

Title

Wrong landing on a non-host occurs under the canopy of a host: the presumed path of the ambrosia beetle *Platypus quercivorus* to approach its host

Alternative language title (Japanese)

非寄主への誤着地は寄主の樹冠下で起こる：カシノナガキクイムシの寄主へのアプローチ経路の推定

Running title

Wrong landing of the ambrosia beetle on a non-host

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Abstract

1. The ambrosia beetle *Platypus quercivorus* is a vector of a pathogenic fungus that causes Japanese oak wilt. Its host is Fagaceae trees, however, these beetles also erroneously bore into unsuitable, non-host tree species, which can be affected by neighboring host tree species and the size of the non-host.

2. We attached sticky sheets to the host and non-host tree species of *P. quercivorus* and counted the number of beetles that landed weekly, in a season of beetle dispersal. We quantified the density of the host canopy above, the basal area of surrounding hosts, and the DBH of each non-host tree.

3. The host canopy density affected the probability of beetles landing on non-hosts, and the host basal area and non-host DBH affected the number of beetles landing on non-hosts. Thus, *P. quercivorus* are probably initially attracted to a dense host canopy, secondly attracted to the high density of the host, and thereafter aggregate onto thick trees, including non-host species.

4. The number of beetles landing on the surrounding host also affected beetle landing on the non-hosts, suggesting that landing on non-hosts is an error that occurs in high frequency during the seasons when many beetles land on the hosts.

Keywords:

Host selection, hurdle model, primary attraction, *Quercus serrata*, warm-temperate secondary forest

Alternative language abstract (Japanese)

1. 養菌性クイクイムシであるカシノナガクイクイムシ *Platypus quercivorus* は、病原菌を媒介することでブナ科樹木萎凋病（ナラ枯れ）を引き起こす。カシノナガクイクイムシの寄主はブナ科の樹木だが、繁殖に不適な非寄主樹種にも穿孔することがある。このような誤穿孔は、近接する寄主樹種や、非寄主樹種の太さに影響されている可能性がある。

2. 本研究では、カシノナガクイクイムシが飛翔分散する時期に寄主樹種と非寄主樹種に粘着トラップを設置し、捕獲された個体数を約1週間間隔で計数した。非寄主樹種への着地に影響する要因として、寄主樹種の樹冠投影図から樹冠密度を計算し、非寄主樹種の周囲の寄主樹種の胸高断面積合計を算出し、非寄主樹種の胸高直径を計測した。

3. 寄主樹種の樹冠密度はカシノナガクイクイムシが非寄主樹種に着地する確率に、寄主樹種の胸高断面積合計と非寄主樹種の胸高直径はカシノナガクイクイムシの非寄主樹種への着地数に影響を及ぼしていた。これらより、カシノナガクイクイムシはまず寄主樹種の樹冠密度が高い場所に、次に寄主樹種の幹密度が高い場所に誘引され、その後非寄主樹種も含めた太い木に集まってくると推定された。

4. 周囲の寄主樹種への着地数も非寄主樹種への着地に影響を及ぼしており、カシノナガクイクイムシの非寄主樹種への着地は寄主樹種への着地が多い時期に起こっているエラーであることが示唆された。

Introduction

Bark and ambrosia beetles spend most of their life in the wood of their host tree (Vega & Hofstetter, 2015). Bark beetles live in and feed on the phloem-cambium layer, and ambrosia beetles live in the xylem and feed on the fungi cultivated there. In both cases, the process of finding their host tree is essential for the beetles. It has been suggested that beetles are primarily attracted to the volatiles emitted from their host tree (Tunset *et al.*, 1993; Brattli *et al.*, 1998; Pureswaran & Borden, 2003), and secondarily attracted to the pheromones emitted from their conspecifics during the process of locating their host (Wood, 1982). Multiple steps in the host selection process may help the beetles locate their host correctly and efficiently. An alternative hypothesis is that beetles randomly land on trees without discrimination (Byers, 1995), however, it has been suggested in another study that beetles are attracted to their host first and land randomly on trees thereafter (Saint-Germain *et al.*, 2007). Therefore, the host selection process of beetles may not be fully random, but somewhat selective.

The ambrosia beetle *Platypus quercivorus* (Murayama) (Coleoptera: Curculionidae: Platypodinae) causes mass mortality of oak trees in Japan, by transporting the pathogenic fungus *Raffaelea quercivora* Kubono et Shin. Ito, also known as Japanese oak wilt (Ito *et al.*, 1998; Kubono & Ito, 2002; Kinuura & Kobayashi, 2006). The sporadic occurrence of this disease was observed before the 1980s (Ito & Yamada, 1998), however, damages caused by it have continuously occurred since then and the affected areas continue to expand in Japan (Kobayashi & Ueda, 2005) to date. It has been suggested that oak coppice forests were abandoned all over Japan because of a fuel revolution in the 1950s, and the matured abandoned coppice forests provided plenty of resources for *P. quercivorus* (Kobayashi & Ueda, 2005). Global warming has also been suggested as a possible factor, causing a recent large-scale damage expansion by this beetle (Kamata *et al.*, 2002; Kobayashi, 2020). Twelve tree species of the Fagaceae family were recognized as hosts of *P. quercivorus*; *Quercus crispula* and *Q. serrata* are the main attack targets of this beetle (Kobayashi & Ueda, 2005). Clarifying the host selection process of *P. quercivorus* is essential for the control of this disease.

Males *P. quercivorus* first fly to their host trees and bore shallow holes in them from June to October, however, the chemicals involved in this initial attack are unknown. The initially attacking beetles produce the aggregation pheromone quercivorol (Kashiwagi *et al.*, 2006), to attract conspecifics, which leads to a mass attack by both males and females (Ueda & Kobayashi, 2001; Tokoro *et al.*, 2007). After the females join the males, they make galleries in the sapwood where they inoculate the symbiotic fungus and oviposit eggs. The hatched larvae feed on the fungi, grow into the 5th larval stage by winter, and start to pupate in spring. New adults start to emerge in June (Soné *et al.*, 1998).

Previous studies have suggested that the host selection process of *P. quercivorus* is

composed of multiple steps, such as the detection of host clusters, evaluation of the host characteristics and status, and discrimination of the host species. Analysis of the distribution of attacked trees showed that beetle attacks occur at places with a high density of host tree species (Yamasaki & Sakimoto, 2009), under a dense host canopy (Yamasaki *et al.*, 2014a), suggesting that *P. quercivorus* first detect the cluster of the host canopy. Analysis of the mortality of attacked trees showed that mortality as a result of mass attack by the beetles frequently occurred in aggregations (Yamasaki *et al.*, 2014b), suggesting that dense clumps of host trees may enhance the attraction for beetles through a greater flux of host volatiles, thereby exacerbating mass attacks. Surveys for two consecutive years revealed that thicker hosts with no beetle infection history were more likely to be attacked (Yamasaki & Futai, 2008), suggesting that the beetles evaluate the characteristics and status of the trees in some way. Comparison of the process of beetle landing and hole boring among the host tree species showed that the proportion of beetles that bored holes out of those that flew to the tree was different among species (Yamasaki & Futai, 2012), suggesting that the beetles discriminate species after landing. Thus, it seems that *P. quercivorus* carefully discriminate and select their host with the best status using these multiple steps.

Careful host selection of *P. quercivorus* has been suggested in former studies, however, the hole-boring activities of these beetles were observed in non-host tree species as well. Nobuchi (1973) listed 4 non-host species, *Cryptomeria japonica*, *Lindera erythrocarpa*, *Prunus* sp., and *Ilex chinensis*, together with 12 host species as hole-boring targets of *P. quercivorus*. Sueyoshi and Taniguchi (1990) described moderate beetle hole densities on 3 non-host species, *Cinnamomum yabunikkei*, *Machilus thunbergia*, and *Cerasus jamasakura*, and light beetle hole densities on 5 other non-host species, *Idesia polycarpa*, *Distylium racemosum*, *Cinnamomum camphora*, *Camellia sasanqua*, and *Cornus controversa*. Soné *et al.* (1995) reported 5 non-host species, *M. thunbergii*, *M. japonica*, *Neolitsea sericea*, *Toxicodendron sylvestre*, and *Carpinus laxiflora*, with low beetle hole densities. *Platypus quercivorus* are unable to reproduce in non-hosts (Tarno *et al.*, 2011), therefore, hole boring in non-hosts should be avoided. There is a process of landing prior to hole boring, however, this process has not yet been studied for non-hosts. Clarifying how often *P. quercivorus* land on a non-host may help understand the host selection process of these beetles. If *P. quercivorus* first respond to odors from oak host foliage in the forest canopy, then they may land on the trunks of non-hosts at a site with a high-density host canopy. If the beetles make errors in the way they fly to host trees, the wrong landing may occur at a place with a high density of host trunks. If they prefer thick trees as their landing target, wrong landing may also occur on thick non-hosts. These errors on non-hosts are thought to occur frequently at times when many beetles attack the surrounding hosts. This is probable because similar phenomena were reported for other beetles such as *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) as spill-over attacks. When too many beetles are attracted to the aggregation pheromone emitted by the beetles which attack the initial

focus tree, some beetles fly to the adjacent trees (Bentz *et al.*, 1996) including non-preferable hosts (Huber *et al.*, 2009); the use of aggregation pheromones as attractants in a field should be carried out carefully for this reason (Progar *et al.*, 2014; Seybold *et al.*, 2018).

Even if a substantial number of *P. quercivorus* wrongly land on non-hosts, former studies have shown that the density of beetle holes on non-hosts is low, therefore, the concentration of the aggregation pheromone which is emitted by successfully colonized pioneer males should be low on these non-hosts. Supposing that wrong landing on non-hosts is also affected by the aggregation pheromone, the landing rate of follower females on these non-hosts should be low. In this context, the sex ratio of the beetle population which lands on non-hosts may be more biased to males as compared to the population on hosts. Clarification of this point may help in understanding the host selection process of the beetle.

In this study, we set up plots in a warm-temperate secondary forest that was suffering damage from Japanese oak wilt and counted the number of *P. quercivorus* that landed on both host and non-host tree species. Host canopy density, host basal area, the number of beetles that landed on surrounding hosts, and the size of non-hosts were examined as factors affecting the number of beetles that landed on non-hosts. Additionally, the sex ratio of landed beetles was compared between the hosts and non-hosts to clarify differences in this population. The flight path of *P. quercivorus* to approach its host was inferred from the results.

Materials and methods

Beetle trapping in a field

This study was conducted in a warm-temperate secondary forest in Kobe Municipal Arboretum, Hyogo, Japan (34.74° N, 135.18° E, Figure 1). The forest is dominated by *Q. serrata*, one of the main attack targets of *P. quercivorus*, and has been suffering from Japanese oak wilt since 2015. Five plots, 20 x 20 m in size, were set up in June 2021 (Plots A, B, C, D, and E in Figure 1). Trees over 10 cm in DBH (diameter at breast height, 130 cm above the ground) inside each plot were recorded according to their species and measured DBH. The location of each tree was measured according to its position using a differential GPS (SXBlue II ; GENEQ Inc., Canada) and laser range finder (TruPulse360B; Laser Technology Inc., Centennial, Colorado). Canopy projection was also made for each tree by positioning several surrounding points of the canopy using the same apparatus described above, and the closure rate of the host canopy was calculated for each plot. A sticky sheet trap (Kamikiri-hoihoi; Earth Biochemical, Tokushima, Japan), 8 x 50 cm in size, was set up on the basal part of each tree trunk (Figure 2a) on June 17, 2021. The sticky sheets were covered with a vinyl-coated wire mesh to prevent other large animals from becoming trapped (Figure 2b). Because we attached sticky sheets of the same size to all the trees, the number of trapped beetles is equivalent to the number per unit area which can be a measure of beetle preference. The disadvantages of this method are that the number of beetles landing on thicker trees is evaluated based on data from a relatively small area and that the heterogeneity of beetle flight direction is ignored. To take into account the second point, the direction of the place to attach the sheet was randomly assigned. After the first setup, counting of the trapped beetles and replacement of the sticky sheets were conducted 12 times until September 15, 2021, in approximately 1-week intervals.

Preparation of variables

DBH was used to estimate the effect of trunk size on the beetles landing on the non-hosts. In cases where the individual trees consisted of multiple stems, the DBH of all the stems was summed up.

To estimate the effect of the host canopy on beetles landing on the non-hosts, the host canopy density above each non-host was calculated. First, a vector of the canopy projection of the host tree species was converted to a raster which was 10 x 10 cm in cell size. Second, the host canopy rasters included in each plot were summed up. Third, buffers with a 1 to 10 m radius were created in 1 m intervals from each non-host tree species. Fourth, summed-up rasters were averaged for each size of each non-host buffer. In cases where the created buffer was intersected by the plot boundary, the average was calculated for that small intersected area. Data processing was conducted using QGIS 3.22 (QGIS Development Team, 2020).

To estimate the effect of the host trunk on beetle landing on the non-hosts, the basal area

of surrounding hosts was calculated. Buffers with a 1 to 10 m radius were created in the same way as described above, and the basal area (cross-sectional area of the trees at breast height, 130 cm above the ground) of surrounding hosts was summed up for each non-host. In cases where the created buffer was intersected by the plot boundary, the basal area was corrected upward by dividing it with the ratio of that small area to the full area of the buffer.

To estimate the effect of beetle landing on surrounding hosts on the beetle landing on non-hosts, buffers with a 1 to 10 m radius were created in the same way as described above, and the number of beetles that landed on the sticky sheets inside each size of the buffer was summed up for each non-host, for each sampling date. In cases where the created buffer was intersected by the plot boundary, the summed-up number of beetles was corrected upward by dividing it with the ratio of that small area to the full area of the buffer. The calculations were done using R 4.1.3 (R Core Team, 2022).

Model construction and selection

Model construction and selection were done by setting the number of beetles that landed on non-hosts on each sampling date as the response variable. The hurdle model was used to account for the excessive number of zero counts (69 %) observed in the data (Zuur *et al.*, 2009). The hurdle model consists of two parts, the zero-hurdle part, and the count part. The former part is equivalent to logistic regression which predicted the probability of beetle landing; the response variable was 0 when no beetles landed and 1 when 1 or more beetles landed. Binomial distribution was assumed for this part. The latter part corresponds to Poisson or negative binomial regression which predicted the number of landed beetles; the response variable was the number of landed beetles when 1 or more beetles landed. Zero-truncated negative binomial distributions were assumed for this part. We regarded the former part of the model as the process of beetles landing on non-hosts or not and the latter part as the process of how many beetles landed on the non-host after the initiation of the first beetle landing.

Candidate explanatory variables of the model were host canopy density, host basal area, the number of beetles that landed on surrounding hosts, and the DBH of non-hosts. The host canopy density and the host basal area were thought to be correlated and the inclusion of both variables may cause multicollinearity. We hypothesized that *P. quercivorus* first detect the host canopy and fly toward the host trunk afterward. Therefore, the host canopy density was incorporated into the zero-hurdle part of the model, and the host basal area was incorporated into the count part of the model. The number of beetles that landed on surrounding hosts and the DBH of non-hosts were incorporated into both parts of the model. Differences in beetle landing could also be affected by tree species, however, the sample size was uneven among the species (Table 1), and detecting this difference would have been difficult. Therefore, we included tree species as random intercepts of the

model. The interval of beetle counting was 6–14 days. The logarithm of the interval period was incorporated into the count part of the model as an offset term to consider this difference.

Model selection was done in 2 steps (Figure 3). The effective scale of variables was possibly different between the two processes described above, therefore, 100 combinations of variables, i.e., the host canopy density averaged for 10 different scales * the number of beetles that landed on the surrounding hosts summed up for the 10 different scales * DBH of the non-host, were set up for the zero-hurdle part of the model, and the host basal area summed up for 10 different scales * the number of beetles that landed on the surrounding hosts summed up for the 10 different scales * DBH of the non-host, were set up for the count part of the model as a set of candidate explanatory variables. Among the 10,000 combinations, the model with the lowest Akaike's information criterion (AIC) value was selected as the full model. AIC is the measure of the goodness of fit penalized for the model complexity, and a lower AIC is better. We expected that the AIC would decrease with an increase in the scale of each parameter, show the lowest value at the most effective scale, and increase afterward. The best-fit model was selected by deleting the insignificant variables one by one from the full model until the deletion caused a significant decrease in the likelihood of the model. Construction and selection of the model were done using the glmmTMB package 1.1.3 (Brooks *et al.*, 2017) and lmttest package 0.9-40 (Zeileis & Hothorn, 2002) of R 4.1.3 (R Core Team, 2022).

Sex ratio

The male sex ratio of beetles that landed on the hosts and non-hosts was estimated and compared using a generalized linear mixed model. For this analysis, we used the number of males and females trapped on a sticky sheet when 1 or more beetles were trapped. We assumed a binomial distribution for the response variable, and used the category of host or non-host, as the explanatory variable. Tree species nested within the host category were included in the model as random intercepts. The analysis was done using lme4 package 1.1-32 (Bates *et al.*, 2015) of R 4.1.3 (R Core Team, 2022).

Results

The tree species distributed in all 5 plots are listed in Table 1. In total, 4 beetle host and 23 non-host species were observed. *Quercus serrata* was the dominant host making up 63 out of the 69 host trees observed on all the plots. The number of the other three *Quercus* species, *Q. myrsinifolia*, *Q. variabilis*, and *Q. glauca* were small. *Ilex pedunculosa* was the most dominant non-host making up 24 out of the 95 non-host trees observed on all the plots. The next most common non-hosts were *Pieris japonica*, *Pinus densiflora*, *Eurya japonica*, and *Cerasus jamasakura*, observed on 3 or more plots.

The canopy projection of the 5 plots is shown in Figure 4 along with the location of each tree trunk. Host density was relatively low (Table 1) and as a result, the host canopy was relatively sparse in Plots B and C. The closure rate of the host canopy was 0.74, 0.54, 0.54, 0.67, and 0.84 for Plots A, B, C, D, and E, respectively.

Changes in the number of beetles that landed on the hosts and non-hosts are shown separately, for each plot, in Figure 5. In total, 17,611 beetles were captured on the 69 hosts (255 beetles per tree on average; a minimum of 1 and a maximum of 1,267) and 3,944 beetles were captured on the 95 non-hosts (42 beetles per tree on average; a minimum of 0 and a maximum of 434). The first peak of beetle landing on the hosts was observed in Plot D, and a relatively large number of beetles were observed in Plot D following this. Thereafter, beetle landing on the hosts started to be observed in Plots A, B, and C from July. The peak of beetle landing on the hosts was observed last in Plot E. Phenology of the beetle landings on the hosts was different among the plots, and a similar pattern was observed in the beetle landings on the non-hosts. In general, the peak of beetle landing on the non-hosts was observed in the same season as that on the hosts. Additionally, the number of beetles landing on non-hosts in Plots B and C, with sparse host canopy densities (Figure 4), was relatively low compared to the other plots.

AIC values of the candidate 10,000 models were plotted against 4 candidate explanatory variables in Figure 6. Expected changes in AIC, increase after decrease with an increase in the scale were observed for 3 variables, though such change was not clear for the host basal area included in the count part. The lowest AIC was observed when the scale of the host canopy density included in the zero-hurdle part was 7 m, that of beetle landing on the surrounding hosts included in the zero-hurdle part was 5 m, that of the host basal area included in the count part was 1 m, and that of beetle landing on the surrounding hosts included in the count part was 5 m. Therefore, the model including variables of these scales and the DBH of the non-hosts for both parts was selected as the full model.

Table 2 shows the results of the selection of the best-fit model to predict beetle landing on non-hosts. Among the 3 variables in the zero-hurdle part which predicted the probability of a beetle landing on a non-host, the host canopy density averaged for the buffer area with a 7 m radius, and the number of beetles that landed on the surrounding hosts summed up for the buffer area with a 5 m

radius were selected for the best-fit model. DBH of the non-host was deleted from the zero-hurdle part of the best-fit model. All 3 variables in the count part which predicted the number of beetles landing on a non-host after the initiation of the first beetle landing, the host basal area summed up for the buffer area with a 1 m radius, the number of beetles that landed on surrounding hosts summed up for the buffer area with a 5 m radius, and DBH of the non-host were selected for the best-fit model.

Relationships between the 3 candidate explanatory variables in the zero-hurdle part of the model and the occurrence of beetle landing on the non-hosts are shown in Figure 7 together with the model prediction. Beetle landing on the non-hosts occurred in high frequency when the host canopy density within a 7 m radius was more than 1, and the model prediction showed an increase in the probability of beetle landing on non-hosts with an increase in host canopy density, though the estimated slope was moderate (Figure 7a). In contrast, a rapid increase in the probability of beetle landing on non-hosts with an increase in the number of beetles landing on the surrounding hosts was predicted, which corresponds to the dense distribution of raw data of beetle landing occurrence when beetle landing on the surrounding hosts was high (Figure 7b). A clear trend was not found in the relationship between the DBH of the non-host and the occurrence of beetle landing (Figure 7c), and DBH was not selected as an explanatory variable of the zero-hurdle part of the model.

Figure 8 shows the relationships between the 3 explanatory variables selected for the count part of the model and the number of beetles that landed on the non-hosts together with the model prediction. Host trees distributed within a 1 m radius of non-hosts were low in frequency, and 88 % of the calculated host basal area for this scale was 0. Though the positive effect of the host basal area on the number of beetles that landed on non-hosts was suggested by the model, the estimated slope was moderate and the confidence intervals were relatively wide (Figure 8a). In Figures 8b and 8c, raw data was concentrated on the bottom left where both the explanatory and response variables were low, and the data were sparse at the right where the explanatory variables were high. Model prediction showed an increase in the number of beetles that landed on the non-hosts with an increase in the number of beetles that landed on the surrounding hosts (Figure 8b). An increase in the response variable was also predicted with an increase in the DBH of the non-hosts (Figure 8c).

Observations that 1 or more beetles were trapped on the sticky sheet were made 521 times on the hosts and 352 times on the non-hosts. According to the constructed model, the male sex ratio of beetles that landed on the hosts was estimated as 53.9 %, and that on the non-hosts was estimated as 59.1 %. The results of the model suggested that the sex ratio of the beetles on non-hosts was significantly more biased to males than that on hosts ($P = 0.0365$).

Discussion

The zero-hurdle part of the constructed model can be regarded as the process of whether beetles land or not, and the count part of the model can be regarded as the process of beetle aggregation after the initiation of the first landing. Host canopy density affects the first process, and the basal area of surrounding hosts and the trunk size of non-hosts affect the second process. The number of beetles that landed on the surrounding hosts affects both processes (Table 2). These results suggest that *P. quercivorus* are attracted to dense host canopies in the process of approaching trees, and thereafter aggregate on thick trees including non-host species at places with a high trunk density of hosts. In addition, variables calculated for a larger scale, 7 m for canopy density, affect the first process, and variables calculated for a smaller scale, 1 m for the basal area of surrounding hosts and DBH of an individual tree, affect the second process. These results show the process by which *P. quercivorus* may narrow their landing target step by step: a big canopy, several candidate trunks, and finally a single trunk while coming down from above the canopy to the forest floor.

Hypothesis explaining the landing of *P. quercivorus* on non-hosts, and the approach path of the beetles to their boring site, based on model results is illustrated in Figure 9. First, the beetles are attracted to the host tree canopy, and the probability of a wrong landing on a non-host (the beetle circled with a dashed line in Figure 9) increases with an increase in the density of the host tree canopy. At this stage, stage 1, all 4 host trees illustrated in Figure 9 affect the probability of a wrong landing by attracting the beetles with their canopies. Second, the beetles fly down from above the canopy by passing through the canopy, and the probability and frequency of a wrong landing increase when many beetles pass through a neighborhood of non-hosts and land on the surrounding hosts as a result. At this stage, stage 2, two host trees (Hosts B and C in Figure 9) affect the probability of a wrong landing. Third, the beetles start to search the trunk to land on the forest floor and the number of beetles that land on non-hosts increases with an increase in the basal area of surrounding hosts. At this stage, stage 3, the adjacent host tree (Host C in Figure 9) affects the number of beetles that land on the non-host. Finally, the beetles land on a tree trunk. At this stage, stage 4, the thickness of the non-host affects the number of beetles that land on it.

The hypothesis described above is just one possibility. Because the hole boring site of *P. quercivorus* is mainly the basal part of their host tree, it is more natural to assume that the beetles which emerge from the basal part fly the lower layer of the forest and approach the host tree from below. In such cases, beetles are thought to use the information from trunks, for example, the volatiles from bark surface and the aggregation pheromone emitted by males that had already established on host trees, to detect their host tree. Results of this study, landing of the substantial number of beetles on non-hosts, can be interpreted as errors occurred when beetles heading towards hosts being attracted by host bark volatiles or the aggregation pheromone. To clarify this point, movement of the beetles at the forest floor around their probable target hosts should be investigated.

Regarding our hypothesis (Figure 9), the canopy is bigger than the trunk in volume, and if the information of the host canopy is detectable to a beetle, it is adaptive for the beetle to use this for the efficient detection of its host trees in a heterogeneous forest. When sticky sheet traps were set up at a height of 0.05–3.5 m on the trunks of *P. quercivorus* targets, the capture of beetles was not concentrated to the basal parts, but observed from the lowest to the highest (Kobayashi & Hagita, 2000), suggesting that beetles approach from a higher position. The flight path of *P. quercivorus* to their boring site, the basal part of their host tree, should be clarified directly by setting up interception traps from the top to the bottom of probable target trees of beetle attack. We captured *P. quercivorus* inside the canopy of their probable target trees by interception traps placed up to a height of 9 m, though the number was low compared to the basal parts (Yamasaki *et al.*, accepted). Traps were not set up in the uppermost part of the canopy in this study and should be carried out in future studies.

There is increasing evidence that the behavior of ambrosia beetles is affected by the tree canopy. In forests dominated by oaks, the abundance and species richness of the ambrosia beetle were high in plots with high canopy closure rates (Holuša *et al.*, 2021). In avocado orchards, a significant effect of canopy cover on the capture of ambrosia beetles was reported (Menocal *et al.*, 2022). In the case of *P. quercivorus*, beetles were more frequently captured under the forest canopies compared to those under forest gaps when sticky screen traps were set up on the forest floor (Igeta *et al.*, 2004), and the probability of a beetle attack was high under a thick host canopy (Yamasaki *et al.*, 2014a). These results suggest that ambrosia beetles are attracted to the tree canopy, and leaf volatiles are the candidate attractants. It has been shown by a laboratory experiment that the redbay ambrosia beetle *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae) was attracted to its host leaf volatiles (Martini *et al.*, 2015). *Platypus quercivorus* was also attracted to volatiles from fresh leaves (Pham *et al.*, 2019), and was more strongly attracted to its host leaf volatiles compared to the non-host leaf volatiles (Pham *et al.*, 2020).

The effect of the basal area of surrounding hosts on the number of beetles that landed on non-hosts was detected (Table 2), though the estimated slope was moderate and its confidence interval was relatively wide (Figure 8a). This high variability of estimates may be partly due to the low variation in the calculated basal area; 88 % of this calculated variable was 0 which corresponds to the situation with no hosts within a radius of 1 m. In addition, the change in the AIC of the candidate models with an increase in the scale to calculate the basal area was not clear compared to the other variables (Figure 6), suggesting that the selected scale is not necessarily the optimum. However, it is easy to interpret the result that a high density of host trunks attracts beetles, and the increase in the beetle flying population causes an increase in wrong landing on the surrounding non-hosts. Former studies have also shown the positive effect of the host trunk density on the attack probability (Yamasaki & Sakimoto, 2009) and subsequent mortality (Yamasaki *et al.*, 2014b) of host

trees.

Attacks by *P. quercivorus* and subsequent mortalities were reported for 12 tree species of the Fagaceae family (Kobayashi & Ueda, 2005). When multiple host species were present in the same stand, the beetles did not discriminate against the host species, but they did discriminate against trunk size at the time of landing (Yamasaki & Futai, 2012). Beetles prefer thicker trees (Akaishi *et al.*, 2006), and disregard trees that are smaller than 9 cm in DBH (Yamasaki & Futai, 2008). The results of this study suggest that *P. quercivorus* may perceive and prefer to land on larger-diameter trees, including non-hosts. Thicker trees may be visually recognized by their silhouette (Mayfield & Brownie, 2013). The preference of beetles for thicker trees is believed to be adaptive because a larger volume of sapwood is available for constructing beetle galleries (Hijii *et al.*, 1991). Another possibility is that the positive effect of tree diameter on the number of beetles that we collected in the sticky traps is because larger diameter trees are more likely than smaller trees to passively intercept flying beetles. In the case of the longhorn beetle *Tetropium fuscum*, the positive effect of tree diameter on the number of beetles trapped to the sticky bands was detected, however, the effect of tree diameter on the number of beetles per unit area was not significant, showing that thicker trees are more likely to be hit by flying beetles (Nelson *et al.*, 2017). However, this possibility can be ruled out in our study because we attached sticky sheets of the same size to all the trees, meaning that the number of trapped beetles was equivalent to the number per unit area.

In a plot scale, the phenology of beetle landing on non-hosts coincided with that of the hosts, in general (Figure 4). The results of the best-fit model showed that both the probability of beetle landing (Figure 7) and the number of landed beetles on the non-hosts (Figure 8) were positively affected by the number of beetles landing on the surrounding hosts at an individual tree level. These results suggest that beetle landing on non-hosts is not an event independent of the surrounding hosts but an error that happens only near hosts and that wrong landing on a non-host occurs in greater frequency when many beetles are flying near host trees to which they are likely orienting.

When the number of landed beetles was summed up for all the seasons, for each tree, the landing rate on host trees was 255 beetles / 400 cm², whereas the landing rate on non-host tree species was 42 beetles / 400 cm² on average. Why does *P. quercivorus* make the error of wrong landing so frequently? The first possible reason is that beetles may not head directly to their boring site. As described above, host canopy detection by *P. quercivorus* has been suggested in former studies as well as this study. If that is the case, beetles are believed to detect the host canopy first, then come down to the basal part of the host trunk, just above the forest floor, to bore holes (Figure 9). The frequency of wrong selection may increase in this process, in which beetles descend from the top of the canopy to the forest floor. On the contrary, in the case of the walnut twig beetle *Pityophthorus juglandis*, wrong landing on non-hosts occurred, but at a lower frequency compared

to this study (Audley *et al.*, 2020). This twig beetle may use information about host twigs, and their boring site, for their host selection and head directly towards that.

The second possible reason for the frequent wrong landing of *P. quercivorus* is that their forest habitat has changed. Originally, *P. quercivorus* was thought to attack the matured big oak tree with a tendency to decline in a natural forest. Such matured trees may be big enough to attract beetles and errors are unlikely to occur when the beetles select the trunk to land on. In recent years, damages caused by *P. quercivorus* are frequently observed in secondary forests (Nakajima & Ishida, 2014). The dense distribution of host and non-host species with a relatively small size compared to a natural forest may increase the frequency of wrong landings in a secondary forest.

It should be noted, however, that wrong hole boring on a non-host by male beetles does not necessarily occur after landing. Boring on a non-host was rarely observed in the study area (personal observation). Former studies have also reported that the number of holes, in the non-hosts, bored by *P. quercivorus* was small (Sueyoshi & Taniguchi, 1990). Therefore, the wrong landing itself is not critical for the fitness of *P. quercivorus* males. This study detected wrong landing on non-hosts by setting up sticky sheets on the trunks. In a natural condition without sticky sheets, the beetles are thought to examine the physical and chemical condition of the bark surface after landing on a non-host and fly away to the next candidate trunk. One of the possible physical cues that beetles use to discriminate between host and non-host species on the bark surface is the angle of the crevice (Kuma *et al.*, 2021).

Females of *P. quercivorus* may be more sensitive than males in the process of discriminating between non-hosts and hosts. The estimated male sex ratio of beetles that landed on the hosts, 53.9 %, was similar to those reported for the population that emerged from host trees: the male sex ratio was 51.5% on *Pasania edulis* (Soné *et al.*, 1998) and 55.3% on *Q. crispula* (Kobayashi & Nozaki, 2003). The estimated male sex ratio of beetles that landed on non-hosts, 59.1 %, was higher than all of these estimates. In the case of *P. quercivorus*, males are pioneers and females are followers in the host selection process. Males that successfully bored holes emit the aggregation pheromone, and females use the aggregation pheromone for their host selection. Because boring on a non-host was rarely observed, the emission of the aggregation pheromone on non-hosts was thought to be low in frequency. This may cause a low landing rate of females on non-hosts, that is, females may avoid non-hosts prior to landing.

With regard to chemical cues, the volatile profiles of bark surfaces are thought to differentiate between host and non-host, and within-host and non-host tree species. These differences may affect beetle behavior, and the resultant number of landings may also differ among the tree species. Tree species were treated as a random effect in the model of this study because of an uneven sample size among the species, therefore, we did not discuss the differences in beetle landing among the tree species. Future studies should take this aspect into account.

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630

Table 1. Number of tree species with greater than 10 cm DBH distributed in the 5 plots set up in a warm-temperate secondary forest in Japan. The species are listed separately as hosts and non-hosts of the ambrosia beetle *Platypus quercivorus*, in order of most to least relevant for each category.

	Plot A	Plot B	Plot C	Plot D	Plot E	Total
Host tree species						
<i>Quercus serrata</i>	18	4	7	21	13	63
<i>Quercus myrsinifolia</i>	1	2	0	0	0	3
<i>Quercus variabilis</i>	0	0	2	0	0	2
<i>Quercus glauca</i>	0	0	0	1	0	1
Non-host tree species						
<i>Ilex pedunculosa</i>	3	4	3	10	4	24
<i>Pieris japonica</i> subsp. <i>japonica</i>	0	2	0	1	7	10
<i>Pinus densiflora</i>	0	2	2	2	1	7
<i>Eurya japonica</i>	1	5	1	0	0	7
<i>Cerasus jamasakura</i>	1	2	2	1	0	6
<i>Acer crataegifolium</i>	0	0	5	0	0	5
<i>Styrax japonica</i>	2	2	0	0	0	4
<i>Fraxinus sieboldiana</i>	0	3	1	0	0	4
<i>Acer palmatum</i>	0	0	0	4	0	4
<i>Gamblea innovans</i>	2	0	1	1	0	4
<i>Clethra barbinervis</i>	0	1	2	0	0	3
<i>Ilex macropoda</i>	0	0	0	0	2	2
<i>Ilex crenata</i>	1	1	0	0	0	2
<i>Diospyros kaki</i>	0	1	1	0	0	2
<i>Lyonia ovalifolia</i> var. <i>elliptica</i>	0	0	0	1	1	2
<i>Aria japonica</i>	0	0	0	0	2	2
<i>Cinnamomum yabunikkei</i>	0	1	0	0	0	1
<i>Camellia japonica</i>	0	0	1	0	0	1
<i>Padus grayana</i>	0	0	1	0	0	1
<i>Albizia julibrissin</i>	0	1	0	0	0	1
<i>Pinus koraiensis</i>	1	0	0	0	0	1
<i>Mallotus japonicus</i>	0	1	0	0	0	1
<i>Carpinus laxiflora</i>	0	1	0	0	0	1

Table 2. Results of a mixed hurdle model predicting the number of ambrosia beetle *Platypus quercivorus* that landed on non-host tree species in a secondary forest in Japan. Three candidate explanatory variables were prepared for the zero-hurdle and count parts, respectively. The estimated slopes, their standard errors, and the Z and P values for the variables selected are described for the best-fit model. Dashes indicate that the particular variable was not selected for the model. The tree species were included as random intercepts of the model.

	Estimate	Std. Err.	Z value	Pr (> z)	
Zero-hurdle part ^{*1}					
Host canopy density (7 m) ^{*2}	-0.845	0.288	-2.937	0.003	**
Beetles landed on surrounding hosts (5 m) ^{*3}	-0.012	0.001	-10.008	< 0.001	***
DBH ^{*4}	-	-	-	-	
Count part					
Host basal area (1 m) ^{*5}	14.950	5.943	2.516	0.012	*
Beetles landed on surrounding hosts (5 m)	0.007	0.001	7.418	< 0.001	***
DBH	0.056	0.009	6.478	< 0.001	***

*1: This part predicts the probability of zero occurrences, i.e., no beetle landing. Minus values of the estimates mean the positive effect of explanatory variables on the occurrence of beetle landing.

*2: Mean number of the canopy layer of the host tree species calculated for the surrounding area of the subject non-host tree within a radius of the distance described in parenthesis.

*3: Total number of beetles that landed on the host tree species calculated for the surrounding area of the subject non-host tree within a radius of the distance described in parenthesis.

*4: Diameter of the subject non-host tree at 1.3 m above ground level.

*5: Cross-sectional area of the host tree species calculated for the surrounding area of the subject non-host tree within a radius of the distance described in parenthesis.

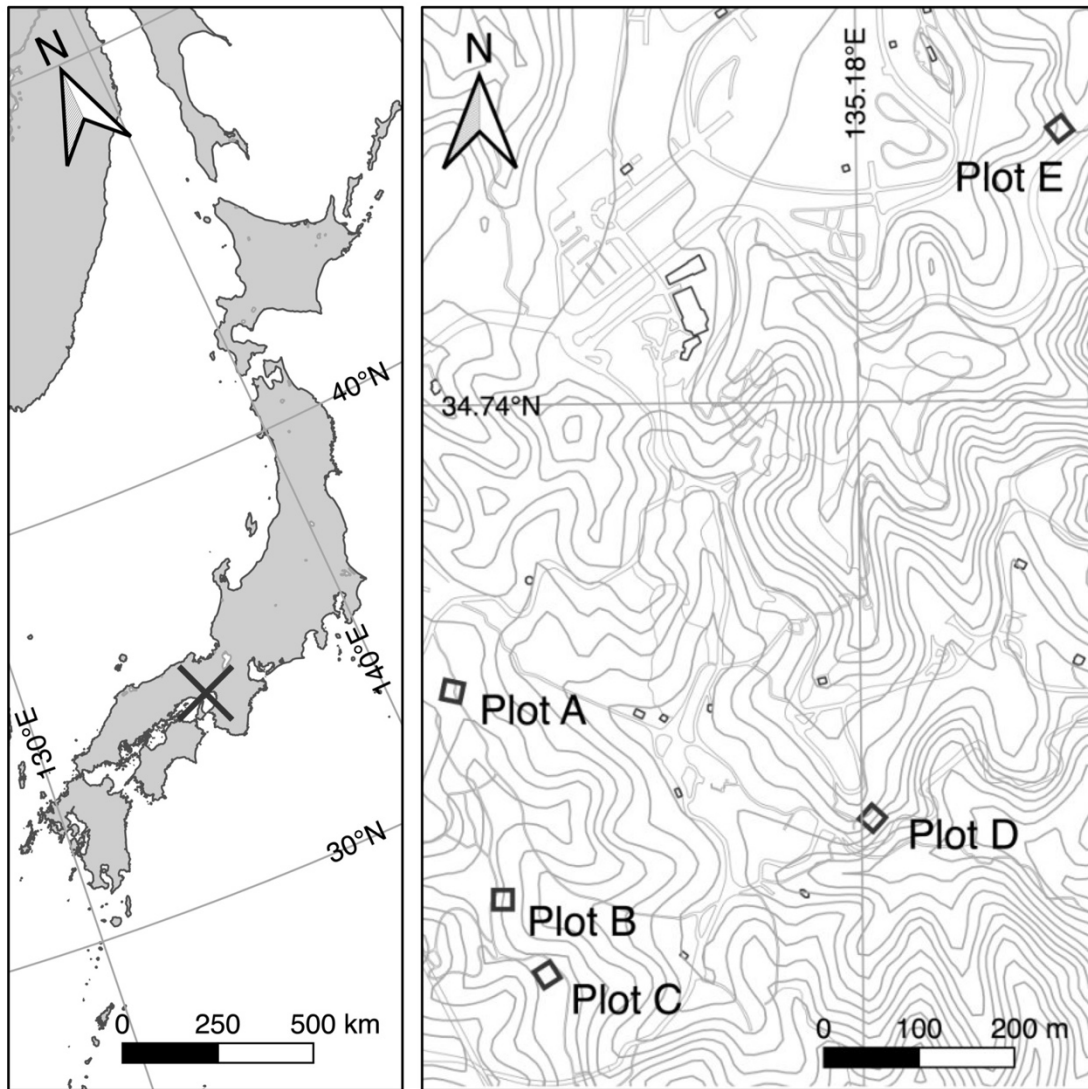


Figure 1. Location of the study site in Japan (left) and arrangement of the 5 plots, 20 x 20 m in size, in this site (right), which were set up in a warm temperate secondary forest to study the landing behavior of the ambrosia beetle *Platypus quercivorus* on their host and non-host species.

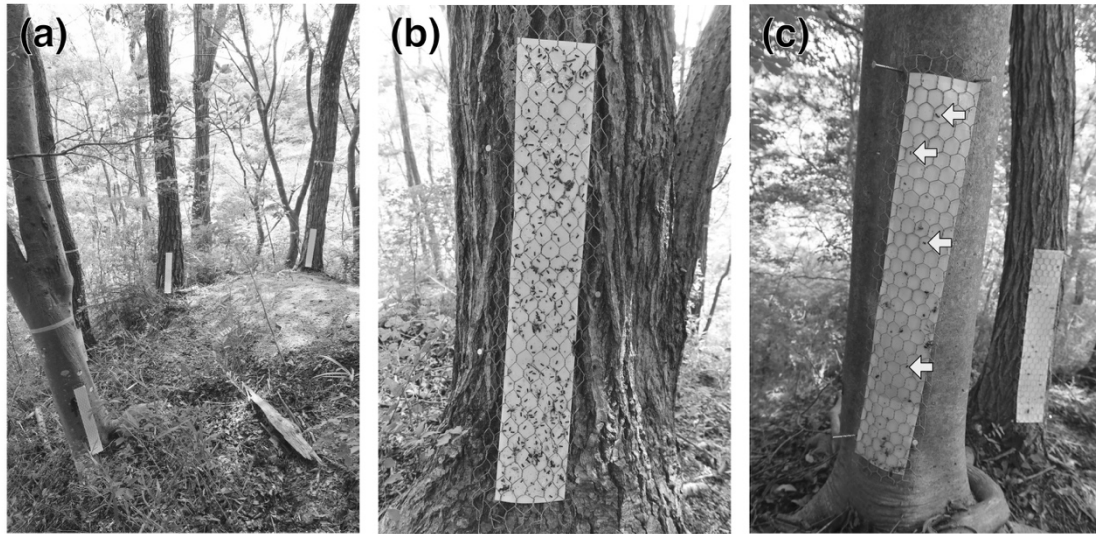


Figure 2. (a) Sticky traps set up on the basal part of the trees on the plot to study the landing behavior of the ambrosia beetle *Platypus quercivorus* on their host and non-host species. (b) Beetles trapped on the sticky trap on the host and (c) beetles trapped on the adjacent non-host. The sticky sheet was covered with a vinyl-coated wire mesh to prevent other large animals from being trapped.

Candidate models (10,000 patterns)

Zero-hurdle part

- host canopy density averaged for any one of 10 scales
- number of beetles landed on surrounding hosts summed up for any one of 10 scales
- DBH of non-host

Count part

- basal area of surrounding hosts summed up for any one of 10 scales
- number of beetles landed on surrounding hosts summed up for any one of 10 scales
- DBH of non-host



Select the model with lowest AIC among candidate models



Full model

Zero-hurdle part

- host canopy density averaged for some scale
- number of beetles landed on surrounding hosts summed up for some scale
- DBH of non-host

Count part

- basal area of surrounding hosts summed up for some scale
- number of beetles landed on surrounding hosts summed up for some scale
- DBH of non-host



Select significant variables out of 6 listed in a full model



Best-fit model

Figure 3. Model selection process of this study. First, 10,000 candidate models were constructed and the model with the lowest AIC was selected as the full model. Second, the best-fit model was selected by deleting insignificant variables one by one from the full model. Refer to the text for details.

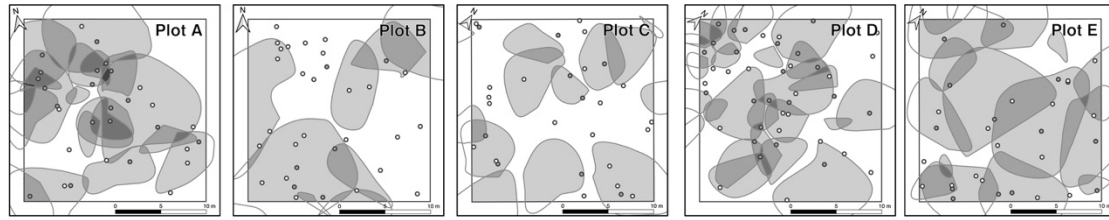


Figure 4. Distribution of the trees inside each plot (Plot A, B, C, D, and E). The grey circles show the location of the trunk base of the ambrosia beetle *Platypus quercivorus* host, and the white circles show the location of the trunk base of the non-host. Projected canopies are shown by grey polygons, only for the host. Because the plots were set up on slopes, the canopies were not necessarily located directly above the trunk base.

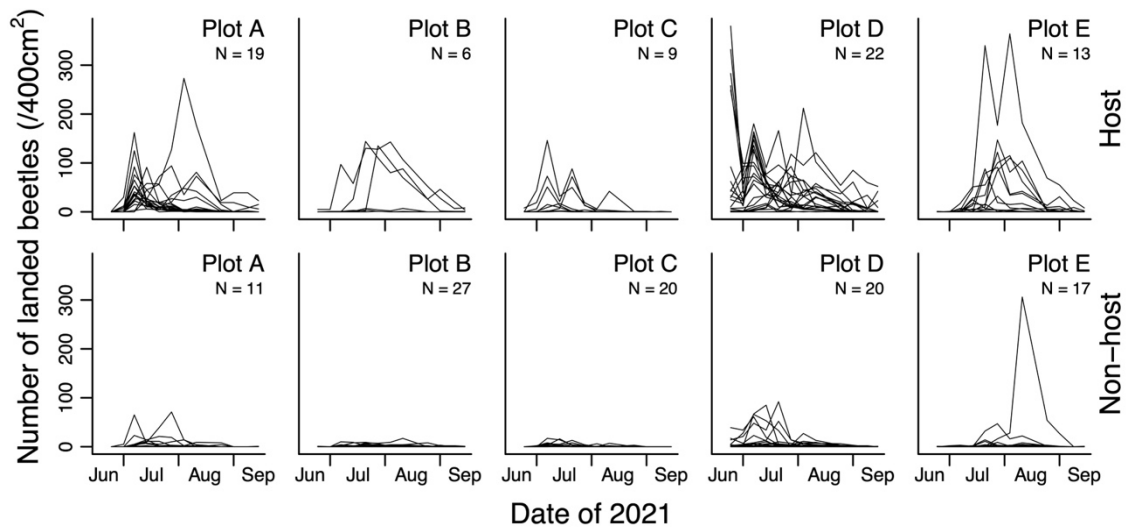


Figure 5. Changes in the number of ambrosia beetles *Platypus quercivorus* which landed and were trapped on the sticky sheets attached to the trunks of their host (top) and non-host species (bottom) in the 5 plots set up in a warm-temperate secondary forest in Japan. The number of trees distributed in each plot is described at the top right of each graph. Each line shows the data of an individual tree.

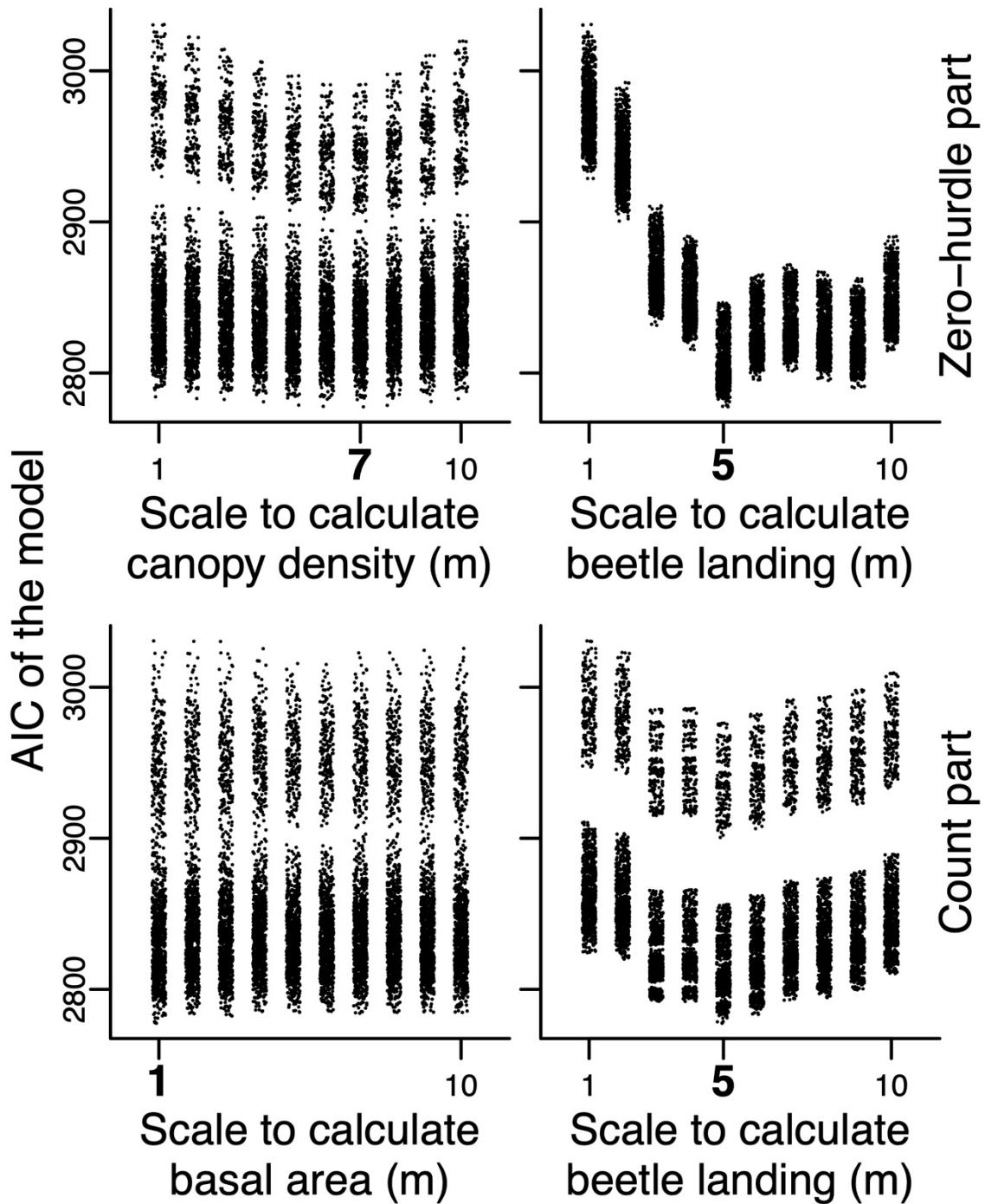


Figure 6. Akaike's information criterion (AIC) of 10,000 different models to predict the number of *Platypus quercivorus* that landed on the non-host. The model was composed of 2 parts, a zero-hurdle and count part, and the host canopy density, host basal area, and number of beetles that landed on the surrounding hosts were calculated within a radius of 1–10 m of the target non-host and were included in each part together with the DBH of the non-host. The numbers with a bold font on each x-axis show the scale of each variable with the lowest AIC obtained. Refer to the text for details.

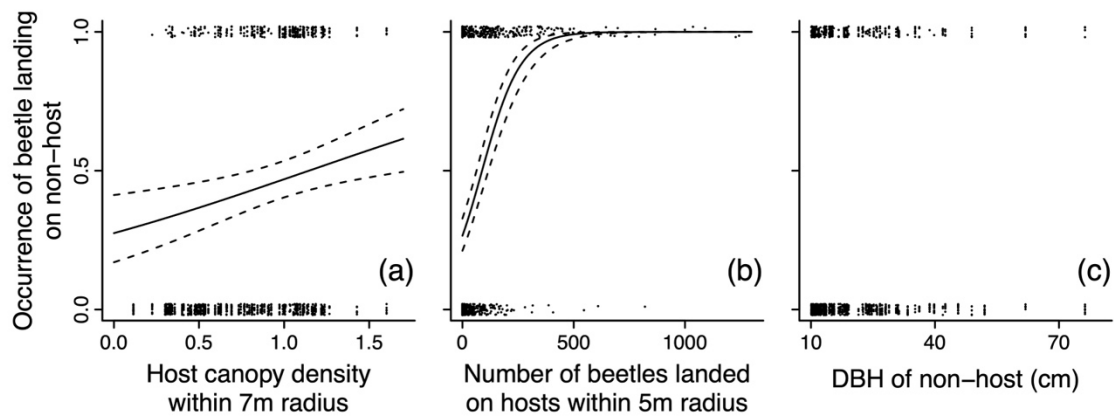


Figure 7. Effects of (a) the host canopy density averaged for the buffer area with a 7 m radius, (b) the number of *Platypus quercivorus* that landed on the hosts in the buffer area with a 5 m radius, and (c) the DBH of the non-host, on the occurrence of the landing of a beetle on the non-host. The small dots show the raw data which were vertically jittered randomly. Value "0" means that no beetles landed, and value "1" means that 1 or more beetles landed. The solid and dashed lines show the values predicted by the zero-hurdle part of the model and their confidence intervals, respectively; they were drawn only for the variables selected for the model.

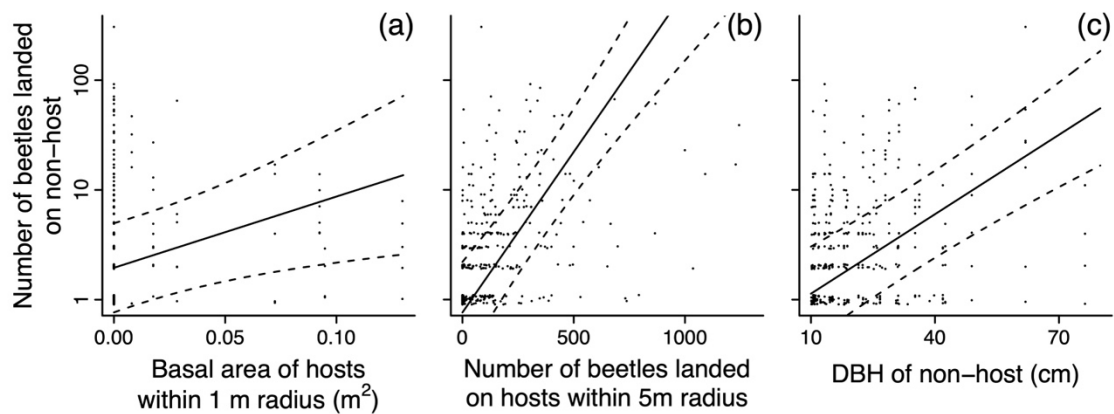


Figure 8. Effects of (a) the basal area of the hosts in the buffer area with a 1 m radius, (b) the number of *Platypus quercivorus* that landed on the hosts in the buffer area with a 5 m radius, and (c) the DBH of the non-host, on the number of *Platypus quercivorus* that landed on the non-host. The small dots show the raw data which were vertically jittered randomly. The solid and dashed lines show the values predicted by the count part of the model and their confidence intervals, respectively. Raw data are shown only for values that are 1 or more in terms of the number of beetles that landed on the non-host.

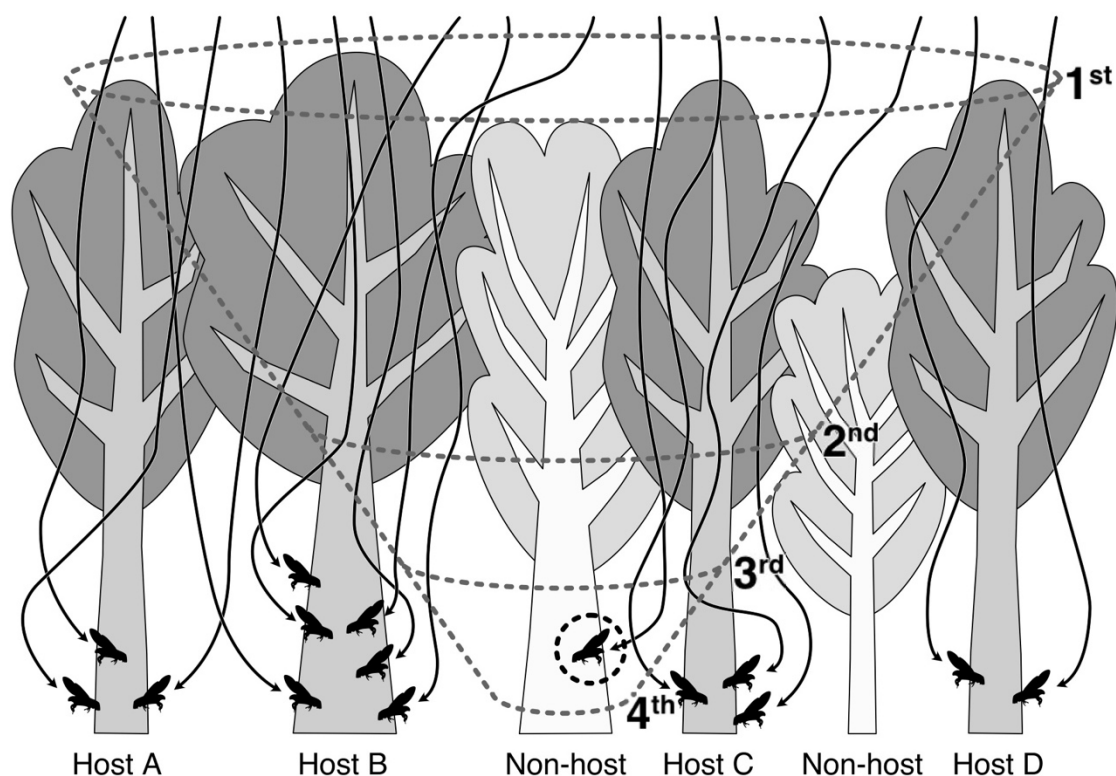


Figure 9. Hypothesis explaining the landing of *P. quercivorus* on non-hosts, and the approach path of the beetles to their boring site, based on model results. The dashed grey lines show the effective scale of the surrounding hosts on the wrong landing. In the 1st stage, the beetles are attracted to the host tree canopy, and the probability of a wrong landing on a non-host (the beetle circled with a dashed line) increases with an increase in the density of the host tree canopy; Hosts A, B, C, and D affect the probability of wrong landing by attracting the beetles with their canopies. In the 2nd stage, the beetles fly down from above the canopy and pass through the canopy, and the probability and frequency of a wrong landing increase when many beetles pass through a neighborhood of non-hosts and land on the surrounding hosts as a result; Hosts B and C affect the probability of a wrong landing. In the 3rd stage, the beetles start to search the trunk to land on the forest floor, and the number of beetles that land on the non-hosts increases with an increase in the basal area of the surrounding hosts; only Host C affects the number of beetles that land on a non-host. In the 4th stage, the beetles land on a tree trunk, and the thickness of the non-host affects the number of beetles that land on it.