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Disentangling the direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of the brown bear *Ursus arctos*

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Elucidating the factors affecting the foraging habitat selection of wildlife can further our understanding of the animal–habitat relationships and inform wildlife conservation and management. Canopy and understory vegetation may directly or indirectly affect the foraging habitat selection of carnivores through changes in habitat structure and prey availability, respectively; however, the relative importance of these two effects remains largely unknown. Dwarf bamboo *Sasa kurilensis* is a predominant understory plant that suppresses regeneration in the forests of northern Japan. The purpose of this study was to disentangle the direct and indirect effects of canopy forest type *Larix kaempferi* plantation versus natural mixed forest) and dwarf bamboo on foraging habitat selection of a large carnivore, the brown bear *Ursus arctos*. In the Shiretoko World Heritage, brown bears dig for cicada nymphs during summer. We evaluated the frequency of brown bear foraging on cicadas by investigating traces of digging for cicada nymphs. A structural equation model was used to statistically disentangle the direct and indirect effects of vegetation. Our results demonstrated that canopy and understory vegetation directly and indirectly affected foraging habitat selection of brown bears. Dwarf bamboo negatively affected cicada nymph density, which positively affected brown bear digging. This suggests that dwarf bamboo also had indirect negative effects on brown bears. Forest type had significant direct and indirect effects via change in cicada nymph density on foraging behavior in brown bears. Forestry managers in northern Japan, including the study site, try to remove dwarf bamboo for assisting natural regeneration. Removal of dwarf bamboo by scarification might not only promote natural regeneration, but also provide a beneficial foraging habitat for bears.

Keywords: digging, direct effects, dwarf bamboo, indirect effects, structural equation model, *Ursus arctos*

Understanding the foraging habitat selection of animals in the natural environment is a major goal of animal ecology (Rosenzweig 1981, Lima and Zollner 1996, Morrison et al. 2012) and can provide useful information for habitat management for conservation (Morris 2003, Mayor et al. 2009). Foraging habitat selection is directly and indirectly affected by many environmental factors such as vegetation biomass and structure or prey availability (Jonkel and Cowan 1971, Risenhoover and Bailey 1985, Heithaus et al. 2009), because environmental factors often show causal relationships among one another. For instance, vegetation can directly and negatively affect carnivores by decreasing prey-searching efficiency (Gorini et al. 2012), but it has indirect and positive effects on carnivores through enhancing prey availability due to increase in plant biomass (Lantschner et al. 2012). Although evaluating the direct and indirect effects of vegetation separately can deepen our understanding of the mechanisms of habitat selection of carnivores and thereby contribute to accurately identifying habitat attributes that should be protected, there is little consideration of these two effects on foraging habitat selection (Eby et al. 2014, Belanger et al. 2020).

Canopy and understory vegetation serve important functions in forest ecosystems, such as enabling nutrient cycling and providing wildlife habitat (Ellison et al. 2005, Nilsson and Wardle 2005, Hagar 2007). Vegetation also influences animal behavior by serving as foraging and resting habitat, or shelter from predators (Ellison et al. 2005, Royo and Carson 2006, Lone et al. 2014, Davies et al. 2016) and strongly influence carnivore habitat selection (Lantschner et al. 2012, Lone et al. 2014, Gastón et al. 2019). For instance, Lone et al. (2014) showed that Eurasian lynx *Lynx lxnx* predation occurred more frequently in areas with dense understory vegetation than in areas with sparse understory

vegetation due to the increased availability of ambush sites. Gastón et al. (2019) showed that the Iberian lynx *Lynx pardinus* preferred broadleaved forests with low canopy cover, possibly due to its indirect effect on lynx through increased prey density (i.e. rabbits). However, the relative importance of direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of carnivores remains largely unknown.

The brown bear *Ursus arctos*, which is one of the most widespread large carnivores in the northern hemisphere, consumes a wide variety of foods from plants to animals (Mattson et al. 1991a, Sato et al. 2005, Shirane et al. 2021). Canopy and understory vegetation provide bears with foods such as herbs, nuts and berries (Nielsen et al. 2004, Martin et al. 2010, McClelland et al. 2020). Even though brown bears mainly consume plant materials, use of herbivorous animals is ubiquitous in bear diets (Mattson et al. 1991b, Kobayashi et al. 2012). Thus, canopy and understory vegetation may also directly and indirectly affect the foraging habitat selection of brown bears. While it is well known that canopy vegetation affects the habitat selection of brown bears (Martin et al. 2010, Milakovic et al. 2012), there are few studies showing the effects of understory vegetation on bears (Nielsen et al. 2004, McClelland et al. 2020).

In the Shiretoko World Heritage (hereafter; SWH), Hokkaido, northern Japan, brown bears dig for final instar nymphs of cicadas *Lyristes bihamatus* during summer (Tomita and Hiura 2020). Tomita and Hiura (2021a) found that their digging for cicada nymphs only occurred in conifer plantations, but not in natural mixed forest, and cicada nymph densities were higher in plantations than in the natural forest. In the SWH site, the dominant understory species is dwarf bamboo *Sasa kurilensis* with tough and dense rhizomes, and thus understory vegetation may negatively affect foraging habitat selection of bears for cicadas through increase in the energy required for digging. Dwarf bamboo may also indirectly affect foraging habitat selection through changes in cicada nymph density because the density of cicada nymphs, which feed on xylem sap, is affected by biomass and composition of understory vegetation (Smith et al. 2006). Accordingly, we predicted that forest type and the presence or absence of understory vegetation might directly or indirectly affect foraging habitat selection of brown bears for cicada nymphs through changes in habitat structure and prey availability (i.e. cicada density), respectively. To independently evaluate the direct and indirect effects of forest type and dwarf bamboo, we used structural equation modelling (SEM), which is a powerful statistical framework to develop causal understanding (Grace 2006).

Material and methods

Study site

This study was conducted in the Horobetsu-Iwaobetsu area (44°09′N, 145°02′E; altitude 120–220 m a.s.l.) located in the western parts of the SWH. This area is certified as the UNESCO World Natural Heritage Site because it represents one of the richest northern temperate ecosystems in the world. The natural forests are conifer–broadleaved mixed forests dominated by Sakhalin fir *Abies sachalinensis* and Mongolian oak *Quercus crispula*. Natural forests account for 82% and plantations account for the remaining 18% of the total forested area at the study site. Sakhalin spruce *Picea glehnii*, Japanese larch *Larix kaempferi* and fir plantations account for 13, 4 and 1% of the total forested area, respectively (Tomita and Hiura 2021a), and most of these plantations were established between 1970s and 1990s (Shoyama 2008). Dwarf bamboo occurs within natural forests and larch plantations, but not in spruce and fir plantations in the study area because of low light availability on the forest floor in the latter ones. Within the study area, at least 11 individual bears were observed to forage on cicada nymphs, including two subadults, two solitary adult females and three females with four cubs (Tomita and Hiura 2020). Individual identification and age classes of bears were determined based on color, marks, body size and family structure using camera traps. Brown bears forage on the final instar nymphs of *L. bihamatus* within conifer plantations, but not within natural mixed forest (Tomita and Hiura 2020, 2021a).

Field survey

In larch plantations without understory dwarf bamboo where the bears frequently dug for *L. bihamatus* nymphs, the emergence density of cicadas in 2018 (20.20 ± 18.71) was lower than that in 2019 (87.07 ± 47.72) (Tomita and Hiura 2021a). Thus, we conducted field surveys in these two years to consider the influence of the annual difference in cicada emergence density on the foraging habitat selection of brown bears. From late August to September, survey plots (100 m^2) were set in the larch plantations and natural forests with and without understory dwarf bamboo (n = 15 for each type). We maintained spatial separation among survey plots with the same vegetation type to avoid spatial autocorrelation (Fig. 1). Because bears dig for cicada nymphs from mid-May to the end of July, during which the final instar nymphs fully emerge (Tomita and Hiura 2020), the chosen survey duration was appropriate for evaluating the foraging behavior of bears and the emergence density of cicadas. Although brown bears dig for cicada nymphs in the spruce and fir plantations (Tomita and Hiura 2021a), we did not use the data collected from these plantations because dwarf bamboo is absent in these forest types. According to our preliminary observations using eight camera traps set in larch plantations where brown bears dug the previous year, bears usually dig for cicada nymphs near tree trunks. Thus, we evaluated the digging frequency per plot as the proportion of all trees (DBH > 2 cm) that had digging traces within 50 cm diameter from the base of a tree. Freshness of digging traces was visually determined, as traces scratched in the current year had no fresh leaf litter on the ground and fluffy soil. The density of cicada nymphs was measured as the density of cicada exuviae collected from all trees (DBH > 2 cm) within the plots. The sampling height of trees was below 3 m, because most exuviae on trees are observed at this height (Tomita and Hiura 2021a). Exuviae on the ground were collected within 1 m of the tree trunk, because most exuviae falling from the tree are found at this distance. We only collected exuviae associated with trees, not dwarf bamboo because *L. bihamatus* use dead branches on tree trunk for oviposition (Tomita and Hiura

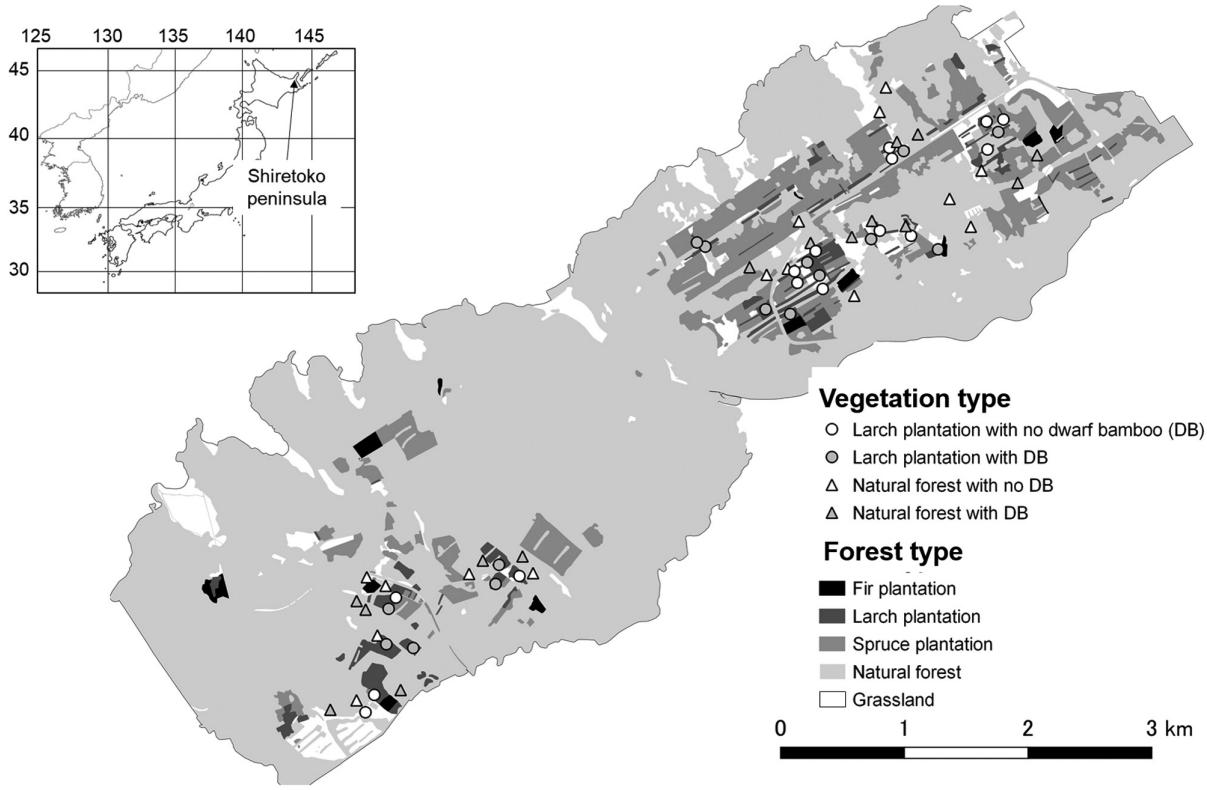

Figure 1. Location of the survey plots in the vegetation map of the study site. This vegetation map is reprinted from Tomita and Hiura (2021a) and created by Shiretoko Nature Foundation (Shiretoko Nature Foundation unpubl. information). This figure was created using QGIS 3.14.0.

2021a) and cicada exuviae were never found on stems and leaves of dwarf bamboo. Cicada exuviae were generally used as an index of cicada nymph density because they empirically reflect the density of underground nymphs (Lee et al. 2010, Moriyama and Numata 2015, Pons 2015). All trees with DBH > 2 cm within the survey plot were measured for quantifying the stand basal area and number of trees per plot in 2018.

Statistical analysis

Generalized linear models (GLMs) with log link and Poisson error distribution were used to test the differences in digging frequencies and cicada nymph densities among vegetation types (i.e. larch plantation and natural forest with and without dwarf bamboo). For digging frequencies, we constrained GLMs only on larch plantations due to no occurrence in natural forests. For GLMs of 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.

In the field of ecology, SEM has recently been used to disentangle the causal relationships among biotic and abiotic factors and independently evaluate the strength of direct and indirect effects based on observational data (Grace 2006, Eisenhauer et al. 2015). In SEMs, an a priori hypothetical model is built following ecologically realistic assumptions and then the path coefficients are estimated (Eisenhauer et al. 2015). Accordingly, a hypothetical path model was constructed for applying SEM to the observational data (Fig. 2), based on the following assumptions. The foraging behavior of brown bears may be affected by the density of cicada nymphs and the presence of dwarf bamboo. Furthermore, brown bears may directly detect the location of belowground cicada nymphs, or indirectly search for them by associating the location with the aboveground landmarks such as forest type (e.g. natural forest versus larch plantation) and stand characteristics (e.g. stand basal area and number of trees) (Tomita and Hiura 2021a). These forest characteristics would also indirectly affect the foraging habitat selection of bears through changes in the density of cicadas, whose life cycle depends on the forest trees. Thus, we assumed that forest characteristics directly and indirectly affect the foraging habitat selection of brown bears for cicada nymphs. To test the effect of forest type in the model, larch plantation and natural forest were converted to dummy variables (i.e. larch plantation = '1', and natural forest = '0'). Thus, the target variables showing higher values in the larch plantation than in the natural forest indicated the positive effects of forest type. We assumed that the density of cicada nymphs is affected by dwarf bamboo and forest characteristics, such as forest type, stand basal area and number of trees, because cicadas depend on forest plants for their life cycle. All count data (i.e. the number of trees and cicada nymphs) were log 10 (n + 1) transformed. The strength of indirect effects was calculated by multiplying the path coefficients of the mediated variables by those of the associated variables. Since the effect size of each variable could be regarded as absolute values of standardized path coefficients (Grace et al. 2010, Ando et al. 2017), we compared the values to evaluate the relative importance of each variable on the foraging habitat selection of bears.

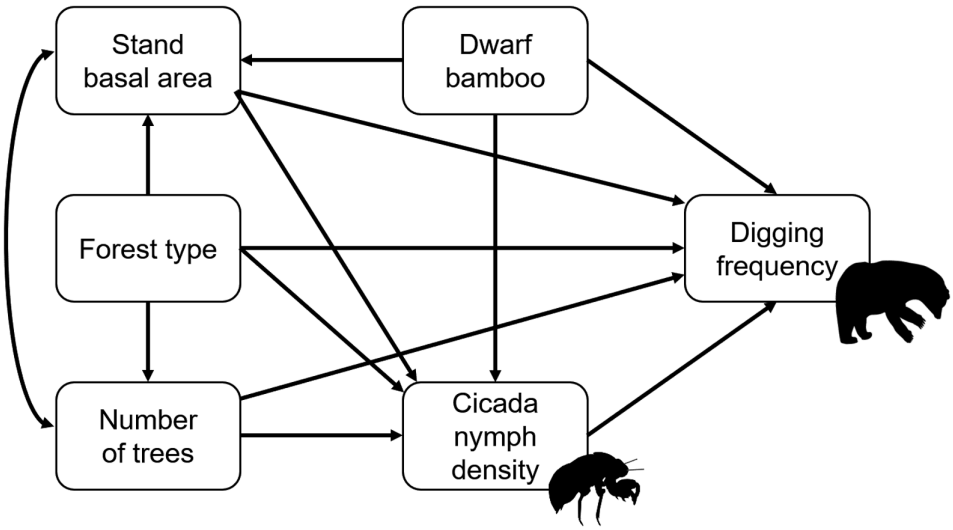

Figure 2. Hypothetical path model to represent the causal relationships among forest characteristics, cicada nymph density and frequency of brown bear digging for cicada nymphs. Cicada nymph density was measured as the number of cicada exuviae within a survey plot. Digging frequency indicates the proportion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

To test the goodness of model fit, we used the root mean square error of approximation (RMSEA) (Steiger 1990) and the comparative fit index (CFI) (Bentler 1990), which examine the absolute fit of the model to the observational data. Values of CFI $\geq$ 0.95 and RMSEA $\leq$ 0.06 suggest an appropriate model fit (Hu and Bentler 1999). Use of multiple measures for testing model fit is recommended to build a highly robust model (Hu and Bentler 1999). All analyses were performed using the lavaan package (Rosseel 2012) of R ver. 3.5.1 (<www.r-project.org>).

Results

In both years, dwarf bamboo had a significant negative effect on digging frequency (Table 1), and forest type had a significant positive effect on cicada nymph density (Table 1).

For SEMs in both years, the RMSEA and CFI values were 0.000 (90% confidence interval: 0.000–0.305) and 1.000 respectively, indicating that the model adequately fit the data. The SEM results (i.e. R^2 values, standardized path coefficients and standard error of each variable) in 2018 and 2019 are summarized in Table 1, and the detailed information is presented in the Supporting information. In both years, the frequency of brown bear diggings for cicada nymphs was positively affected by the density of cicada nymphs and negatively by the presence of dwarf bamboo. Forest type had the largest positive effect on digging frequency (Table 1). Digging frequencies, including densities of cicada exuviae, were greatest in larch forests without a dwarf bamboo understory (Fig. 3). The direct effect of dwarf bamboo presence on digging frequency (2018: −0.22, 2019: −0.12) was stronger than the indirect effect via cicada nymph density (2018: $-0.61 \times 0.14 = -0.08$; 2019: $-1.03 \times 0.09 = -0.09$) (Fig. 4). The direct effect of forest type on digging frequency (0.38) was stronger than the indirect effect via cicada nymph density ($1.44 \times 0.14 = 0.20$) in 2018, whereas the direct effect (0.14) was same as or slightly weaker than the indirect effect ($1.75 \times 0.09 = 0.16$) in 2019 (Fig. 4). In both years, cicada nymph density was positively affected by forest type (2018: 1.44; 2019: 1.75) but negatively affected by dwarf bamboo presence (2018: −0.61; 2019: −1.03), respectively (Fig. 4). No significant effects of stand basal area and number of trees were observed, indicating that these factors did not affect cicada nymph density. The presence of dwarf bamboo negatively affected stand basal area (−0.24). Forest type positively affected stand basal area, indicating stand basal area in larch plantations was higher than in natural forests.

Discussion

In the present study, we evaluated the direct and indirect effects of canopy and understory vegetation on the foraging habitat selection of brown bears. Although there were differences in direct and indirect effect sizes, these two effects of forest type and dwarf bamboo were significantly positive and negative, respectively. To the best of our knowledge, this is the first study to independently evaluate the direct and indirect effects of vegetation on the foraging habitat selection of carnivores.

Factors affecting the foraging habitat selection of brown bears

The direct effect of dwarf bamboo on the digging frequency was stronger than the indirect effect through decrease in the density of cicada nymphs (Fig. 4), indicating that dwarf bamboo physically interferes with digging behavior of brown bears. Our results demonstrate that understory vegetation such as dwarf bamboo may obstruct foraging behavior in brown bears. The selection of digging site by brown bears is determined by the balance between the energy for excavating soil and energy gain from food (Mattson 1997). It may be energetically costly to dig up the surface ground covered with dwarf bamboo because bear claws get caught in their tough and dense rhizomes. Likewise, dwarf bamboo would interfere with the digging behavior of other wildlife in natural environments.

Table 1. Summary of the structural equation model showing standardized path coefficients and standard errors (SE) in 2018 and 2019. R^2 show the coefficient of determination indicating the variability explained for each variable. Underlined places indicate the pathways directly associated with our predictions.

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

Significant at ***p < 0.001, **p < 0.01, *p < 0.05 and †p=0.054.

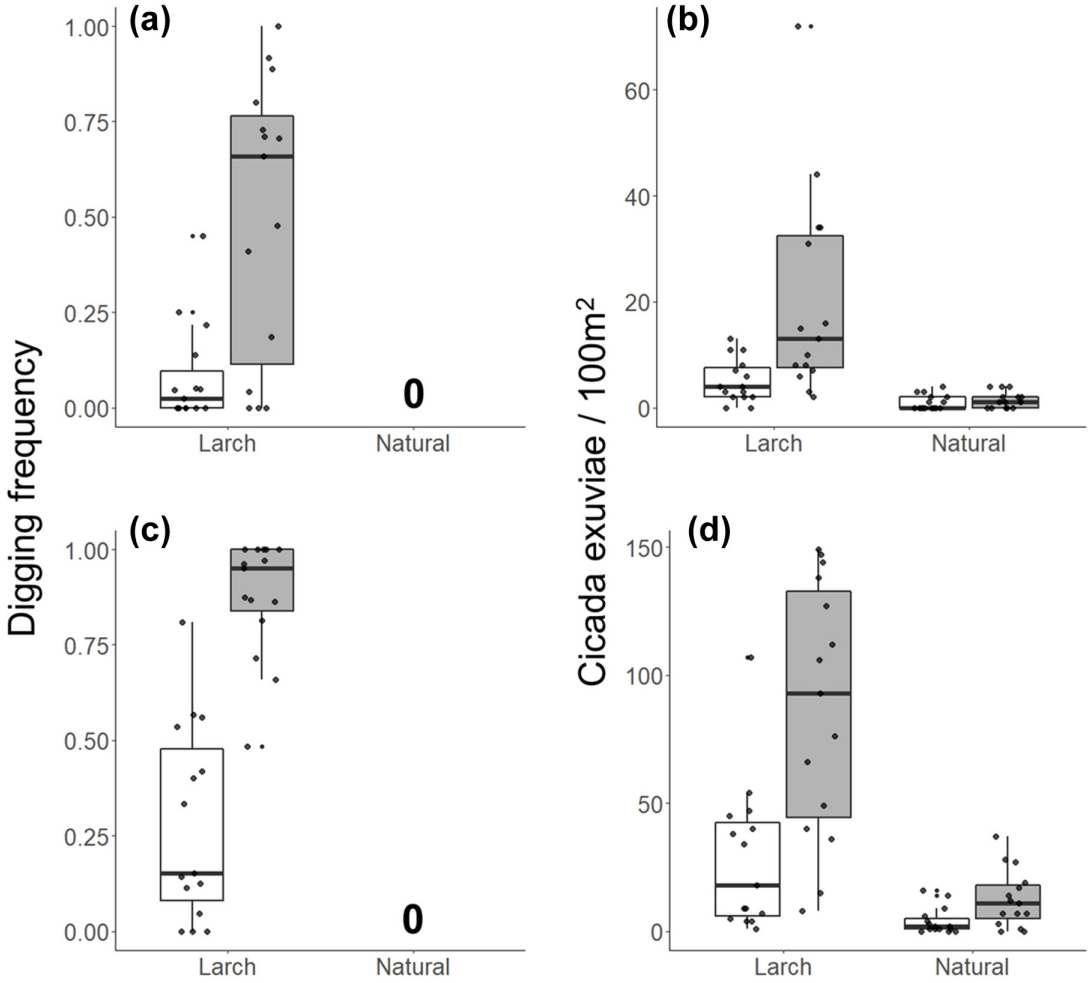

Figure 3. The frequencies of brown bear digging (a, c) and the number of cicada *Lyristes bihamatus* exuviae (b, d) between larch plantation and natural forest with (white bar) and without understory dwarf bamboo (gray bar) in 2018 (a, b) and 2019 (c, d).

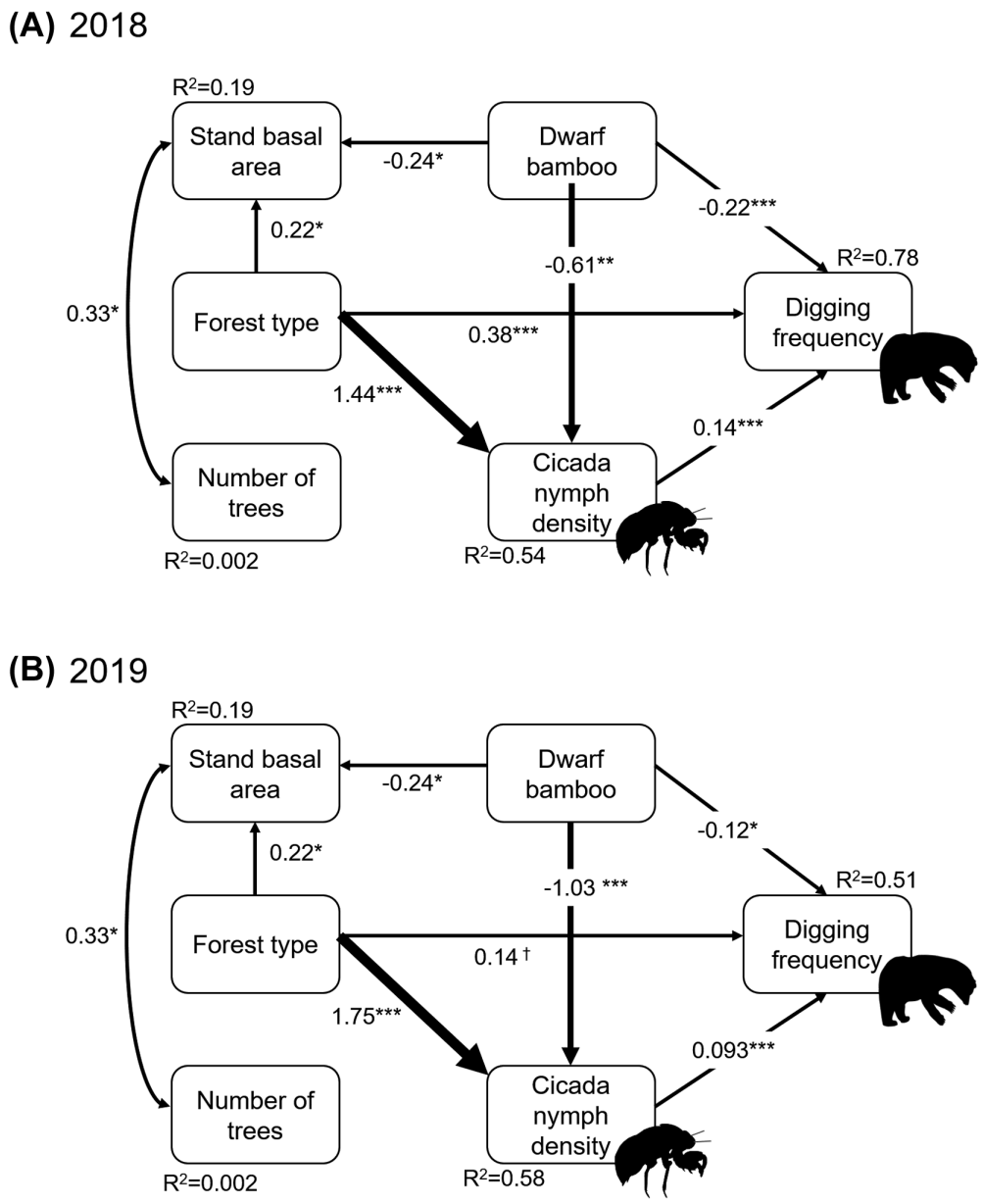

Figure 4. Structural equation model showing the causal relationships among forest characteristics, cicada *Lyristes bihamatus* nymph density and frequency of brown bear digging for cicada nymphs in 2018 (a) and (a) 2019. All paths described in the figure are statistically significant ($p < 0.05$). Numbers 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.

Although the reason bears intensively dig for cicada nymphs in the larch plantations may be the higher cicada availability in plantations than in natural forests, they also directly selected the plantations regardless of the density of cicada nymphs (direct effect of forest type on digging in 2018, Fig. 4a). Moreover, the absolute values of direct effect of forest type on brown bears were stronger than that of dwarf bamboo, indicating that canopy vegetation has a larger effect on bears than understory dwarf bamboo. Brown bears may have learned to associate nymphs with larch trees, because these trees are an introduced species, and cicada nymphs occur within the larch plantations at the study site. Learning which is an important process determining the behavior of bears (Mazur and Seher 2008), may yield a strong and direct association between their foraging behavior and forest type.

Factors affecting cicada nymph density

A possible reason for the positive effect of the larch plantations on cicada nymph density might be the fact that larches harbor more oviposition sites for cicadas than broadleaved trees. Cicada species in Japan usually lay eggs on dead branches attached to living trees (Moriyama et al. 2016). Conifer plantations usually have more attached dead branches than natural forests (Yoshida and Hijii 2006). Another possible reason is that the nutrient content of the

xylem sap of larches is higher than that of the xylem sap of broadleaved trees in natural forests. Consequently, adult cicadas would intensively oviposit on larches because the oviposition preference of herbivorous insects is typically positively correlated with larval performance (Thompson 1988, Yang and Karban 2009).

A possible mechanism underlying the negative effect of dwarf bamboo on cicada nymph density is the decrease in the nutrient content of tree xylem sap, which is a food source for cicada nymphs, due to competition with dwarf bamboo for resource such as soil nutrients (e.g. inorganic nitrogen) and water (Ishii et al. 2008). The belowground competition between dwarf bamboo and trees is supported by the negative effect of bamboo on stand basal area (Fig. 4). We observed no consistent effect of stand basal area on cicada nymph density. Although cicada nymph density may have been positively correlated with root biomass, resource quality (e.g. nutrient content of xylem sap) rather than quantity (i.e. root biomass) would be a more important factor affecting viability of cicada nymphs. Even if cicada nymphs can forage on the xylem sap of dwarf bamboo, its nutrient content would not be higher than that of the xylem sap of trees occurring in forests without dwarf bamboo due to belowground competition.

Differences in SEM results between 2018 and 2019

Even though the emergence density of cicadas in 2018 was lower than that in 2019 (Tomita and Hiura 2021a), the direction of the effect of cicada nymph density and dwarf bamboo presence on brown bear digging was consistent between both years, indicating that our SEM results provide robust estimation of the foraging habitat selection of brown bears for cicada nymphs. Conversely, the indirect effect of forest type via cicada nymph density was weaker and stronger (or the same) than the direct effect in 2018 and 2019, respectively. This difference suggests that in 2018, brown bears directly searched for the nymphs associated with the larch plantations regardless of cicada nymph density. It may be more difficult for brown bears to find cicada nymphs in years with a low emergence density of cicadas than with a high emergence density, because foraging efficiency usually decreases with decrease in prey availability (Bell 1991). In such years, bears might be more dependent on larch trees as aboveground landmarks to search cicada nymphs.

Implication for the roles of understory vegetation as brown bear habitat

Even though it is assumed that understory vegetation plays roles as brown bear habitat through food supply and structural modification on the ground surface, there are few studies considering its effects on the foraging habitat selection of brown bears possibly due to the difficulties of separation between canopy and understory layer from satellite images (Nielsen et al. 2004, Martinuzzi et al. 2009, McClelland et al. 2020). In contrast with our results, previous studies in Canada suggested that understory vegetation such as *Vaccinium* spp. are heavily utilized by bears in summer (Nielsen et al. 2004, McClelland et al. 2020). While McClelland et al. (2020) suggested that encouraging growth of understory vegetation could maximize food resources regionally for brown bears, our results suggest that understory bamboo impedes bear foraging. Given the dominant understory species generally differ among ecoregions where brown bears inhabit (e.g. Hokkaido, Japan: dwarf bamboo (Hiura et al. 1996), Alberta in Canada and Sweden: berries (Nilsson and Wardle 2005, Franklin et al. 2019), Carpathian Mountain, Poland: ferns and berries (Ciarkowska and Miechówka 2019)), evaluation of the role of the understory in brown bear ecology and management should carefully consider regional differences. Additionally, understanding spatial patterns of habitat selection can assist prediction of bear–human conflict (Northrup et al. 2012). However, dwarf bamboo may affect bear habitat selection in other ways we did not address in this study.

Management implications

We separately evaluated the direct and indirect effects of vegetation on carnivores. Our study can provide important implications for wildlife management. Understanding the mechanisms of wildlife resource use can help to solve problems in wildlife habitat management (Morris 2003, Hebblewhite et al. 2005). The indirect effect of vegetation via changes in prey availability is an overlooked pathway affecting the foraging behavior of carnivores. Given their foraging habitat selection is strongly affected by the distribution patterns of herbivorous animals that are determined by the distribution of vegetation, the indirect effect may be important for shaping their foraging habitat. Therefore, considering the indirect effects of vegetation would be able to help us to understand how the foraging habitat of carnivores determines and possibly improves their habitat conservation.

Because dwarf bamboo suppress natural regeneration due to its dense cover, forestry managers in northern Japan, including the study site, try to remove dwarf bamboo for assisting natural regeneration (Yamazaki and Yoshida 2020). Given the negative effects of dwarf bamboo on brown bear foraging as shown by this study, bamboo scarification might have a positive effect on bears through reducing the cost of digging for food and increasing prey availability. Thus, it is possible that scarification can not only promote natural regeneration, but also provide a beneficial foraging habitat for bears. Since the goal of sustainable forest management is to maintain a balance between timber production and environmental values (Dennis et al. 2008), scarification of dwarf bamboo may be an option for sustainable forestry in the study site. However, application of scarification should be carefully considered because of unknown effects on other wildlife species.

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Author contributions

KT conceived the ideas and designed the methodology. KT collected data and performed the statistical analyses. KT wrote the manuscript. KT and TH contributed to the drafts and gave final approval for publication.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.xgxd254hc> (Tomita and Hiura 2021b).

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Supplementary information (available online as Appendix wlb-00886 at <www.wildlifebiology.org/appendix/wlb-00886>).