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Title

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

Authors

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Abstract (315/400 words)

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

Keywords: Variable retention; Green-tree retention; Silvicultural treatment; Clear-felling; Chiroptera; Sakhalin fir

Main text

1. Introduction

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

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

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

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

2. Materials and Methods

2.1. Study region and sites

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

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

2.2. Bat survey

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

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

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

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

$$\log (Richness_{ij}) = \beta * \text{treatment}_i + SeasonSite\ ID_{ij}$$

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

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

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

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

4. Discussion

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

Our results imply that clear-cutting Todo fir plantations negatively impacted the activity of cluttered-space and edge species of bats, decreasing the observed genus richness. The habitat preferences of each bat species are strongly associated with their flight morphology. Cluttered-space species with 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

393 species frequently use conifer forests (Patriquin and Barclay, 2003; Ober et al., 2020; Buchholz et al.,
394 2021). Mature conifer plantations may therefore have a high value for open-space species.
395 In contrast, the pattern of lower activity at clear-cut sites may be explained by a biased
396 distribution of prey resources at clear-cut sites or the preferences of each bat species for the forest
397 edge. Studies have shown that the density of prey insects is higher near the edges of forest and clear-
398 cut areas (Grindal and Brigham, 1999; Burford et al., 1999). Therefore, prey resources for bats may
399 have been scarce around our sampling points at clear-cut sites 40 m from the forest edges. In
400 addition, *Nyctalus* spp., treated as an open-space species, may actually prefer the open spaces near
401 edges, as is the case for *Nyctalus noctula* (Rachwald, 1992; Heim et al., 2018). The relatively high
402 activity of *Nyctalus* spp. at the high-level retention sites supports this assumption (Fig. 4a, Appendix
403 S3, Table S7e). Future research should examine bat activity or behavior considering distances from
404 linear edges created between unharvested and harvested forests to understand the effects of
405 harvesting on this group.
406
407 **4.4. Limitations and future direction**
408 Our assessment offers a snapshot of the period just after harvesting; thus, the annual variations and
409 long-term changes in the response of bats to retention forestry remain to be determined. Toyoshima
410 et al. (2013), focusing on birds in Hokkaido, showed that young plantations created by clear-cutting
411 functioned as early successional environments (i.e., open habitats) for approximately 10 years. For
412 cluttered-space and edge species of bats, their activity in clear-cut areas will likely be low for more
413 than 10 years after harvesting. In contrast, retention forestry may foster more rapid recovery of the
414 activity of these groups than clear-cutting (Fedrowitz et al., 2014). The survival and growth of
415 retained trees and their effect on bat activity should be monitored (Rosenvald et al., 2019).
416 Furthermore, it is unclear how retention forestry can be used to conserve bats at the individual-
417 tree and landscape scales. At the individual-tree scale, tree characteristics (e.g., size and species),
418 microhabitats (e.g., cavities and barks), or location can affect bat roost use and activity (Crampton
419 and Barclay, 1998; Froidevaux et al., 2022). Large broad-leaved trees with cavities make promising
420 roosts (Kikuchi et al., 2013; Yui and Ishii, 1994). It is essential to identify retention targets with high
421 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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758
759

Figure legends

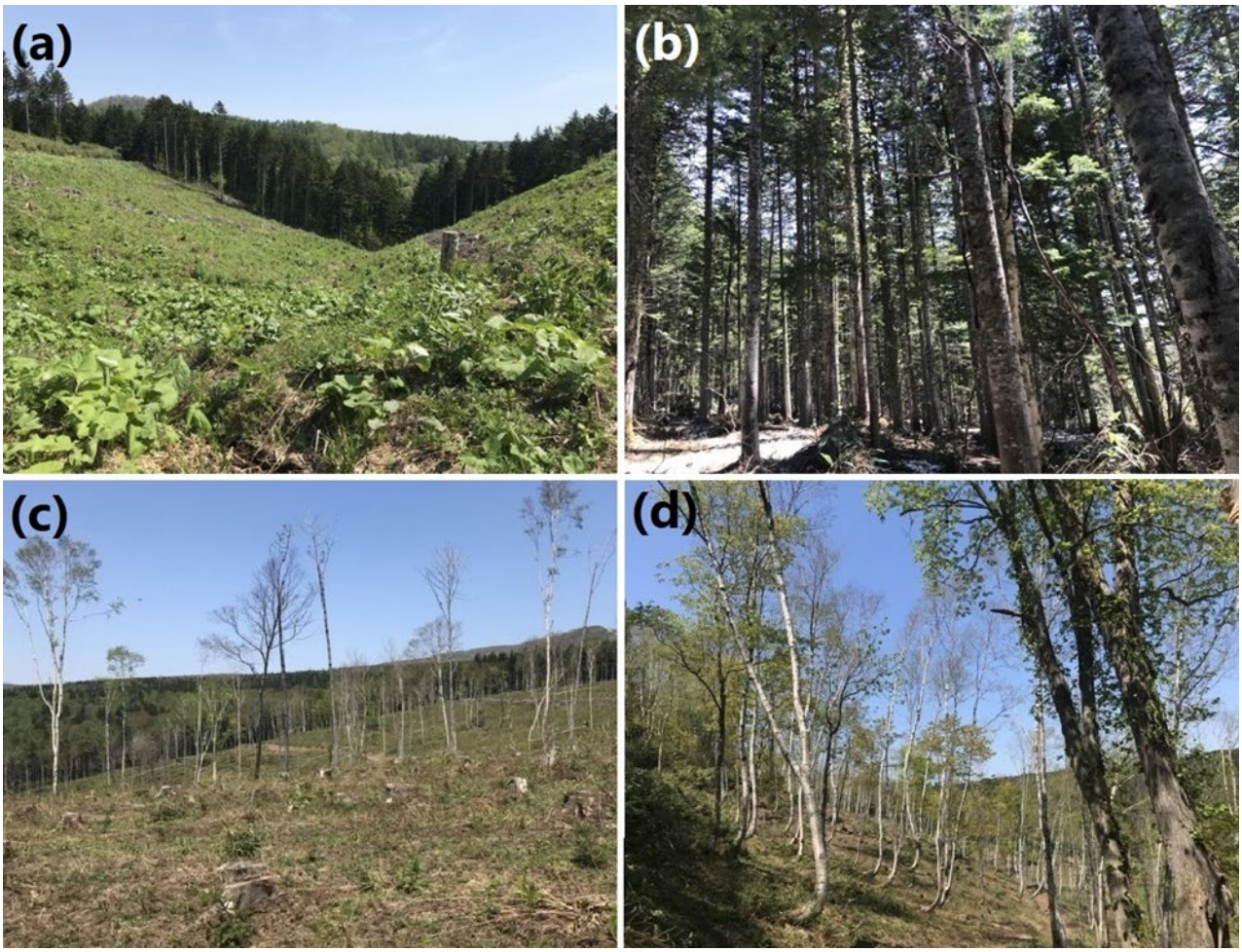
Fig. 1. Photographs of representative sites for each treatment: (a) clear-cut (CC), (b) unharvested conifer plantation (UP), and (c) medium-level dispersed broad-leaved tree retention (50 trees/ha) (MR) (number basis: 7.3–10.8%, basal area basis: 5.7–12.9%, volume basis: 4.1–11.9%), (d) high-level dispersed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

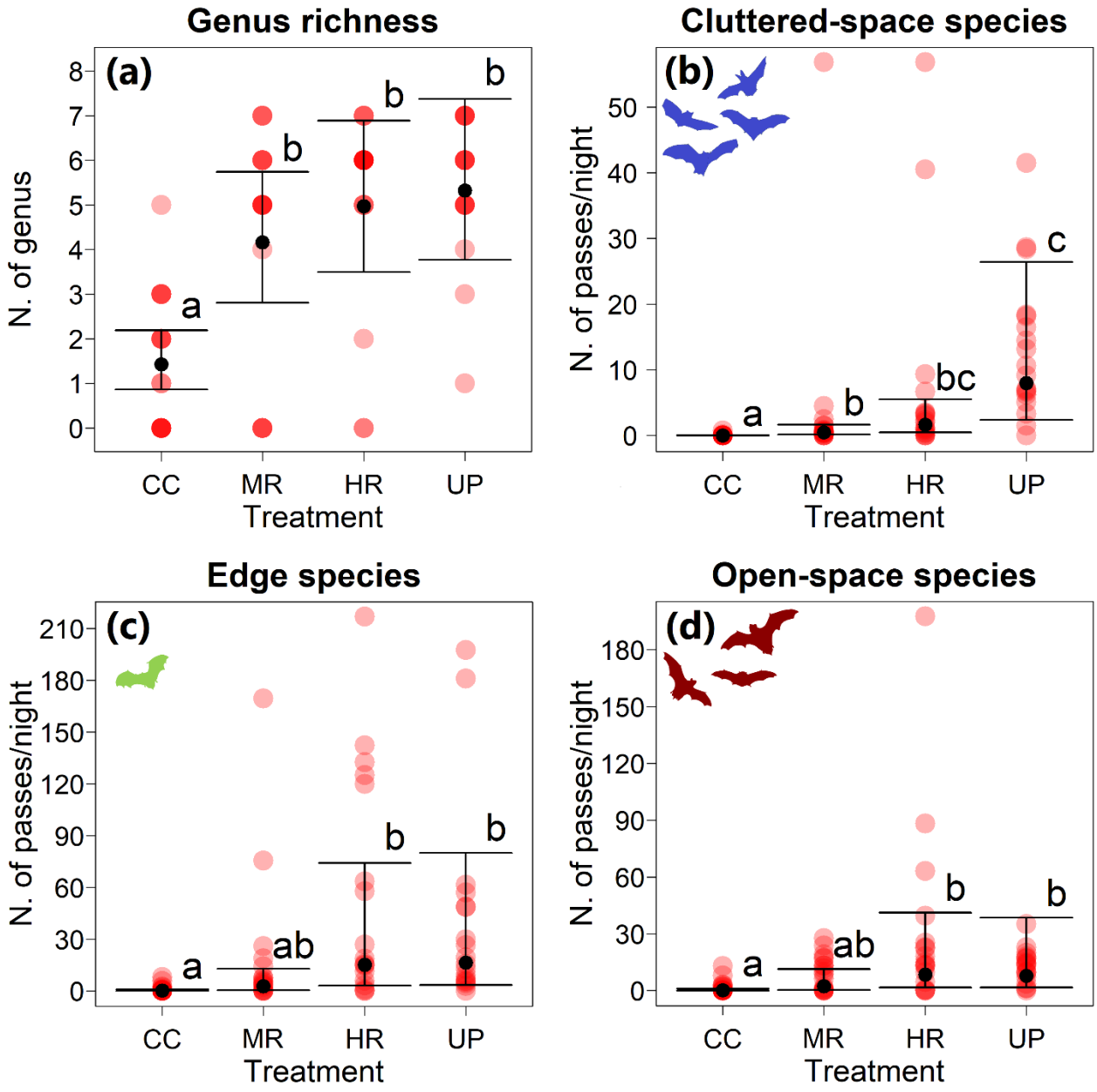
Fig. 2. Genus richness and the activity of each group in each treatment: (a) genus richness, (b) activity of cluttered-space species, (c) activity of edge species (*Myotis* spp.), and (d) the activity of open-space species. Closed dots and solid bars indicate the expected values (estimates of the mean 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.

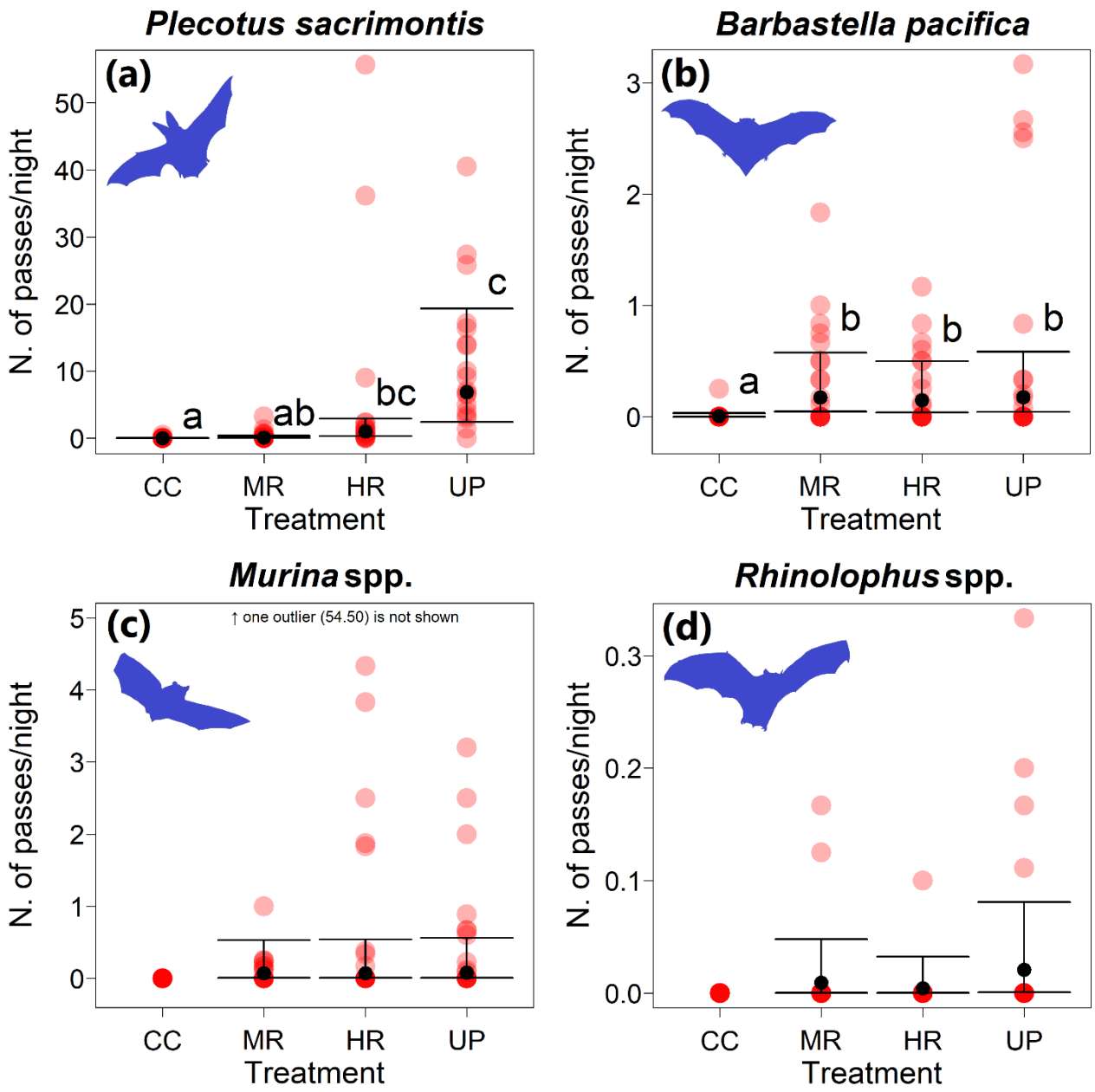
Fig. 3. Activity of each genus of cluttered-space species in each treatment: (a) *Plecotus sacrimontis*, (b) *Barbastella pacifica*, (c) *Murina* spp., and (d) *Rhinolophus* spp. Note that the outlier value of the activity at the medium-level retention (MR) site (54.50 passes/night) is not shown in (c).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

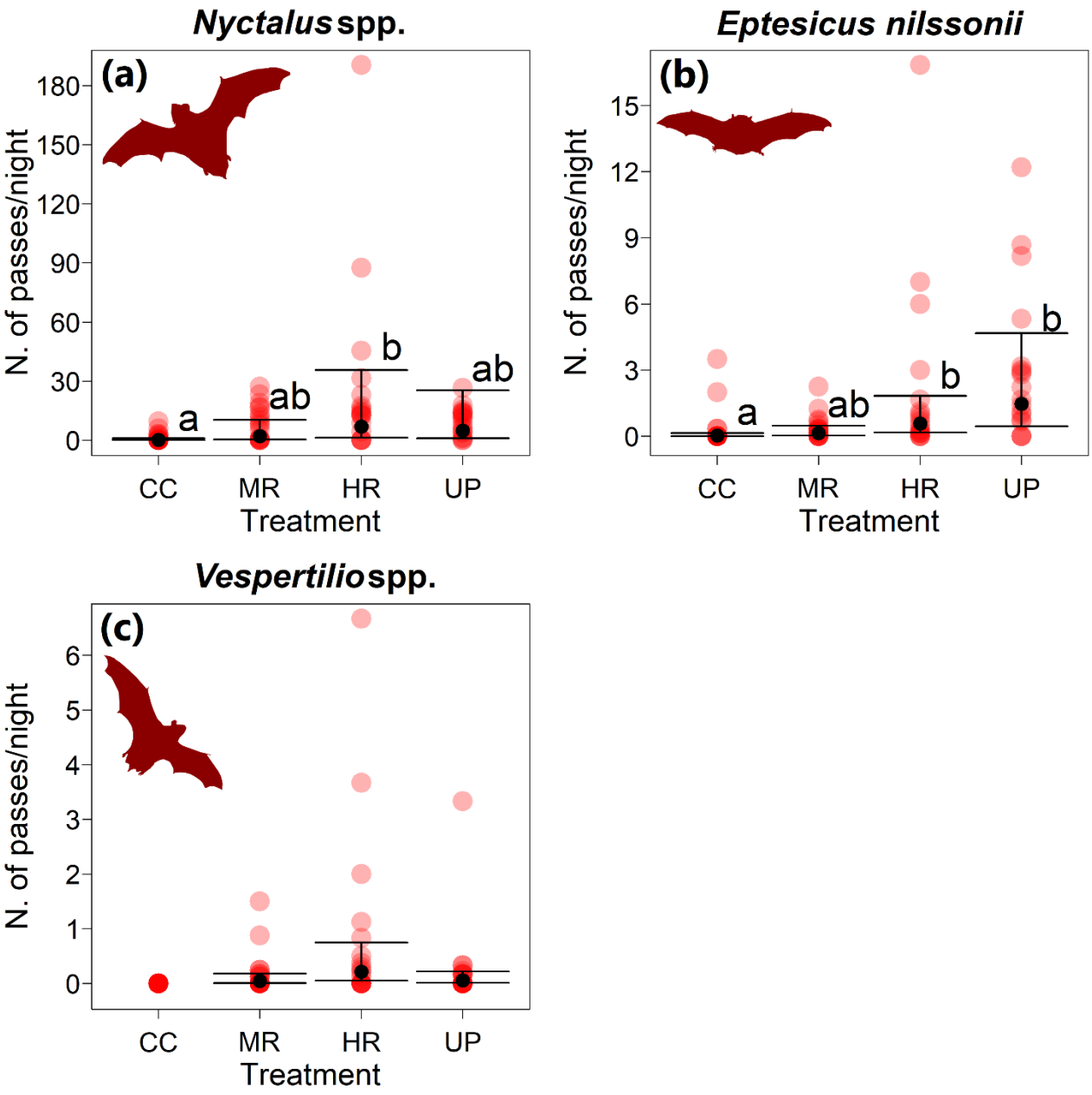
Fig. 4. Activity of each genus of open-space species in each treatment: (a) *Nyctalus* spp., (b) *Eptesicus nilssonii*, and (c) *Vespertilio* spp. See details in Fig. 2.

Figure 1




Genus richness
(a)
N. of genus
0
1
2
3
4
5
6
7
8
a
b
b
b
CC
MR
HR
UP
Treatment
Cluttered-space species
(b)
N. of passes/night
0
10
20
30
40
50
a
b
bc
c
CC
MR
HR
UP
Treatment
Edge species
(c)
N. of passes/night
0
30
60
90
120
150
180
210
a
ab
b
b
CC
MR
HR
UP
Treatment
Open-space species
(d)
N. of passes/night
0
30
60
90
120
150
180
a
ab
b
b
CC
MR
HR
UP
Treatment


Plecotus sacrimontis
(a)
N. of passes/night
50
40
30
20
10
0
a
ab
bc
c
CC
MR
HR
UP
Treatment
Barbastella pacifica
(b)
N. of passes/night
3
2
1
0
a
b
b
b
CC
MR
HR
UP
Treatment
Murina spp.
(c)
↑ one outlier (54.50) is not shown
N. of passes/night
5
4
3
2
1
0
CC
MR
HR
UP
Treatment
Rhinolophus spp.
(d)
N. of passes/night
0.3
0.2
0.1
0.0
CC
MR
HR
UP
Treatment


Nyctalus spp.
(a)
N. of passes/night
180
150
120
90
60
30
0
a
ab
b
ab
CC
MR
HR
UP
Treatment
Eptesicus nilssonii
(b)
N. of passes/night
15
12
9
6
3
0
a
ab
b
b
CC
MR
HR
UP
Treatment
Vespertilio spp.
(c)
N. of passes/night
6
5
4
3
2
1
0
CC
MR
HR
UP
Treatment