1   Title: Emergence of a novel interaction between brown bear and cicada

2   due to anthropogenic habitat modification

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Abstract

14   Novel species interactions have generally emerged in ecosystems that are highly

15   modified by human activities. Anthropogenic habitat modification, such as

16   afforestation, is one possible driver of novel species interactions; however, empirical

17   evidence remains scarce. In this study, we show that a novel predator-prey interaction

18   between the brown bear (*Ursus arctos*) and nymphs of a cicada species (*Lyristes*

19   *bihamatus*) is generated by anthropogenic habitat modification. We evaluated the

20   frequency of brown bear predation on cicada nymphs and the density of cicada

21   nymphs between natural forests and plantations, which are a typical type of human-

22   modified habitat. We found that brown bear predation on cicada nymphs occurred

23   only in the plantations. The density of cicada nymphs in the plantations was

24   significantly higher than in the natural forest. Our results indicate that the plantation

25   leads to the emergence of the bear-cicada interaction due to increasing the density of

26   cicada nymphs. The study draws attention to the overlooked effects of anthropogenic

27   habitat modification on species interactions.

Introduction

Species interactions vary depending on environmental change. During the Anthropocene, many species now inhabit novel ecosystems characterized by a changing climate, non-native species, and a human-modified habitat [1,2]. In these novel ecosystems, species interactions occur among species that previously never interacted (hereafter: novel interaction) [3–5]. Native species can be susceptible to negative consequences from novel interactions as they lack a co-evolutionary history with their interactors [6,7]. It is difficult to predict when and where novel interactions will emerge, and whether their outcome is positive or negative for native species, as little empirical evidence of novel interactions exist [8,9]. Therefore, understanding the causes and consequences of novel interactions is important for ecosystem management and conservation [8,10].

Most studies on novel interactions focus on interactions between exotic and native species caused by biological invasion [4,11,12]. On the other hand, human-induced environmental changes, such as anthropogenic habitat modification (e.g. land use change) and climate change (e.g. global warming), have been overlooked as a cause of novel interactions, even though these changes alter the behaviour, abundance, and phenology of species, which significantly influences species interactions [13–15]. Moreover, these environmental changes provide consumers with opportunities for acquiring novel resources [8,16]. However, to our knowledge, there are no studies showing empirical evidence that anthropogenic habitat modification generates novel interactions among native species (but suggested by Fagan et al. [17]).

We focus on a predator-prey interaction between the brown bear (*Ursus arctos*) and

51 nymphs of a cicada species (*Lyristes bihamatus*) in the Shiretoko World Natural

52 Heritage (hereafter: SWH), northern Japan. This is a case of a novel interaction

53 between native species because both species are native but brown bears have only

54 started preying on cicada nymphs since 2000 in the area [18]. The interaction is

55 generated by a driver that is not associated with the invasion of either predator or prey

56 species. The plantation, a typical type of human-modified habitat [19], is one possible

57 driver of the bear-cicada interaction, given brown bear predation on cicada nymphs

58 were frequently observed in larch (*Larix kaempferi*) plantations [18].

59 In this study, we evaluated the frequency of predation and the density of

60 cicada nymphs between the natural forest and the plantations. We made the following

61 predictions according to our previous findings [18]: (1) brown bear predation on cicada

62 nymphs occurs more frequently in the plantations than in the natural forest; (2) the

63 density of cicada nymphs is higher in the plantations than in the natural forest; (3)

64 there is a positive relationship between predation frequency and the density of cicada

65 nymphs.

66

Materials & Methods

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(a) Site Description

69

70 The study was conducted in forests located on the western parts of the Shiretoko

71 Peninsula (Fig. S1). The elevation ranged from 120 m to 220 m. UNESCO has certified

72 the area as a World Heritage site because it represents one of the richest northern

73   temperate ecosystems in the world (http://whc.unesco.org/en/list/1193). The natural

74   forests are conifer-broadleaved mixed forests, mainly consisting of Sakhalin fir (*Abies*

75   *sachalinensis*) and Mongolian oak (*Quercus crispula*). Natural forests account for 82%

76   of the forest area in the study site, while plantations account for 18% of the total forest

77   area. Spruce (*Picea glehnii*), larch and fir plantations account for 13%, 4%, and 1% of

78   the total forest area, respectively. Most of the larch and fir plantations were

79   established during the late 1970s, whereas the spruce plantations were established

80   during the early 1990s [20]. The vegetation map of the study site is shown in Fig. S2.

81   The SWH has one of the highest densities of brown bear in the world[21]. Within the

82   study site, food items of the brown bears change across seasons; that is, herbaceous

83   plants are consumed in spring, herbaceous plants, ants and cicada nymphs are

84   consumed in summer, and *Q. crispula* acorns and anadromous salmon are consumed in

85   autumn [18,22,23]. Within the study area at least 11 individual bears were preying on

86   cicada nymphs, including two subadults, two solitary female adults, and three females

87   with cubs [18]. Two native cicada species, *Lyristes bihamatus* and *Terpnosia nigricosta*,

88   occur in the SNH and emerge during late summer and spring to early summer,

89   respectively. In the study site, brown bears prey on the nymphs of *L. bihamatus*, but

90   not *T. nigricosta* [18]. Hence, this study focuses on *L. bihamatus* as a prey item of bears

91   and the term "cicada" refers to *L. bihamatus*.

92

93   (b) Field Survey

94   From late August to September 2018**,** 100 m^2 survey plots were set in the following

95   forest types: larch plantations (N = 15), fir plantations (N = 12), spruce plantations (N =

96   15), and natural forests (N = 30). The location of the survey plots is shown in Fig. S2. A

97   larger number of plots were in the natural forest, as this is the highest proportion of

98   forest for all forest types. Stand characteristics of each forest type are shown in Table 1.

99   The density of cicada nymphs was measured using the density of cicada exuviae

100   collected from all trees (diameter breast height, DBH > 2 cm) within the plots. Sampling

101   heights of trees were less than 3 m. Brown bear predation on cicada nymphs was

102   measured by observing digging traces of brown bears, as the bears dig up soil when

103   preying on cicada nymphs [18]. According to our preliminary observations by camera

104   traps, brown bears usually dig for cicada nymphs near the base of a tree. We evaluated

105   the predation frequency per each plot as the proportion of trees that had digging

106   traces within a 50 cm radius from the base of a tree for all trees (DBH > 2 cm) in the

107   plot.

108   (c) Statistical Analysis

109   Generalized linear models (GLMs) with a log link, Poisson error distribution and

110   Tukey post hoc tests were used to examine the differences in predation frequency and

111   the density of cicada nymph among the forest types. When the GLM indicated a

112   significant difference (*p-value* < 0.05) of one forest type from others, we performed a

113   multiple comparison between the forest types. In the GLM analysis for predation

114   frequency, we introduced an offset term as the number of trees (log-transformed) to

115   adjust for differences in the number of trees among the survey plots. To examine the

116   effects of cicada nymph density on predation frequency, we used GLMs with log links

117   and Poisson error distributions for each forest type. Number of trees (log-transformed)

118   were included as an offset term in the GLMs. All statistical analyses were conducted in

119   R version 3.5.1 [24].

120

Results

122   The GLMs indicated a significant effect of forest type on predation frequency and the

123   density of cicada nymphs. Surprisingly, brown bear predation on cicada nymphs only

124   occurred in plantation plots, not the natural forest plots even in which mainly

125   composed of fir species (Fig. 1A). The density of cicada nymphs was lowest in the

126   natural forest plots (Fig. 1B). The predation frequency was highest in the larch

127   plantation plots, but the density of cicada nymphs did not differ from in the fir

128   plantation plots, which had a lower predation frequency (Fig. 1). The spruce plantation

129   plots had a lower predation frequency and the density of cicada nymphs than other

130   types of plantation plots (Fig. 1). The density of cicada nymphs positively affected the

131   predation frequency in all plantation types (GLM, $p < 0.05$ Fig. 2), suggesting that

132   predation occurred more frequently as the density of cicada nymphs increased.

133

Discussion

135   The results of our study generally supported the predictions. In particular, brown

136   bear predation on cicada nymphs only occurred in the plantations, not the natural

137   forests. Furthermore, in the SWH, the plantations were established during the late

138   1970s, with trees reaching maturation around 2000 [20,25]. Because cicada nymphs

139   generally grow under mature trees [26], they could inhabit the plantations since 2000

140   in this area. These indicate the high density of cicada nymphs have occurred in the

141   plantation since about 2000; consequently, the bear-cicada interaction has emerged. To

142   our knowledge, this is the first study presenting empirical evidence of a novel

143   interaction between native species due to anthropogenic habitat modification.

144   Our results indicate that the differences in predation frequency among forest types

145   can generally be explained by the density of cicada nymphs (Figs. 1,2). However, the

146   predation frequency in larch plantation was higher than in fir plantation despite no

147   differences in the density of cicada nymphs between these types of plantations. The

148   most plausible reason for this is that the density of cicada nymphs in the larch

149   plantations was underestimated. The use of cicada exuviae as a proxy for the nymph

150   density may have resulted in an underestimation of actual nymph density because it

151   does not account for nymphs that were already preyed upon by the brown bears.

152   Another reason is that brown bears had fewer chances of encountering fir plantations

153   than larch plantations because the total area of larch plantations was larger than fir

154   plantations at the study site (Fig. S2). One final reason is the social transmission of

155   information from mothers to their cubs that cicada nymphs were abundant in larch

156   plantations, which might constrain brown bears to prey on nymphs within the larch

157   plantations. Tomita & Hiura [18] showed that bears preying on cicada nymphs mainly

158   consisted of solitary adult females and females with cubs. Since socially learned

159   foraging behaviours in bears are expected to be female biased [27,28], the predatory

160   behaviour might propagate through the brown bear population via social learning.

161   Moreover, because brown bears in the SWH show female-biased philopatry [29],

162   female bears learning the behaviour may stay within the study site.

163   Consistent with our results, other studies have shown high densities of cicada

164   nymphs in human-modified habitats, such as forest edges and plantations [30–32],

165   though the reasons are unclear (but see Yang [33]). This suggests that anthropogenic

166   habitat modifications provide high quality habitat for cicadas. Since some birds and

167   mammals prey on cicadas [18,34,35], anthropogenic habitat modifications can

168   positively affect these predators via increasing availability of cicada nymphs.

169   Although the density of cicada nymphs in the larch, fir, and spruce plantations was

170   underestimated compared to natural forests due to predation by brown bears, the

171   density in these plantations was still significantly higher than in the natural forests (Fig.

172   1B). This indicates the positive effects of plantations on the cicada population

173   compensate for the negative effects of increased predation. Therefore, the bear-cicada

174   interaction does not seem to lead to negative consequences for the cicada population,

175   a notion supported by the fact that the interaction has continued for 20 years at the

176   study site [18].

177   Detecting novel interactions among native species is challenging because it can be

178   difficult to determine whether they are novel or are pre-existing interactions that have

179   been overlooked. Therefore, we might be failing to notice how anthropogenic habitat

180   modifications generate novel interactions among native species, even though the

181   impacts of anthropogenic habitat modification on native species assemblages

182   continues to strengthen around the world [36]. Our study draws attention to an

183   overlooked aspect of the effects of anthropogenic habitat modification on species

184   interactions. Furthermore, our results showed that this bear-cicada interaction does

185   not seem to have negative consequences for the cicada population. On the other hand,

186   Liu et al. [37] showed how global warming caused a novel interaction between a native

187   herbivore and a native plant that had significant negative impacts on plant

188   reproduction. Further studies are needed to understand the consequences of novel

189   interactions caused by anthropogenic environmental changes, such as habitat

190   modification and climate change.

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Acknowledgments

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298   capacity. *Ecology* **92**, 1201–1207. (doi:10.1890/10-2060.1)

299

Figures & Table

300

301 Table 1 Stand characteristics across the forest types.

Forest type(Number of plots)	Dominant tree species (%Basal area)	Density of trees (Trees $100m^{-2}$)	Basal area (m^2 $100m^{-2}$)
Larch plantation (N=15)	*Larix kaempferi* (97%)	32.06 ± 7.78	0.12 ± 0.04
Fir plantation (N=12)	*Abies sachalinensis* (84%)	30.17 ± 10.80	0.11 ± 0.04
Spruce plantation (N=15)	*Picea glehnii* (95%)	27.14 ± 6.36	0.09 ± 0.03
Natural forest (N=30)	*Abies sachalinensis* (31%) *Quercus crispula* (28%)	30.87 ± 10.73	0.10 ± 0.05

302   Figure 1

303   (A) Frequency of predation of brown bear on cicada nymphs and (B) the
304   density of cicada nymphs in larch plantations, fir plantations, spruce
305   plantations, and natural forests. Different letters indicate significant
306   differences (Tukey test, p < 0.05).
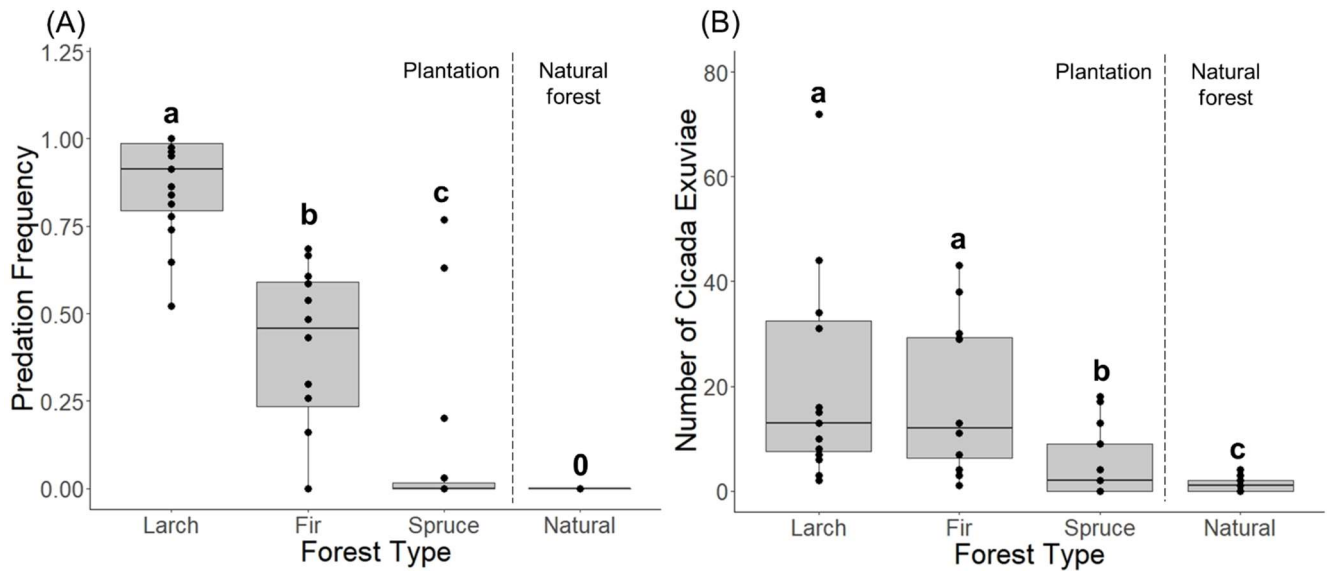
307   Figure 2

308   Relationships between the predation of brown bear on cicada nymphs and
309   the density of cicada nymphs. Dashed lines show the linear model
310   predictions with shaded areas indicating the 95% CI. The relationships are
311   significantly positive in larch plantation (Left), fir plantation (Center),
312   spruce plantation (Right) (GLM, p < 0.05).

313