

1 **Title**

2 The response of bats to dispersed retention of broad-leaved trees in harvested conifer plantations in
3 Hokkaido, northern Japan

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21

22 **Abstract** (315/400 words)

23 The area of tree plantations has been expanding globally. While plantations generally support less
24 biodiversity than natural forests, the habitat function of plantations can be enhanced by management.
25 Retention forestry is a promising method to mitigate the negative impacts of harvesting on forest-
26 dependent species through retaining some vital habitat structures for organisms. Bats are highly
27 dependent on forests and have an important pest-control function; however, their response to
28 retention forestry remains unknown. We surveyed bat activity at clear-cut sites, sites with dispersed
29 broad-leaved tree retention (medium-level retention: 50 trees/ha, high-level retention: 100 trees/ha),
30 and unharvested Todo fir (*Abies sachalinensis*) plantations in Hokkaido, northern Japan. We
31 analyzed the effects of these treatments on genus richness and the activity of three groups preferring
32 different degrees of habitat openness (cluttered-space species, open-space species, and edge species).
33 Genus richness and the activity of cluttered-space species were higher at retention sites than at clear-
34 cut sites. Similarly, the activity of edge species was higher at high-level retention sites than at clear-
35 cut sites and comparable to that at unharvested plantations. Unexpectedly, the pattern of open-space
36 species was similar to that of edge species. The increase in bat activity due to high-level retention
37 was predicted to be 3.4 and 6.1 times that of medium-level retention for cluttered-space and edge
38 species, respectively. Our results imply that dispersed broad-leaved tree retention in conifer
39 plantations mitigates the negative impacts of harvesting on cluttered-space and edge species, and
40 high-level retention is more effective. Thus, retaining large numbers of trees in a few harvested
41 compartments and clear-cutting in others can be more effective for conserving bat activity than
42 retaining a smaller number of trees in each of many compartments. For biodiversity conservation in
43 plantation landscapes, it would be worthwhile to consider not only the common strategy of low
44 retention in each of many harvested compartments but also a management strategy that retains many
45 trees in a few compartments.

46
47 **Keywords:** Variable retention; Green-tree retention; Silvicultural treatment; Clear-felling;
48 Chiroptera; Sakhalin fir

49 **Main text**

50 **1. Introduction**

51 Planted forests have been expanding worldwide and account for 7% of the global forest area (FAO,
52 2020). Planted forests dominate many landscapes; for example, the proportion of planted forest
53 among the total forest area is 36% in East Asia and 30% in Europe, excluding the Russian Federation
54 (FAO, 2020). Planted forests that are intensively managed (composed of one or two species, even
55 age class, and regular spacing of trees) are defined as tree plantations (FAO, 2020). Planted forests,
56 especially plantations, generally support less biodiversity than natural forests because the forest
57 composition and structure are less diverse (Brockhoff et al., 2008; Chaudhary et al., 2016).
58 Conversely, abundance or species richness for a range of taxa in planted forests can be enhanced by
59 management activities, such as the tree species selection, stand maturation, or maintenance of native
60 trees within stands (Hartley, 2002; Castaño-Villa et al., 2019; López-Bedoya et al., 2021). In
61 landscapes dominated by plantations, the conservation of forest-dependent species in plantations can
62 be an important means to maintain or enhance regional biodiversity, and specific management
63 methods have recently been proposed to achieve this aim (Yamaura et al., 2012; Demarais et al.,
64 2017; McFadden and Dirzo, 2018).

65 One of the main purposes of plantations is timber production (FAO, 2020). In 2012, planted
66 forests, almost half of which were plantations, produced 46.3% of global industrial round wood
67 despite their small area (Payn et al., 2015). Conserving biodiversity in plantations requires
68 management methods that are compatible with timber production (Yamaura et al., 2012; Demarais et
69 al., 2017). Clear-cutting is a common timber-harvesting technique, but results in a huge decline of
70 forest-dependent species following tree removal (Paillet et al., 2010; Chaudhary et al., 2016).
71 Retention forestry has been proposed to mitigate the negative impact of harvesting (Franklin et al.,
72 1997). In this silvicultural system, some important components for organisms and ecosystems are
73 retained in harvested areas (Gustafsson et al., 2012; Lindenmayer et al., 2012). Retention forestry has
74 been used mainly in natural forests or naturally regenerated forests in many parts of the world (Pastur
75 et al., 2020). Its effectiveness for biodiversity conservation has been demonstrated in several meta-
76 analyses (Rosenvald and Löhmus, 2008; Fedrowitz et al., 2014; Mori and Kitagawa, 2014).

77 Retention forestry also likely contributes to biodiversity conservation in plantations (Demarais
78 et al., 2017; McFadden and Dirzo, 2018), but this benefit has not been investigated (Gustafsson et al.,
79 2012; Lindenmayer et al., 2012; Yamaura et al., 2018). In conifer plantations, which are common in
80 boreal and temperate zones (FAO, 2006), mixed broad-leaved trees are essential for many species as
81 prey resources or roosting/nesting sites, e.g., for insects (Ohsawa, 2007) and birds (Lindbladh et al.,
82 2017). Broad-leaved tree retention is therefore considered a promising approach for conserving
83 biodiversity in conifer plantations (Yamaura et al., 2018, 2019). Its effectiveness for ground beetles
84 was demonstrated in a large-scale experiment in Japan (Yamanaka et al., 2021). However, the effects
85 of retention forestry are likely to vary across taxa (Rosenvald and Löhmus, 2008; Fedrowitz et al.,
86 2014; Mori and Kitagawa, 2014), and the responses of various taxa need to be evaluated before
87 retention forestry can be promoted in plantations.

88 Most bats in temperate forests are nocturnal insectivores and have important roles in controlling
89 pest populations in plantations (Charbonnier et al., 2014). Many studies have revealed that forest
90 harvesting profoundly affects bat communities, although the effects differ among species. Intensive
91 harvesting (i.e., removing most trees from stands) decreases the activity of species that prefer the
92 forest interior or edges (cluttered-space species and edge species, respectively), but increases the
93 activity of species preferring open habitats (open-space species) (Law et al., 2016; Węgiel et al.,
94 2019; Loeb, 2020). In contrast, mature conifer plantations with flying spaces under the canopies can
95 be suitable habitats for cluttered-space and edge species (Starbuck et al., 2015; Law et al., 2016), and
96 mixed broad-leaved trees likely support their activity (Charbonnier et al., 2016). Thus, retaining
97 broad-leaved trees in harvested conifer plantations may mitigate the impact of harvesting on
98 cluttered-space and edge species. However, few studies have focused on the effects of retention
99 forestry on bats (but see Hogberg et al., 2002; Law and Law, 2011), and none have been conducted in
100 planted forests.

101 In Japan, plantations account for 41% of the total forest area, and are principally monocultures
102 of conifer trees (Yamaura et al., 2012; Forestry Agency, 2017a). Plantations largely replaced natural
103 forests after clear-cutting from the 1950s to 1980s, and they have matured and remain unharvested
104 because of the decline of forestry over the subsequent decades (Yamaura et al., 2012). Recently
105 clear-cutting of mature plantations has occurred across Japan to increase the domestic wood supply;

106 however, the Forestry Agency has also stressed the need to improve biodiversity and the provision of
107 ecosystem services in plantations as a measure to achieve sustainable development (Kakizawa et al.,
108 2018; Forestry Agency, 2020). Two recent meta-analyses in Japan revealed that Pinaceae plantations
109 are important as habitats for various taxa, with mature stands supporting a higher abundance and
110 richness of birds and woody plants than younger ones (Spake et al., 2019; Kawamura et al., 2021).
111 Yoshikura et al. (2011) compared bat communities and forest structures between Pinaceae plantations
112 and old-growth natural forests and stressed the importance of restoring the features of old-growth
113 forests (e.g., large or dead trees) in plantations for supporting forest-dependent bat species. It is
114 therefore crucial for the conservation of forest biodiversity, including bats, to evaluate the effects of
115 retention forestry in Pinaceae plantations in Japan.

116 The aim of this study was to evaluate the responses of bats to broad-leaved tree retention in
117 harvested Pinaceae plantations in Hokkaido, northern Japan. Specifically, we recorded the
118 echolocation calls of bats at different harvested sites, including clear-cutting and two levels of tree
119 retention (medium and high), as well as unharvested Todo fir *Abies sachalinensis* plantations. We
120 compared bat activity and the genus richness among treatments. Considering the differences in
121 harvesting effects on bats according to habitat preference, we categorized each genus or species into
122 one of three groups (cluttered-space, edge, and open-space species) based on wing morphologies and
123 echolocation call characteristics. Separate analyses were then conducted for each group.

124

125

126 **2. Materials and Methods**

127 **2.1. Study region and sites**

128 The study was conducted in 2019 using sites from the Retention Experiment for Plantation Forestry
129 in Sorachi, Hokkaido (REFRESH project) (43°34'37"–39°26"N, 142°05'27"–09°33"E). In Hokkaido,
130 Pinaceae plantations have replaced broad-leaved natural forests, particularly those of native Todo fir,
131 which constitute more than half of the plantation area (Forestry Agency, 2017b; Yamaura et al.,
132 2018). The study sites were in forested landscapes dominated by Todo fir plantations, and the
133 remaining natural forests were composed mainly of broad-leaved trees (Yamaura et al., 2018).

134 Among the REFRESH sites, we selected plantation harvesting sites that had received three
135 different treatments (clear-cut [CC], medium-level retention [MR] and high-level retention [HR]),
136 and an unharvested Todo fir plantation [UP] as a control (hereafter, the term treatment is used to
137 describe all four types of sites; Fig. 1). At the MR and HR sites, dispersed 50 and 100 broad-leaved
138 trees/ha were retained, respectively, mainly birch (*Betula platyphylla*, *B. ermanii*, and *B.*
139 *maximowicziana*), linden (*Tilia japonica*), and Mongolian oak (*Quercus crispula*). The proportion of
140 broad-leaved trees retained among all trees before harvesting was as follows: MR (number basis:
141 7.3–10.8%, basal area basis: 5.7–12.9%, volume basis: 4.1–11.9%) and HR (number basis: 15.0–
142 18.1%, basal area basis: 18.6–26.5%, volume basis: 16.7–26.5%). Broad-leaved trees were mixed at
143 the UP sites, accounting for 18.2–27.5% of all trees based on the number of trees, and 8.1–10%
144 based on the basal area, based on the results of a survey of seven 20 × 20-m plots at each site (Akashi
145 et al., 2017). Each treatment had three replicates (i.e., 12 sites were surveyed in total) that were not
146 spatially clustered (Appendix S1). The distance between sites was greater than 360 m. Within a 1-km
147 radius from the center of each site, forest accounted for 86–100% of the area. The percentages of
148 broad-leaved natural forests in the same radius for the three replicates at each site were as follows:
149 CC, 21%, 23%, and 27%; MR, 15%, 16%, and 34%; HR, 11%, 18%, and 20%; and UP, 17%, 18%,
150 and 26%. The area of each site was 5.87–7.94 ha (Akashi et al., 2017). The stand ages of the three
151 UPs were 52, 52, and 55 years when the surveys were conducted, and the other sites were studied at
152 3–5 years post-harvesting (Akashi et al., 2017; Yamaura et al., 2018). Todo fir seedlings had been
153 planted at the harvested sites, and weeding had been conducted once or twice annually (Akashi et al.,
154 2017; Yamaura et al., 2018). The details of this experiment were described in Yamaura et al. (2018).

155

156 **2.2. Bat survey**

157 We recorded the echolocation calls of bats to evaluate bat activity using bat detectors (Song Meter
158 SM4BAT FS, Wildlife Acoustics, Inc., USA). We placed bat detectors connected to microphones
159 (SMM-U2, Wildlife Acoustics, Inc.) at three sampling points at each site. Each sampling point was at
160 least 50 m from the next-nearest sampling point. Bat activity was likely to be high near the edges
161 between harvested and unharvested areas, potentially because cluttered- and open-space species
162 avoid open spaces and the forest interior, respectively, or because there are abundant prey resources

163 (Morris et al., 2010; Law and Law, 2011). We selected sampling points near the center of sites for a
164 harvesting treatment (at least 40 m from the edges between harvested and unharvested forests) to
165 reduce the edge effects and assess the differences in bat activity among treatments. We placed
166 microphones 1.2 m above the ground to reduce the recording of natural noise near the ground (e.g.,
167 the sound of grass swaying in the wind) and prevent microphone damage by small animals. The
168 microphones were directed toward the sky to record bat calls from all directions.

169 The surveys were conducted from June 13 to October 2, 2019. To consider the lifecycle of bats
170 in Hokkaido, the surveys at each site were conducted twice across the breeding and dispersal
171 seasons. The first period was from the evening of June 13 to the early morning of July 31, 2019, and
172 the second was from the evening of July 31 to the early morning of October 2, 2019 (Ohdachi et al.,
173 2009). The bat detectors were activated automatically from 30 min before sunset to 30 min after
174 sunrise. We obtained data derived from 4–12 nights without rain in each survey period at each site. In
175 this study, the bat detectors recorded a sequence of sounds for 15 s once they detected a high-
176 frequency sound and then saved it as a single observation; any sounds that continued for longer than
177 15 s were recorded as multiple observations. The average temperature, precipitation, and average
178 wind velocity during the survey period (June to October) were 17.24°C, 113.2 mm, and 1.82 m/s,
179 respectively, which did not differ from those in the previous 10 years ($17.25 \pm 1.11^\circ\text{C}$, $135.69 \pm$
180 55.68 mm, and 1.98 ± 0.21 m/s, respectively).

181 Temperature can affect bat activity because the activity of their insect prey is likely reduced
182 during periods with low temperatures (Rydell et al., 1996). Following Fukui et al. (2011), who
183 conducted a study in the same region, we examined whether there were any days with a temperature
184 $< 10^\circ\text{C}$ at sunset (1900 h) at Ashibetsu, a nearby observation station of the Japanese Meteorological
185 Agency (<https://www.data.jma.go.jp/gmd/risk/obsdl/index.php>; accessed on September 1, 2021).
186 There were no such days during the first period, and there were only 2 days during the second period.
187 Of these 2 days, a single datum from September 19 was excluded from the analyses because the
188 temperature was low for a long time, even at noon before the survey (maximum: 11.8°C), and no bat
189 calls were recorded. We therefore used all the data except for that collected on September 19. Finally,
190 we considered the total calls recorded at each sampling point in each survey period as the analysis
191 unit and obtained 72 samples (12 sites \times three sampling points \times two periods).

192

193 **2.3. Sound analysis and bat grouping**

194 The recorded sound data were displayed as sonograms using Kaleidoscope analysis software
195 (Wildlife Acoustics, Inc.). Following Fukui et al. (2004) and Ohdachi et al. (2009), each call was
196 visually identified to each genus and two different activity types (commuting pass or feeding buzz;
197 hereafter, pass and buzz, respectively). Eight genera were identified at the study sites, and for three
198 of them (*Plecotus*, *Barbastella*, and *Eptesicus*) only one species occurs in the region (Ohdachi et al.,
199 2009). Therefore, we treated them as the following species: Japanese long-eared bat (*Plecotus*
200 *sacrimontis*), Japanese barbastelle (*Barbastella pacifica*), and Northern bat (*Eptesicus nilssonii*).
201 Ultimately, we counted the numbers of sound data points consisting of passes or buzzes for each
202 genus/species and used them as an index of bat activity. Differences in the numbers of survey nights
203 were considered when constructing models, as outlined in Section 2.4.

204 We categorized each genus/species into the following three groups according to their wing
205 morphologies and echolocation call characteristics: cluttered-space species with wide, short, and
206 rounded wings and high-frequency calls, adapted to flying slowly in cluttered spaces (*P. sacrimontis*,
207 *B. pacifica*, *Murina* spp., and *Rhinolophus* spp.); open-space species with narrow, long, and pointed
208 wings and low-frequency calls, adapted for fast flight in open environments (*Nyctalus* spp., *E.*
209 *nilssonii*, and *Vespertilio* spp.); and edge species with intermediate morphologies between cluttered-
210 and open-space species, which prefer to use the edge space between forests and open habitats
211 (*Myotis* spp.) (Norberg and Rayner, 1987; Fukui et al., 2011). There is little information available
212 regarding the ecology of *B. pacifica* (Kruskop et al., 2019), but in many studies this species has been
213 captured mainly within continuous mixed conifer and broad-leaved forests (e.g., Sato et al., 2008;
214 Sugai et al., 2011), especially in cluttered spaces (Akasaka et al., 2004). Akasaka et al. (2004)
215 captured seven individuals on an abandoned (almost vanished) forest road, but did not find them on
216 four other active forest roads. Thus, we categorized *B. pacifica* as a cluttered-space species. Among
217 the *Myotis* genus, Ikonnikov's bat (*M. ikonnikovi*), Fraternal myotis (*M. frater*), and Japanese large-
218 footed bat (*M. macrodactylus*) were present in the study area (Ohdachi et al., 2009). Of these
219 species, *M. ikonnikovi* and *M. macrodactylus* are considered to be edge species in Japan (Fukui et
220 al., 2004). Although the ecology of *M. frater* is poorly understood, the sound structure of its

221 echolocation call is similar to that of other *Myotis* species that are considered to be edge species
222 (Masuda et al., 2017). This species has been observed in linear open spaces in Japan (Endo, 1967)
223 and five individuals were caught at the intersection of scrub-covered hills and cedar forest, primary
224 oak forest, and forest edges in India (Chakravarty et al., 2020). Therefore, we collectively
225 categorized *Myotis* as edge species.

226 Although each sampling point was arranged to be spatially independent, multiple bat detectors
227 at the same site may have recorded the same call (i.e., duplicate recordings). This was a particular
228 issue for open-space species because these species make low-frequency calls, which can easily travel
229 long distances. After sorting the data, we found that echolocation calls were recorded at multiple
230 sampling points at the same time (2 s before and after) only for *Nyctalus* spp., which accounted for
231 less than 2% of the total calls for the open-space species. The percentages were 15%, 25%, and 32%
232 for the periods 10, 20, and 30 s before and after, respectively, which implied that duplicate recordings
233 were rare.

234

235 **2.4. Statistical analysis**

236 We analyzed the treatment effects on bat communities using a generalized linear mixed model
237 (family = Poisson, link function = log). The response variables were genus richness and the number
238 of passes (i.e., activity) of each group or genus/species in each survey period at each sampling point.
239 We considered each treatment (CC, MR, HR, and UP) as four categorical explanatory variables. The
240 intercept of the linear predictor was omitted (cell means method: Kéry, 2010) to facilitate
241 comparison of expected values among treatments. For the convergence of the models for some
242 genus/species, we excluded the data from CC sites where no calls were recorded. Considering the
243 linear increase in bat activity with survey effort, we added a logarithmically transformed form of the
244 number of survey nights [$\log(\text{survey nights})$] as an offset term [$\exp(x + \log(\text{survey nights})) =$
245 $(\text{survey nights}) * \exp(x)$].

246 Although duplicate recordings were rare, multiple bat detectors at the same site could have
247 observed the same individual over a short period (i.e., pseudo-replication). Moreover, three samples
248 from the same site in the same period may have exhibited similar values due to factors other than the
249 treatments or pseudo-replication (e.g., landscape composition and seasonal behavior of bats; Vasko et

al., 2020; Froidevaux et al., 2021). In contrast, the variation in bat activity among samples could be large even for the same site and period due to local-scale environments (e.g., the amount of prey or roost resources; Akasaka et al., 2010). Therefore, we added two random effects: *SeasonSite ID*, which accounted for differences in bat activity among sites and seasons and for pseudo-replication among samples; and *Sample ID*, which accounted for large variations among samples for bat activity, i.e., overdispersion. The following equation was used to analyze bat activity at sampling point i during survey period j ($Activity_{ij}$):

$$\log (Activity_{ij}) = \beta_i * treatment_i + SeasonSite ID_{ij} + Sample ID_{ij} + \log (survey night_{ij})$$

where β is a coefficient. In preliminary analyses, we confirmed that the model incorporating these two random effects performed better (lowest Akaike information criterion value) than models with other possible combinations (Appendix S2). We calculated the 95% confidence intervals of each coefficient. We interpreted the difference as significant when the intervals did not overlap between the two treatments. In addition, to compare the conservation effectiveness between MR and HR, we calculated the increases in the activity of cluttered-space and edge species at MR and HR sites compared to that at CC sites, using the expected values of activity (i.e., the estimates of the mean value) derived from the constructed models.

For all genera/species in this study, fewer buzzes were recorded than passes (Appendix S3). In addition, the numbers of buzzes and passes were highly correlated (*Murina* spp.: $r = 0.997$, *Myotis* spp.: $r = 0.793$, *Nyctalus* spp.: $r = 0.874$). Thus, we focused only on passes for the analyses. Appendix S3 describes the results on buzzes in the preliminary analyses and the comparisons with those for passes.

We conducted sensitivity analyses to examine the effects of any temporal autocorrelation, which may have originated from the situation in which many calls of the same individual were recorded in the same place in a short duration. We constructed models using data where multiple series of calls of the same species within 1 minute were counted as one. Because these estimates were almost identical to those using the original data, we used the original data for the analyses (Appendix S4).

In the analysis of genus richness, the increase in the richness with the number of survey nights may not be directly proportional and could level off when most genera were recorded. In preliminary analyses, we confirmed that the effects on results of differences in the numbers of survey nights were

negligible (Appendix S5). We removed *Sample ID*, which accounted for overdispersion, from random variables because the variation among samples was smaller than the variation in the activity of each group/genus (Appendix S2). Thus, the following equation was used to analyze genus richness:

$$\log(Richness_{ij}) = \beta * treatment_i + SeasonSite ID_{ij}$$

where *Richness* is the genus richness during each survey period at each sampling point. We performed all of these analyses using “lme4” ver. 1.1.27 (Bates et al., 2015) in R ver. 4.1.0 (R Core Team, 2021).

3. Results

The following eight genera of bats were recorded: four genera of cluttered-space species (*P. sacrimontis*, *B. pacifica*, *Murina* spp., and *Rhinolophus* spp.), one genus of edge species (*Myotis* spp.), and three genera of open-space species (*Nyctalus* spp., *E. nilssonii*, and *Vespertilio* spp.). The most frequently recorded genus was *Myotis* spp. (total number of recorded passes: 14,959). The most recorded genus of cluttered-space species was *P. sacrimontis*, followed by *Murina* spp., *B. pacifica*, and *Rhinolophus* spp. (total number of passes for each species: 2,050, 505, 168, and 8, respectively). Of the open-space species, most passes were recorded for *Nyctalus* spp., followed by *E. nilssonii* and *Vespertilio* spp. (total number of passes for each species: 6,633, 681, and 152, respectively).

For genus richness and the activity of cluttered-space species, the values were highest at the UP sites, followed by the HR, MR, and CC sites. The values were significantly higher at the UP, HR, and MR sites than at the CC sites (Fig. 2a, b, Table S6a, b in Appendix S6). Cluttered-space species were less active at MR sites than in UPs, and their activity at HR sites tended to be low, but the difference from UPs was not significant (Fig. 2b, Table S6b). This pattern mainly reflected that of *P. sacrimontis*, but the activity of this species did not differ significantly between the MR and CC sites (Fig. 3a, Table S7a in Appendix S7). Meanwhile, *B. pacifica* was more active at the UP, HR, and MR sites than at the CC sites, and there were no significant differences among sites, except at CC sites (Fig. 3b, Table S7b). *Murina* spp. and *Rhinolophus* spp. were not detected at CC sites, and the

307 differences among the other sites were not significant (Fig. 3c, d, Table S7c, d). Furthermore, no
308 buzzes of cluttered-space species were recorded at CC sites (Fig. S3.1 in Appendix S3). For
309 cluttered-space species, the increases in activity were predicted to be 0.49 and 1.66 passes/night at
310 the MR and HR sites compared to the CC sites, respectively, indicating that HR was 3.41 times more
311 effective than MR for the conservation of the activity of these species.

312 Edge species (*Myotis* spp.) exhibited a pattern similar to that of cluttered-space species. The
313 expected activity was highest in UPs, followed by the HR, MR, and CC sites, and the values were
314 higher at UP and HR sites than at CC sites (Fig. 2c, Table S6c). In contrast to cluttered-space species,
315 the activity of edge species at HR sites was comparable to that at UP sites, and the activity at MR
316 sites did not differ significantly from that at the other sites (Fig. 2c, Table S6c). For edge species, the
317 increases in activity were 2.48 and 15.04 passes/night for the MR and HR sites compared to the CC
318 sites, respectively, indicating that HR was 6.07 times more effective than MR for conserving the
319 activity of these species.

320 For open-space species, the expected activity was highest at HR sites, followed by the UP, MR,
321 and CC sites, and the values were significantly higher at the HR and UP sites than at the CC sites
322 (Fig. 2d, Table S6d). This pattern mainly reflected that of *Nyctalus* spp., but the activity of this
323 species in UPs did not differ significantly from that at CC sites (Fig. 4a, Table S7e). The activity of
324 *E. nilssonii*, was higher at the UP and HR sites than at the CC sites (Fig. 4b, Table S7f). *Vespertilio*
325 spp. was not detected at the CC sites, and the differences among the other sites were not significant
326 (Fig. 4c, Table S7g).

327

328

329 **4. Discussion**

330 **4.1. Effects of plantation clear-cutting on cluttered-space and edge species**

331 Our results imply that clear-cutting Todo fir plantations negatively impacted the activity of cluttered-
332 space and edge species of bats, decreasing the observed genus richness. The habitat preferences of
333 each bat species are strongly associated with their flight morphology. Cluttered-space species with
334 broad wings and high-frequency calls are adapted to flying in cluttered spaces and forage in forest

interiors (Norberg and Rayner, 1987; Müller et al., 2012). *Myotis* spp., with intermediate morphologies between cluttered- and open-space species, were edge species at our sites, and their activity generally increased in the small canopy gaps created by natural or artificial disturbances (e.g., Humes et al., 1999; Fukui et al., 2011). In the region near our study sites, cluttered-space and edge species avoid treefall gaps with an area of 1 ha (Fukui et al., 2011). For these two groups with low-speed flight adapted to forested areas, large open spaces would present a high risk of being caught by predators or a high cost of flying due to wind (Limpens and Kapteyn, 1991; Grindal and Brigham, 1999). Therefore, clear-cut land is likely unsuitable for foraging or commuting activities for both cluttered-space and edge species. Although we did not compare the habitat functions of plantations and broad-leaved natural forests, maintaining mature plantations would assist the conservation of these two groups.

4.2. Effects of dispersed broad-leaved tree retention on cluttered-space and edge species

We found that retaining dispersed broad-leaved trees mitigated the negative impacts of conifer-plantation harvesting on cluttered-space and edge species (Fig. 2b, c). To our knowledge, this is the first study to show the effectiveness of dispersed retention for bat conservation. Two previous studies on bats showed only the effectiveness of retaining small unharvested patches (i.e., aggregated retention; Hogberg et al., 2002; Law and Law, 2011). Although Law and Law (2011) also evaluated the effects of dispersed retention in Tasmania, they concluded that dispersed tree retention on a 10% basal-area basis was less effective than aggregated retention. Compared to their study, the number of retained trees in our study was higher (maximum 27% on a basal area basis). In addition, the value of retained trees compared to harvested trees may have been higher in our study than in their study, in which eucalyptus trees were retained and harvested, because broad-leaved trees are considered to have higher values for bats, e.g., as a source of prey insects, than conifer trees (Yui and Ishii, 1994; Ohsawa, 2007). For these reasons, the effects of retention would have been easy to detect in this study.

Dispersed trees in harvested areas likely provide forest-dependent species with suitable environments for activity and rest (Franklin et al., 1997). Our results support this assumption, in that cluttered-space species were more active at the retention sites than at the clear-cut sites (Fig. 2b; Fig.

3). Some of the spaces within or close to the canopies of retained broad-leaved trees can support the activity of cluttered-space species. In particular, *B. pacifica* and *Murina* spp. use not only cluttered spaces but also small open spaces or edges (Dewa, 2010; Russo et al., 2015, 2020). Dispersed retention would be more effective for these species with higher tolerance to decreased tree density (Fig. 3b, c). In contrast, *P. sacrimontis* exhibited relatively low activity at the retention sites (Fig. 3a). A closely related species, Common long-eared bat (*Plecotus auratus*) flies slowly and catches insects from surfaces while hovering, and thus has a strong preference for the forest interior (Entwistle et al., 1996). Even high-level retention sites may therefore be inferior habitats for *P. sacrimontis* compared to unharvested plantations.

Edge species (*Myotis* spp.) were more active at HR sites than at clear-cut sites (Fig. 2c). Studies have indicated that the activity of this group is high in thinned forests or small clear-cut areas (Humes et al., 1999; Dodd et al., 2012). In retention forestry, the spaces around the retained trees likely function as edges, as expected by Baker et al. (2013). However, retaining 50 trees/ha would be insufficient for this group, and no significant effects were detected for medium-level retention sites. Conversely, unharvested plantations had similar activity levels to those of high-level retention sites. In the unharvested plantations, the trees were spaced regularly and linearly and the tree density had been managed by thinning (Akashi et al., 2017). There was no dense understory (i.e., dwarf bamboo) that suppressed the other plant species in these plantations (Akashi et al., 2021). Therefore, the unharvested plantations provided suitable environments for the flight of edge species under canopies. Our results indicate that retaining 100 broad-leaved trees/ha maintained habitat function for edge species (*Myotis* spp.) at a level comparable to that of an unharvested Todo fir plantation.

4.3. Responses of open-space species to harvesting

Unexpectedly, the activity of open-space species was relatively high at the high-level retention and unharvested plantation sites (Fig. 2d). Some studies have suggested that open-space bat species (mainly *Nyctalus* spp. in the study area) are less sensitive to disturbances because they fly over canopies (e.g., Menzel et al., 2005; Müller et al., 2013). The habitat function of unharvested forests for open-space species can be high in some regions or for some species, e.g., *Nyctalus leisleri* (Waters et al., 1999) and *E. nilssonii* (Kaňuch et al., 2008). It has also been reported that open-space

species frequently use conifer forests (Patriquin and Barclay, 2003; Ober et al., 2020; Buchholz et al., 2021). Mature conifer plantations may therefore have a high value for open-space species.

In contrast, the pattern of lower activity at clear-cut sites may be explained by a biased distribution of prey resources at clear-cut sites or the preferences of each bat species for the forest edge. Studies have shown that the density of prey insects is higher near the edges of forest and clear-cut areas (Grindal and Brigham, 1999; Burford et al., 1999). Therefore, prey resources for bats may have been scarce around our sampling points at clear-cut sites 40 m from the forest edges. In addition, *Nyctalus* spp., treated as an open-space species, may actually prefer the open spaces near edges, as is the case for *Nyctalus noctula* (Rachwald, 1992; Heim et al., 2018). The relatively high activity of *Nyctalus* spp. at the high-level retention sites supports this assumption (Fig. 4a, Appendix S3, Table S7e). Future research should examine bat activity or behavior considering distances from linear edges created between unharvested and harvested forests to understand the effects of harvesting on this group.

4.4. Limitations and future direction

Our assessment offers a snapshot of the period just after harvesting; thus, the annual variations and long-term changes in the response of bats to retention forestry remain to be determined. Toyoshima et al. (2013), focusing on birds in Hokkaido, showed that young plantations created by clear-cutting functioned as early successional environments (i.e., open habitats) for approximately 10 years. For cluttered-space and edge species of bats, their activity in clear-cut areas will likely be low for more than 10 years after harvesting. In contrast, retention forestry may foster more rapid recovery of the activity of these groups than clear-cutting (Fedrowitz et al., 2014). The survival and growth of retained trees and their effect on bat activity should be monitored (Rosenvald et al., 2019).

Furthermore, it is unclear how retention forestry can be used to conserve bats at the individual-tree and landscape scales. At the individual-tree scale, tree characteristics (e.g., size and species), microhabitats (e.g., cavities and barks), or location can affect bat roost use and activity (Crampton and Barclay, 1998; Froidevaux et al., 2022). Large broad-leaved trees with cavities make promising roosts (Kikuchi et al., 2013; Yui and Ishii, 1994). It is essential to identify retention targets with high habitat functions to improve conservation effectiveness (Asbeck et al., 2021). At a larger scale,

retention forestry can create more complex mosaic landscapes, where some features of old-growth forests (i.e., forests with stand ages older than the rotation cycle) are maintained in each stand. In general, individual bats have a large home range and multiple roosts across stands (Crampton and Barclay, 1998; Ancillotto et al., 2022). It is therefore important to determine whether retention forestry enhances the suitability of the forest for bat commuting and roosting, and supports bat communities across the whole landscape.

4.5. Implications for conservation and forest management

Genus richness and the activity of cluttered-space and edge species were higher at high-level retention sites than at clear-cut sites, and the values did not differ significantly between the high-level retention and unharvested plantation sites. Thus, we recommend adopting the retention of > 100 broad-leaved trees/ha for the management of conifer planted forests in areas with a high priority for the conservation of cluttered-space or edge species of bats. This strategy may be easier to apply in regions where broad-leaved trees are more common within plantations due to better natural regeneration and lower management intensity. In Japan, this could include cool regions using Pinaceae as the planted tree species or snowy regions with unsuccessful plantations (Masaki et al., 2004; Yamaura et al., 2019).

However, retaining large numbers of trees in all harvested compartments could lead to an increase in the area harvested to meet wood demands because the wood production per area will decrease as the number of trees retained increases (Yoshida et al., 2005; Santaniello et al., 2017). This could explain why a minimum retention amount in each harvested compartment has been proposed in previous studies, e.g., 5–10% (Gustafsson et al., 2012) and 10 snags/ha (Newton, 1994), and applied in practice to managed forests in many regions, e.g., northern Europe (Gustafsson et al., 2012; Kuuluvainen et al., 2019). However, in this study, the increase in bat activity due to high-level retention was predicted to be 3.4 and 6.1 times that of medium-level retention for cluttered-space and edge species, respectively, despite there being only twice the number of retained trees. Therefore, in areas where there is a need to reconcile bat conservation and forestry, retaining a large number of trees (> 100 trees/ha) only in compartments with a high conservation value could be more practical than retaining a small number of trees (< 50 trees/ha) in each of many compartments (cf. ‘Triad’

zoning; Betts et al. 2021). To conserve biodiversity more effectively and prepare more options for forest managers, it would be worthwhile to consider a conservation goal not only for each harvested compartment but also for each area of landscape containing multiple stands.

CRedit author contribution statement

Conceptualization: NT, KK, TA, SY, FN; Methodology: NT, KK, TA, SY; Investigation: NT, KK, TA, SY; Formal analysis: NT, KK, TA, SY; Writing - original draft: NT, KK; Writing - review & editing: TA, SY, FN; Project administration: FN.

Data availability statement

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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Figure legends

Fig. 1. Photographs of representative sites for each treatment: (a) clear-cut (CC), (b) unharvested conifer plantation (UP), and (c) medium-level dispersed broad-leaved tree retention (50 trees/ha) (MR) (number basis: 7.3–10.8%, basal area basis: 5.7–12.9%, volume basis: 4.1–11.9%), (d) high-level dispersed broad-leaved tree retention (100 trees/ha) (HR) (number basis: 15.0–18.1%, basal area basis: 18.6–26.5%, volume basis: 16.7–26.5%).

Fig. 2. Genus richness and the activity of each group in each treatment: (a) genus richness, (b) activity of cluttered-space species, (c) activity of edge species (*Myotis* spp.), and (d) the activity of open-space species. Closed dots and solid bars indicate the expected values (estimates of the mean value) and 95% confidence intervals, respectively. Red translucent dots represent each observation, where the color becomes darker when similar values are recorded. The letters of the alphabet attached to the right shoulder of the bar indicate statistical significance, and two treatments with a significant difference do not contain the same letter. Abbreviations: CC, clear-cut; MR, medium-level retention of dispersed broad-leaved trees; HR, high-level retention of dispersed broad-leaved trees; UP, unharvested plantation control.

Fig. 3. Activity of each genus of cluttered-space species in each treatment: (a) *Plecotus sacrimontis*, (b) *Barbastella pacifica*, (c) *Murina* spp., and (d) *Rhinolophus* spp. Note that the outlier value of the activity at the medium-level retention (MR) site (54.50 passes/night) is not shown in (c). See details in Fig. 2.

Fig. 4. Activity of each genus of open-space species in each treatment: (a) *Nyctalus* spp., (b) *Eptesicus nilssonii*, and (c) *Vespertilio* spp. See details in Fig. 2.

Figure 1

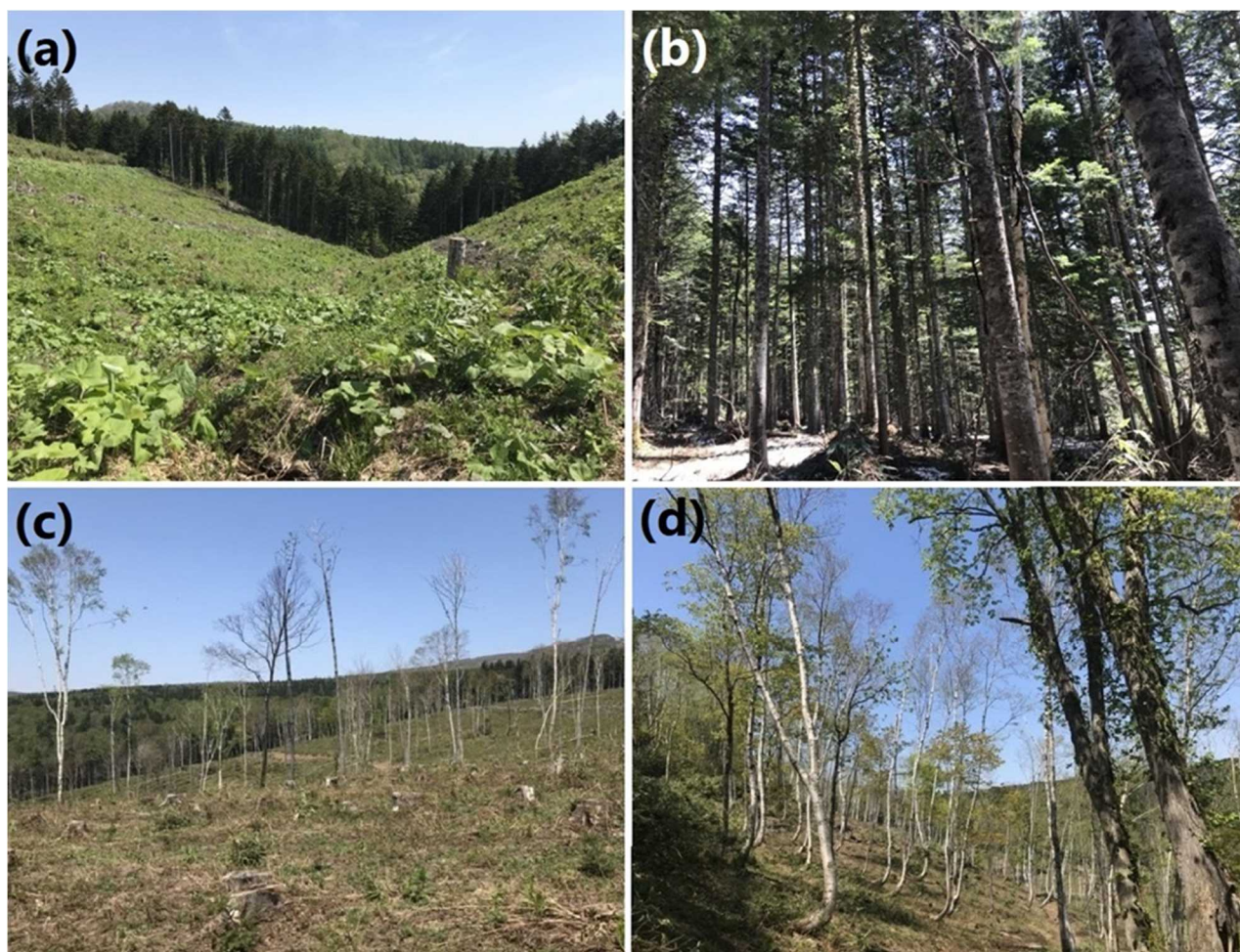


Figure 2

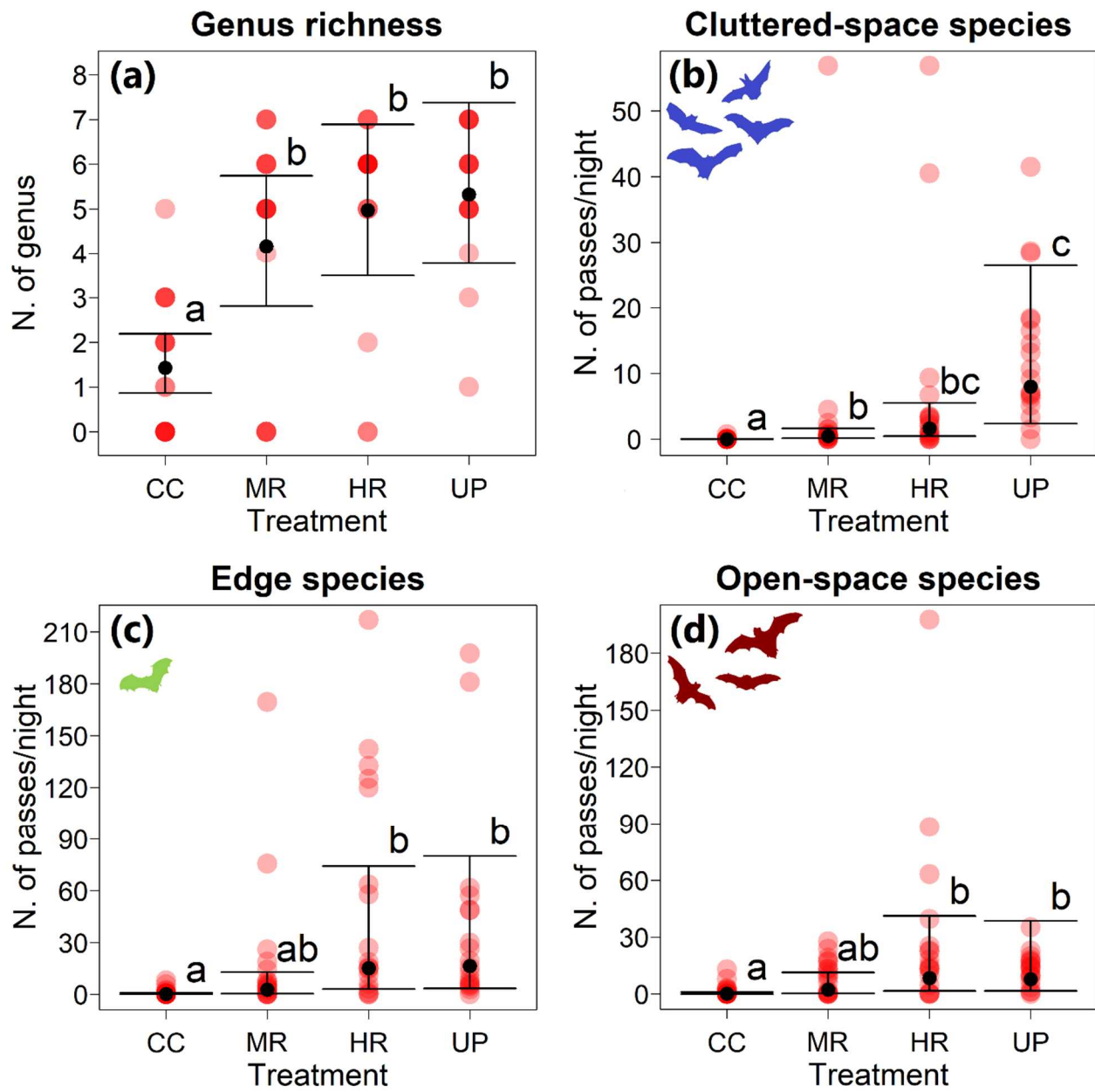


Figure 3

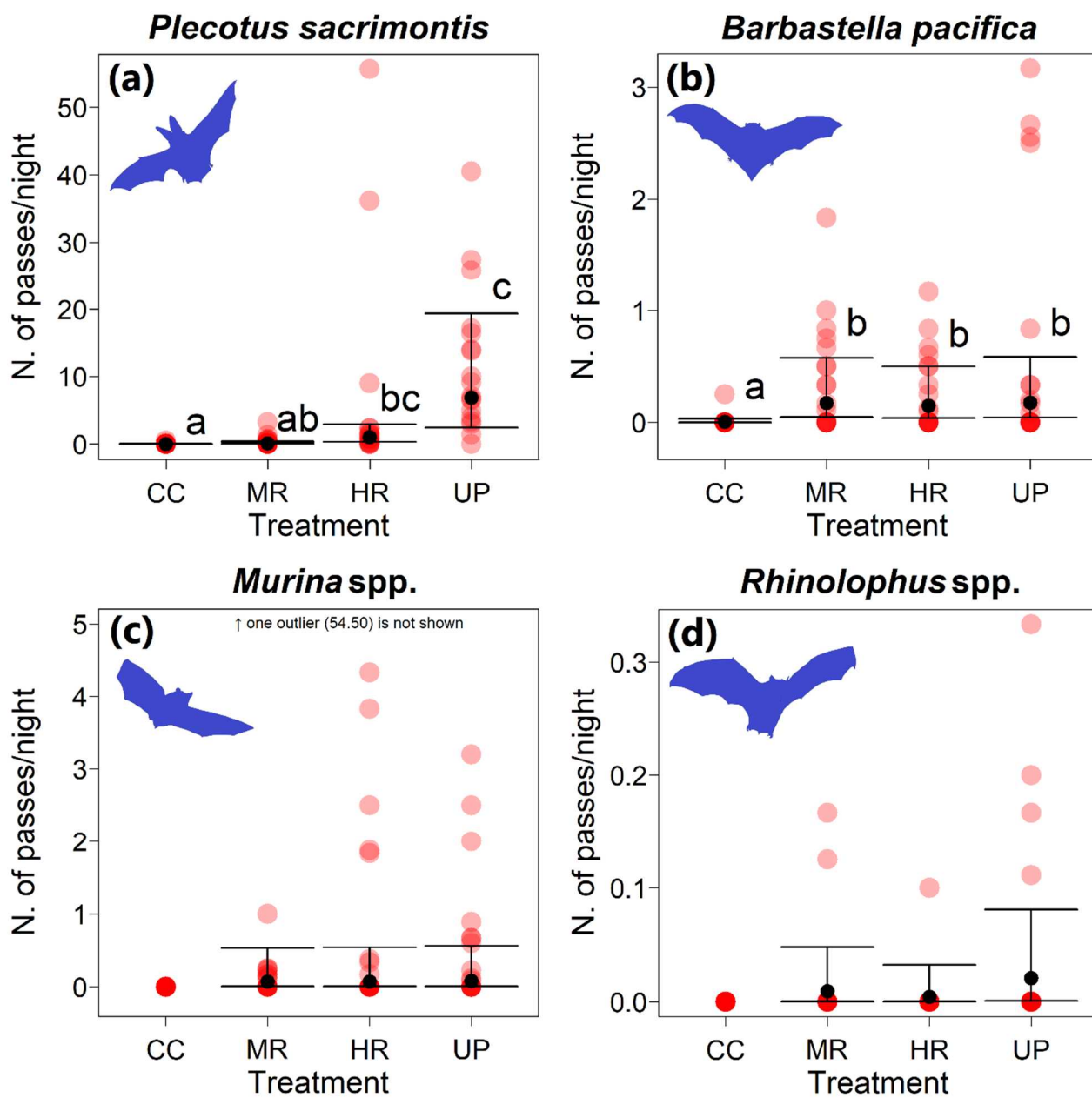
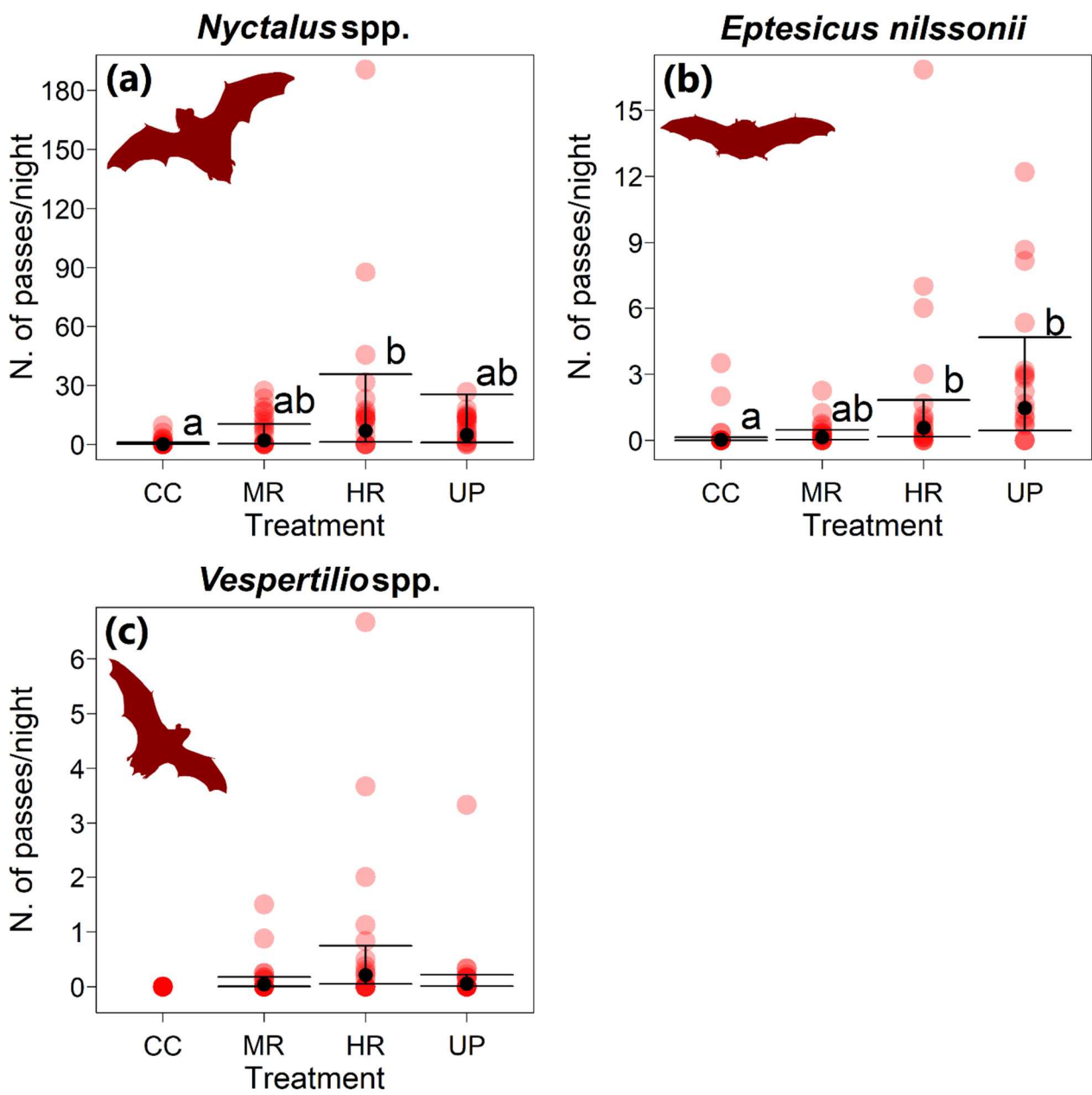


Figure 4



Appendix

Forest Ecology and Management

The response of bats to dispersed retention of broad-leaved trees in harvested conifer plantations in Hokkaido, northern Japan

Nanoka Teshima, Kazuhiro Kawamura, Takumi Akasaka, Satoshi Yamanaka, Futoshi Nakamura

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Appendix S1. Details of study region and sites

Spatial arrangement of study sites and landscape compositions in this region.

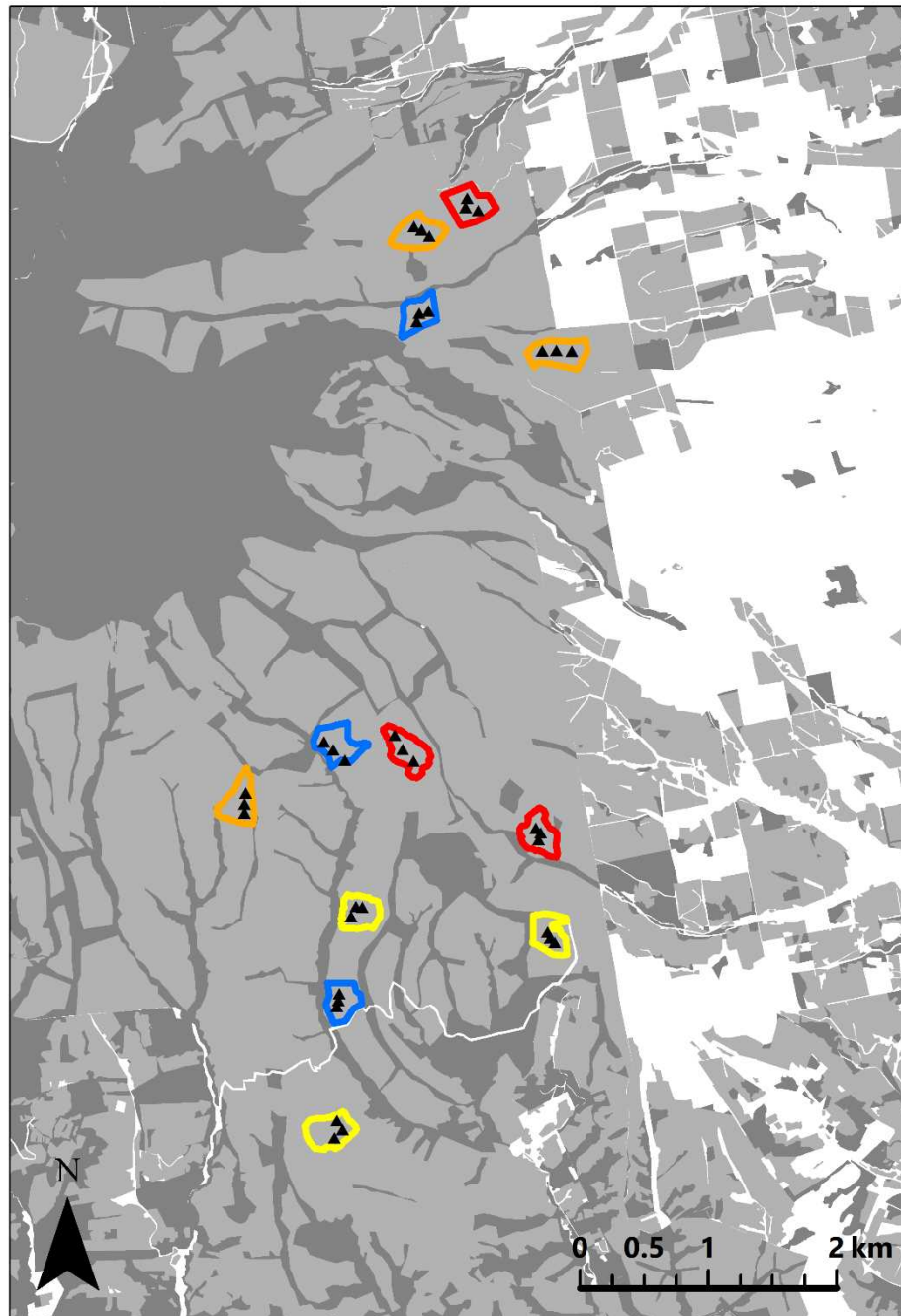


Fig. S1. Distribution of study sites and landscape compositions. Yellow, orange, red, and blue bold lines represent sites of clear-cut, medium-level retention (50 trees/ha), high-level retention (100 trees/ha), and unharvested plantations, respectively. Triangles indicate sampling points with bat detectors in each site. The light-gray background represents conifer plantations, the dark-gray one represents broad-leaved natural forests, and the white one represents other land uses, mainly farmlands and pastures.

Appendix S2. Consideration for different sets of random effects

To include appropriate random effects into models, we considered multiple combinations of random effects potentially affecting the results.

Table S2. Comparison among GLMMs with different combinations of random effects. We treated the activity of each group and genus richness as response variables, treatment as an explanatory variable. In analyses for activity, log (the number of survey nights) was added as an offset term. Values in the table indicate the AIC of each model. *Site ID* was a random effect that considers six data derived from the same site (3 sampling points \times 2 seasons) as one group, accounting for site differences in bat activity and pseudo-replication among samples. *Season ID* was a random effect that considers all sampling points in each season as one group, accounting for seasonality in bat activity. *SeasonSite ID* means the interaction term between *Season ID* and *Site ID*, treating three sampling points in the same site during the same season (i.e., same date) as one group. *Sample ID* was a random effect that considers each sampling point in each season as one group, accounting for over-dispersion due to large variation in bat activity data. A Cross indicates that models did not converge. Abbreviation: Cluttered-space, cluttered-space species; Open-space, open-space species.

Random intercept	Cluttered-space	Edge species	Open-space	Genus richness
<i>SeasonSite ID</i> + <i>Sample ID</i>	510.5	765.4	717.9	317.9
<i>Site ID</i> + <i>Sample ID</i>	516.7	781.2	733.0	321.6
<i>Season ID</i> + <i>Sample ID</i>	516.7	781.2	729.4	317.6
<i>Site ID</i> + <i>Season ID</i> + <i>Sample ID</i>	512.5	×	730.6	319.3
<i>SeasonSite ID</i>	2196.8	8975.4	4601.1	315.9
<i>Site ID</i>	3124.5	14313.6	7557.0	319.6
<i>Season ID</i>	4908.8	24607.3	9201.1	315.6
<i>Site ID</i> + <i>Season ID</i>	2963.5	14097.4	7237.1	317.3

Results and interpretation

In the analyses for activities of all three groups, the model containing *SeasonSite ID* and *Sample ID* as random effects showed the lowest AIC. This suggests that three data obtained in the same site during the same season were similar, and variation among each sampling point of bat activity was also large. In the analysis for genus richness, the model containing *Season ID* as a random effect showed the lowest AIC; however, the model considering the *SeasonSite ID* random effect also performed well ($\Delta\text{AIC} < 2$). Moreover, the models including *Sample ID* show higher AIC, which suggests that the variation among each sample was smaller compared to those of the activity of each group/genus. Based on these results, we added *SeasonSite ID* as a random effect for all analyses and added *Sample ID* in analyses for activity.

Appendix S3. Analysis for the effects of treatment on the number of feeding buzzes and comparison with the pattern of commuting passes

We conducted preliminary analyses on the buzzes of each bat group and genus to confirm that patterns of feeding buzzes and commuting passes were similar.

Table S3. Results from GLMMs for preliminary analyses the effects of treatment on feeding activity [(a) cluttered-space species, (b) edge species (*Myotis* spp.), (c) open-space species, (d) *Murina* spp., (e) *Nyctalus* spp.]. We treated the number of buzzes of each group and genus as response variables, treatments as explanatory variables, and *SeasonSite ID* and *Sample ID* as random variables (See details of random variables in Appendix S2). *Sample ID* was excluded for model convergence in the analysis for cluttered-space species. *95CI.l* and *95CI.u* represent upper and lower limits of 95% confidence intervals, calculated by ‘confint.merMod’ function. For the analyses of the edge species (*Myotis* spp.), open-space species, *Murina* spp., and *Nyctalus* spp., the default setting of the method for computing the confidence intervals, “profile” did not produce results, so “Wald” was used. Dashes indicate that the treatment was not included in models (no buzzes were recorded in CC). We did not analyze for genera recorded in a few treatments (Japanese long-eared bat *Plecotus sacrimontis*, Japanese barbastella *Barbastella pacifica*, *Rhinolophus* spp., Northern bat *Eptesicus nilssonii*, *Vespertilio* spp.). Abbreviation: Estimate, partial regression coefficient; SE, standard error; SD, standard deviation; CC, clear-cutting; MR, medium-level dispersed broad-leaved tree retention; HR, high-level dispersed broad-leaved tree retention; UC, unharvested plantation control.

(a) Cluttered-space species				
Treatment	Estimate	SE	95CI.l	95CI.u
CC	—	—	—	—
MR	−3.19	1.36	−6.80	−0.71
HR	−2.74	1.33	−6.35	−0.31
UC	−2.75	1.23	−5.88	−0.33
Random effects				
	Variance	SD		
<i>SeasonSite ID</i>	7.14	2.67		

Table S3, continued

(b) Edge species (*Myotis* spp.)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	-4.14	1.03	-6.16	-2.13
MR	-1.67	0.85	-3.33	0.00
HR	0.31	0.79	-1.23	1.86
UP	0.62	0.78	-0.91	2.14

Random effects

	Variance	SD
<i>SeasonSite ID</i>	3.01	1.73
<i>Sample ID</i>	1.6	1.3

(c) Open-space species

Treatment	Estimate	SE	95CI.l	95CI.u
CC	-4.23	0.99	-6.18	-2.29
MR	-1.84	0.79	-3.39	-0.29
HR	-0.50	0.74	-1.95	0.95
UC	-2.56	0.81	-4.14	-0.98

Random effects

	Variance	SD
<i>SeasonSite ID</i>	2.27	1.5
<i>Sample ID</i>	1.99	1.4

(d) *Murina* spp.

Treatment	Estimate	SE	95CI.l	95CI.u
CC	—	—	—	—
MR	-4.93	1.69	-9.67	-1.96
HR	-3.57	1.68	-8.76	-0.69
UC	-5.60	1.80	-10.70	-2.63

Random effects

	Variance	SD
<i>SeasonSite ID</i>	8.75	2.96
<i>Sample ID</i>	3.27	1.81

Table S3, continued

(e) *Nyctalus* spp.

Treatment	Estimate	SE	95CI.l	95CI.u
CC	-4.24	1.00	-6.20	-2.29
MR	-1.93	0.80	-3.51	-0.36
HR	-0.66	0.75	-2.12	0.81
UC	-2.57	0.81	-4.16	-0.98

Random effects

	Variance	SD
<i>SeasonSite ID</i>	2.28	1.51
<i>Sample ID</i>	2.01	1.42

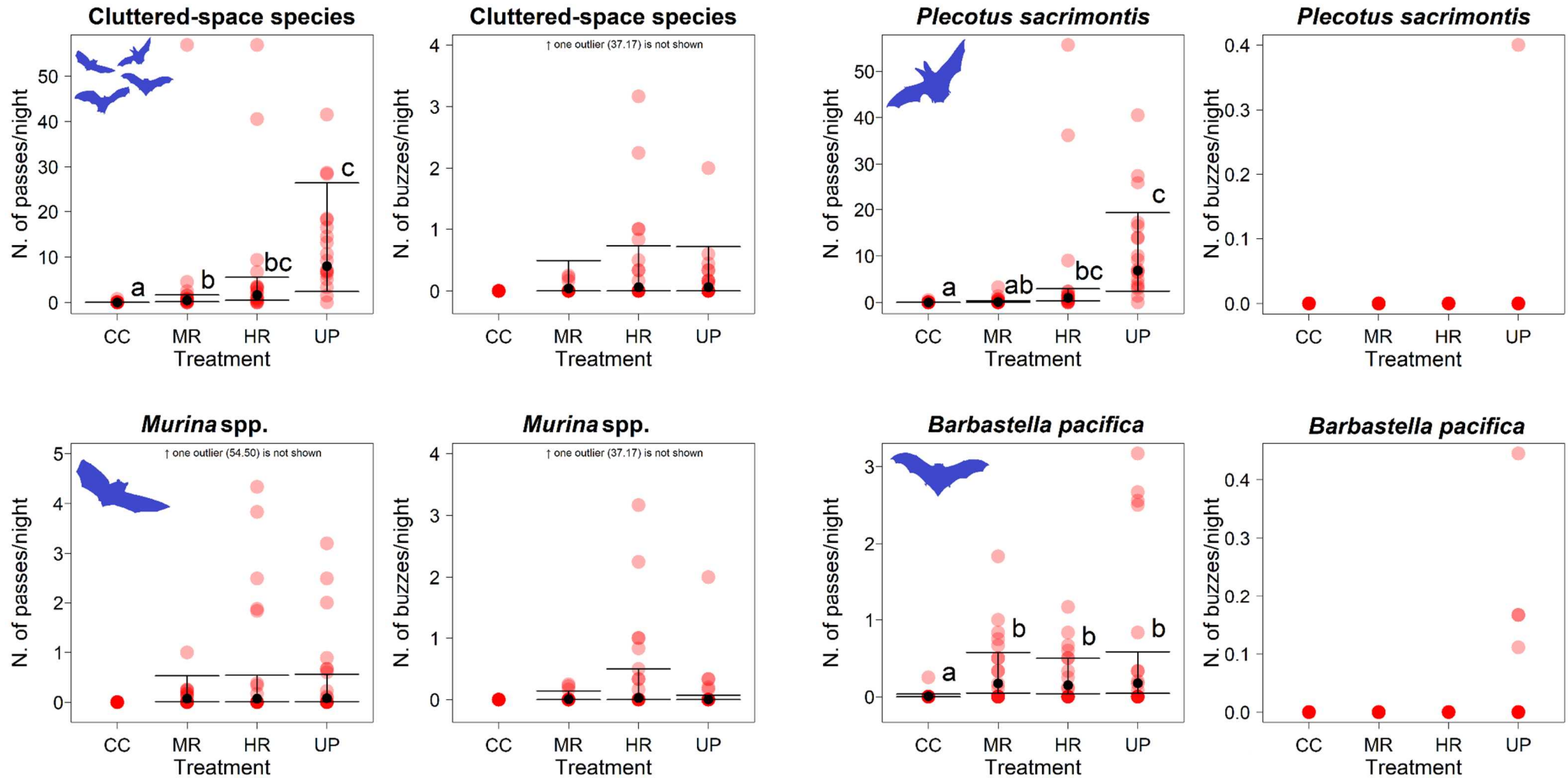


Fig. S3.1. Comparison of patterns between passes (left) and buzzes (right) for cluttered-space species. Closed dots and solid bars indicate the expected values (the estimates of the mean value) and its 95% confidence intervals, respectively. Red translucent dots represent each of the observations (i.e., the color becomes darker when a similar value is recorded). Letters of alphabet attached to the right shoulder of the bar indicate statistical significance, and two treatments with a significant difference do not contain the same letter. Note that the outlier values of the activity in MR were not shown [buzzes of this group and *Murina* spp (37.17), and passes of *Murina* spp. (54.50)]. See abbreviations of each treatment in Table S3. See results on passes in Appendix S6, S7. In addition, the buzzes of *Rhinolophus* spp. were not recorded on any sites.

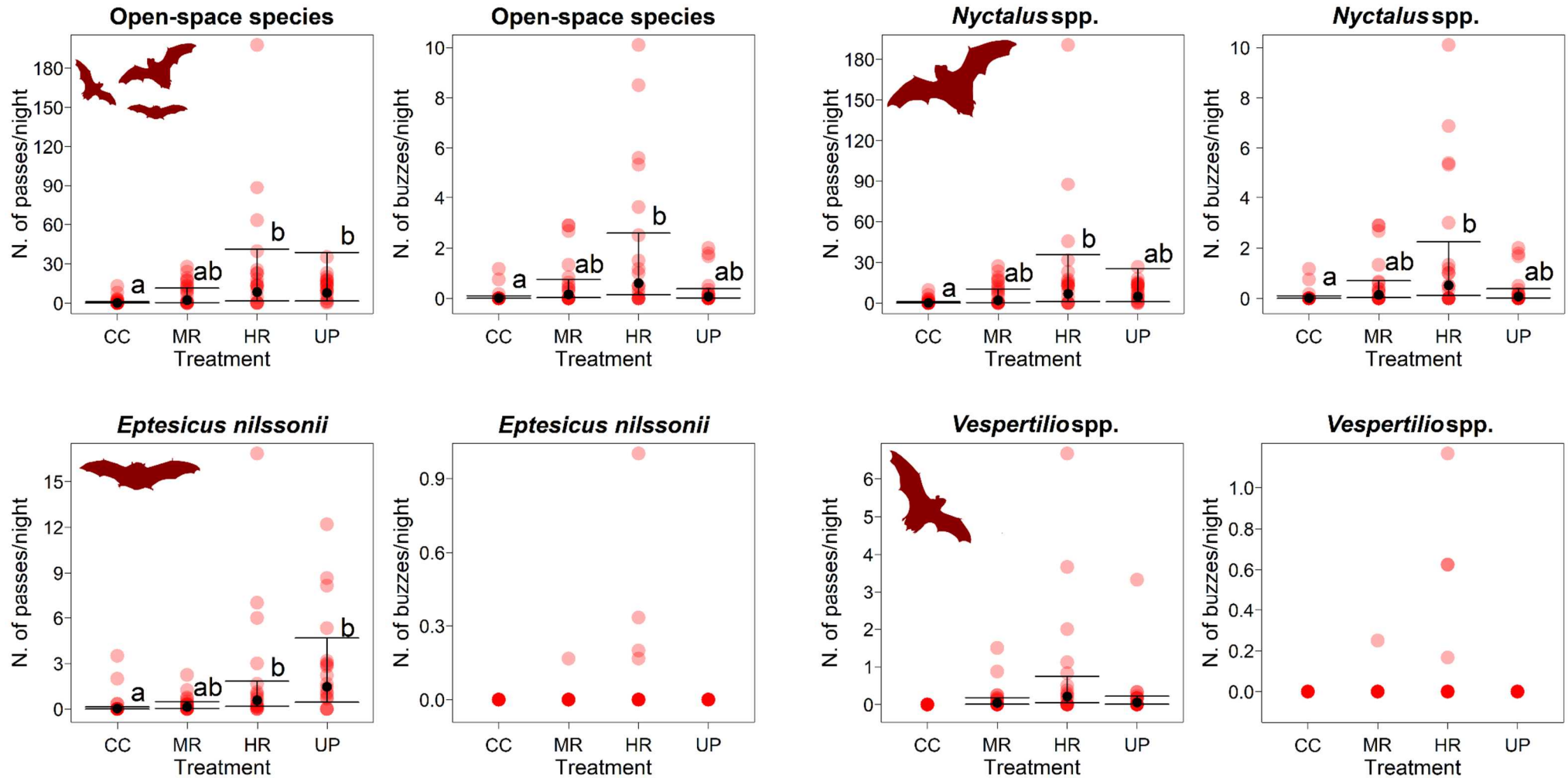


Fig. S3.2. Comparison of patterns between passes (left) and buzzes (right) for open-space species. Closed dots and solid bars indicate the expected values (the estimates of mean value) and its 95% confidence intervals, respectively. Red translucent dots represent each of the observations (i.e., the color becomes darker when a similar value is recorded). Letters of alphabet attached to the right shoulder of the bar indicate statistical significance, and two treatments with a significant difference do not contain the same letter. See abbreviations of each treatment in Table S3. See results on passes in Appendix S6, S7.

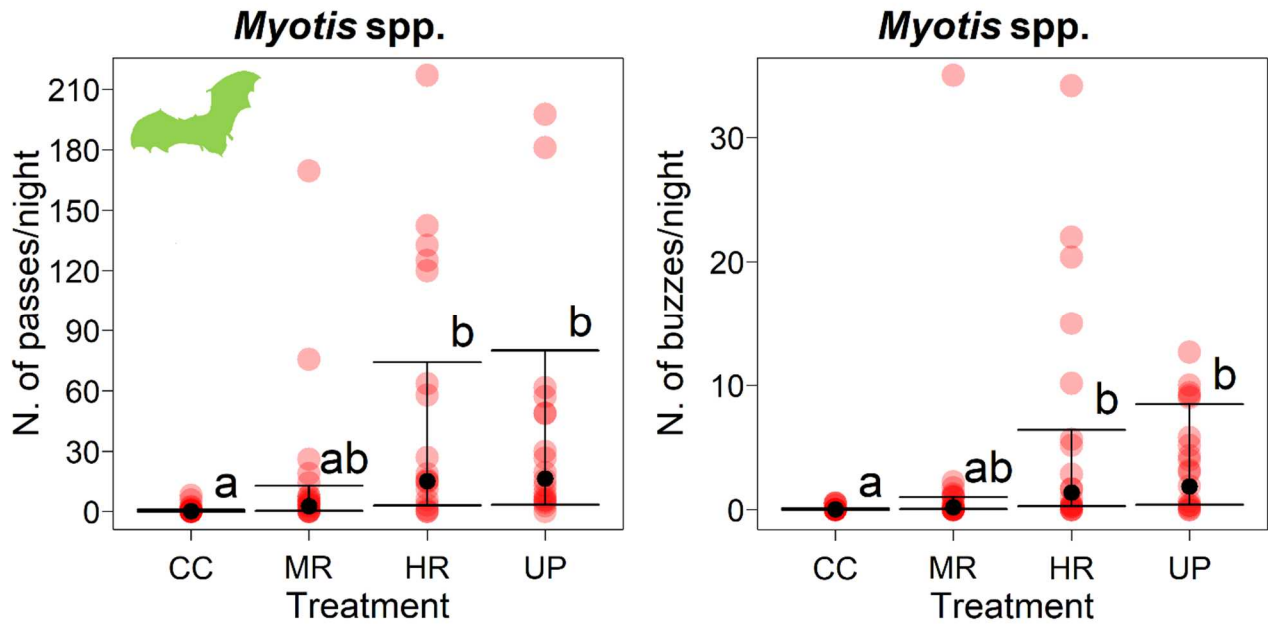


Fig. S3.3. Comparison of patterns between passes (left) and buzzes (right) for edge species (*Myotis* spp.). Closed dots and solid bars indicate the expected values (the estimates of the mean value) and its 95% confidence intervals, respectively. Red translucent dots represent each of the observations (i.e., the color becomes darker when a similar value is recorded). Letters of alphabet attached to the right shoulder of the bar indicate statistical significance, and two treatments with a significant difference do not contain the same letter. See abbreviations of each treatment in Table S3. See results on passes in Appendix S6, S7.

Results and interpretation

From the results of GLMMs, we interpreted the overall trend as common between passes and buzzes. However, possibly there were some differences for Japanese barbastella *Barbastella pacifica* and open-space species.

The buzzes of *Barbastella pacifica* were recorded only in UP, in contrast to the case of passes that were also recorded in MR and HR. For the group of open-space species and *Nyctalus* spp., the expected number of buzzes was highest in HR, followed by MR, UP, and CC, and the value was lower in CC and tended to be low in UP compared to in HR. Of open-space species, no buzzes of Northern bat *Eptesicus nilssonii* were recorded in UP, even though their passes were recorded frequently in this treatment.

Appendix S4. Sensitivity analysis for the effects of temporal autocorrelation in bat activity

To examine the effects of temporal autocorrelation, derived from the situation that many calls of the same individual were recorded in the same place in a short duration, we constructed the models using the data where multiple series of calls of the same species within one minute were counted as one and compared the result to that using original data.

Table S4. Comparison of GLMMs using original data and the data dealing with temporal autocorrelation. We considered the number of passes of each group as response variables, treatments as explanatory variables, and *SeasonSite ID* and *Sample ID* as random variables (See details of random variables in Appendix S2). Abbreviation: Estimate, partial regression coefficient; SE, standard error; CC, clear-cutting; MR, medium-level dispersed broad-leaved tree retention; HR, high-level dispersed broad-leaved tree retention; UP, unharvested plantation control.

Group	Treatment	Original data		Data considering autocorrelation	
		Estimate	SE	Estimate	SE
Cluttered-space species	CC	−4.50	0.90	−4.51	0.88
	MR	−0.70	0.60	−0.74	0.56
	HR	0.51	0.58	0.43	0.54
	UP	2.08	0.57	1.96	0.53
Edge species (<i>Myotis</i> spp.)	CC	−1.59	0.84	−1.54	0.79
	MR	0.99	0.78	0.84	0.73
	HR	2.72	0.76	2.44	0.72
	UP	2.80	0.76	2.52	0.71
Open-spaced species	CC	−1.61	0.85	−1.63	0.77
	MR	0.85	0.79	0.65	0.71
	HR	2.13	0.77	1.81	0.69
	UP	2.06	0.76	1.86	0.69

Results and interpretation

The expected values of activity (estimates of the mean value) and differences among treatments were nearly identical when using either data. We, therefore, considered that the effects of this temporal autocorrelation on results were negligible.

Appendix S5. Consideration for the effects of survey efforts on genus richness

For analysis of genus richness, the relationship between observed richness and the number of survey nights is likely to be not directly proportional because the richness can increase for a short term and then level off when most genera are observed. Thus, we constructed three types of models and examined the effects of the number of survey nights.

Table S5. Comparison of GLMMs with differently treating the number of survey nights, in the analysis for genus richness. We considered genus richness as the response variable, treatments as explanatory variables, and *SeasonSite ID* as a random variable (See details of random variables in Appendix S2). We constructed the model containing log (the number of survey nights) as an offset term, the model adding it as an explanatory variable, and the model not considering the number of survey nights. Dashes indicate that log (the number of survey nights) was not included as an explanatory variable in models. Abbreviation: Estimate, partial regression coefficient; SE, standard error; SD, standard deviation; CC, clear-cutting; MR, medium-level dispersed broad-leaved tree retention; HR, high-level dispersed broad-leaved tree retention; UP, unharvested plantation control.

	Not considering difference in survey days (AIC: 315.9)		Considering as explanatory variables (AIC: 317.4)		Considering as offset terms (AIC: 327.9)	
Explanatory variable	Estimate	SE	Estimate	SE	Estimate	SE
CC	0.36	0.23	0.73	0.54	−1.42	0.30
MR	1.43	0.17	1.84	0.55	−0.49	0.24
HR	1.60	0.16	2.02	0.56	−0.28	0.24
UP	1.67	0.15	2.11	0.58	−0.28	0.23
log(days)	—	—	−0.22	0.29	—	—
Random effects						
	Variance	SD	Variance	SD	Variance	SD
<i>SeasonSite ID</i>	0.08	0.28	0.08	0.27	0.26	0.51

Results and interpretation

Adding \log (the number of survey nights) as an explanatory variable or an offset term did not lead to a decrease in AIC. Based on this result, we considered that the effects of the number of survey nights were negligible for the analysis of genus richness.

Appendix S6. Details of results on genus richness and the activity of each group

Table S6. Results of GLMMs for examining the effects of treatment on genus richness and the activity of each group (the number of passes/night) [(a) genus richness, (b) cluttered-space species, (c) edge species (*Myotis* spp.), (d) open-space species]. We considered *SeasonSite ID* as a random variable for all analyses and added *Sample ID* for analyses for activity (See details of random variables in Appendix S1). For analyses for activity, we also added log (the number of survey nights) as an offset term. Abbreviation: Estimate, partial regression coefficient; SE, standard error; 95CI.l, lower limits of 95% confidence intervals; 95CI.u, upper limits of 95% confidence intervals; SD, standard deviation; CC, clear-cutting; MR, single broad-leaved tree retention in medium amount; HR, single broad-leaved tree retention in large amount; UP, unharvested plantation control.

(a) Genus richness

Treatment	Estimate	SE	95CI.l	95CI.u
CC	0.36	0.23	−0.15	0.78
MR	1.43	0.17	1.03	1.75
HR	1.60	0.16	1.25	1.93
UP	1.67	0.15	1.33	2.00

Random effects

	Variance	SD
<i>SeasonSite ID</i>	0.08	0.28

(b) Cluttered-space species

Treatment	Estimate	SE	95CI.l	95CI.u
CC	−4.50	0.90	−6.55	−2.88
MR	−0.70	0.60	−2.00	0.51
HR	0.51	0.58	−0.73	1.71
UP	2.08	0.57	0.88	3.27

Random effects

	Variance	SD
<i>SeasonSite ID</i>	1.45	1.20
<i>Sample ID</i>	1.49	1.22

Table S6, continued

(c) Edge species (*Myotis* spp.)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	-1.59	0.84	-3.44	0.04
MR	0.99	0.78	-0.69	2.56
HR	2.72	0.76	1.13	4.31
UP	2.80	0.76	1.22	4.38

Random effects

	Variance	SD
<i>SeasonSite ID</i>	2.82	1.68
<i>Sample ID</i>	1.95	1.40

(d) Open-space species

Treatment	Estimate	SE	95CI.l	95CI.u
CC	-1.61	0.85	-3.49	0.04
MR	0.85	0.79	-0.84	2.43
HR	2.13	0.77	0.52	3.72
UP	2.06	0.76	0.47	3.65

Random effects

	Variance	SD
<i>SeasonSite ID</i>	2.79	1.67
<i>Sample ID</i>	2.07	1.44

Appendix S7. Details of results on the activity of each genus/species

Table S7. Results of GLMMs for examining the effects of treatment on the activity of each genus (the number of passes/night) [cluttered-space species: (a) Japanese long-eared bats *Plecotus sacrimontis*, (b) Japanese barbastelle *Barbastella pacifica*, (c) *Murina* spp., (d) *Rhinolophus* spp.; open-space species: (e) *Nyctalus* spp., (f) Northern bat *Eptesicus nilssonii*, (g) *Vespertilio* spp.]. We considered *SeasonSite ID* and *Sample ID* as random variables, and added log (the number of survey nights) as an offset term. For the analysis of *Plecotus sacrimontis*, when calculating 95% using ‘confint.merMod’ function, the default setting of the method for computing the confidence intervals, “profile” did not produce results, so “Wald” was used. Dashes indicate that the treatment was not included in models (no passes were recorded in CC). Abbreviation: Estimate, partial regression coefficient; SE, standard error; 95CI.l, lower limits of 95% confidence intervals; 95CI.u, upper limits of 95% confidence intervals; SD, standard deviation; CC, clear-cutting; MR, single broad-leaved tree retention in medium amount; HR, single broad-leaved tree retention in large amount; UP, unharvested plantation control.

(a) *Plecotus sacrimontis* (cluttered-space species)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	−4.62	0.89	−6.37	−2.88
MR	−2.14	0.62	−3.35	−0.93
HR	0.00	0.55	−1.07	1.08
UP	1.93	0.53	0.89	2.96

Random effects

	Variance	SD
<i>SeasonSite ID</i>	1.09	1.05
<i>Sample ID</i>	1.67	1.29

(b) *Barbastella pacifica* (cluttered-space species)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	−5.42	1.20	−8.54	−3.45
MR	−1.75	0.60	−3.07	−0.55
HR	−1.91	0.61	−3.23	−0.69
UP	−1.73	0.62	−3.10	−0.54

Random effects

	Variance	SD
<i>SeasonSite ID</i>	1.54	1.24
<i>Sample ID</i>	0.67	0.82

Table S7, continued

(c) *Murina* spp. (cluttered-space species)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	—	—	—	—
MR	−2.66	1.01	−4.95	−0.63
HR	−2.63	1.06	−5.14	−0.62
UP	−2.56	1.04	−5.04	−0.58

Random effects

	Variance	SD
<i>SeasonSite ID</i>	4.11	2.03
<i>Sample ID</i>	2.36	1.54

(d) *Rhinolophus* spp. (cluttered-space species)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	—	—	—	—
MR	−4.70	1.15	−8.26	−3.04
HR	−5.44	1.36	−9.61	−3.43
UP	−3.88	0.97	−7.15	−2.52

Random effects

	Variance	SD
<i>SeasonSite ID</i>	0.07	0.27
<i>Sample ID</i>	1.41	1.19

(e) *Nyctalus* spp. (open-space species)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	−1.74	0.88	−3.67	−0.04
MR	0.72	0.81	−1.03	2.34
HR	1.94	0.79	0.28	3.57
UP	1.60	0.79	−0.04	3.23

Random effects

	Variance	SD
<i>SeasonSite ID</i>	2.18	1.48
<i>Sample ID</i>	2.95	1.72

Table S7, continued

(f) *Eptesicus nilssonii* (open-space species)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	−3.28	0.76	−5.07	−1.92
MR	−1.94	0.61	−3.29	−0.74
HR	−0.56	0.57	−1.80	0.60
UP	0.38	0.55	−0.79	1.54

Random effects

	Variance	SD
<i>SeasonSite ID</i>	1.12	1.06
<i>Sample ID</i>	1.88	1.37

(g) *Vespertilio* spp. (open-space species)

Treatment	Estimate	SE	95CI.l	95CI.u
CC	—	—	—	—
MR	−3.08	0.73	−4.80	−1.72
HR	−1.55	0.64	−3.03	−0.29
UP	−2.88	0.70	−4.46	−1.53

Random effects

	Variance	SD
<i>SeasonSite ID</i>	1.34	1.16
<i>Sample ID</i>	1.75	1.32