



Bark beetles on pine logs: forecasting winter colonisation dynamics based on trap catches and temperature records

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Abstract

Seasonality influences the abundance and activity of forest insects. Harvesting during periods of reduced activity could minimise colonisation risk on logs and reduce the need for phytosanitary treatments. We describe the winter colonisation dynamics of *Pinus radiata* logs in operational harvest sites in New Zealand and assess the probability of log colonisation as a function of captures in flight interception traps. After 15 days, 3% and 1% of logs were colonised by *Hylastes ater* and *Hylurgus ligniperda* (Coleoptera: Scolytinae), respectively, and 1% by *Xenocnema spinipes* (Coleoptera: Curculionidae). The same three species were captured in traps. Our observations showed that logs exposed for ≥ 2 weeks are predicted to have a more than 1% probability of bark beetle colonisation, whereas logs removed from forests within 24 or 48 h had predicted colonisation rates of 0.13% and 0.26%, respectively. A positive relationship between trap capture and log colonisation was also observed. Average catches of < 1 bark beetle per trap, three bark beetles per trap or ten bark beetles per trap equated to estimated log colonisation rates of $< 10\%$, 14–98% or $> 98\%$ log colonisation. A positive relationship was also shown between log colonisation rates and temperature. A 12.3 °C temperature threshold predicted colonisation rates of 5, 50 and 95% with thermal sums of 10, 20 and 30 degree-hours, respectively. Models based on exposure time, trap catches, or environmental factors can estimate seasonal probability of insect colonisation, which aids identification of periods of low pest pressure when treatments could be avoided or reduced.

Keywords Area of low pest prevalence (ALPP) · *Pinus radiata* · *Hylurgus ligniperda* · *Hylastes ater* · *Xenocnema spinipes* · Kairomone trap · Systems approach

Key message

- Insect activity in temperate forests is largely influenced by season.
- Here, we quantify the winter colonisation of *Pinus radiata* logs by saproxylic insects in operational harvest sites in New Zealand plantation forests.

- Our data showed that removing logs from the forest within a 24- to 48-h period significantly reduces colonisation risks during winter.
- We provide models based on exposure time, trap catches, or temperature records to estimate the seasonal probability of log colonisation.

Introduction

Insect pests are considered to be one of the most significant forest disturbance agents worldwide (van Lierop et al. 2015). Bark beetles, wood/shoot borers and defoliators that attack healthy trees directly (or indirectly) affect the environment and human well-being through ecosystem modification (Boyd et al. 2013). During outbreaks, the most aggressive species may substantially reduce forest productivity and can be responsible for large economic losses in affected areas (Kautz et al. 2017). Less aggressive species that colonise

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weakened trees or the bark and wood of recently dead or harvested trees can also be of concern (Paine et al. 1997; Weed et al. 2015). For example, beetles in the families Curculionidae, Cerambycidae and Buprestidae, and Siricidae can reduce the economic value of harvested wood products (Grégoire et al. 2015). When infestations are associated with exported wood commodities, they represent a phytosanitary risk (Lanfranco et al. 2004; Pawson et al. 2014) that can lead to the establishment of alien species in new geographic ranges (Meurisse et al. 2018). The economic, environmental or social impacts of such establishments in the receiving environment are difficult to predict (Aukema et al. 2011; Grégoire et al. 2015).

A range of phytosanitary measures have been developed through bilateral agreements between the exporting and importing countries, to minimise the risk of transporting pest species with trade (Ormsby and Brenton-Rule 2017). These include phytosanitary treatments, such as heat (Nursultanov et al. 2019), chemical sprays and fumigants (Najar-Rodriguez et al. 2015), or systems approaches that combine two or more interventions to achieve satisfactory control (Allen et al. 2017). For example, managing phytosanitary risks using a systems approach to control pest risks associated with timber trade takes into account options to reduce the exposure of logs to colonising insects both during harvest and at temporary storage facilities and ports prior to export (Lanfranco et al. 2004).

New Zealand, the second largest log exporter in the world after Russia, exported 19.2 million m³ of roundwood logs from plantation forests in 2017 (MPI 2019a). Logs are produced from exotic *Pinus radiata* D. Don plantations that are managed in single species, even aged stands (MPI 2019b). Introduced to New Zealand, *P. radiata* has few insect defoliators and no aggressive insect species that kill live trees except the woodwasp *Sirex noctilio* F. (Hymenoptera: Siricidae). However, *S. noctilio* has no economic impact because of established and effective biological controls (Bain et al. 2012). Hence, post-harvest colonisation of logs by saproxylic species (i.e. species dependent upon deadwood habitats during some part of their life cycle) during their periods of flight activity is the principal phytosanitary risk. *Arhopalus ferus* (Mulsant) (Coleoptera: Cerambycidae) and two bark beetles, *Hylurgus ligniperda* (F.) and *Hylastes ater* (Paykull) (Coleoptera: Scolytinae), are the most abundant saproxylic insects in New Zealand plantations and colonise recently harvested *P. radiata* (Pawson et al. 2021). *Arhopalus ferus* adults are not active in winter, and the two bark beetles have minimal flight activity in winter (Pawson et al. 2021). Low wintertime flight activity is expected due to the strong relationship between maximum hourly temperature and the probability of flight (Pawson et al. 2017). The seasonal differences in adult activity provide an opportunity to use alternative

risk-based approaches to mitigate phytosanitary risks. For instance, the establishment and declaration of a temporal area of low pest prevalence or ALPP (IPPC 2005) provides confidence that the infestation rate of logs leaving the forests is below an acceptable threshold. For pine plantations in New Zealand, the winter season and its low post-harvest risk profile may meet ALPP requirements, provided that the seasonal probability of colonisation of recently harvested logs by species of concern can be quantified.

Here, we address the following questions:

1. Which insect species fly and subsequently colonise harvested logs during the Southern Hemisphere winter in New Zealand?
2. What is the probability that a log is colonised in winter by individual pest species of potential phytosanitary importance?
3. What is the relationship between the rate of log colonisation and the number of individuals caught in traps?
4. What meteorological factors influence the rate of colonisation of recently cut logs by these insect species?

Understanding these questions will allow the development of monitoring devices (e.g. traps baited with semiochemicals) and models based on meteorology and insect habitat abundance in the landscape to quantify insect abundance (Pawson et al. 2017, 2021) and the probability of log colonisation (this study). Defining these risk factors in space and time, as a function of measurable metrics (i.e. trap catch data), allows the identification of ALPP (IPPC 2016) and an important step towards the development of a systems approach for the management of export phytosanitary risk for forest products (Allen et al. 2017).

Materials and methods

Study region

The survey was conducted in the central North Island (CNI), which is New Zealand's main *P. radiata* growing region (Fig. 1). The CNI summer climate is typically warm and dry, with daytime maximum air temperatures ranging from 21 to 26 °C and rarely exceeding 30 °C. The winter climate is cooler, with heterogeneous distribution of rainfall, daytime maximum air temperatures ranging from 10 to 14 °C and frosts occurring when conditions are clear and calm (NIWA 2007). The region is sheltered by mountains to the south and east and has less wind than many other parts of New Zealand. The rainfall average is 1100 to 1400 mm in most places with 2000 to 2100 h of sunshine annually (NIWA 2007).

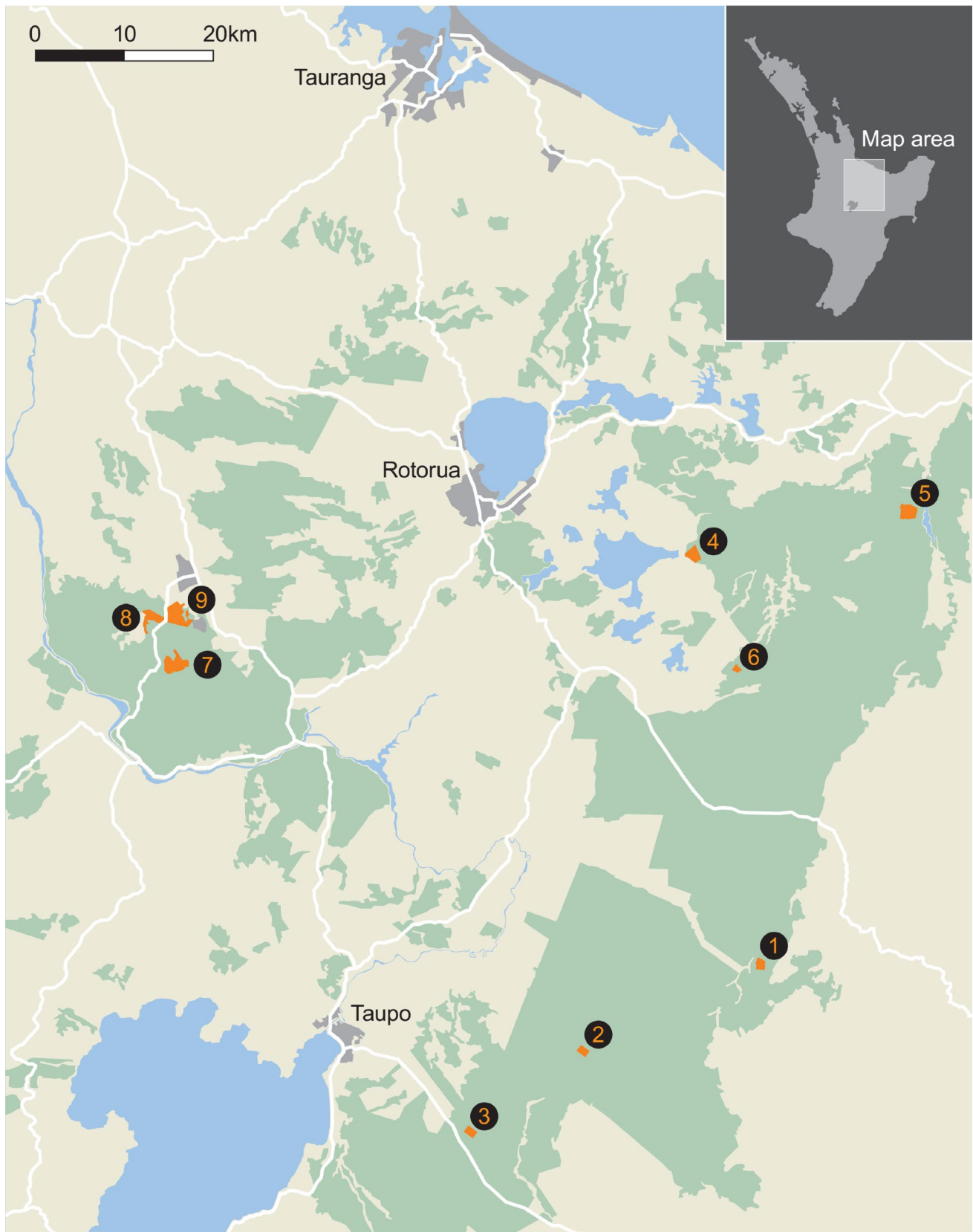


Fig. 1 Map of the study region in central North Island, New Zealand, showing the distribution of plantation forests, primarily *Pinus radiata* (green shaded areas), and the nine clearcut harvesting sites where the

study was performed (orange-filled stands). Sites 1–3 are located in Kaingaroa Forest, 4 in Tarawera Forest, 5 in Matahina Forest, 6 in Rerewhakaaitu Forest and 7–9 in Kinleith Forest

Study sites, experimental design and data collection

Study sites were established in nine operational harvest sites scattered over an area of about 500,000 ha (Fig. 1). Harvest operations were still active in most sites at the start of the experiment with tree cutting, stem piling and removal operations occurring 100–300 m from our sampling equipment. A square (80 m × 80 m) study area was delimited at each harvest site within an area that had been clearcut harvested 1 to 4 weeks before the study was initiated (Fig. 2).

Focal species

Hylastes ater and *H. ligniperda* are quarantine pests of India and China, respectively (MPI 2021a, b). Because of their regulated status, we focused our analyses on the colonisation of *P. radiata* logs by the females of these two species. Both *Hylastes* spp. and *Hylurgus* spp. are non-aggressive, saprophytic bark beetles (Weed et al. 2015) that do not need to overwhelm tree defences like primary bark beetles and, for this reason do not exhibit a capacity for long-range adult aggregation [i.e. a pheromone-based colonisation behaviour (Wood 1982; Byers 2004)]. In contrast, their host colonisation relies essentially on primary attraction to volatiles emitted by recently cut logs or other deteriorating tree material.

Logs

Logs were placed in the study areas to expose them to insect colonisation. The logs (40 cm in length by 15–25 cm in diameter) were sourced from 18-year-old *P. radiata* trees in Whakarewarewa forest (38.157°S, 176.270°E). The logs were harvested 4 to 8 days before they were placed in the study area. In the meantime, they were kept under shade and at ambient temperature in an insect-proof enclosure. At time of harvest and on the day prior to exposure in the field, all logs were visually inspected for external symptoms of insects or fungal infection. The cut ends of each log were waxed to prevent desiccation.

Three logs were placed side by side at the midpoint on each side of the study area (Fig. 2) on 12, 13 and 14 July 2015 for a cluster of nine logs at each midpoint and a total of 36 logs at each study site. Three logs were subsequently removed from each cluster of logs (12 logs total from each study site) after 3-, 8- or 15-d exposure to insect colonisation (Supplementary Fig. 1).

Traps

Kairomone interception traps were installed at the centre and each corner of the study square (Fig. 2). Traps were custom-made four-vane, black panel traps with funnels and dry collecting cups, suspended on steel posts at 1.4 m height. The collecting cups were coated with alpha-cypermethrin

Fig. 2 Five traps and four log piles arranged in an 80 × 80 m square area illustrate a typical study site within a clearcut harvested stand. Background image sourced from Land Information New Zealand (2017), location 43.455°S, 172.711°E, orthophotography dated summer (Southern Hemisphere) 2015–2016. Locations of logs and traps within each study area could not be completely randomised because health and safety issues within the operational harvest areas restricted the placement of sampling equipment



(RipCord Plus, BASF New Zealand Limited, Auckland, New Zealand) to kill all captured insects. Each trap was baited on the day it was placed in the field with two 150-mL polyethylene dispensers (150 μm thick), one dispenser containing a mixture of α -pinene and β -pinene, and the other containing ethanol (see Supplementary Fig. 2). Host plant volatiles, especially α -pinene and β -pinene present in live pine tissues, and ethanol that is produced in decaying pine phloem and sapwood tissues, provide the best lures known to date for bark beetles in the genera *Hylastes* and *Hylurgus* (Rudinsky and Zethner-Møller 1967; Phillips 1990; Reay and Walsh 2002; Kerr et al. 2016). Release rates for the α -pinene/ β -pinene and ethanol dispensers were previously estimated to ~ 0.76 g/day and ~ 0.02 g/day, respectively (Kerr et al. 2017). These estimates were obtained in summer conditions, and average release rates in this experiment were certainly lower than these because temperatures in winter in New Zealand CNI are usually inferior to summer temperatures by about 10 °C (minimum, maximum and mean daily, see Supplementary Material 2). The traps were operating during the entire log exposure period (12–29 July 2015).

Temperature loggers

Temperatures at each study site were monitored at 15-min intervals over the entire log exposure period using iButton temperature loggers (DS1922L-F5# Thermochron iButton, Maxim, San Jose, California, USA). A temperature logger was placed inside a Stevenson screen, a dedicated meteorological shelter designed to shield the instruments placed therein from both long- and shortwave radiation, while allowing a free flow of air to circulate freely around them. The Stevenson screen was attached at ~ 1.4 m height to the steel post that supported the trap in the centre of the study site (Fig. 2). This trap in the centre was otherwise equipped the same way as the four traps in the corners of the study square, with α -pinene and ethanol dispensers, and a collecting cup.

Assessment of log colonisation and trap catches

Traps were checked during each site visit (11 checks over the 17-day log exposure period, Supplementary Fig. 1), and all insects in the collecting cups were brought to the laboratory for identification.

The logs were inspected externally before they were removed from the study sites to observe for the presence of insects or symptoms of insect activity, such as frass, boring holes, sawdust, or unusual resin flows. All symptoms were described and photographed for subsequent laboratory identification. The logs were then enclosed in plastic bags or plastic boxes and stored between 2 and 33 days (mean: 18 days) under shade and at ambient temperature in

a containment facility before the bark was removed and the logs were destructively examined for insect contamination. All insects found in the logs were counted and identified. Bark beetles were sexed by inspecting *H. ater* for characters described by Clark (1932) and Anonymous (1946), and *H. ligniperda* for characters described by Fabre and Carle (1975) and Liu et al. (2008).

Meteorological data collection

Short-term fluctuations in temperature were smoothed prior to analysis by applying a one-hour rolling mean window to the iButton data. Daily minimum and maximum temperatures from 1 January 1990 to 31 December 2014 were obtained from a meteorological station in Taupō (located 15–90 km from the study sites, 38.743°S, 176.081°E (NIWA 2018) to derive 25-year normal temperatures for comparison with the conditions during our study period. Hourly rainfall data were also obtained from the Taupō station.

Statistical analyses

All analyses were performed using the statistical package R, version 3.4.0 for Windows (R Core Team 2017).

Log colonisation by *H. ater* and *H. ligniperda*

Log colonisation rates were first analysed separately for females of *H. ater* and *H. ligniperda*, and then for both species combined. Estimates were calculated across the three periods of exposure (3, 8 or 15 days, $n = 108$ logs for each duration), and associated 95% confidence intervals were estimated using exact binomial tests (*binom.test*, Clopper and Pearson 1934).

Temporal dynamics of colonisation by bark beetles

The probability of log colonisation by bark beetles, irrespective of species, was analysed with generalised linear models (GLMs), using a binomial error structure and a “logit” link function. The number of logs colonised by females was used as a response variable (out of a total of 12 logs in each site, Supplementary Fig. 1). Log exposure time, in days, was used as a fixed effect. Initially, the proportion of logs colonised was modelled using a GLMM that also incorporated site as a random effect (*glmmTMB*, R package *glmmTMB* (Magnusson et al. 2018)). A likelihood ratio test suggested that the same model with the random effect was not justified (Supplementary Material 1), and a final GLM model was then fitted without consideration of site as a random effect (*brglm*, R package *brglm* (Kosmidis 2017)). In this final model, the bias-reduction method of Firth (1993) was used instead

of traditional maximum likelihood estimation methods to account for the rarity of colonisation events. Associated 95% confidence intervals were estimated on the parameters (*confint*), and a 95% confidence envelope was estimated on the predictions from the predictive values ± 1.96 SE excluding the random effects.

Although models such as GLMs provide convenient phenomenological descriptions of observed ecological processes, their predictions may be unrealistic when explanatory conditions lie outside of the range of tested values. To provide a mechanistic explanation for log colonisation, as well as a model that would be more reliable for long-term predictions (> 15 days of exposure), we also analysed the probability of log colonisation with nonlinear mixed-effect models. The proportion of logs colonised by females was used as a response variable (Supplementary Fig. 1), exposure time as a fixed effect and site as a random effect. The functional form of the nonlinear mixed model was derived from probability theory, where $PropFinal_t$ corresponds to the proportion of colonised logs after t days and $PropDaily$ corresponds to the average proportion of logs infested each day (Eq. 1, McArdle 1990).

$$PropFinal_t = 1 - (1 - PropDaily)^t \quad (1)$$

Comparisons were performed between models varying in: (1) the inclusion of site as a random effect (using mixed-effect models) and (2) the consideration of heteroscedasticity in the variance (using an exponential variance model structure). All models were fitted using maximum likelihood, with the *gnls* function for models without a random effect, and the *nlme* function for models with a random effect (R package *nlme* Pinheiro et al. 2016). The 95% confidence intervals were estimated for model parameters (*intervals*, R package *nlme*), and a symmetrical 95% confidence envelope was estimated for the predictions using variance calculation based on Taylor series expansion (Wutzler 2013).

Relationship between log colonisation and trap catches

We examined the relationship between log colonisation and trap catch with GLMs and generalised linear mixed models (GLMMs), using a binomial error structure and a “logit” link function (*glmmTMB*, R package *glmmTMB* (Magnusson et al. 2018)). The number of logs colonised by female bark beetles was used as a response variable. Numbers were estimated from four logs in each site, which corresponds to each of nine periods of exposure/trapping (Supplementary Fig. 1). The number of bark beetles captured in traps was used as a fixed effect. A first analysis considered only females, while a second analysis included both sexes. We also used derived models to: (1) test for the significance of site as a random effect (using mixed models); and (2) account for the large

numbers of zero trap catch and colonisation events (using zero-inflated models). All models were compared using the second-order criterion Akaike Information Criterion (AIC_c), and likelihood ratio tests to determine whether a model was significantly better performing than another one. A difference in the AIC_c score ≤ 2 indicates that models are similar, in which case the simpler model (i.e. with less parameters) was favoured (Burnham and Anderson 2002). Associated 95% confidence intervals were also estimated for parameters of the best model (*confint*).

Relationship with meteorological conditions

GLM and GLMMs were used to investigate the effects of temperature on log colonisation rates and trap catches. Minimum (T_{\min} , Eq. 2), mean (T_{mean} , Eq. 3) and maximum (T_{\max} , Eq. 4) air temperatures, and the thermal sum of effective temperatures for flight (SET , Eq. 5), were calculated on hourly temperature data (T_i), for each site and each period of log exposure. For SET calculation, we used a flight activity threshold of 12.3 °C ($T_{\text{threshold}}$). This corresponds to the lowest cut point value for hourly temperature identified in models by Pawson et al. (2017) and is associated with increasing flight activity for *H. ligniperda*. This lowest value also corresponds to a steep increase in observed trap catches (Pawson et al. 2017, Supplementary material, Fig. S3). Higher thresholds were not considered as temperatures during our trial rarely exceeded other cut points (14.6 °C and 17.5 °C) identified by Pawson et al. (2017).

$$T_{\min} = \min(T_i) \quad (2)$$

$$T_{\text{mean}} = \text{mean}(T_i) \quad (3)$$

$$T_{\max} = \max(T_i) \quad (4)$$

$$SET = \sum_i (T_i - T_{\text{threshold}}) \quad (5)$$

Total rainfall ($Rain_{\text{total}}$, Eq. 6) was calculated on rainfall hourly data ($Rain_i$), for each period of log exposure.

$$Rain_{\text{total}} = \sum_i (Rain_i) \quad (6)$$

Before using GLMMs, we calculated the variance inflation factor (VIF) for all temperature variables (*vifcor*, R package *usdm* (Naimi 2017)). T_{\min} and T_{mean} were associated with VIFs of 7.6 and 7.4, respectively, indicating high intercorrelation (Graham 2003, p. 20). We removed T_{\min} to provide a set of explanatory variables that did not contain collinearity (VIFs < 3 (Zuur 2009)).

Using the remaining temperature variables as explanatory fixed factors, we fitted GLMs and GLMMs to: (1) the number of logs colonised by female bark beetles (out of four logs in each site/trapping period), using a binomial error structure and a “logit” link function; and (2) the count responses of bark beetle individuals captured in traps (for five traps in each site/trapping period), using a Poisson and negative binomial error structure and a “log” link function (*glmmTMB*, R package *glmmTMB* (Magnusson et al. 2018)). Comparisons were performed between models varying in: (1) the inclusion of a site random effect (using mixed models) and (2) the consideration of the large number of zeros (using zero-inflated models). All models were compared using the Akaike Information Criterion (AIC). A difference in the AIC score ≤ 2 indicates that models are similar, in which case the simpler model (i.e. with less parameters) was favoured. Associated 95% confidence intervals were estimated on the parameters of the best model (*confint*).

Results

General patterns of insect log colonisation and trap catches

Fewer insects were found associated with logs than were captured in flight intercept traps. A total of 19 individuals representing four species were found on nine of the 324 logs (2.8%) (Table 1). In comparison, 73 individuals of at least 17 different species were captured in 37 of the 45 flight intercept traps (82%) (Table 1). The difference in abundance between logs and traps persisted irrespective of the duration of exposure (3, 8 or 15 days for logs, and 17 days for traps) with an observed bark beetle colonisation rate that averaged 0.0068 per log- per day and an observed trap catch rate that averaged 0.095 per trap-day.

The bark beetles *H. ater* and *H. ligniperda* and the short-nosed kauri weevil *Xenocnema spinipes* Wollaston (Coleoptera: Curculionidae) were the only species associated with obvious signs of establishment on logs (i.e. active adult beetles boring into the bark) that were also observed in flight intercept traps. Both *H. ater* and *H. ligniperda* were also observed on logs during intermediate checks along with two other adult beetles, an unidentified Staphylinidae and an unidentified Tenebrionidae, that were not considered in the analyses but are listed in Supplementary Table 1.

Log colonisation by *H. ater* and *H. ligniperda*

A total of five female *H. ater* and one female *H. ligniperda* colonised a total of five logs at two of the nine study sites (Table 1). No bark beetles were found in logs exposed for 3 days (Table 1). Females were found in one (0.9%) of the

logs exposed for 8 days (*H. ater*), and four (3.7%) of the logs exposed for 15 days (2.8% by *H. ater* and 0.9% by *H. ligniperda*) (Table 1, Fig. 3). Another log exposed for 15 days was colonised by a single male *H. ater*. Confidence estimates around the estimated percentages of bark beetle colonisations are provided in Supplementary Table 2.

Temporal dynamics of colonisation by bark beetles

Estimates from the final GLM (Fig. 4), fitted without consideration of the site factor, were comparable to the results observed during the study period. Model extrapolation to longer exposure periods predicted larger estimates for longer exposures, for example, 0.22% colonisation after 24 h (1 day), 0.28% after 48 h (2 days), 0.8% after a week (7 days), 3.4% after two weeks (14 days), and 51% after a month (30 days) (Fig. 4).

The nonlinear mixed-effect model estimated the proportion of logs colonised by female bark beetles to be $1.3e^{-3}$ per day (Fig. 5). This corresponds to an almost linear colonisation rate over time, with 0.13% after 24 h (1 day), 0.26% after 48 h (2 days), 0.9% after a week (7 days), 1.8% after two weeks (14 days) and 3.6% after a month (28 days).

Relationship with trap catches

Bark beetles were captured in flight intercept traps at four of the nine study sites, including the two sites where *H. ater* and *H. ligniperda* colonised logs (Table 1). However, in contrast to the number of *H. ater* that was observed in logs, *H. ligniperda* was far more abundant in traps (ten males and ten females) than *H. ater* (one male).

A comparison of GLMs versus GLMMs to model the relationship between log colonisation and trap catch indicated that the best models were based on catches of bark beetles of both sexes without the inclusion of a zero-inflated component (Supplementary Material 1). The GLMM (with site as random effect) did not represent a significant improvement ($\Delta AIC = 1.7$, $P = 0.054$) relative to the simpler GLM (Supplementary Material 1), which was therefore favoured (Fig. 6). Average catches of one bark beetle per trap were estimated to be associated with a level of log colonisation of 4% (95% CI 1.7%, 10%). Higher catches were associated with greater uncertainties. For instance, an average catch of three bark beetles per trap would indicate a 72% colonisation rate at the site (CI 14%, 98%). Ten bark beetles would suggest colonisation rates above 99% (CI 98%, 100%).

Relationship with meteorological conditions

Temperatures fluctuated widely during the study (Supplementary Material 2). The coldest recorded temperature was -7.3 °C (at site 2), and the warmest was 21.5 °C (at site 8).

Table 1 Post-harvest observations on logs, and trap catches of flying insects between the 12 and 29 July 2015 at nine clearcut harvested sites in central North Island, New Zealand

Order family species	Log observations			Trap catches		
	<i>N</i>	Logs (<i>n</i> = 108)	Sites (<i>n</i> = 9)	<i>N</i>	Traps (<i>n</i> = 45)	Sites (<i>n</i> = 9)
Blattodea						
Blattidae	–	–	–	1	1	1
Coleoptera						
Agyrtidae						
<i>Zeanecrophilus</i> sp.	–	–	–	1	1	1
Anthribidae	–	–	–	2	2	2
Carabidae						
<i>Laemostenus complanatus</i> ^{ex}	–	–	–	19	16	5
Unidentified	0/1/0	0/1/0	0/1/0	1	1	1
Curculionidae						
<i>Catoptes binodis</i>	–	–	–	1	1	1
<i>Hylastes ater</i> ^{*, ex, ^}	0/3/7	0/1/4	0/1/2	1	1	1
Females only	0/1/4	0/1/3	0/1/2	0	0	0
<i>Hylurgus ligniperda</i> ^{*, ex, ^}	0/0/1	0/0/1	0/0/1	20	11	4
Females only	0/0/1	0/0/1	0/0/1	10	8	4
<i>Pactola variabilis</i>	–	–	–	1	1	1
<i>Xenocnema spinipes</i> [*]	2/0/5	1/0/3	1/0/3	1	1	1
Leiodidae ¹	–	–	–	1	1	1
Melandryidae	–	–	–	3	3	1
Nitidulidae						
<i>Eपुरaea zealandica</i>	–	–	–	1	1	1
Scarabaeidae						
<i>Costelytra</i> sp.	–	–	–	2	2	2
<i>Odontria</i> sp.	–	–	–	12	9	2
Staphylinidae	–	–	–	5	5	2
Orthoptera						
Anostomatidae	–	–	–	1	1	1
Total	2/4/13	1/2/6	1/2/3	73	37	9

Three series of 12 logs per site, and five traps baited with α -pinene and ethanol, were set up at each site. Numbers separated with “/” represent records on different series of logs (set up for 3, 8 or 15 days, respectively)

¹Subf. Leoninae

*Species associated with *Pinus radiata*

^{ex}Species exotic to New Zealand

[^]Species listed as a quarantine pest by at least one trading partner of New Zealand (Pawson et al. 2014)

Temperature differences between the sites were also noticeable (Supplementary Material 2). Negative temperatures were recorded in all but one site (site 4). Temperatures above the identified 12.3 °C threshold for *H. ligniperda* flight activity were recorded in all sites. The highest recorded thermal sums (i.e. for 15-day periods) ranged between 0.3 (at site 3) and 16.9 degree-hours (at site 7).

In the study region, rain events (> 1 mm rain in 24 h) occurred at night on 15–16 July, all day on 18 July, at night on 20–21 July, and intermittently between 27 and 29 July. Most of these events were short (< 1 day), and with moderate rainfall (< 10 mm). None of the logs was exposed to rain (> 0.1 mm / hour) for more than 20% of the time.

Comparisons of GLMs and GLMMs investigating the relationship between bark beetle activity and temperature variables indicated that the best models were based on only one temperature predictor, the thermal sum (*SET*). The inclusion of other temperature predictors, or rainfall, did not enhance model predictions (Supplementary Material 1).

To predict log colonisation, the GLMM (with consideration of site as a random effect) did not represent a significant improvement (Δ AIC = 1.9, P = 0.79) relative to the simpler GLM (Supplementary Material 1), which was therefore favoured (Fig. 7). This model predicted a large increase in colonisation events when logs are exposed for several hours of temperatures above the flight activity threshold.

Fig. 3 Infestation rates of female *Hylastes ater* and *Hylurgus ligniperda* bark beetles colonising *P. radiata* logs exposed for either 3, 8 or 15 days in recent clearcut harvest sites in central North Island, New Zealand. $N=108$ logs for each duration of exposure. The error bars represent the associated 95% confidence intervals as estimated from exact binomial tests

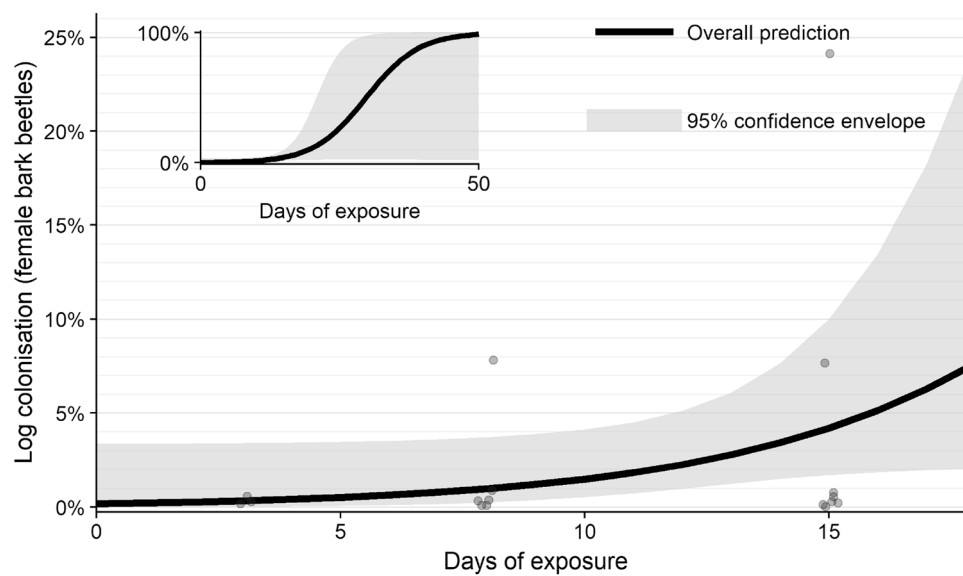
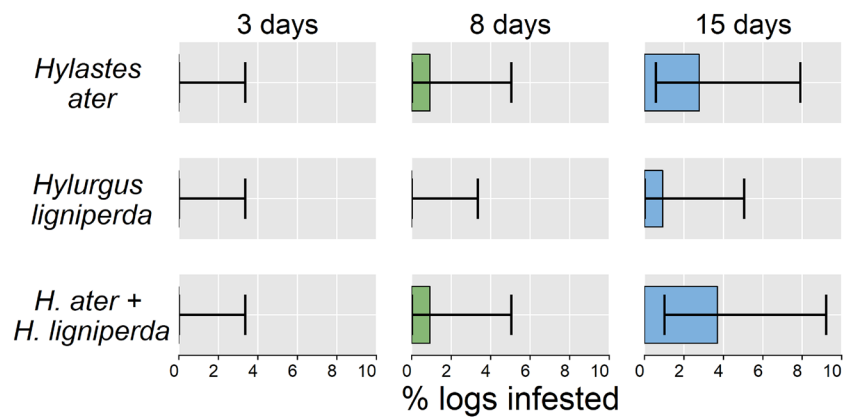


Fig. 4 Generalised linear model prediction of *P. radiata* log colonisation by female *Hylastes ater* and *Hylurgus ligniperda* as a function of exposure time in recent clearcut harvest sites. The model was fitted to the proportion of logs colonised across nine harvest sites, for each period of exposure (3, 8 or 15 days). $N=81$ (binomial responses out of 12 logs). Prediction function: $\text{logit}(y) = -6.32 + 0.213 \times (\text{inter}$

$\text{cept SE} = 1.51$; intercept 95% CI = $-13.1, -4.0$; linear coefficient $\text{SE} = 0.112$; linear coefficient 95% CI = $0.022, 0.666$). A small amount of jittering has been applied to the data points in order to make overlapping records more visible. The inset provides predictions over a 50-day period

For example, thermal sum requirements of 10, 20 and 30 degree-hours are predicted to result in colonisation levels of 5%, 50% and 95%, respectively.

To predict trap catch numbers, the best GLMM (with negative binomial error structure) provided a much better fit than its GLM counterpart ($\Delta\text{AIC} = 17.3$, $P = 1.1 \times 10^{-5}$). This model predicted an exponential increase of the number of bark beetles captured, with increasing thermal sums (Supplementary Material 1). Thermal sums of 10, 20 and 30 degree-hours, for instance, correspond to average trap catches of 0.1, 1.2 and 14.0 bark beetles per trap, respectively. The inclusion of a zero-inflated component did not improve any of the models.

Discussion

Forestry pests colonising pine logs in winter

Eight insect species potentially associated with *P. radiata* log material from New Zealand are classed as quarantine pests by one or more trading partners: *Arhopalus ferus*, *Platypus apicalis* White (Coleoptera: Curculionidae), *P. gracilis* Broun, *Hylurgus ligniperda*, *Hylastes ater*, *Mitrastethus baridioides* Redtenbacher (Coleoptera: Curculionidae), *Oemona hirta* (F.) (Coleoptera: Cerambycidae), and *Sirex noctilio* (Pawson et al. 2014). However, most of these species have no adult activity during winter

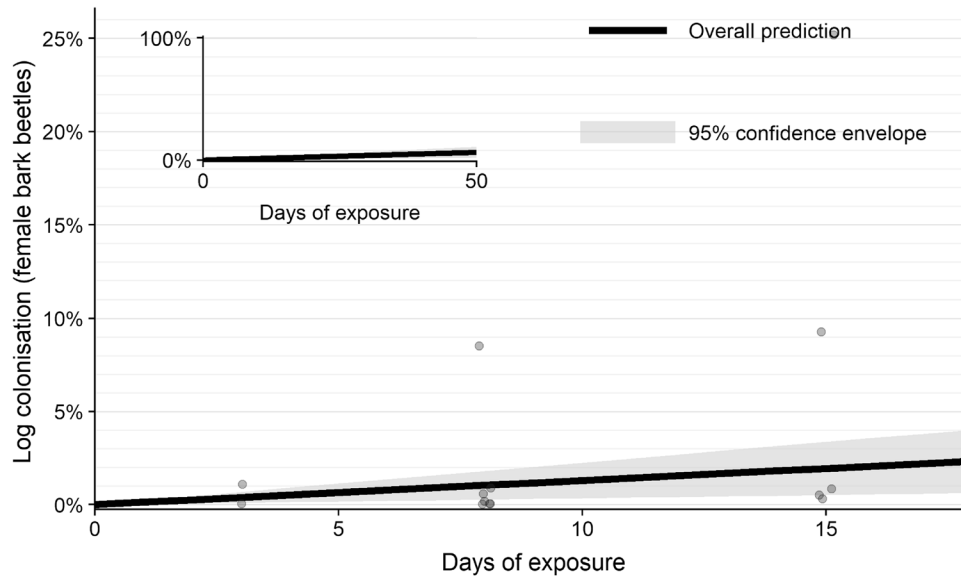


Fig. 5 Nonlinear mixed model predictions of *P. radiata* log colonisation by female *Hylastes ater* and *Hylurgus ligniperda* as a function of exposure time in recent clearcut harvest sites. The model was fitted to the proportion of logs colonised across nine harvest sites, for each duration of exposure (3, 8 or 15 days). $N=27$ (%

colonisation calculated out of 12 logs). Overall prediction function: $y = 1 - (1 - \text{DailyProb})^x$, where $\text{DailyProb} = 1.31e^{-3}$ ($SE = 4.94e^{-4}$; $95\% \text{ CI} = 0.29e^{-4}, 2.32e^{-3}$). A small amount of horizontal jitter has been applied to the X -axis in order to make overlapping records more visible. The inset provides predictions over a 50-day period

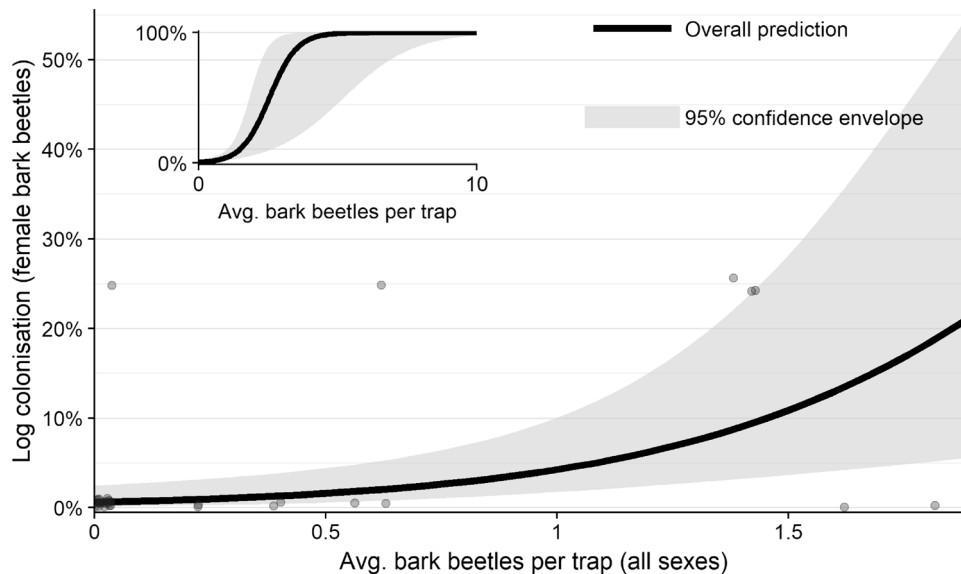


Fig. 6 Generalised linear model predictions of *P. radiata* log colonisation by female *Hylastes ater* and *Hylurgus ligniperda* as a function of bark beetle catch (all sexes) in traps. The model was fitted to the proportion of logs colonised across nine harvest sites, for each period of exposure (3, 8 or 15 days). $N=81$ (binomial responses out of 4 logs). Prediction function: $\text{logit}(y) = -5.13 + 0.404 \times (\text{inter-}$

$\text{cept } SE = 0.74$; intercept $95\% \text{ CI} = -6.58, -3.68$; linear coefficient $SE = 0.126$; linear coefficient $95\% \text{ CI} = 0.157, 0.651$). A small amount of jittering has been applied to the data points in order to make overlapping records more visible. The inset provides predictions over a 50-day

(Pawson et al. 2021) or are infrequently associated with *P. radiata* as a host, e.g. *O. hirta*.

Our results show that the rate of colonisation by *H. ater* and *H. ligniperda* in New Zealand's CNI in winter is positively correlated with insect flight activity and strongly

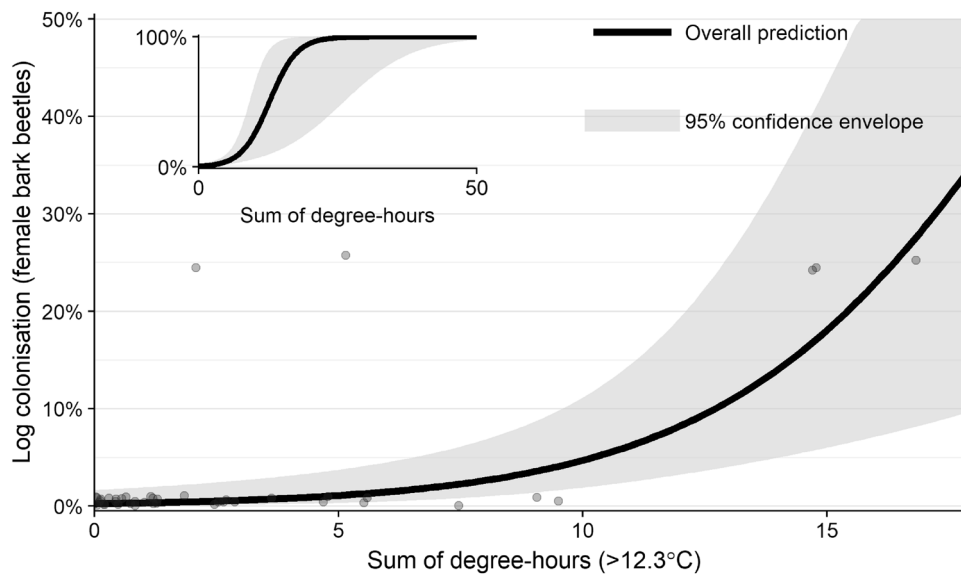


Fig. 7 Generalised linear model predictions of *P. radiata* log colonisation by female *Hylastes ater* and *Hylurgus ligniperda* as a function of a sum of degree-days above the flight temperature threshold. The model was fitted to the proportion of logs colonised across nine harvest sites, for each period of exposure (3, 8 or 15 days). Prediction function: $\text{logit}(y) = -6.01 + 0.300 \times (\text{intercept SE} = 0.98; \text{intercept}$

$95\% \text{ CI} = -7.92, -4.10; \text{linear coefficient SE} = 0.084; \text{linear coefficient } 95\% \text{ CI} = 0.134, 0.466). N = 81$ (binomial responses out of 4 logs). A small amount of horizontal jitter has been applied to the data points on the x -axis in order to make overlapping records more visible. The inset provides predictions over a 50-day period

influenced by prevailing meteorological conditions, particularly temperature. Periods with temperature conditions like those observed in our study regularly occur in winter in CNL as well as in other regions throughout New Zealand (Supplementary Material 3).

In addition to the widespread exotic bark beetles *H. ater* and *H. ligniperda*, our study also identified pine log colonisation in winter by *X. spinipes*. Although we found this species in both the traps and logs, the *X. spinipes* is scarcely documented in the scientific literature. Records from the New Zealand Forest Health Database (FHDB 2018) indicate that *X. spinipes* can occasionally be associated with mature, recently harvested *P. radiata* logs, but is far less common than *H. ligniperda* or *H. ater*.

Log colonisation as a function of duration of exposure

In our winter study period, we observed colonisation of freshly cut logs by bark beetles at a rate of $\sim 0.2\%$ per day (for a 40-cm-long *P. radiata* log). After 15 days of exposure in the forest, 3% and 1% of the logs were colonised by *H. ater* and *H. ligniperda*, respectively (4% for both species). Our data were collected across nine harvest sites for one winter season (July 2015), and although the study accounted for a total of 2808 log exposure days, colonisation occurred on less than 3% of the 324 logs in two of the nine sites. The result was that a clear site effect could not be

identified because of the small proportion of logs that were colonised. Greater understanding of the potential for site effects, e.g. landscape context, would be a high priority for future research. Nevertheless, when considering both bark beetle species, 1% to 9% log colonisation can be expected after 15 days (Supplementary Table 2). The phenomenological (GLM) and mechanical (nonlinear model) models fitted to the colonisation data provided similar estimates within the range of exposure times tested (i.e. 3 to 15 days); however, long-term predictions differed significantly between models. The GLM predicted an exponential increase in log colonisation rates (associated with a large uncertainty), while the nonlinear model predicted a linear increase even over a long period (< 50 days).

Mechanism of log colonisation

In the absence of a long-range aggregation pheromone, we do not expect a rapid increase in the rate of log colonisation for either *H. ater* or *H. ligniperda*. Hence, the mechanistic (model nonparametric) should be favoured. Our preferred model predicts about 0.9% of the logs would be colonised after 7 days and 3.6% after 28 days. This is assuming a relatively constant colonisation rate, which is an unlikely scenario over longer periods due to changing meteorological conditions.

Bark beetle activity and primary attraction to pine logs vary over time due to seasonal variations in insect

abundance, actual meteorological conditions and temperature regimes (Crowhurst 1969; Tribe 1991a; Mausel et al. 2007). Furthermore, in operational harvest conditions, logs are stacked in decks and those that are not in ground contact are less likely to be colonised by bark beetles (Mausel et al. 2007). Our results, from individual logs in direct contact to the ground, are thus conservative, and the true colonisation rate for logs in decks is likely to be less than we observed.

Phloem degradation and/or boring activity by the initially established beetles (i.e. autoxidation, Borden et al. 1986) may also elicit increased attraction over time in some circumstances (Tunset et al. 1993). Nonetheless, in a plantation forest setting, the primary attraction of bark beetles towards recently harvested logs is influenced by “competing” odour responses to volatiles emitted by standing trees and other dead pine wood material. The volatiles communally define a unique olfactory landscape that may affect the colonisation patterns of harvested logs by bark beetles.

Relationship between log colonisation and trap catches

There is little published information that simultaneously quantifies pine bark beetle colonisation of logs (or stumps) and trap catches. Mausel et al. (2007) provided a description of coincident log colonisations and trap records for *H. ater* and *H. ligniperda* in Chile. Their observations, performed in spring, nonetheless do not quantify the relationship that would relate the risk of log infestation to trap catches.

We described this relationship for *P. radiata* plantations in New Zealand in winter conditions. Trap catches provide a potential indicator of log establishment because bark beetle response to traps and logs is thought to be influenced by the same factors, notably their local abundance and activity (Raffa et al. 2016). In similar meteorological conditions, the semiochemical blends released by traps and logs are similar and the olfactory landscape that may “dilute” the insect responses to these olfactory cues (see above, Mechanism of log colonisation) is the same. Both catch and establishment counts also conveniently integrate the temporal dimension whereby the establishment of a functional relationship does not require explicit consideration of time.

Relative population estimates, such as trap catches, are known to be useful in work on species distributions or to monitor changes in activity (Southwood and Henderson 2009). Our study demonstrated the simplicity of implementing a system to monitor trap catch as an indicator of potential colonisation. In particular, trap catches do not require the consideration of several factors that may influence the colonisation of log material by bark beetles. These factors can relate to the beetle’s

activity (actual population sizes, life stages composition), their interactions with the logs (behavioural “phases,” responses to visual or chemical stimuli) and the environment (meteorological factors, visual and olfactory landscape).

In our study, counts of both males and females of the two species provided the best prediction, demonstrating that quick field estimates of colonisation can be made without the need to discriminate between species or sexes. Sex determination of *H. ligniperda* collected at time of emergence or captured in traps suggests that adults have an approximately even sex ratio (Meurisse and Pawson 2017). Although the sex ratio of *H. ater* adults is unknown in field conditions, there is no evidence to indicate it might be different than *H. ligniperda*. Species in both genera share similar life-history traits as saprophytes of conifer woody debris, in which adults are characterised by outbreeding and a monogynous mating system (Kirkendall et al. 2015).

The capture of one individual bark beetle in a trap (on average) was indicative of a mean log colonisation rate of 4% for the same period (95% CI 1.7%, 10%). Our model also provided estimates for larger trap catches, for instance the capture of three beetles corresponds to a mean 72% log colonisation (CI 14%, 98%), and the capture of ten or more beetles corresponds to a probability that mean log colonisation is above 99% (CI 98%, 100%).

However, these predictions must be considered with caution because they fall well beyond the catch rates and colonisation percentiles recorded during this study. Bark beetle catches in winter generally consist of a few individuals per trap over periods of several weeks. Pawson et al. (2021) used similar traps to monitor *H. ater* and *H. ligniperda* in New Zealand young *P. radiata* plantations between 2013 and 2016. In the CNI, average monthly captures were at their lowest from mid-winter to early summer (July–December) for *H. ater*, and in early winter (June–July) for *H. ligniperda*. During these months, capture rates never exceeded three individuals per trap. Similar rates have been observed for most other forest regions but were higher in parts of the South Island for *H. ater* (> 10 beetles per trap per month from July to December in Nelson, and the West Coast), and in parts of the North Island for *H. ligniperda* (> 10 beetles per trap per month in June–July in Northland, East Cape, Hawke’s Bay). *Hylurgus ligniperda* is also generally less abundant in parts of the South Island (West Coast and Southland/Otago) where its average capture rate in June–July was < 0.5 beetles per trap. Importantly, trap catch during these periods was strongly influenced by maximum temperature and the daily probability of flight varied considerably and most activity occurred on only a few days per month (Pawson et al. 2021).

Relationship between temperature and log colonisation by *Hylastes ater* and *Hylurgus ligniperda*

Temperature is regarded as the key driver of forest insect larval development in *P. radiata* plantations (Logan and Barington 2015). Other factors, such as the length of day, relative humidity or wind speed, are also known to affect adult emergence and flight activity (Pawson et al. 2017). We found that during winter in New Zealand, temperature expressed as the thermal sum of temperatures above a 12.3 °C threshold was a suitable predictor of log colonisation risk at sites occupied by *H. ater* and *H. ligniperda* (i.e. most *P. radiata* plantations in New Zealand). Notably, the accumulation of more than 10 degree-hours was almost always associated with some level of flight activity and subsequent log colonisation, and according to model predictions, a thermal sum of 35 degree-hours or more indicated a very high probability of log colonisation.

In New Zealand, Meurisse and Pawson (2017) reported *H. ligniperda* flying during relatively cold days in autumn (air temperature of 13 to 15 °C), which confirmed earlier observations made in France in early spring (Fabre and Carle 1975). Although Pawson et al. (2017) observed activity peaks for both *H. ater* and *H. ligniperda* between 17 and 18 °C during spring and summer trapping in New Zealand, activity at lower temperatures was also recorded.

Winter activity of *Hylastes ater* and *Hylurgus ligniperda*

Hylastes ater was most frequently observed colonising *P. radiata* logs, and *H. ligniperda* was the most common species found in kairomone-baited traps. The phenology of *H. ater* and *H. ligniperda* in exotic plantation forests in New Zealand is relatively well known based primarily on trap catch records (Reay and Walsh 2001; Brockerhoff et al. 2006a; Kerr et al. 2016; Chase et al. 2017), but also by investigations of attack symptoms on trap logs (Crowhurst 1969), or on seedlings (Sopow et al. 2015) or stressed trees (Be et al. 2017). However, most of the cited studies focussed on periods of known activity and did not evaluate winter activity (except Crowhurst 1969). Recently, a comprehensive trapping survey that was performed over 3.5 years in eight regions in New Zealand (Pawson et al. 2021) confirmed that the seasonality of flight activity for *H. ater* and *H. ligniperda* varied around the country. *Hylastes ater* is usually characterised by a unimodal flight activity peak in autumn (while spring peaks are observed in some parts of the South Island). *Hylurgus ligniperda* is usually characterised by bimodal flight activity peaks in spring and summer/autumn (except a unimodal spring/summer peak pattern in the West Coast of the South Island); however, evidence of three periods exists

in some regions (Pawson et al. 2021). Both *H. ater* and *H. ligniperda* were observed flying during the colder months, but the probability of flight is negligible compared to peak activity periods (Pawson et al. 2021).

No study on the seasonal colonisation of cut logs is available in New Zealand for *H. ligniperda*, where it was discovered in 1974 (Bain 1977). Previously, Crowhurst (1969) made a qualitative description of seasonal pine log colonisation by *H. ater*; however, no quantitative results were provided and the results were replicated in only one region in the South Island (Canterbury). Crowhurst (1969) found that freshly cut *P. radiata* logs were attractive to *H. ater* whenever the adults were flying and adults were observed to arrive almost immediately on logs cut in July and in August. The arrival of *H. ater* adults continued for up to 25 weeks after the first beetles arrived (Crowhurst 1969). Crowhurst (1969) also described *H. ater* adults invading logs from the cut end first, in preference to boring through the bark, and he observed that the boring adults were females which, in the winter months (July–August), started to lay eggs 4–9 weeks after the initial invasion. In contrast, our observations in the CNI found colonisation at cut parts, at branch insertions and into plain bark (for both *H. ater* and *H. ligniperda*) and we observed roughly equal numbers of males and females boring into logs, but no eggs (< 4 weeks after field exposure).

Comparisons with other countries

In pine plantations in Araucanía, Chile, Mausel et al. (2007) observed peak trap catches of *H. ater* and *H. ligniperda* in spring/early summer and (or) autumn, with reduced catch of both species in winter. The same authors observed active colonisation of 2m-long *P. radiata* logs in spring, peaking in November for *H. ater* (about 2–100 individuals per log), and in October for *H. ligniperda* (about 20–200 individuals per log). Although Mausel et al. (2007) only investigated log colonisation patterns in spring (September–November), their records indicate that, at the onset of the spring period, *Hylastes ater* adults had only colonised one or two logs of a 6-log sample, whereas *H. ligniperda* had colonised most, if not all, of the exposed logs. Most colonisation by *H. ater* occurred with a delay after the peak flight period was observed, which relates to the fact that the adult beetles of this species perform maturation feeding on stems of seedlings before colonising and ovipositing in dead wood material (Sopow et al. 2015). Nonetheless, the authors hypothesise that winter colonisation by both *H. ater* and *H. ligniperda* is probable in the warmest regions of Chile. Temperature conditions in early spring in the Chilean study (31 August–14 September, daily maximum average: 12 °C) were colder than those recorded in winter in our New Zealand study (12–29 July: 15 °C).

In the Western Cape Province of South Africa, Tribe (1991b) exposed a series of 1m-long logs at two sites over a period of five years to investigate the seasonal colonisation of *P. radiata* logs by *H. ligniperda*. They observed variable colonisation rates between sites and large variation between both years and between weeks within a year. For the winter months of July and August, about 15% of the logs exposed over 2-week periods were colonised at one site (six out of 40 logs, from graph inspection), and 77.5% of the logs at another site (31 out of 40 logs). Tribe (1991b) attributed winter colonisation rates to the site level abundance of *H. ligniperda* each year with seasonal meteorological conditions likely to affect colonisation success. However, the winter conditions in South Africa differ from New Zealand where average weekly temperatures never dropped below 8 °C (over a period of 5 years) compared to 6 °C during our 17-day study period (Supplementary Material 2).

Earlier studies in south-eastern France by Fabre and Carle (1975) reported peak periods of *H. ligniperda* activity from late winter to early summer, and again from late summer to late autumn. Reduced log colonisation was observed in winter (December–February in the Northern Hemisphere) (Fabre and Carle 1975). Nonetheless, in all countries the colonisation of pine logs by *H. ligniperda* was shown to be strongly affected by meteorological and other environmental conditions, with large variations within and between years, and between locations (Fabre and Carle 1975; Tribe 1991b; Mausel et al. 2007).

Systems approaches

Insect pests breeding in the phloem of recently cut conifers, especially invasive pine bark beetles in the genera *Orthotomicus*, *Hylastes* and *Hylurgus*, are among the most abundant and common species in pine forests worldwide (Brockerhoff et al. 2006a; Miller and Rabaglia 2009; Faccoli et al. 2020). They are also easily transported on trade routes, especially when bark is still present on timber and wood packaging material (Brockerhoff et al. 2006b; Haack 2006; Meurisse et al. 2018).

Some of these species such as *H. ater* and *H. ligniperda* are still on the phytosanitary regulated lists for some countries, and as available chemical-based treatments become increasingly regulated, the need for alternative, but often costlier, options become critical (Pawson et al. 2014; Najar-Rodriguez et al. 2020). Systems approach, as “a pest risk management option that integrates different measures, at least two of which act independently, with cumulative effect” (IPPC 2002), represents a good option for pest risk reduction in situations where pesticide options are limited. They also minimise the transportation risk for a range of pests as opposed to a single target (Allen et al. 2017).

For the export of logs from production forests for instance, measures used in a systems approach may be applied pre- and/or post-harvest, either at the place of production or at any point during the transport and distribution of the logs. The rapid removal of harvested logs from forests comes as one of the first recommendations as part of a systems approach to manage the potential phytosanitary risks presented by bark beetles and other pests (Lanfranco et al. 2004). For pine logs harvested in winter in New Zealand CNI, our nonlinear model shows removal of logs after 24 and 48 h reduces the colonisation risk to 0.13 and 0.16%, respectively. Improving our ability to forecast seasonal post-harvest log colonisation risk also supports additional risk reduction objectives applied against successive production stages (Van Klinken et al. 2020). First, the ability to distinguish low and high pest prevalence periods can allow harvesting to be scheduled at times that minimise exposure to pests. Recommendations may include targeted harvesting in areas and periods of low bark beetle prevalence and activity (e.g. by establishing and declaring an ALPP), possibly associated with the development of risk reduction methods associated with log storage (e.g. decking logs in less exposed areas, stacking or treating them in a way that reduce the possibility for colonisation, or removing them quickly out of the forest). Second, predictions of log colonisation probabilities, for instance based on monitoring of temperature or insect activity (e.g. using traps), allow selection of measures to manage the infestation rate of selected consignments. Such measures could include the segregation of at-risk log stocks for treatment application to importing country or market’s phytosanitary requirements (MPI 2019c), or alternatively to be diverted for local processing without treatment. Eventually, a combination of proactive measures taken to minimise exposure with reactive measures to manage more heavily colonised wood consignments could provide the basis for the implementation of a systems approach guaranteeing an appropriate level of protection for log exports.

Conclusion

To support alternative risk-based approaches to phytosanitary measures, i.e. an ALPP, our results show that *P. radiata* logs should be removed from the forest within 24 to 48 h after harvest during winter. This is consistent with Lanfranco et al. (2004) who advocated for rapid log removal from high-risk zones, such as harvest areas in Chile. Reducing exposure risk by minimising the time between harvest and transportation from the forest should be implemented as best practice by the forest industry to reduce the potential phytosanitary risks associated with the global trade of wood products. Such practices also enhance product quality by reducing timber degradation by bark- and wood-boring

insects. During winter months, additional economic benefits may accrue from avoided phytosanitary treatment costs when it can be shown that the phytosanitary risk does not exceed the acceptable pest limit of a trading partner. This assurance can be provided by the predictive models we demonstrated in our study with ongoing validation by site specific trapping during winter harvesting. The implementation of risk-based phytosanitary measures will require further work to understand the log colonisation risk throughout the entire supply chain, e.g. transitional facilities and ports (Pawson et al. 2020), the potential effects of log size (as we used log sections in this study) and the interannual variation in log colonisation risk. We showed that, in winter, a simple model of temperature sums can be used to predict the rate of colonisation of logs by bark beetles in recently harvested sites. However, greater understanding of meteorological determinants of flight risk (begun by Pawson et al. 2017) could lead to the use of meteorological forecasts as a simple management tool to predict bark beetle activity, and hence colonisation risk, over time and at large spatial scales.

Author contributions

NM and SP conceived and organised the experimental work. CS and NM performed the statistical analysis and prepared figures. NM prepared tables. NM wrote the initial manuscript draft with contributions from SP and CS. All authors reviewed and approved the manuscript.

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Availability of data and material The data generated or analysed during this study are included in summarised form in this published article and its supplementary information files. The completed datasets generated during the current study are available from the corresponding author on reasonable request.

Code availability The R code used for analyses and to generate some of the figures presented in this published article and its supplementary information files is available from the corresponding author on reasonable request.

Declarations

Conflict of interest Authors declare that they have no conflict of interests or competing interests.

Ethics approval This article does not contain any studies with human participants or vertebrates performed by any of the authors.

Consent to participate This article does not contain any studies with human participants performed by any of the authors.

Consent for publication This article does not contain any studies with human participants performed by any of the authors.

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