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Reforestation provides a foraging habitat for brown bears by increasing cicada density in the Shiretoko World Heritage site

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Abstract

Reforestation, which converts abandoned farmland back into forestland by planting woody species, can provide habitat for wildlife, including the brown bear (*Ursus arctos* Linnaeus, 1758). In the Shiretoko World Heritage site, northern Japan, where brown bears occur at high density, conifers have been planted since the 1970s to reforest abandoned farmland. In this area, brown bears were first observed digging for cicada nymphs (*Lyristes bihamatus* Motschulsky, 1861) from 2000. Our preliminary observations suggested the emergence of digging behavior might be associated with reforestation. We examined whether reforestation provided a foraging habitat for brown bears. We found that digging occurred only within the restored conifer forests, but not within the natural forest. The densities of cicada nymphs in the restored forests were higher than in the natural forest. These results indicate that the reforestation of abandoned farmland provides a foraging habitat for brown bears by increasing the availability of cicada nymphs in the Shiretoko World Heritage site.

KEY WORDS cicada nymph, *Lyristes bihamatus,* digging, Hokkaido, large carnivore, plantation, restoration, brown bear, *Ursus arctos*

Introduction

Forests, which occupy one third of terrestrial ecosystems, harbor the highest biodiversity in the world (Millenium Ecosystem Assessment 2005). From the 1700s to the 1990s, approximately 20 % of forests were converted to farmland, and consequently a wide range of forest habitat was lost around the world (Goldewijk 2001). Since the 1900s, large areas of farmland have also been abandoned in developed countries because of declines in human population in agricultural areas as a result of aging populations and migration to urban areas (Ramankutty and Foley 1999). Reforestation, which is a major ecological restoration action in forest ecosystems, aims to convert abandoned farmland to forestland by planting woody species (Chazdon 2008; Aerts and Honnay 2011). The goals of reforestation are not only re-establishment of forest cover, but also the enhancement of forest ecosystem functions such as carbon sequestration, biodiversity conservation and wildlife habitat (Block et al. 2001; Le et al. 2012; Cunningham et al. 2015; Derhé et al. 2016). Because reforestation cannot fully restore the original forest ecosystem, it does not necessarily succeed in recovering forest ecosystem functions. Therefore, it is important for the evaluation of reforestation success to understand the ecological functions of the restored forest (Le et al. 2012).

The direction and magnitude of reforestation's influence on wildlife, differs among species and taxonomic groups depending on their ecology such as habitat requirements (Law et al. 2017; Whytock et al. 2018; Fuentes-Montemayor et al. 2020). Thus, it is important for deepening the understanding of a function of reforestation as wildlife habitat to clarify the response per each species and taxonomic groups.

The brown bear (*Ursus arctos* Linnaeus, 1758), which is one of the most widespread and largest carnivores in terrestrial ecosystems, plays important ecological roles as an apex predator and long-distance seed disperser, and transport of marine-derived nutrients (Reimchen 2000; Helfield and Naiman 2006; Ripple et al. 2014; Steyaert et al. 2019). Brown bears sensitively respond to anthropogenic habitat changes due to forestry (e.g. afforestation and deforestation), cultivation and industrial development (Cristescu et al. 2015; Frank et al. 2015; Sorensen et al. 2015; Penteriani et al. 2018). In fact, woodland conversion to cropland leads to an increased attraction of bears to human settlements for crop raiding, and consequently increases their human-caused mortality (Hata et al. 2017; Penteriani et al. 2018). In forest ecosystems, clearcuts temporarily change in resource availability for bears via increasing light environment and biomass of coarse woody debris, and influence their habitat selection (Nielsen et al. 2004*a*, 2004*b*; Frank et al. 2015). For example, in west-central Alberta, Canada, grizzly bears select clearcut sites, which provide some foraging resources such as ants, herbaceous plants and berries, during summer (Nielsen et al. 2004a, 2004b). On the other hand, it is unknown how brown bears respond to reforestation, which significantly alters the habitat from farmland to forest.

In the Shiretoko World Heritage site (hereafter; SWH), Hokkaido, northern Japan, a reforestation project started in the 1970s was led by the local government and residents to recover forest landscape from abandoned farmland. In the reforested sites of the SWH, brown bears have been observed digging for cicada nymphs (*Lyristes bihamatus* Motschulsky, 1861) during the summer season since 2000 (Tomita and Hiura 2020). Tomita and Hiura (2020) showed some preliminary observations that this behavior was frequently found in reforested larch plantations (*Larix kaempferi* (Lamb.) Carrière) , and that the density of cicada nymphs in the plantations was over 30-fold higher than in natural forests. These preliminary results suggest that reforestation has increased the availability of cicadas for brown bears. However, there is no quantitative data on this behavior, information such as the frequency of this digging behavior between the restored forests and natural forest has yet to be studied. Because cicada emergence density usually fluctuates between years (Sato and Sato 2015), to elucidate if reforestation has provided a foraging habitat for bears, we should examine whether cicada emergence density in the plantations is higher than in natural forests across years.

We compared the frequency of this digging behavior and the density of cicada nymphs between the natural forest and plantations. Based on our previous findings (Tomita and Hiura 2020), we made the following predictions: (1) brown bears digging for cicada nymphs occurs more frequent in the restored plantations than in the natural forests, (2) the density of cicada nymphs is higher in the plantations than in the natural forests, (3) there is a positive relationship between digging frequency and the density of cicada nymphs.

Material and Methods

Study site

This study was conducted in the Horobetsu-Iwaobetsu area (44°09=N, 145°02=E) located in the western parts of the SWH (Fig. 1). The elevation ranges from 120 to 220 m. The annual mean temperature at the study site is 6.2 °C. and monthly mean temperature ranged from –10.4 °C in February to 15.1 °C in August (1981–2010). The annual mean precipitation is 1,149 mm (1981–2010). UNESCO certified this area as a World Natural Heritage site because it represents one of the richest northern temperate ecosystems in the world (http://whc.unesco.org/en/list/1193). In the study area, approximately 40% of the conifer-broadleaved mixed forests were converted to farmland for grazing by cattle during the post-war period from the 1940s to the 1960s (Shoyama 2008). Agricultural crops such as corn and sugar beet were rarely cultivated in this area. During the period of high economic growth in Japan, from the late 1960s to the 1970s, all the farmland was abandoned because farmers immigrated to urban areas. Since 1977, reforestation of the abandoned farmland has been conducted by the local government and residents through a national trust movement.

Coniferous trees such as Japanese larch, Sakhalin spruce (*Picea glehnii* (F.Schmidt) Mast) and Sakhalin fir (*Abies sachalinensis* (F.Schmidt) Mast), have been planted on the abandoned farmland for the purpose of reforestation. Most of the larch and fir plantations were established during the 1970s, whereas the spruce plantations were established during the early 1990s. The restored plantations accounted for 18 % of the total forest area (Shoyama 2008), with Sakhalin spruce, Japanese larch and Sakhalin fir plantations account for 13 %, 4 %, and 1 %, respectively. The natural forests are conifer-broadleaved mixed forests, mainly consisting of Sakhalin fir and Mongolian oak (*Quercus crispula* Blume) and maple (*Acer mono* Maxim.), and account for 82 % of the forest area in the study site. The stand characteristics for each forest type are shown in Table 1. On the abandoned farmland, pasture grass such as *Miscanthus sinensis* Andersson and *Anthoxanthum odoratum* L. are dominant and soft mast species such as *Rubus* spp., which are a common food for bears in summer, rarely grow (Ministry of the Environment, the Government of Japan 2017).

The SWH has one of the highest densities of brown bears in the world (Shimozuru et al. 2020*a*). In the study area, food items of the brown bears change across the seasons, depending on resource availability. Herbaceous plants are consumed in spring, and herbaceous plants, ants and cicada nymphs in summer, from June to August. *Q. crispula* acorns, *Vitis coignetiae* (Pulliat) berries, and anadromous salmons (*Oncorhynchus gorbuscha* Walbaum, 1792) are consumed in autumn, from September to November (Ohdachi and Aoi 1987; Matsubayashi et al. 2014; Tomita and Hiura 2020). Home range size of adult female bears is estimated at 26.5 km^2 in the study area (Kohira et al. 2009). Bear viewing is a major tourism activity in this region which generates an estimate 3 million dollars in revenue (Kubo and Shoji 2014). At the study site in 2018, 11 individual bears were observed digging for cicada nymphs, consisting of 2 sub adults and 2 solitary female adults, and 3 females with cub(s) (Tomita and Hiura 2020). Individual identification and age classes were determined based on color, marks, body size, and family structure of bears. Two native cicada species, *L. bihamatus* and *Yezoterpnosia nigricosta* (Motschulsky, 1866), only occur in forest of the SWH and emerge during late summer and spring to early summer, respectively. No cicada nymphs occur on the farmland because the nymphs feed from tree roots. In the study site, brown bear preys on the final instar nymphs of *L. bihamatus*, but not

Y. nigricosta (Tomita and Hiura 2020). Hence, this study focuses on the final instar nymph of *L. bihamatus* as a prey of bears; the term “cicada” represents *L. bihamatus*.

Field Survey

We conducted field surveys in two successive years. From late August to September 2018 and 2019, 100 m^2 survey plots were set on the following forest types: larch plantations (n = 15), fir plantations (n = 12), spruce plantations (n = 15), and natural forests (n= 30). Since bears dig for cicada nymphs until the end of July when the final instar nymphs fully emerge (Tomita and Hiura 2020), this survey's duration is appropriate for the evaluation of this behavior and cicada emergence density. The locations of the survey plots are shown in Fig. 1. We set more plots in the natural forest because it made up the highest proportion of all forest types. The availability of cicada nymphs was determined by the density of cicada exuviae collected from all trees (diameter breast height, DBH > 2 cm) within the plots, since brown bears forage on only the nymphs in their final instar (Tomita and Hiura 2020). Cicada exuviae attached to trees were collected from trunks and branches under 3 m from the ground, as most exuviae on trees can be observed under this height. We also collected the exuviae on the ground within 1 m from the trunk of a tree, because most exuviae falling from the tree were found within 1 m of the trunk. Since final instar cicada nymphs usually attach to the tree trunk when they emerge, the exuviae density in a survey plot can be regarded as the total emergence density from a given plot. Although exuviae could move a short distance due to the wind, the plot size (i.e. 100 m^2) is large enough to cover for passive movement of the exuviae after emergence. Digging marks were regarded as evidence of brown bears foraging on cicada nymphs. According to our preliminary observations using 8 camera traps set in larch plantations where brown bears dug the previous year, brown bears usually dig for cicada nymphs near tree trunks. Thus, we evaluated the digging frequency per plot as the proportion of trees which had the digging traces within 50 cm diameter from the base of a tree, to all trees (DBH > 2 cm) in the plot.

Statistical Analysis

Generalized linear models (GLMs) with log link, Poisson error distribution and Tukey post hoc test were used to examine the differences in the digging frequencies and the densities of cicada nymphs among the forest types. When the GLMs indicated a significant difference (*p-value* < 0.05) of one forest type from others, we performed multiple comparisons among the forest types. The GLMs were used to compare the digging frequency and the density of cicada nymphs between 2018 and 2019. In GLMs for digging frequency, we introduced an offset term as the log-transformed number of trees to adjust for differences in the number of trees among the survey plots. To examine the effects of the density of cicada nymphs on the digging frequency, we performed GLMs for each forest type. All statistical analyses were conducted in R version 3.5.1 (R Core Team 2018).

Biomass measurement of cicada nymphs

In mid-June 2019, we collected 10 cicada final instar nymphs from the larch plantation. In the laboratory, these nymphs were measured individual using dry mass after a 48 hour at 60 ℃ drying period. The biomass of cicada final instar nymphs per 100 m^2 were calculated by multiplying individual dry mass of the nymph by the density of cicada exuviae.

Results

Across all survey plots, we collected a total of 629 and 3344 cicada exuviae in 2018 and 2019, respectively and recorded a total of 2176 trees with or without digging traces.

The GLMs found a significant effect of forest type on digging frequency and the density of cicada nymphs. Surprisingly, brown bears only dug for cicada nymphs in the restored plantation plots, even when the natural forest plots were mainly composed of fir species (Fig. 2). Digging frequency in the larch plantations was highest in all forest types in both years, but significantly differed between years (Fig. 2). The density of cicada nymphs in the larch plantations did not differ from the fir plantations, which had a lower digging frequency (Fig. 3). The density of cicada nymphs was lowest in the natural forest (Fig. 3). The spruce plantation plots had a lower digging frequency and density of cicada nymphs than other types of plantation plots (Fig. 2, 3). The densities of cicada nymphs across all forest types in 2019 were significantly higher than in 2018 ($p < 0.001$, Fig. 3). The density of cicada nymphs positively correlated to the digging frequencies in fir and spruce plantations ($p < 0.001$), but not in larch plantations in 2018 ($p = 0.19$) (Fig. 4). Individual dry mass of the final instar nymphs was evaluated at 1.12 ± 0.20 g (mean ± SD), and the biomass density of nymphs in each forest type is shown in Table 2.

Discussion

The results of this study generally supported our predictions. In particular, brown bears foraged on cicada nymphs only in plantations, not in natural forests (Fig. 2). This clearly indicates that reforestation provided a foraging habitat for brown bears by increasing the availability of cicada nymphs. To our knowledge, this is the first study showing that reforestation provides a foraging habitat for brown bears.

Our results indicate that the difference in the digging frequency among forest types can generally be explained by the density of cicada nymphs (Figs. 2, 3, 4). The digging frequency showed that brown bears preferentially dug for cicada nymphs in the larch plantations, although there were no differences in the density of cicada nymphs between larch and fir plantations (Figs. 2, 3). Brown bears might indirectly search for the nymphs by using larch trees as an aboveground landmark for detecting the location of underground cicada nymphs. In the study site, larch trees do not occur in the natural forest because larches are an introduced plantation species. Thus, brown bears may have learned to associate nymphs with larch trees. This potential explanation is supported by our finding that a lower density of cicada nymphs did not affect digging frequency in larch plantations during 2018 (Fig. 4A). Another possible explanation is that brown bears have fewer chances of encountering fir plantations than larch plantations, because the total area of larch plantations is larger than that of fir plantations in the study site.

Within the same forest type, digging frequencies were positively affected by the density of cicada nymphs (Fig. 4B-F). This indicates that brown bears can accurately detect the location of the cicada nymphs within a certain distance, perhaps using their remarkable olfactory senses (Gittleman 1991; Rosell et al. 2011). Other fossorial mammals can use the smell of volatile signals from unseen belowground resources to detect food (Sörensen et al. 2019; Stephens et al. 2020). Thus, bears may identify locations where there are high densities of cicada nymphs by smelling the volatile signals. We note that it is unclear yet whether cicada nymphs emit volatile signals to the surface.

If bears rely on olfaction while searching for cicada nymphs, the relationship between digging frequency and cicada density should be significantly positive in the larch plantations. The possible reason is that the searching tactics of bears are different among individuals;

some bears rely on spatial learning, associating cicada with larches, while others use olfactory cues. Behavioral differences among individuals are common in bears (Leclerc et al. 2016; Lesmerises and St-Laurent 2017). Data based on the digging behavior of individuals is required to deepen our understanding of how bears search for cicada nymphs.

Across all forest types, the density of cicada nymphs in 2019 were significantly higher than that of 2018 (Fig.2), suggesting that emergence density of *L. bihamatus* varies among years. Emergence densities of annual cicada vary among years because of the age structure in the nymphal stage (Sato and Sato 2015), so this inter-annual difference is probably a general pattern for cicada species. Importantly, the emergence densities of cicadas in the restored forests were significantly higher than in the natural forest, despite the different density of cicadas over the study period. Given that the plantations are located proximate to the natural forests in the study site (see Fig.1) and dispersal distance in adult cicadas is estimated at about 100-250 m (Andrade et al. 2020), adult cicadas can easily come and go between the plantations and the natural forest. Since emergence schedule in cicada is usually homogeneous within same population (e.g. periodical cicadas (Dybas and Lloyd 1974)), periodicity of cicada emergence doesn’t differ between the plantations and natural forests. These strongly indicate that the restored forests play a role as foraging habitat for brown bears across years.

We speculate that the reason for high densities of cicada nymphs in the conifer plantations is because adult cicadas intensively oviposit on coniferous species. The spatial distribution of cicada nymphs is determined by the oviposition preference of adult cicadas because the nymphs cannot move a long distance in the soil (Oberdörster and Grant 2006). A study showed that oviposition density of the periodical cicada (*Magicicada sp*.) increased with increasing canopy openness (Yang 2006). Although the canopy openness of larch plantations was higher than natural forests, fir and spruce plantations were similar to the natural forests (Table 1), suggesting that variations in light among forest types was insufficient for explaining the difference in cicada density. Another possible factor is the host tree architecture (Mattingly and Flory 2011). Several annual cicada species in Japan lay their eggs on dead branches attached to living trees (e.g. *Cryptotympana facialis* (F. Walker, 1858), Moriyama et al. (2016)). In the study site, oviposition scars by *L. bihamatus* were frequently observed on dead branches of the living larch trees (K. Tomita *personal observation*), suggesting that this species also deposits its eggs on the dead branches of living trees. Since conifer plantations usually have a larger number of attached dead branches than natural forests (Yoshida and Hijii 2006) , the former would have a higher availability of oviposition sites for cicadas than the latter.

Our previous study showed that the proportion of cicada nymphs in bear scats was estimated at 14.3% (Tomita and Hiura 2020). Given that brown bears forage on cicada nymphs only in the restored plantations (Fig.2), the plantation could contribute to the bears' summer diet to some extent, even though it only accounts for 18% of the total forest area. Insects such as ants (Formicidae) and the army cutworm moth (*Euxoa auxiliaris* Grote, 1873) are some of the most important summer foods for brown bears around the world (Mattson et al. 1991*a*, 1991*b*; Elgmork and Kaasa 1992; Sato et al. 2005; Bojarska and Selva 2012). Mattson et al. (1991*b*) estimated the proportion of army cutworm moths in bear scats during summer was at 42-77% in alpine areas of the Yellowstone National Park, North America. The proportions of ants, the most common insect prey for bears across their distributional range, in Sweden, North America, Slovenia and Japan was reported at 16%, <5%, 25% and 18%, respectively (Swenson et al. 1999; Mattson 2001; Große et al. 2003; Sato et al. 2005). These suggest that the dependency of brown bears on cicada nymphs in this area seems to be to the same extent as ants in other regions, though not as significant as army cutworm moths in Yellowstone National Park.

The dry biomass of the final instar nymphs of cicada in the larch plantation was estimated at 22.62 and 97.51 g/100 m^2 in 2018 and 2019, respectively (Table 2). In Sweden, Slovenia and Japan, the dry biomass of ants was estimated at 96, 1.35 and 0.59 g/100 m^2, respectively (Swenson et al. 1999; Große et al. 2003; Yamazaki et al. 2012). This indicates that the biomass density of the nymphs in the plantations is more or equal than that of ants, which is a major summer food for bears. Nevertheless, this does not mean that the total biomass of cicada nymphs in the whole forest is higher than that of ants or other food sources, because a large biomass of cicada nymphs only occurs in the restored plantations, accounting for a small proportion (ca. 18%) of the study site. Further data on the foraging ecology, such as the nutrients provided by the nymphs and energetic cost of the digging behavior, are required to deepen our understanding of the value of cicadas as a food resource for bears.

In the SWH, the body condition of brown bears declines from June to August (Shirane et al. 2020), suggesting that their nutritional status is lowest in summer. Because their body condition rapidly increases during autumn, from September to November (Shirane et al. 2020), how bears overcome poor nutrition in the summer might be important for their fitness. The restored plantations, in which bears dig for cicada nymphs, might play a role in mitigating the poor nutrition in summer, to some extent, via food supplementation in summer (i.e. cicada nymphs).

Concluding Remarks

The primary goal of the reforestation program in the SWH to recover the forest landscape from abandoned farmland has already been achieved (Shoyama 2008), but its ecological functions remain largely unknown (but see Fujii et al. (2017)). Our findings shed light on an ecological function of the restored forests for brown bears via providing a food resource (i.e. cicadas). In the SWH, brown bears play important roles in ecological and economical services, such as the transporting of salmon-derived nutrients and nature tourism

(Koshino et al. 2013; Kubo and Shoji 2014). However, bear appearances along the roads have often occurred in the study site (Shimozuru et al. 2020*b*), and this is a potential cause for increasing human-bear conflicts like "bear jams" (Herrero et al. 2005). Because large areas of the restored plantations located near the roads are frequently used by tourists (Fig.1), bears would need to approach the roads to forage on cicada nymphs. In fact, wildlife managers often observed bears digging for the nymphs within the plantations adjacent roads (Shiretoko Nature Foundation *personal communication*). Perhaps, the plantations might not only provide a foraging habitat for bears, but also intensify human-bear conflict by attracting bears towards the roads. Of course, it is also possible that human-habituated bears mainly dig for the nymphs in the plantations. Testing this hypothesis requires more data on space use by bears.

We found that brown bears foraged on cicada nymphs only in the monoculture plantations, but not the natural forests with higher tree diversity. Nevertheless, it doesn't mean that monocultures are an overall more valuable habitat for bears than natural forests because tree diversity assumes to enhance the ecological value of forests as wildlife habitat

(Stephens and Wagner 2007). Recently, there is growing evidence indicating that monoculture plantations are more valuable as wildlife habitat than previously thought (Brockerhoff et al. 2008; Sakamaki and Enari 2012). Given this evidence, including our finding, monocultures might be regarded as distinct habitat compared with mixed forests, not as less valuable habitat for wildlife. Especially, larch, one of the typical pioneer tree species, can rapidly recover forest canopy. Moreover, due to high light availability on the forest floor of larch plantations, biomass of herbaceous species on the plantation have same extent as natural forests and deciduous broadleaved trees can easily invade into the plantation (Kitaoka and Koike 2004; Takafumi and Hiura 2009). Larch plantations with high availability of cicadas are the potential foraging habitat for predators consuming cicadas (e.g. birds (Pons 2020), mammals (Lovari et al. 1994; Way 2008; Tomita and Hiura 2020)). Therefore, larch may be a candidate species for tentative reforestation on abandoned land although it should consider that in the Hokkaido island, larch is now an alien species but had distributed during the last glacial period (Ooi et al. 1997). When selecting tree species for reforestation, we need to consider the ecological functions of the species, not only following an assumption that the value of restored forests increases as tree diversity increases.

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References

Aerts, R., and Honnay, O. 2011. Forest restoration, biodiversity and ecosystem functioning. BMC Ecol. **11**(1): 29. doi:10.1186/1472-6785-11-29.

Andrade, S.C., Rossi, G.D., and Martinelli, N.M. 2020. Dispersion Pattern of Giant Cicada (Hemiptera: Cicadidae) in a Brazilian Coffee Plantation. Environ. Entomol. **49**(5): 1019–1025. doi:10.1093/ee/nvaa096.

Block, W.M., Franklin, A.B., Ward, J.P., Ganey, J.L., and White, G.C. 2001. Design and Implementation of Monitoring Studies to Evaluate the Success of Ecological Restoration on Wildlife. Restor. Ecol. **9**(3): 293–303. doi:10.1046/j.1526-100x.2001.009003293.x.

Bojarska, K., and Selva, N. 2012. Spatial patterns in brown bear Ursus arctos diet: The role of geographical and environmental factors. Mamm. Rev. **42**(2): 120–143. doi:10.1111/j.1365-2907.2011.00192.x.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., and Sayer, J. 2008. Plantation forests and biodiversity: Oxymoron or opportunity? Biodivers. Conserv. **17**(5): 925–951. doi:10.1007/s10531-008-9380-x.

Chazdon, R.L. 2008. Beyond Deforestation: Restoring Forests and Ecosystem Services on Degraded Lands. Science, **320**(5882): 1458–1460. doi:10.1126/science.1155365.

Cristescu, B., Stenhouse, G.B., and Boyce, M.S. 2015. Grizzly bear diet shifting on reclaimed mines. Glob. Ecol. Conserv. **4**: 207–220. doi:10.1016/j.gecco.2015.06.007.

Cunningham, S.C., Mac Nally, R., Baker, P.J., Cavagnaro, T.R., Beringer, J., Thomson, J.R., and Thompson, R.M. 2015. Balancing the environmental benefits of reforestation in agricultural regions. Perspect. Plant Ecol. Evol. Syst. **17**(4): 301–317. . doi:10.1016/j.ppees.2015.06.001.

Derhé, M.A., Murphy, H., Monteith, G., and Menéndez, R. 2016. Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. J. Appl. Ecol. **53**(6): 1714–1724. doi:10.1111/1365-2664.12728.

Dybas, H.S., and Lloyd, M. 1974. The habitats of 17-year periodical cicadas (Homoptera: Cicadidae: Magicicada Spp.). Ecol. Monogr. **44**(3): 279–324. doi:10.2307/2937032.

Elgmork, K., and Kaasa, J. 1992. Food habits and foraging of the brown bear Ursus arctos in central south Norway. Ecography **15**(1): 101–110. doi:10.1111/j.1600-0587.1992.tb00013.x.

Frank, S.C., Steyaert, S.M.J.G., Swenson, J.E., Storch, I., Kindberg, J., Barck, H., and Zedrosser, A. 2015. A “clearcut” case? Brown bear selection of coarse woody debris and carpenter ants on clearcuts. For. Ecol. Manage. **348**: 164–173. doi:10.1016/j.foreco.2015.03.051.

Fuentes-Montemayor, E., Ferryman, M., Watts, K., Macgregor, N.A., Hambly, N., Brennan, S., Coxon, R., Langridge, H., and Park, K.J. 2020. Small mammal responses to long-term large-scale woodland creation: the influence of local and landscape-level attributes. Ecol. Appl. **30**(2). doi:10.1002/eap.2028.

Fujii, S., Mori, A.S., Koide, D., Makoto, K., Matsuoka, S., Osono, T., and Isbell, F. 2017. Disentangling relationships between plant diversity and decomposition processes under forest restoration. J. Appl. Ecol. **54**(1): 80–90. doi:10.1111/1365-2664.12733.

Gittleman, J.L. 1991. Carnivore olfactory bulb size: allometry, phylogeny and ecology. J. Zool. (Lond.) **225**(2): 253–272. doi:10.1111/j.1469-7998.1991.tb03815.x.

Goldewijk, K.K. 2001. Estimating global land use change over the past 300 years: The HYDE database. Global Biogeochem. Cycles, **15**(2): 417–433. doi:10.1029/1999GB001232.

Große, C., Kaczensky, P., and Knauer, F. 2003. Ants: A food source sought by Slovenian brown bears (Ursus arctos)? Can. J. Zool. **81**(12): 1996–2005. doi:10.1139/z03-151.

Hata, A., Takada, M.B., Nakashita, R., Fukasawa, K., Oshida, T., Ishibashi, Y., and Sato, Y. 2017. Stable isotope and DNA analyses reveal the spatial distribution of crop-foraging brown bears. J. Zool. (Lond.) **303**(3): 207–217. doi:10.1111/jzo.12479.

Helfield, J.M., and Naiman, R.J. 2006. Keystone interactions: Salmon and bear in riparian forests of Alaska. Ecosystems, **9**(2): 167–180. doi:10.1007/s10021-004-0063-5.

Herrero, S., Smith, T., DeBruyn, T.D., Gunther, K., and Matt, C.A. 2005. Brown bear habituation to people—safety, risks, and benefits. Wildl. Soc. Bull. **33**(1): 362–373. doi:10.2193/0091-7648(2005)33[362:ftfbbh]2.0.co;2.

Kitaoka, S., and Koike, T. 2004. Invasion of broad-leaf tree species into a larch plantation: seasonal light environment, photosynthesis and nitrogen allocation. Physiol. Plant. **121**(4): 604–611. doi:10.1111/j.1399-3054.2004.00359.x.

Kohira, M., Okada, H., Nakanishi, M., and Yamanaka, M. 2009. Modeling the effects of human-caused mortality on the brown bear population on the Shiretoko Peninsula, Hokkaido, Japan. Ursus, **20**(1): 12–21. doi:10.2192/1537-6176-20.1.12.

Koshino, Y., Kudo, H., and Kaeriyama, M. 2013. Stable isotope evidence indicates the incorporation into Japanese catchments of marine-derived nutrients transported by spawning Pacific Salmon. Freshw. Biol. **58**(9): 1864–1877. doi:10.1111/fwb.12175.

Kubo, T., and Shoji, Y. 2014. Spatial tradeoffs between residents' preferences for brown bear conservation and the mitigation of human-bear conflicts. Biol. Conserv. **176**: 126–132. doi:10.1016/j.biocon.2014.05.019.

Law, B.S., Chidel, M., Brassil, T., Turner, G., and Gonsalves, L. 2017. Winners and losers among mammals and nocturnal birds over 17 years in response to large-scale eucalypt plantation establishment on farmland. For. Ecol. Manage. **399**: 108–119. doi:10.1016/j.foreco.2017.05.022.

Le, H.D., Smith, C., Herbohn, J., and Harrison, S. 2012. More than just trees: Assessing reforestation success in tropical developing countries. J. Rural Stud. **28**(1): 5–19. doi:10.1016/j.jrurstud.2011.07.006.

Leclerc, M., Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J., and Pelletier, F. 2016. Quantifying consistent individual differences in habitat selection. Oecologia, **180**(3): 697–705. doi:10.1007/s00442-015-3500-6.

Lesmerises, R., and St-Laurent, M.-H. 2017. Not accounting for interindividual variability can mask habitat selection patterns: a case study on black bears. Oecologia, **185**(3): 415–425. doi:10.1007/s00442-017-3939-8.

Lovari, S., Valier, P., and Lucchi, M.R. 1994. Ranging behaviour and activity of red foxes *(Vulpes vulpes:* Mammalia) in relation to environmental variables, in a Mediterranean mixed pinewood. J. Zool. (Lond.) **232**(2): 323–339. doi:10.1111/j.1469-7998.1994.tb01576.x.

Matsubayashi, J., Morimoto, J., Mano, T., Aryal, A., and Nakamura, F. 2014. Using stable isotopes to understand the feeding ecology of the Hokkaido brown bear (Ursus arctos) in Japan. Ursus, **25**(2): 87–97. doi:10.2192/ursus-d-12-00015.1.

Mattingly, W.B., and Flory, S.L. 2011. Plant architecture affects periodical cicada oviposition behavior on native and non-native hosts. Oikos, **120**(7): 1083–1091.

doi:10.1111/j.1600-0706.2010.18994.x.

Mattson, D.J. 2001. Myrmecophagy by Yellowstone grizzly bears. Can. J. Zool. **79**(5): 779–793. doi:10.1139/cjz-79-5-779.

Mattson, D.J., Blanchard, B.M., and Knight, R.R. 1991*a*. Food habits of Yellowstone grizzly bears, 1977-1987. Can. J. Zool. **69**(6): 1619–1629. doi:10.1139/z91-226.

Mattson, D.J., Gillin, C.M., Benson, S.A., and Knight, R.R. 1991*b*. Bear feeding activity at alpine insect aggregation sites in the Yellowstone ecosystem. Can. J. Zool. **69**(9): 2430–2435. doi:10.1139/z91-341.

Ministry of the Environment the Government of Japan. 2017. Report on a survey for evaluating the impacts of deer herbivory on vegetation structure [in Japanese].

Moriyama, M., Matsuno, T., and Numata, H. 2016. Dead-twig discrimination for oviposition in a cicada, Cryptotympana facialis (Hemiptera: Cicadidae). Appl. Entomol. Zool. **51**(4): 615–621. doi:10.1007/s13355-016-0438-z.

Nielsen, S.E., Boyce, M.S., and Stenhouse, G.B. 2004*a*. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. For. Ecol. Manage. **199**(1): 51–65. doi:10.1016/j.foreco.2004.04.014.

Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B., and Boyce, M.S. 2004*b*. Grizzly bears and forestry: II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. For. Ecol. Manage. **199**(1): 67–82. doi:10.1016/j.foreco.2004.04.015.

Oberdörster, U., and Grant, P.R. 2006. Predicting emergence, chorusing, and oviposition of periodical cicadas. Ecology, **87**(2): 409–418. doi:10.1890/05-0547.

Ohdachi, S., and Aoi, T. 1987. Food Habits of Brown Bears in Hokkaido, Japan. Bears: Their Biology and Management, **7**: 215. doi:10.2307/3872627.

Ooi, N., Tsuji, S.I., Danhara, T., Noshiro, S., Ueda, Y., and Minaki, M. 1997. Vegetation change during the early last Glacial in Haboro and Tomamae, northwestern Hokkaido, Japan. Rev. Palaeobot. Palynol. **97**(1–2): 79–95. doi:10.1016/S0034-6667(96)00052-8.

Penteriani, V., Delgado, M.D.M., Krofel, M., Jerina, K., Ordiz, A., Dalerum, F., Zarzo-Arias, A., and Bombieri, G. 2018. Evolutionary and ecological traps for brown bears Ursus arctos in human-modified landscapes. Mamm. Rev. **48**(3): 180–193. doi:10.1111/mam.12123.

Pons, P. 2020. True cicadas (Cicadidae) as prey for the birds of the Western Palearctic: A review. Avian Res. **11**(1): 1–9. doi:10.1186/s40657-020-00200-1.

QGIS Development Team (2020) QGIS geographic information system. Open source geospatial foundation project. https://qgis.osgeo.org

R Core Team. 2018. R: A language and environment for statistical computing. Available from https://www.r-project.org/.

Ramankutty, N., and Foley, J.A. 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. Global Biogeochem. Cycles, **13**(4): 997–1027. doi:10.1029/1999GB900046.

Reimchen, T.E. 2000. Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. Can. J. Zool. **78**(3): 448–457. doi:10.1139/z99-232.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al. 2014. Status and Ecological Effects of the World’s Largest Carnivores. Science,

343(6167): 1241484. doi:10.1126/science.1241484.

Rosell, F., Jojola, S.M., Ingdal, K., Lassen, B.A., Swenson, J.E., Arnemo, J.M., and Zedrosser, A. 2011. Brown bears possess anal sacs and secretions may code for sex. J. Zool.(Lond.) **283**(2): 143–152. doi:10.1111/j.1469-7998.2010.00754.x.

Sakamaki, H., and Enari, H. 2012. Activity-specific evaluation of winter habitat use by Japanese macaques in snow areas, northern Japan: Implications for conifer plantation management. For. Ecol. Manage. **270**: 19–24. doi:10.1016/j.foreco.2012.01.010.

Sato, Y., Mano, T., and Takatsuki, S. 2005. Stomach contents of brown bears Ursus arctos in Hokkaido, Japan. Wildl. Biol. **11**(2): 133–144. doi:10.2981/0909-6396(2005)11[133:SCOBBU]2.0.CO;2.

Sato, Y., and Sato, S. 2015. Spring Temperature Predicts the Long-Term Molting Phenology of Two Cicadas, Cryptotympana facialis and Graptopsaltria nigrofuscata (Hemiptera: Cicadidae). Ann. Entomol. Soc. Am. **108**(4): 494–500. doi:10.1093/aesa/sav036.

Shimozuru, M., Shirane, Y., Jimbo, M., Yamanaka, M., Nakanishi, M., Ishinazaka, T., et al. 2020*a*. Male reproductive input, breeding tenure, and turnover in high-density brown bear (Ursus arctos yesoensis) populations on the Shiretoko Peninsula, Hokkaido, Japan. Can. J. Zool. **98**(3): 175–185. doi:10.1139/cjz-2019-0061.

Shimozuru, M., Shirane, Y., Yamanaka, M., Nakanishi, M., Ishinazaka, T., Kasai, S., et al. 2020*b*. Maternal human habituation enhances sons' risk of human-caused mortality in a large carnivore, brown bears. Sci. Rep. **10**(1): 16498. doi:10.1038/s41598-020-73057-5.

Shirane, Y., Mori, F., Yamanaka, M., Nakanishi, M., Ishinazaka, T., Mano, T., et al. 2020. Development of a noninvasive photograph-based method for the evaluation of body condition in free-ranging brown bears. PeerJ **8**: e9982. doi:10.7717/peerj.9982.

Shoyama, K. 2008. Reforestation of abandoned pasture on Hokkaido, northern Japan: Effect of plantations on the recovery of conifer-broadleaved mixed forest. Landsc. Ecol. Eng. **4**(1): 11–23. doi:10.1007/s11355-008-0034-7.

Sorensen, A.A., Stenhouse, G.B., Bourbonnais, M.L., and Nelson, T.A. 2015. Effects of habitat quality and anthropogenic disturbance on grizzly bear (Ursus arctos horribilis) home-range fidelity. Can. J. Zool. **93**(11): 857–865. doi:10.1139/cjz-2015-0095.

Sörensen, I., Amundin, M., and Laska, M. 2019. Meerkats (Suricata suricatta) are able to detect hidden food using olfactory cues alone. Physiol. Behav. **202**: 69–76. doi:10.1016/j.physbeh.2019.02.002.

Stephens, R.B., Trowbridge, A.M., Ouimette, A.P., Knighton, W.B., Hobbie, E.A., Stoy, P.C., and Rowe, R.J. 2020. Signaling from below: rodents select for deeper fruiting truffles with stronger volatile emissions. Ecology, **101**(3). doi:10.1002/ecy.2964.

Stephens, S.S., and Wagner, M.R. 2007. Forest plantations and biodiversity: A fresh perspective. J. For. **105**(6): 307–313. doi:10.1093/jof/105.6.307.

Steyaert, S.M.J.G., Hertel, A.G., and Swenson, J.E. 2019. Endozoochory by brown bears stimulates germination in bilberry. Wildl. Biol. **2019**(1): 1–5. doi:10.2981/wlb.00573.

Swenson, J.E., Jansson, A., Riig, R., and Sandegren, F. 1999. Bears and ants: Myrmecophagy by brown bears in central Scandinavia. Can. J. Zool. **77**(4): 551–561. doi:10.1139/z99-004.

Takafumi, H., and Hiura, T. 2009. Effects of disturbance history and environmental factors on the diversity and productivity of understory vegetation in a cool-temperate forest in Japan. For. Ecol. Manage. **257**(3): 843–857. doi:10.1016/j.foreco.2008.10.020.

Tomita, K., and Hiura, T. 2020. Brown bear digging for cicada nymphs: a novel interaction in a forest ecosystem. Ecology, **101**(3). doi:10.1002/ecy.2899.

Way, J.G. 2008. Eastern Coyotes, Canis latrans, observed feeding on periodical Cicadas, Magicicada septendecim. Can. Field-Nat. **122**(3): 271–272. doi:10.22621/cfn.v122i3.614.

Whytock, R.C., Fuentes-Montemayor, E., Watts, K., Barbosa De Andrade, P., Whytock, R.T., French, P., Macgregor, N.A., and Park, K.J. 2018. Bird-community responses to habitat creation in a long-term, large-scale natural experiment. Conserv. Biol. **32**(2): 345–354. doi:10.1111/cobi.12983.

Yamazaki, K., Kozakai, C., Koike, S., Morimoto, H., Goto, Y., and Furubayashi, K. 2012. Myrmecophagy of Japanese black bears in the grasslands of the Ashio area, Nikko National Park, Japan. Ursus, **23**(1): 52–64. doi:10.2192/URSUS-D-10-00012.1.

Yang, L.H. 2006. Periodical cicadas use light for oviposition site selection. Proc. R. Soc. B Biol. Sci. **273**(1604): 2993–3000. doi:10.1098/rspb.2006.3676.

Yoshida, T., and Hijii, N. 2006. Spatiotemporal distribution of aboveground litter in a Cryptomeria japonica plantation. J. For. Res. **11**(6): 419–426. doi:10.1007/s10310-006-0235-6.

Table

Table 1 Stand characteristics across the forest types. Mean ± SD

Forest type (Number of plots)	Dominant tree species (%Basal area)	Density of trees (Trees 100 m^{-2})	Basal area (m^{2} 100 m^{-2})	Canopy openness (%)
Larch plantation (*n*=15)	Larix kaempferi (97%)	32.07 ± 7.78	0.12 ± 0.04	12.69 ± 2.63
Fir plantation (*n*=12)	Abies sachalinensis (84%)	30.17 ± 10.34	0.11 ± 0.04	2.41 ± 0.62
Spruce plantation (*n*=15)	Picea glehnii (95%)	27.33 ± 6.19	0.09 ± 0.03	1.83 ± 0.82
Natural forest (*n*=30)	Abies sachalinensis (31%) Quercus crispula (28%)	31.57 ± 10.36	0.10 ± 0.05	2.20 ± 1.06

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

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

Figure captions

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 (QGIS Development Team 2020).

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 ($p < 0.001$).

Figure 3 The number of cicada *Lyristes bihamatus* exuviae across all forest types in 2018 (dark grey) and 2019 (grey). 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 number of cicada exuviae between 2 years by generalized linear model ($p < 0.001$).

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.

Figure 1

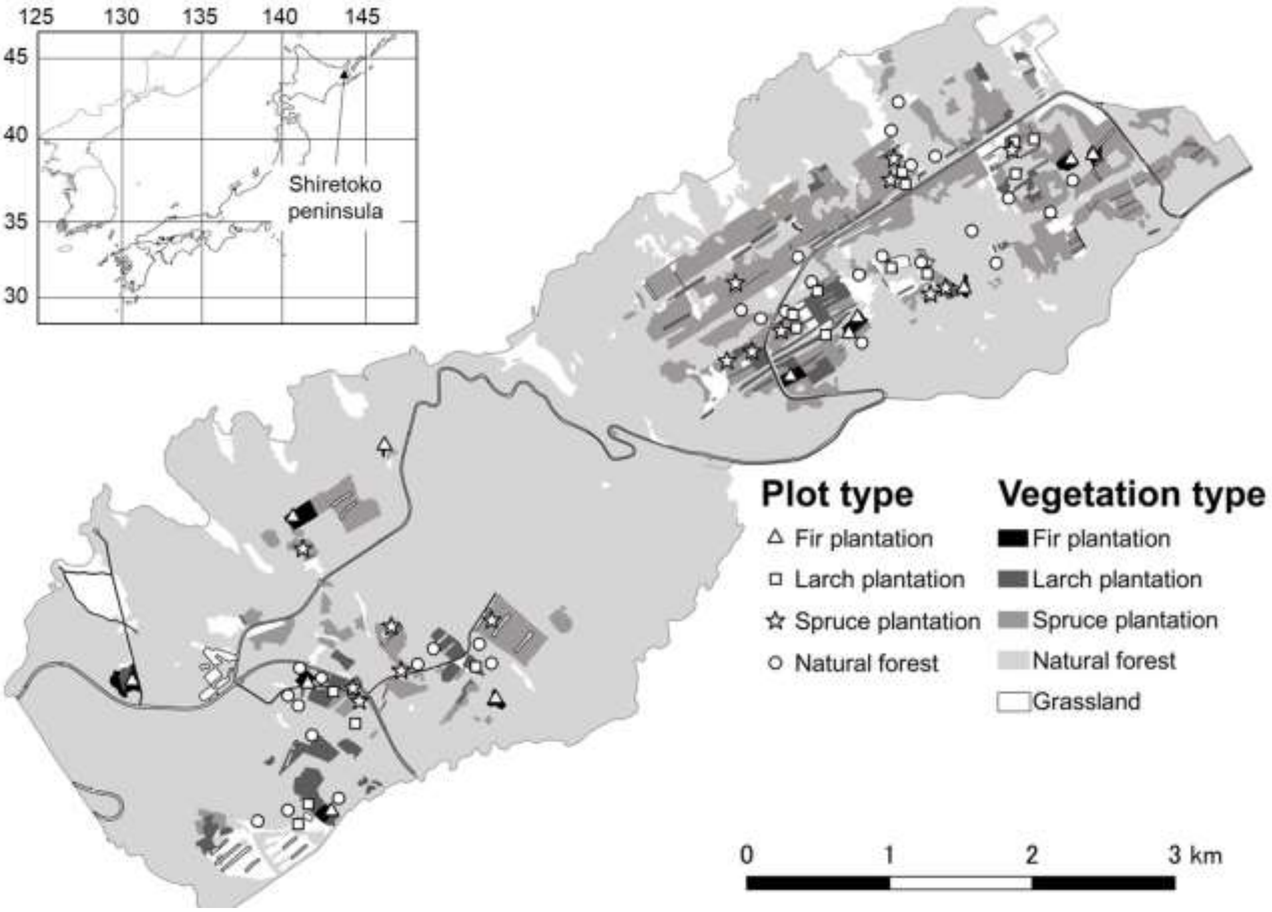

125
130
135
140
145
45
40
35
30
Shiretoko peninsula
Plot type
△ Fir plantation
□ Larch plantation
☆ Spruce plantation
○ Natural forest
Vegetation type
■ Fir plantation
■ Larch plantation
■ Spruce plantation
■ Natural forest
☐ Grassland
0
1
2
3 km

Figure 2

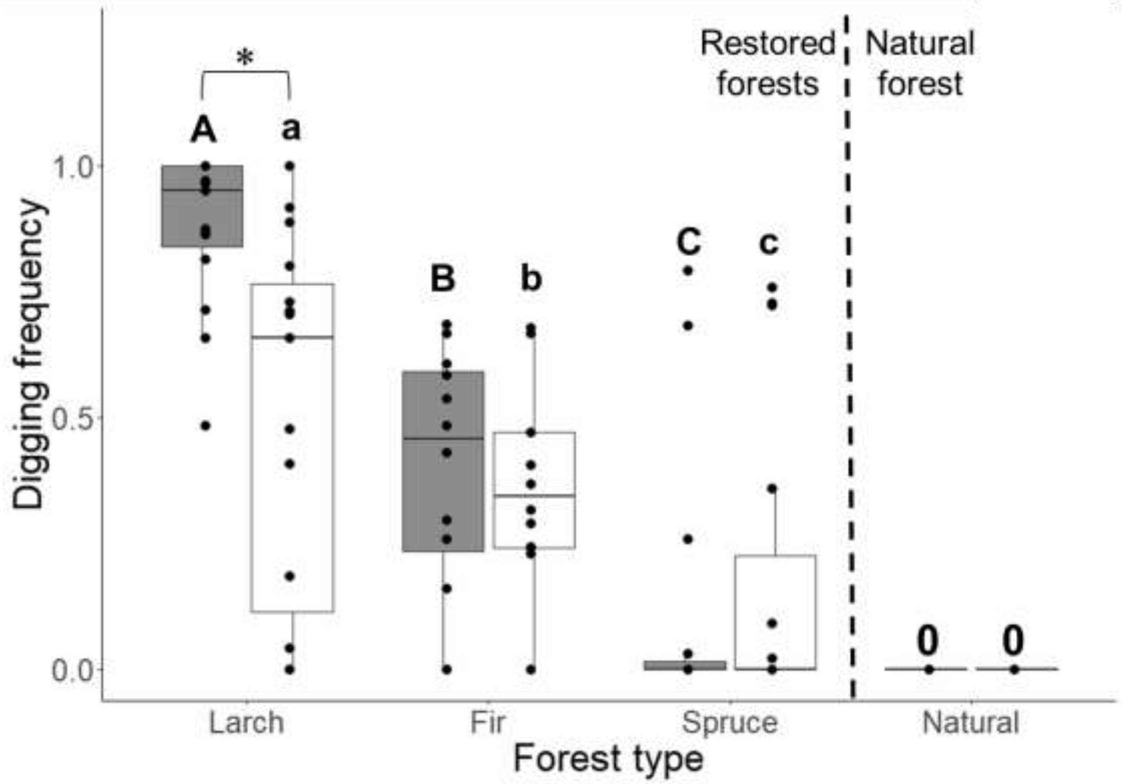
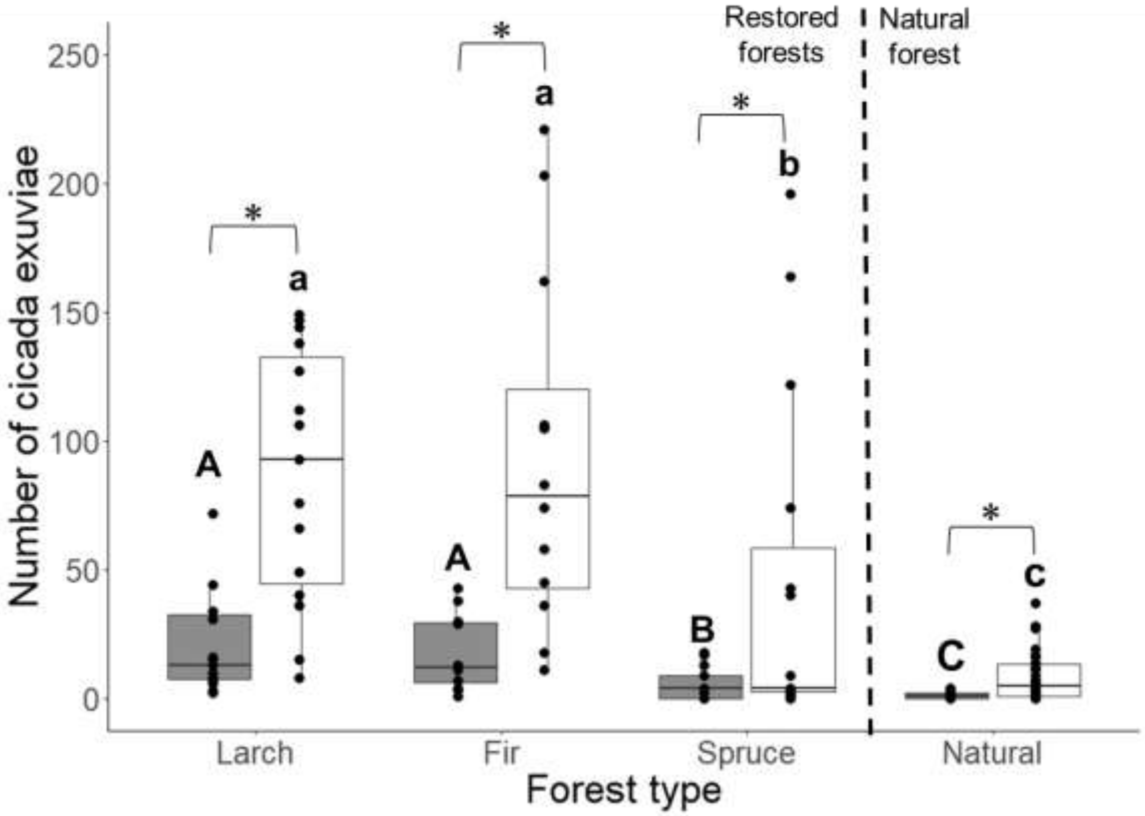
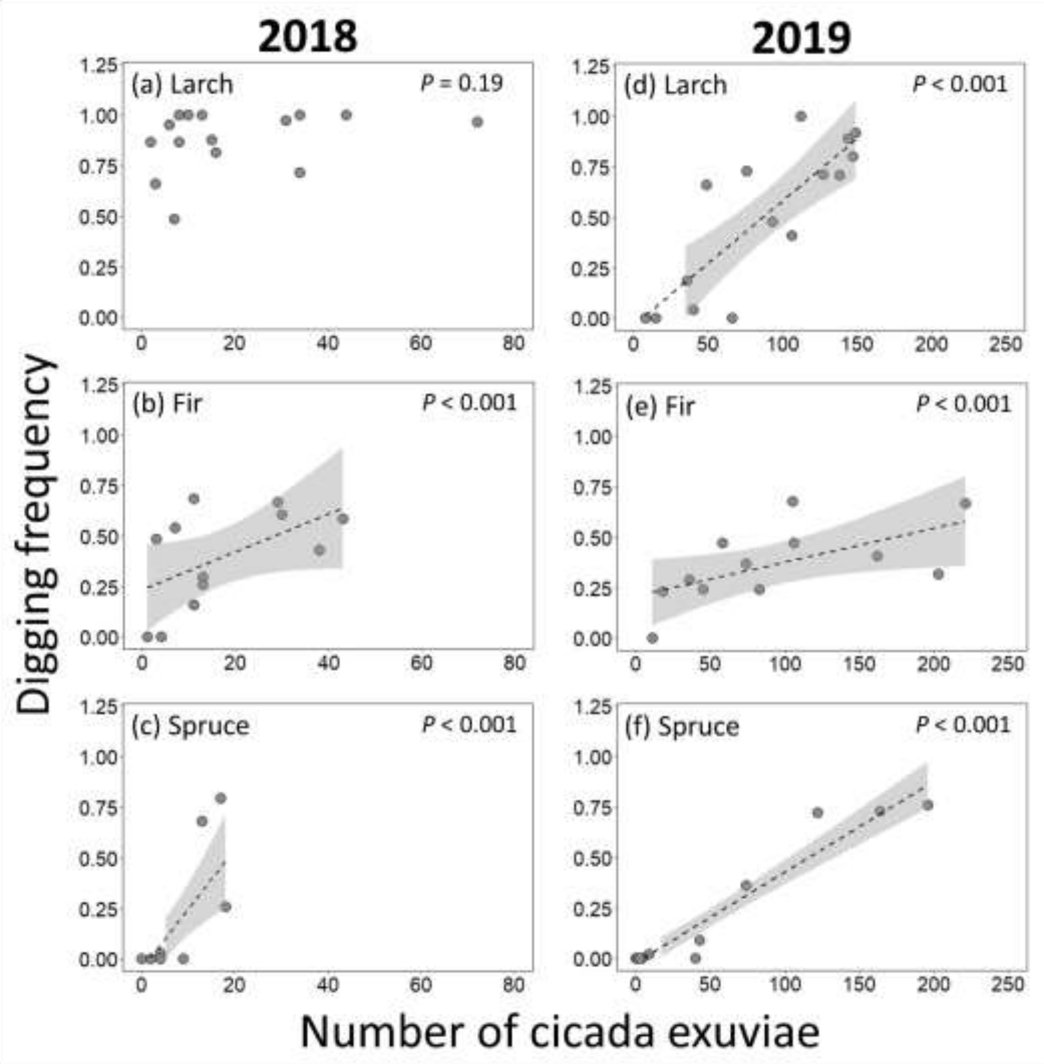

*
A
a
B
b
C
c
0
0
Restored forests
Natural forest
Digging frequency
1.0
0.5
0.0
Larch
Fir
Spruce
Natural
Forest type

Figure 3



Restored forests
Natural forest
Number of cicada exuviae
250
200
150
100
50
0
*
a
A
b
B
c
C
Larch
Fir
Spruce
Natural
Forest type

570 **Figure 4**


2018
2019
(a) Larch
P = 0.19
(b) Fir
P < 0.001
(c) Spruce
P < 0.001
(d) Larch
P < 0.001
(e) Fir
P < 0.001
(f) Spruce
P < 0.001
Digging frequency
1.25
1.00
0.75
0.50
0.25
0.00
0
20
40
60
80
0
50
100
150
200
250
Number of cicada exuviae