Cycles* 13: 997–1027.
- 2123 Reich, P. B., Walters, M. B., Kloeppel, B. D., & Ellsworth, D. S. (1995). Different  
2124 photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree  
2125 species. *Oecologia*, 104(1), 24–30. <https://doi.org/10.1007/BF00365558>
- 2126 Reichman, O. J., & Seabloom, E. W. (2002). The role of pocket gophers as subterranean  
2127 ecosystem engineers. *TREE* 17: 44 - 49.
- 2128 Reimchen, T.E. (2000). Some ecological and evolutionary aspects of bear-salmon interactions in  
2129 coastal British Columbia. *Canadian Journal of Zoology* 78: 448–457.
- 2130 Ripple, W.J., et al. (2014). Status and Ecological Effects of the World’s Largest Carnivores.  
2131 *Science*, 343: 1241484.
- 2132 Risch, A. C., S. Wirthner, M. D. Busse, D. S. Page-Dumroese, and M. Schütz. (2010). Grubbing  
2133 by wild boars (*Sus scrofa* L.) and its impact on hardwood forest soil carbon dioxide  
2134 emissions in Switzerland. *Oecologia* 164: 773–784.
- 2135 Risenhoover, K. L. and Bailey, J. A. (1985). Foraging Ecology of Mountain Sheep: Implications  
2136 for Habitat Management. *Journal of Wildlife Management* 49: 797.
- 2137 Rosell, F., Jojola, S.M., Ingdal, K., Lassen, B.A., Swenson, J.E., Arnemo, J.M., and Zedrosser,  
2138 A. (2011). Brown bears possess anal sacs and secretions may code for sex. *Journal of*  
2139 *Zoology* 283: 143–152.
- 2140 Rosenzweig, M. L. (1981). A Theory of Habitat Selection. *Ecology* 62: 327–335.
- 2141 Rosseel, Y. 2012. Lavaan: An R package for structural equation modeling. *Journal of Statistical*  
2142 *Software* 48: 1-36.
- 146

- 2143 Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive*  
2144 *Sciences*, 9: 250–257. <https://doi.org/10.1016/j.tics.2005.03.005>
- 2145 Roth, H. U. (1980). Defecation rates of captive brown bears. *Bears: their biology and*  
2146 *management* 4: 249-253
- 2147 Royo, A. A. and Carson, W. P. (2006). On the formation of dense understory layers in forests  
2148 worldwide: Consequences and implications for forest dynamics, biodiversity, and  
2149 succession. *Canadian Journal of Forest Research* 36: 1345–1362.
- 2150 Sakamaki, H., and Enari, H. 2012. Activity-specific evaluation of winter habitat use by Japanese  
2151 macaques in snow areas, northern Japan: Implications for conifer plantation management.  
2152 *Forest Ecology and Management*. 270: 19–24.
- 2153 Sanborn, A. F., & Phillips, P. K. (2013). Biogeography of the cicadas (Hemiptera: Cicadidae) of  
2154 North America, north of Mexico. *Diversity* 5: 166-239.
- 2155 Sato, Y., Mano, T., & Takatsuki, S. (2005). Stomach contents of brown bears *Ursus arctos* in  
2156 Hokkaido, Japan. *Wildlife Biology* 11: 133–144.
- 2157 Sato, Y., and Sato, S. 2015. Spring Temperature Predicts the Long-Term Molting Phenology of  
2158 Two Cicadas, *Cryptotympana facialis* and *Graptopsaltria nigrofuscata* (Hemiptera:  
2159 Cicadidae). *Annals of the Entomological Society of America* 108(4): 494–500.
- 2160 Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the  
2161 functioning of forest ecosystems. *Biological Reviews* 81: 1–31.
- 2162 Schmitz, O. J., Grabowski, J. H., Peckarsky, B. L., Preisser, E. L., Trussell, G. C., & Vonesh, J.  
2163 R. (2008). From Individuals to Ecosystem Function: Toward an Integration of Evolutionary  
2164 and Ecosystem Ecology. *Ecology* 89: 2436–2445.

- 2165 Schmitz, O. J., Krivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-  
2166 mediated indirect interactions. *Ecology letters* 7: 153-163.
- 2167 Seko, T., Kawata, S., Tezuka, M., Uesugi, T., & Akihito (2008). Seasonal Food Habits of the  
2168 Raccoon Dog, *Nyctereutes procyonoides*, in the Imperial Palace, Tokyo. *Bull. Natl. Mus.*  
2169 *Nat. Sci., Ser. A* 34: 63–75 [in Japanese with English abstract]
- 2170 Shen, Y., Santiago, L. S., Shen, H., Ma, L., Lian, J., Cao, H., Lu, H., & Ye, W. (2014).  
2171 Determinants of change in subtropical tree diameter growth with ontogenetic stage.  
2172 *Oecologia*, 175: 1315–1324.
- 2173 Shimozuru, M., et al. (2020). Male reproductive input, breeding tenure, and turnover in high-  
2174 density brown bear (*Ursus arctos yesoensis*) populations on the Shiretoko Peninsula,  
2175 Hokkaido, Japan. *Canadian Journal of Zoology* 98: 175–185.
- 2176 Shirane, Y. et al. (2021). Dining from the coast to the summit: Salmon and pine nuts determine  
2177 the summer body condition of female brown bears on the Shiretoko Peninsula. *Ecology*  
2178 *and Evolution* 11: 5204–5219.
- 2179 Shirane, Y., et al. (2020). Development of a noninvasive photograph-based method for the  
2180 evaluation of body condition in free-ranging brown bears. *PeerJ* 8: e9982.
- 2181 Shoyama, K. (2008). Reforestation of abandoned pasture on Hokkaido, northern Japan: Effect  
2182 of plantations on the recovery of conifer-broadleaved mixed forest. *Landscape Ecology*  
2183 *and Engineering* 4: 11–23.
- 2184 Shoyama, K., & Braimoh, A. K. (2011). Analyzing about sixty years of land-cover change and  
2185 associated landscape fragmentation in Shiretoko Peninsula, Northern Japan. *Landscape*  
2186 *and Urban Planning* 101: 22–29.



- 2187 Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of  
2188 behavioural syndromes. *Ecology Letters* 15: 278–289.
- 2189 Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to  
2190 human-induced rapid environmental change. *Evolutionary Applications* 4: 367–387.
- 2191 Siljander, M., Kuronen, T., Johansson, T., Munyao, M. N., & Pellikka, P. K. (2020). Primates on  
2192 the farm—spatial patterns of human–wildlife conflict in forest-agricultural landscape mosaic  
2193 in Taita Hills, Kenya. *Applied Geography* 117: 102185.
- 2194 Smith, D. M., Kelly, J. F., & Finch, D. M. (2006). Cicada emergence in southwestern riparian  
2195 forest: Influences of wildfire and vegetation composition. *Ecological Applications* 16:  
2196 1608–1618.
- 2197 Somaweera, R., J. et al. (2020). The ecological importance of crocodylians: towards evidence-  
2198 based justification for their conservation. *Biological Reviews* 95:936–959.
- 2199 Sorensen, A.A., Stenhouse, G.B., Bourbonnais, M.L., and Nelson, T.A. (2015). Effects of  
2200 habitat quality and anthropogenic disturbance on grizzly bear (*Ursus arctos horribilis*)  
2201 home-range fidelity. *Canadian Journal of Zoology* 93: 857–865.
- 2202 Steiger, J. H. (1990). Structural Model Evaluation and Modification: An Interval Estimation  
2203 Approach. *Multivariate Behavioral Research* 25: 173–180.
- 2204 Stephens, R.B., Trowbridge, A.M., Ouimette, A.P., Knighton, W.B., Hobbie, E.A., Stoy, P.C.,  
2205 and Rowe, R.J. (2020). Signaling from below: rodents select for deeper fruiting truffles  
2206 with stronger volatile emissions. *Ecology* 101: e02964.
- 2207 Stephens, S.S., and Wagner, M.R. (2007). Forest plantations and biodiversity: A fresh  
2208 perspective. *Journal of Forestry* 105: 307–313.

- 2209 Stewart, P. S., Hill, R. A., Stephens, P. A., Whittingham, M. J., & Dawson, W. (2021). Impacts  
2210 of invasive plants on animal behaviour. *Ecology Letters* 24: 891-907.
- 2211 Steyaert, S. M. J. G., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J. E., &  
2212 Zedrosser, A. (2016). Human shields mediate sexual conflict in a top predator. *Proceedings*  
2213 *of the Royal Society B: Biological Sciences* 283: 20160906.
- 2214 Steyaert, S.M.J.G., Hertel, A.G., and Swenson, J.E. (2019). Endozoochory by brown bears  
2215 stimulates germination in bilberry. *Wildlife Biology* 2019: 1–5.
- 2216 Stock, W. D., Finn, H., Parker, J., & Dods, K. (2013). Pine as fast food: foraging ecology of an  
2217 endangered cockatoo in a forestry landscape. *PLoS One* 8: e61145.
- 2218 Suzuki, K. F., et al. (2021). The potential role of an alien tree species in supporting forest  
2219 restoration: Lessons from Shiretoko National Park, Japan. *Forest Ecology and*  
2220 *Management* 493: 119253.
- 2221 Swenson, J.E., Jansson, A., Riig, R., and Sandegren, F. (1999). Bears and ants: Myrmecophagy  
2222 by brown bears in central Scandinavia. *Canadian Journal of Zoology* 77: 551–561.
- 2223 Sörensen, I., Amundin, M., and Laska, M. 2019. Meerkats (*Suricata suricatta*) are able to detect  
2224 hidden food using olfactory cues alone. *Physiology and Behavior*. 202: 69–76.
- 2225 Takafumi, H., and Hiura, T. 2009. Effects of disturbance history and environmental factors on  
2226 the diversity and productivity of understory vegetation in a cool-temperate forest in Japan.  
2227 *Forest Ecology and Management* 257: 843–857.
- 2228 Takahashi, K., Uemura, S., Suzuki, J.-I., & Hara, T. (2003). Effects of understory dwarf bamboo  
2229 on soil water and the growth of overstory trees in a dense secondary *Betula ermanii* forest,  
2230 northern Japan. *Ecological Research* 18: 767–774.

- 2231 Tardiff, S. E., and J. A. Stanford. (1998) Grizzly bear digging: effects on subalpine meadow  
2232 plants in relation to mineral nitrogen availability. *Ecology* 79: 2219–2228.
- 2233 Tateno, R., T. Hishi, and H. Takeda. (2004). Above- and belowground biomass and net primary  
2234 production in a cool-temperate deciduous forest in relation to topographical changes in soil  
2235 nitrogen. *Forest Ecology and Management* 193:297–306.
- 2236 Thompson, J. N. (1988). Evolutionary ecology of the relationship between oviposition  
2237 preference and performance of offspring in phytophagous insects. *Entomologia*  
2238 *Experimentalis et Applicata* 47: 3–14.
- 2239 Tomita, K. (2021). Camera traps reveal interspecific differences in the diel and seasonal  
2240 patterns of cicada nymph predation. *The Science of Nature* 108: 52.
- 2241 Trussell, G. C., Ewanchuk, P. J., & Matassa, C. M. (2006). Habitat effects on the relative  
2242 importance of trait- and density- mediated indirect interactions. *Ecology letters* 9: 1245-  
2243 1252.
- 2244 Tucker, M. A., et al. (2018). Moving in the Anthropocene: Global reductions in terrestrial  
2245 mammalian movements. *Science* 359: 466–469.
- 2246 Umetsu, F., & Pardini, R. (2007). Small mammals in a mosaic of forest remnants and  
2247 anthropogenic habitats—evaluating matrix quality in an Atlantic forest  
2248 landscape. *Landscape Ecology* 22: 517-530.
- 2249 Valentine, L. E., Ruthrof, K. X., Fisher, R., Hardy, G. E. St. J., Hobbs, R. J., & Fleming, P. A.  
2250 (2018). Bioturbation by bandicoots facilitates seedling growth by altering soil properties.  
2251 *Functional Ecology* 32: 2138–2148.

- 2252 Verdon, S. J., Gibb, H., & Leonard, S. W. (2016). Net effects of soil disturbance and herbivory  
2253 on vegetation by a re-established digging mammal assemblage in arid zone  
2254 Australia. *Journal of Arid Environments* 133: 29-36.
- 2255 Villar, N., & Medici, E. P. (2021). Large wild herbivores slow down the rapid decline of plant  
2256 diversity in a tropical forest biodiversity hotspot. *Journal of Applied Ecology* 58: 2361–  
2257 2370.
- 2258 Watanabe, M., Watanabe, Y., Kitaoka, S., Utsugi, H., Kita, K., & Koike, T. (2011). Growth and  
2259 photosynthetic traits of hybrid larch F1 (*Larix gmelinii* var. *Japonica* × *L. kaempferi*) under  
2260 elevated CO<sub>2</sub> concentration with low nutrient availability. *Tree Physiology* 31 965–975.
- 2261 Way, J.G. (2008). Eastern Coyotes, *Canis latrans*, observed feeding on periodical Cicadas,  
2262 *Magicicada septendecim*. *Canadian Field-Naturalists* 122: 271–272.
- 2263 Whytock, R.C. et al. (2018) Bird-community responses to habitat creation in a long-term, large-  
2264 scale natural experiment. *Conservation Biology* 32: 345–354.
- 2265 Wilby, A., Shachak, M., & Boeken, B. (2001). Integration of ecosystem engineering and trophic  
2266 effects of herbivores. *Oikos* 92: 436-444.
- 2267 Wilson, M. W., Ridlon, A. D., Gaynor, K. M., Gaines, S. D., Stier, A. C., & Halpern, B. S.  
2268 (2020). Ecological impacts of human-induced animal behaviour change. *Ecology Letters*  
2269 23: 1522–1536.
- 2270 Wirthner, S., Schütz, M., Page-Dumroese, D. S., Busse, M. D., Kirchner, J. W., & Risch, A. C.  
2271 (2012). Do changes in soil properties after rooting by wild boars (*Sus scrofa*) affect  
2272 understory vegetation in Swiss hardwood forests? *Canadian Journal of Forest Research*  
2273 42: 585–592.

- 2274 Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments.  
2275 *Behavioral Ecology* 26: 665–673.
- 2276 Wootton, J. T. (1994). The nature and consequences of indirect effects in ecological  
2277 communities. *Annual Review of Ecology and Systematics* 25: 443-466.
- 2278 Wright, J. P., & Jones, C. G. (2004). Predicting Effects of Ecosystem Engineers on Patch-Scale  
2279 Species Richness from Primary Productivity. *Ecology* 85: 2071–2081.
- 2280 Yamanaka, M. & T. Aoi. (1988) Brown bear. Pages 181– 223 in N. Ohtaishi and H. Nakagawa,  
2281 editors. *Animals of Shiretoko*. Hokkaido University Press, Sapporo, Japan. [In Japanese  
2282 with an English abstract.]
- 2283 Yamazaki, H., & Yoshida, T. (2020). Various scarification treatments produce different  
2284 regeneration potentials for trees and forbs through changing soil properties. *Journal of*  
2285 *Forest Research* 25: 41-50.
- 2286 Yamazaki, K., Kozakai, C., Koike, S., Morimoto, H., Goto, Y., & Furubayashi, K. (2012).  
2287 Myrmecophagy of Japanese black bears in the grasslands of the Ashio area, Nikko  
2288 National Park, Japan. *Ursus* 23: 52–64.
- 2289 Yang, B., Wen, X., & Sun, X. (2015). Seasonal variations in depth of water uptake for a  
2290 subtropical coniferous plantation subjected to drought in an East Asian monsoon region.  
2291 *Agricultural and Forest Meteorology* 201: 218-228.
- 2292 Yang, L. H. & Karban, R. (2009). Long-term habitat selection and chronic root herbivory:  
2293 Explaining the relationship between periodical cicada density and tree growth. *American*  
2294 *Naturalists* 173: 105–112.
- 2295 Yang, L. H. (2004). Periodical cicadas as resource pulses in North American forests. *Science*  
2296 306: 1565-1567.

- 2297 Yang, L.H. (2006). Periodical cicadas use light for oviposition site selection. *Proceedings of the*  
2298 *Royal Society B: Biological Sciences* 273: 2993–3000.
- 2299 Yoshida, T., and Hijii, N. (2006). Spatiotemporal distribution of aboveground litter in a  
2300 *Cryptomeria japonica* plantation. *Journal of Forest Research* 11: 419–426.
- 2301 Yurkewycz, R. P., Bishop, J. G., Crisafulli, C. M., Harrison, J. A., & Gill, R. A. (2014). Gopher  
2302 mounds decrease nutrient cycling rates and increase adjacent vegetation in volcanic  
2303 primary succession. *Oecologia* 176: 1135–1150.
- 2304 Zedrosser, A., Støen, O. G., Sæbø, S., & Swenson, J. E. (2007) Should I stay or should I go?  
2305 Natal dispersal in the brown bear. *Animal Behaviour* 74: 369– 376.