

Long-distance dispersal of non-native pine bark beetles from host resources

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Abstract. 1. Dispersal and host detection are behaviours promoting the spread of invading populations in a landscape matrix. In fragmented landscapes, the spatial arrangement of habitat structure affects the dispersal success of organisms.

2. The aim of the present study was to determine the long distance dispersal capabilities of two non-native pine bark beetles (*Hylurgus ligniperda* and *Hylastes ater*) in a modified and fragmented landscape with non-native pine trees. The role of pine density in relation to the abundance of dispersing beetles was also investigated.

3. This study took place in the Southern Alps, New Zealand. A network of insect panel traps was installed in remote valleys at known distances from pine resources (plantations or windbreaks). Beetle abundance was compared with spatially weighted estimates of nearby pine plantations and pine windbreaks.

4. Both beetles were found ≥ 25 km from the nearest host patch, indicating strong dispersal and host detection capabilities. Small pine patches appear to serve as stepping stones, promoting spread through the landscape. *Hylurgus ligniperda* (F.) abundance had a strong inverse association with pine plantations and windbreaks, whereas *H. ater* abundance was not correlated with distance to pine plantations but positively correlated with distance to pine windbreaks, probably reflecting differences in biology and niche preferences. Host availability and dispersed beetle abundance are the proposed limiting factors impeding the spread of these beetles.

5. These mechanistic insights into the spread and persistence of *H. ater* and *H. ligniperda* in a fragmented landscape provide ecologists and land managers with a better understanding of factors leading to successful invasion events, particularly in relation to the importance of long-distance dispersal ability and the distribution and size of host patches.

Key words. Biological invasions, Coleoptera: Scolytinae, exotic bark beetles, inverse distance weighting.

Introduction

Which traits make wood and bark-boring beetles one of the most successful groups of biological invaders? In addition to high propagule pressure (Brockerhoff *et al.*, 2014), good

dispersal ability, effective host detection, and the availability of host resources are also clearly associated with colonisation success (Byers, 1996; Skarpaas & Økland, 2009). One group of successful colonisers are bark and ambrosia beetles, which can accidentally be transported in logs shipped overseas or in wooden pallets, crates, and dunnage (Brockerhoff *et al.*, 2006a; Piel *et al.*, 2008; Liebhold *et al.*, 2012). After transport, emerging populations may establish, potentially causing major ecological and economic damage (e.g. *Ips grandicollis* Eichhoff, *Dendroctonus valens* LeConte, and *Xyleborus glabratus*

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Eichhoff) (Morgan, 1967; Yin, 2000; Rabaglia *et al.*, 2006). In total, 8286 interceptions of Scolytinae were recorded by port inspectors from 1984 to 2008 in the United States and more than 1500 in New Zealand from 1950 to 2000 (Brockerhoff *et al.*, 2006a; Haack *et al.*, 2014). After establishment, populations may subsequently expand their range into regions with a suitable habitat; this spread occurs as a combined result of both population growth and dispersal (Skellam, 1951; Williamson, 1996; Liebhold & Tobin, 2008).

While the majority of spreading insect individuals typically disperse relatively short distances, a small fraction may disperse very long distances, passively (e.g. anthropogenic transport), actively (e.g. flying), or semi-passively (e.g. an actively flying insect carried by the wind), to novel habitat locations (Coulson, 1979; Shigesada *et al.*, 1995; Suarez *et al.*, 2001; Liebhold & Tobin, 2008). The consequences of such a 'fat-tailed' dispersal kernel can include increased rates of range expansion, dampened inbreeding depression, escape from predators and parasitoids, and reduced intra-specific competition (Dytham, 2009). Risks and costs associated with long-distance dispersal include arrival at locations with a low-quality habitat (or unsuitable habitat) or dispersal beyond the climatic limit of the species (Dytham, 2009; Bonte *et al.*, 2012). Additionally, low numbers of colonising propagules are subject to Allee effects (inverse density dependence), potentially resulting in establishment failure and a slower spread (Kot *et al.*, 1996; Keitt *et al.*, 2001; Taylor & Hastings, 2005; Kanarek *et al.*, 2014).

The ability of a dispersing organism to detect a suitable host and reproduce is a critical component of successful establishment (Moeck *et al.*, 1981). Bark beetles can be attracted to host tree volatiles such as alcohols and terpenes (Person, 1931; Moeck *et al.*, 1981; Borden, 1989; Miller, 2006). Trees that are physiologically stressed or mechanically wounded can attract the first colonising bark beetles (Raffa & Berryman, 1983; Phillips *et al.*, 1988; Wallin & Raffa, 2000, 2002; Pureswaran *et al.*, 2004). In some bark beetle species, pioneer beetles produce aggregation pheromones that attract conspecifics, sometimes causing mass-aggregation on hosts that allow the beetles to overcome host defenses (Wood, 1982; Raffa & Berryman, 1983). At close range, visual cues may also become important in host detection by colonising bark beetles (Hynum & Berryman, 1980; Wood, 1982; Saint-Germain *et al.*, 2007).

The goal of the present study was to determine how far invading bark beetles disperse from host resources, to improve our understanding of dispersal dynamics during biological invasions. Specifically, we investigated long-distance dispersal and the abundance of two non-native bark beetles in relation to host plant density in remote regions of New Zealand at varying distances from pine plantations and pine windbreaks (also called shelterbelts) across diverse landscapes. We also related abundance to spatially weighted estimates of pine density.

Methods and material

Study system

Hylastes ater Payk. and *Hylurgus ligniperda* F., both native to Eurasia, are two of the world's most successful bark beetle

colonisers and have established in many southern hemisphere countries with pine plantations, including South Africa, Chile, Argentina, Australia, and New Zealand (Brockerhoff *et al.*, 2006a). Although neither species kills living trees, as they are saprophytic (dead wood infesting) insects, both species are facilitators of timber-degrading ophiostomatoid fungi in the genera *Ophiostoma* and *Leptographium* (McCarthy *et al.*, 2013). *Hylastes ater* was detected in New Zealand in 1929 (Clark, 1932) and *H. ligniperda* in 1974 (Bain, 1977). Since their introduction, both species have spread to most pine plantations throughout both the North and South Islands of New Zealand.

In New Zealand, there are no native species in the family Pinaceae; however, many species have been introduced for ornamental and timber production purposes and 18 species have become naturalised (Webb *et al.*, 1988). Non-native plantation forests (including *Pinus* spp. and Douglas fir *Pseudotsuga menziesii*) cover ~1.7 Mha and are a major component of the New Zealand economy (NZFOA, 2014). Unfortunately, wilding pine and Douglas fir trees have become important invaders in New Zealand covering at least 500 000 ha in the South Island alone (Ledgard, 2001; Gous *et al.*, 2014). Many wilding conifer stands are young and vigorous with little dead wood and thus should not currently provide suitable host material for *H. ater* and *H. ligniperda* to breed in. However, as these stands mature or trees are killed to limit the spread of wilding conifers, the stands could provide suitable bark beetle host material.

Trapping network

To sample dispersing *H. ater* and *H. ligniperda*, we deployed 169 traps across 12 study areas (11 areas in the Southern Alps and one area on Stewart Island) and 10 control (possible beetle-source) areas (five pine plantations, two wilding pine areas, and three pine windbreaks) throughout the South Island of New Zealand from October 2012 to March 2013 (Fig. 1, Table 1). Study areas were selected to vary in distance and isolation from operational pine plantations, including several areas located in remote valleys vegetated by grasslands and surrounded by mountains with native vegetation and no pines. In all study areas, the dominant vegetation type was recorded (obtained from the Landcare LRIS portal, Land Cover Database v4.0 [Informatics Team Landcare Research, 2015]) within each valley (Table 1).

Traps consisted of black panel insect traps (Kerr *et al.*, 2016) baited with the host (*Pinus* spp.) primary attractants α -pinene (release rate of *c.* 0.76 g day⁻¹) and ethanol (release rate of *c.* 0.02 g day⁻¹) (Kerr *et al.*, 2016) that are known to attract both *H. ater* and *H. ligniperda* (Reay & Walsh, 2002; Petrice *et al.*, 2004; Brockerhoff *et al.*, 2006b; Costa *et al.*, 2013). Currently, no secondary attractants (i.e. sex pheromones) are known from either species of bark beetle (Perttunen, 1957; Petrice *et al.*, 2004; Brockerhoff *et al.*, 2006b). Lures consisted of attractant baits with 150 ml of each attractant in separate, sealed polyethylene bags. All panel traps were hung from metal fence posts (~1.5 m tall) deployed in pairs separated by ~0.5 km and located along transects with at least 3 km between trap pairs (mapped using a handheld GPS). The length of each transect and

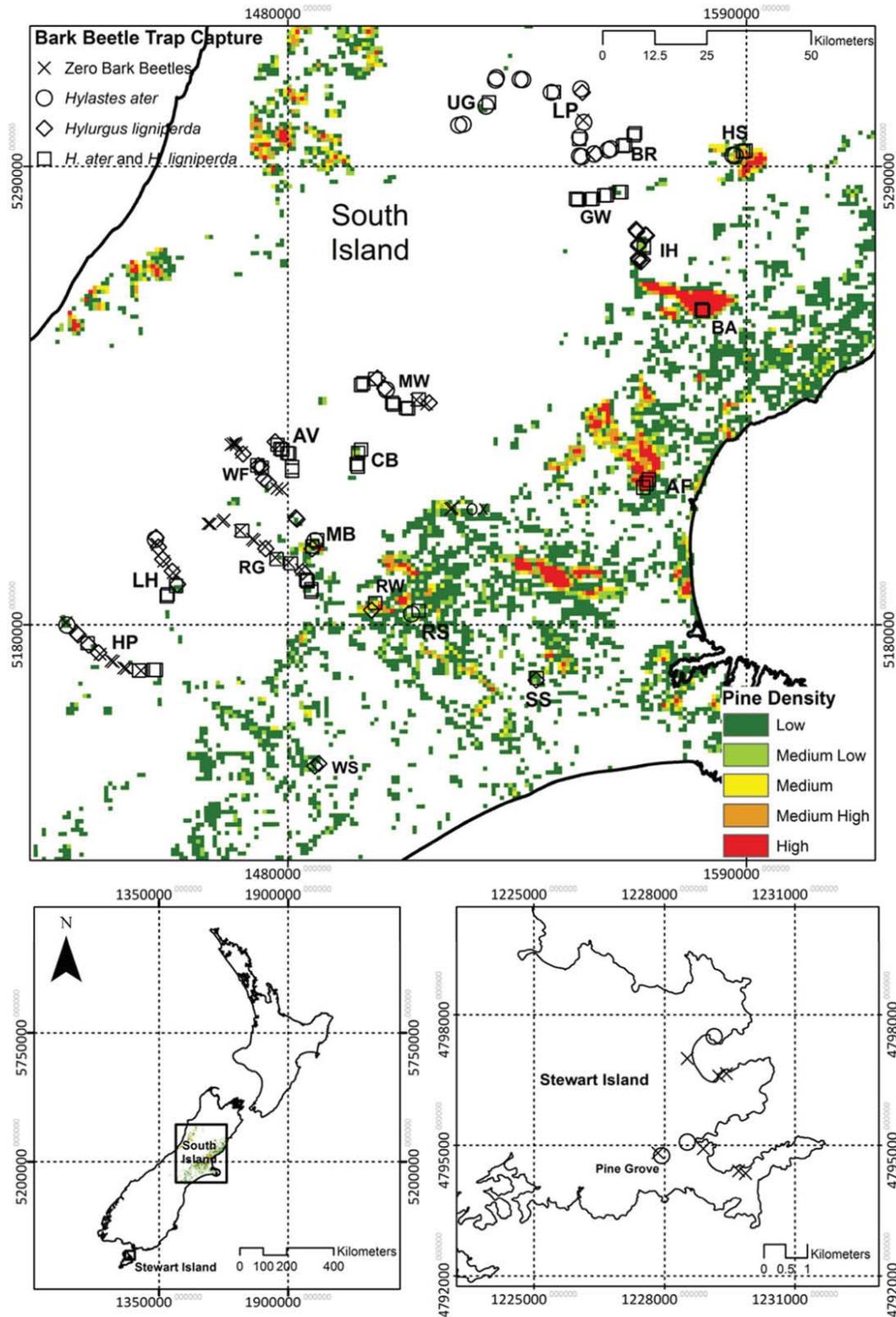


Fig. 1. Location of the 156 traps in the Southern Alps and 10 traps in Stewart Island, and local density of pines derived from the Landcare LRIS portal, Land Cover Database v4.0. Refer to Table 1 for categorisation of study and control sites and for codes to site names. Pine density represents the following % cell coverage: low = 0.1–17; medium low = >17–36; medium = >36–57; medium high = >57–81; high = >81–100. White pixels on land represent zero pine density. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 1. Site characteristics and trapping results across South Island and Stewart Island, New Zealand.

Site	Vegetation type	# Traps	Trapping period (month/year)	# Trap days	Nearest pine plantation (~km)*	<i>Hylurgus ligniperda</i> /trap/week	<i>Hylastes ater</i> / trap/week
Ashley forest (AF) [†]	Exotic Forest	3	10/13–4/14	188	0	75.05	2.45
Balmoral forest (BF) [†]	Exotic Forest	2	10/13–4/14	149	0	3.68	0.43
Rockwood forest (RW) [†]	Exotic Forest	2	10/13–1/14	181	0	3.17	0.02
Hanmer Springs forest (HS) [†]	Exotic Forest	4	11/13–4/14	144	0	0.72	0.57
Oxford forest (OX) [†]	Exotic Forest	2	10/13–4/14	181	0	0.00	0.00
Selwyn windbreak (SS) [†]	Exotic Forest, exotic grassland	2	10/13–4/14	181	23	0.40	0.04
Westerfield windbreak (WS) [†]	Exotic Forest, exotic grassland	2	10/13–4/14	181	27	0.04	0.00
Rockwood windbreak (RS) [†]	Exotic Forest, exotic grassland	2	10/13–4/14	181	2	0.02	0.04
Cragieburn wilding pine (CB) [‡]	Exotic Forest, exotic grassland	4	9/13–4/14	202	1	0.77	0.75
Mt. Barker wilding pine (MB) [‡]	Exotic Forest, exotic grassland	4	9/13–4/14	218	16	0.16	0.05
Island Hills (IH) [‡]	Exotic grassland, exotic forest, kanuka and manuka forest	12	11/13–2/14	103	0	7.15	0.05
Mt. White (MW) [‡]	Exotic grassland and grey scrub	14	9/13–4/14	202	13	0.29	0.74
Glynn Wye (GW) [‡]	Exotic grassland and exotic forest	8	11/13–3/14	144	15	0.47	0.54
Avoca river (AV) [‡]	Exotic and tussock grassland, grey scrub	10	9/13–4/14	218	18	0.20	0.07
Wilberforce river (AV) [‡]	Exotic grassland and grey scrub	14	9/13–4/14	218	22	0.0005	0.00
Rakaia river (RG) [‡]	Exotic grassland	20	9/13–4/14	188	24	0.09	0.06
Boyle river (BR) [‡]	Exotic grassland	10	11/13–3/14	134	25	0.2	0.27
Upper Grey (UG) [‡]	Indigenous forest and exotic grassland	6	12/13–3/14	106	29	0.03	5.66
Haketere (HP) [‡]	Exotic and tussock grassland	16	11/13–4/14	132	33	0.07	0.08
Lake Heron (LH) [‡]	Herbaceous freshwater vegetation, grey scrub and exotic grassland	12	9/13–4/14	199	34	0.18	0.03
Lewis Pass (LP) [‡]	Exotic grassland	10	12/13–3/14	132	40	0.03	0.2
Stewart Island [‡]	Indigenous forest and broadleaved indigenous hardwoods	10	1/14–4/14	89	40	0.00	0.09

Two letter codes can be used to identify sites in Fig. 1.

*Straight line distance from nearest operational pine plantation to center of transect.

[†]Control site.

[‡]Study site

number of trap pairs varied with the length of the study area. Each pine windbreak area ($N = 3$) contained one pair of traps, and both wilding pine areas contained two pairs of traps.

The number of traps placed in *Pinus radiata* pine plantations varied from two to four. Traps placed in Ashley Forest (a pine plantation) were part of a national forest insect survey programme (S. M. Pawson, unpublished). The two traps from the Oxford Forest plantation were not included in the analysis because they were filled with pine needles at every trap check, which prevented bark beetles from entering and/or allowed them to escape. All *Pinus radiata* plantations used in this study received at least one stand harvest within ~2 years of trapping

to ensure suitable breeding material (recently dead stumps and slash) was available to populations of *H. ligniperda* and *H. ater*.

Sampling periods varied from 89 days (Stewart Island) to 218 days (Wilberforce and Avoca; Table 1), according to local weather conditions and site access restrictions. The variation in duration of trapping periods may present a temporal bias, but we accounted for this in the statistical analysis (see below).

The identity of *H. ater* adult samples trapped on Stewart Island was confirmed by John Bain (New Zealand Forest Research Institute/Scion) and specimens deposited in the National Forest Insect Collection at the New Zealand Forest Research Institute,

Rotorua, as this was the first record of this species on Stewart Island.

Distance measurements

The distance from individual traps to the nearest operational pine plantation was measured in ArcMap (version V 10.1; ESRI, 2011) using the New Zealand mainland exotic vegetation layer imported from the Landcare LRIS portal, Land Cover Database v4.0. A straight-line distance was measured from the edge of the nearest pine plantation to the centrepoint of the trap pair to obtain distance.

Although we expected most bark beetles captured to originate from pine plantations containing large amounts of the host material (stumps and dead woody material in contact with the ground), it is possible that dead pine tree material in agricultural landscapes with windbreaks and small stands of pines also provide host material for small populations to persist. Therefore, we also measured the distance from individual traps to the nearest pine windbreak. Distances were individually measured in Google Earth (Version 7.1.4.1529) because the Land Cover Database layer does not show all windbreaks. Distance measurements were taken from satellite imagery taken on 29 September 2013. We defined a windbreak as a continuous stretch of *Pinus* spp. at least 25 m in length, except for Stewart Island where a small private plantation of *Pinus* spp. was used for the analysis, as it is the only continuous patch of *Pinus* spp. on the island. Wilding pine areas in the geographic area were generally young and vigorous stands (i.e. unsuitable bark beetle habitat) and were hence not considered in the analysis as it is highly unlikely that they contain any suitable breeding material. A straight-line distance was measured from the trap to the edge of the nearest pine windbreak.

Inverse distance weighted estimates

To quantify the effect of local pine density on bark beetle capture, we calculated inverse-distance weighted average estimates of pine densities around each trap. Data on pine densities were extracted from a national (New Zealand) vector GIS layer of pine forest cover (Informatics Team Landcare Research, 2015). Individual pine trees and very small windbreaks are not accounted for in this GIS layer. This coverage was converted into a 1-km raster layer with each raster cell coded as the proportion of the cell covered by pine forests. This vector-to-raster conversion was performed using ArcGIS software (ESRI, 2011).

Two matrices (*c* and *d*) were used to delineate a fixed neighbourhood of pine density and distance from a focal point (insect trap) (Liebhold *et al.*, 1993). The first matrix, *c*, contained $1 \times 1 \text{ km}^2$ cells with values of conifer density based on the New Zealand mainland exotic raster layer used previously for straight-line distances. Note that the original vector coverage corresponded to all conifers and we could not separate Douglas fir (*Pseudotsuga menziesii*) from *Pinus* species. However, the area of Douglas fir was small (<16%) so the density estimates should be dominated by pines. The second matrix, *d*, was created

using a distance decay function (Euclidean distance):

$$\sqrt{((x_{lim} + 1) - x_i)^2 + ((y_{lim} + 1) - y_i)^2}$$

where *xlim* and *yylim* sets a maximum extent of the *c* matrix included to obtain estimates from the focal point x_i and y_i . The maximum extent used was 50 km (i.e., 100×100 cells) because this distance would include at least one operational pine plantation for all traps and we observed bark beetles up to 40 km from any pine plantation (Table 1). Furthermore, because of the nature of the inverse distance weighting function, points more distant than 50 km would have a negligible effect on estimates.

Spatially weighted average pine density *w* around each trap was computed from all raster cells within 50 km of each trap location using an inverse distance power weight function,

$$w = \frac{\sum \frac{x_i}{d_i^p}}{\sum \frac{1}{d_i^p}}$$

where *p* = a power parameter that was varied to obtain the best fit in the regression of trap capture on weighted pine density. The inverse density function gives greater weight to nearby locations, but the parameter *p* determines the rate at which the distant areas decrease in their contribution to the estimate. Specifically, if the best-fit model had a low value of *p* (e.g. 0.5), beetle catch was affected even by remote pine stands, implying that dispersal was effective over long distances, whereas if the best fit model had a high value of *p* (e.g. 3.0), beetle catch was affected mainly by local sources, implying limited long-distance dispersal (see Lu & Wong, 2008). We tested models with a *P*-value of 0.1, 0.5, 1, 1.5, 2, 2.5, and 3 and used the best-fit value of *p* for all subsequent analyses for that species. Weighted average pine densities were computed using a script written in the R language (V. 3.2.3, R Development Core Team, 2015, Supporting information Appendix S1).

Statistical analysis

Counts (bark beetle trap⁻¹; *N* = 167 traps) of *H. ligniperda* and *H. ater* were analysed using negative binomial generalised linear models with a log link in the statistical software R version 3.2.3 (R Development Core Team, 2015; R package MASS, Venables & Ripley, 2002). Negative binomial models were used to account for overdispersion and to allow model comparisons based on the Akaike Information Criterion (AIC) (Akaike, 1973). We did not run models with combinations of weighted average pine density, *w*, as these values would be highly autocorrelated because of the nested structure of the data. Potential outliers that could cause confounding effects on regression models were checked using Cook's distance considering a value of 1 as a threshold (Fox, 2002), but no influential outliers were found. Likelihood ratio tests were used to assess the significance of the fixed term(s) in each regression model (drop1 command in R, Zuur *et al.*, 2009). For each model, we also calculated the explained deviance, also known as pseudo *R*², according to Dobson (2002).

Four models were run for each species containing the following predictors: (i) distance to the nearest pine plantation; (ii) distance to nearest pine windbreak; (iii) weighted estimate of pine density using a best-fit value of P as described above; (iv) a multiple regression including distance to plantation, distance to windbreak, and weighted pine density estimate. We used an offset function in all models to account for the variation in number of trapping exposure days (Zuur *et al.*, 2009).

Results

Pine distance and density effects on Hylurgus ligniperda

We captured 4900 *H. ligniperda* in pine plantations (84% of all those captured). As expected, the highest trap catch of *H. ligniperda* occurred in a pine plantation (Ashley Forest, mean = 75.5 trap⁻¹ week⁻¹). For traps away from plantations, we captured 844 *H. ligniperda* across all 11 sites in the Southern Alps, but none on Stewart Island (Table 1). A total of 23 and 112 *H. ligniperda* were captured across the windbreak and wilding pine sites, respectively. The most remote location at which *H. ligniperda* was captured was 40.4 km from the nearest pine plantation and 26.3 km from the nearest pine windbreak.

Hylurgus ligniperda trap capture significantly decreased with increasing distance to pine resources in all modelled scenarios (Figs 2 and 3); it was negatively correlated with distance to pine plantation (L = likelihood ratio test statistic; $L = 229.31$, $df = 1$, $P < 0.001$, deviance explained = 58%) and distance to pine windbreak ($L = 34.77$, $df = 1$, $P < 0.001$, deviance explained = 17%; Fig. 2). The best distance power function for weighted pine density for *H. ligniperda* was $p = 0.5$ [AIC = 861.3, next lowest AIC = 866.51 ($P = 0.1$)], meaning that distant pines constitute important sources of local catch rates (i.e. long-distance dispersal is effective). Using this value of p , *H. ligniperda* catch was significantly positively related to pine density w ($L = 260.52$, $d.f. = 1$, $P < 0.001$, deviance explained = 61%; Fig. 3a). The multiple regression model, which included distance to pine plantation, distance to pine windbreak, and weighted density, was the best predictor of *H. ligniperda* (i.e. the model with the highest explained deviance) showing that all three different estimates of pine resources made independent contributions to predicted catches (Table 2).

Pine distance and density effects on Hylastes ater

We captured 217 *H. ater* in pine plantations. Unexpectedly, more *H. ater* were captured at non-plantation sites (Upper Grey Valley: 37% of total capture, mean = 5.7 trap⁻¹ week⁻¹, Mount White Station: 31% of total capture) than in pine plantations (17% of total capture). A total of 1059 *H. ater* were captured across the 12 non-plantation study sites in the Southern Alps and on Stewart Island. *Hylastes ater* was captured at all 12 sites apart from Wilberforce (Table 1), including on Stewart Island (this is the first known record of *H. ater* on Stewart Island). A total of four *H. ater* were captured across the three windbreak sites in the Canterbury plains. At the wilding pine sites, 97 *H. ater* were captured. The most distant captures of *H. ater* occurred 43.0 km from the nearest pine plantation and 27.6 km from the nearest pine windbreak.

Hylastes ater abundance was not significantly correlated with trap distance from the nearest pine plantation ($L = 2.49$, $df = 1$, $P = 0.11$, deviance explained = 2%). Unexpectedly, the trap catch was significantly positively correlated with increasing distance to the nearest pine windbreak ($L = 23.95$, $df = 1$, $P < 0.001$, deviance explained = 64%) (Fig. 2). The best-fit-power function for *H. ater* abundance in relation to pine density occurred at $p = 0.1$ [AIC = 853.09, next lowest AIC = 847.23 ($P = 0.5$)], a very low value indicating that catches were affected strongly by even distant pine stands. Relatively high numbers of *H. ater* were observed at the highest values of pine density w but the highest abundances occurred at intermediate values of pine density ($L = 8.65$, $d.f. = 1$, $P = 0.003$, deviance explained = 5%; Fig. 3b). The multiple regression model including distance to the plantation, distance to windbreak, and weighted pine density w was the best fit model overall, showing that for *H. ater* these three different measures of pine resource all contributed to predicted trap catch rates.

Discussion

The Eurasian bark beetles *H. ater* and *H. ligniperda* are invasive pests that have successfully colonised most pine-growing countries in the Southern Hemisphere. Our results show that one contributing factor to their invasion success could be their effective long-distance dispersal, as indicated by their abundance as a function of host availability. The very low values for the spatial scaling function p , and trap captures in some sites tens of kilometers from the nearest pine resources all indicate surprisingly high levels of long-distance dispersal in these two bark beetles. Overall, the present study provides new insight into traits positively associated with the spread and establishment of two non-native bark beetles and it has wider implications for bark beetle ecology and biological invasions.

At the start of this study, we expected to find remote areas, distant from, and typically devoid of pine resources (including windbreaks and wilding pines), to be absent of *H. ater* and *H. ligniperda*. As a general rule, the trap catch of forest insects is usually strongly positively correlated with greater host density (Hayes *et al.*, 2009; Chase *et al.*, 2014), even at the landscape scale (Zausen *et al.*, 2005). Yet, this was not consistently the case. Instead, we captured both bark beetles in almost every area we looked, often on more than one occasion throughout the flight season. The observed relationships between trap capture rates and distance from the host material (i.e. pine resources) differed markedly between the two bark beetles. The trap catch rate of *H. ligniperda* was closely associated with higher values of pine density (i.e. pine plantations) whereas the clustering of *H. ater* also occurred at intermediate values of pine density (i.e. larger pine windbreaks).

Another unexpected result of this study was that in some of the remote sites we captured more *H. ater* than *H. ligniperda*. Previous studies indicate that *H. ligniperda* is the more abundant species in New Zealand and Chile (Reay & Walsh, 2001; Brockerhoff *et al.*, 2006b; Mausel *et al.*, 2007; McCarthy *et al.*, 2010), but all of these studies took place in or near pine

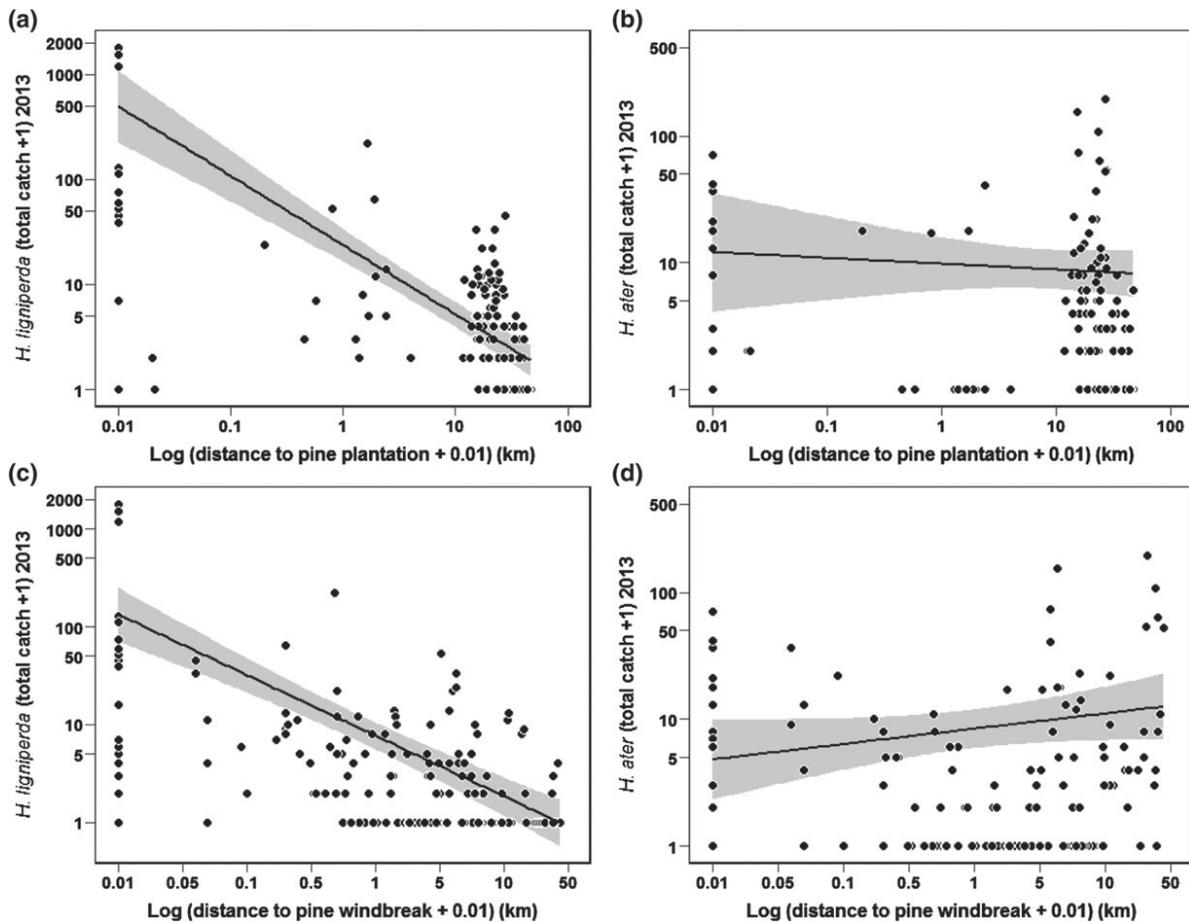


Fig. 2. Trap captures of *H. ligniperda* (left) and *H. ater* (right) as a function of distance to the nearest pine plantation (upper) or windbreak (lower). Lines represent significant negative binomial generalized linear model fits; grey areas indicate 95% confidence intervals. $N = 167$ traps. Each point represents one individual insect trap.

plantations. We propose five possible (not mutually exclusive) explanations for finding greater abundances of *H. ater* in remote locations: (i) *H. ater* can colonise the root systems of damaged trees (Chararas, 1962; Sopow *et al.*, 2015) in pine windbreaks, thereby using these resources as ‘stepping stones’ (Saura *et al.*, 2014) to spread through and persist in the landscape. In a recent study, *H. ater* was captured in emergence traps placed around the buttresses of damaged windbreak trees in New Zealand (Be *et al.*, unpublished data); (ii) *H. ater* has been in New Zealand *c.* 35 years longer than *H. ligniperda* which might have allowed it to colonise more remote sites with low-density host material; (iii) within pine plantations, *H. ater* could be an inferior competitor compared to *H. ligniperda*, which would be consistent with the greater abundance of the latter in areas with a high density of pines; (iv) *H. ater* may be able to better tolerate colder temperatures and wetter climates than *H. ligniperda*. Initially, *Hylastes ater* was much more common in plantation forests after establishing but has since declined in areas where *H. ligniperda* is present (Reay, 2000). However, in the southern half of the South Island where temperatures are cooler and where *H. ligniperda* has invaded more recently (post 2004) and populations are still very low, *H. ater* was still found

at higher populations than *H. ligniperda* (Brockerhoff *et al.*, 2006b); (v) *H. ater* may be more prone to enter wind-aided long distance dispersal than *H. ligniperda*. Species within the genus *Hylastes* are particularly known to disperse long distances via the wind (see paragraph below), and this may explain why in the mountainous, windy regions of the Southern Alps we found high numbers of *H. ater* at great distances away from pine resources.

Dispersal aided by wind (also known as anemochorous dispersal) is an important mechanism for spread that allows some bark beetles to disperse great distances (Nilssen, 1978, 1984; Compton, 2002; Nathan *et al.*, 2003). Bark beetles can enhance wind-assisted dispersal by flying higher into the air column where winds are stronger. For example, Nilssen (1978) found evidence of wind-aided long-distance dispersal by examining fish guts in high mountain lakes ~180 km from the nearest major spruce forests. Most relevant to the current study, Nilssen (1984) captured both *Hylastes cunicularius* Erichson and *H. brunneus* Erichson in either pine or spruce billets 171 km from the nearest major spruce forest and ~78 km from the nearest pine forest, indicating that *Hylastes* species can be particularly widely dispersed. In the same study, the bark beetle *Dryocoetes hectographus* Reitter and the bark-feeding weevil *Hylobius abietis* L.

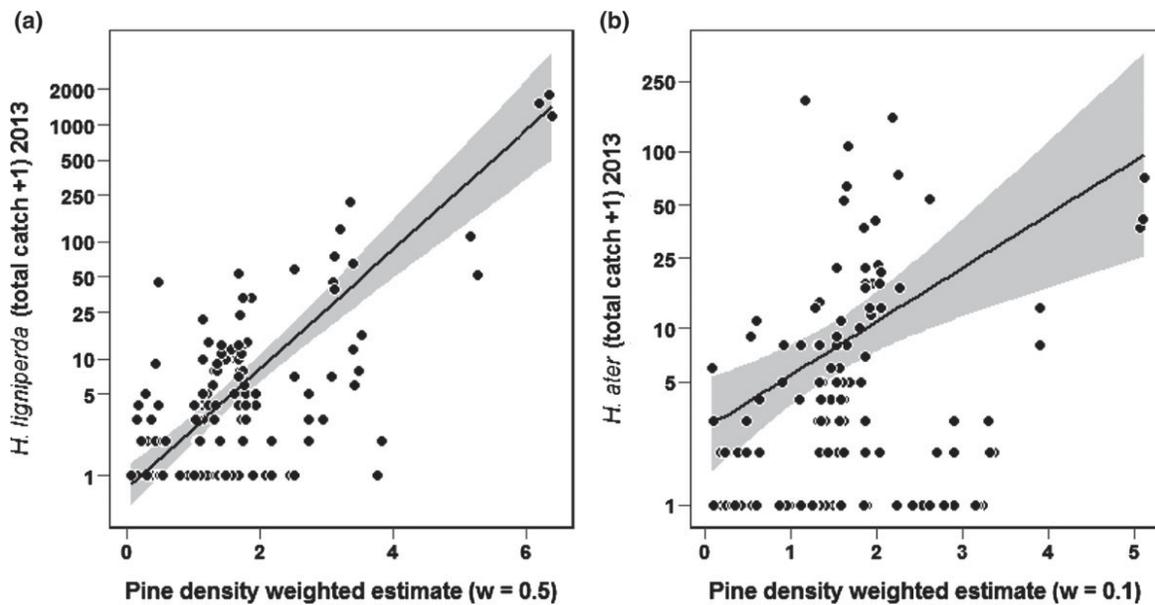


Fig. 3. Total beetle catch per trap as a function of pine density weighted estimate for (a) *H. ligniperda* and (b) *H. ater*. Lines represent significant negative binomial generalised linear model fits using weighted pine density, calculated using the best-fit power scaling function p given on the x-axis. Grey areas indicate 95% confidence intervals. Note differences in y-axis values.

Table 2. Multiple regression negative binomial GLM output from the `drop1` function in R predicting bark beetle trap capture across all sites, 2013–2014, predicted from distance to nearest plantation, distance to nearest windbreak, and weighted pine density (w).

Bark beetle	Predictor	d.f.	Deviance	LRT	Pr (>Chi)	Deviance explained
<i>Hylurgus ligniperda</i>	Null	–	167.12	–	–	67%
	Distance plantation	1	184.5	17.38	<0.001	–
	Distance windbreak	1	177.31	10.19	0.001	–
	Weighted density	1	194.14	27.04	<0.001	–
<i>Hylastes ater</i>	Null	–	158.85	–	–	26%
	Distance plantation	1	162.61	3.75	0.05	–
	Distance windbreak	1	194.29	35.44	<0.001	–
	Weighted density	1	163.66	4.81	0.03	–

Weighted density was calculated using best-fit estimates for power function p (0.5 for *H. ligniperda*, 0.1 for *H. ater*), see text.

were also found at these distances (Nilssen, 1984 and references within). Wind-aided dispersal of *H. abietis* was also investigated by Solbreck (1980) who estimated that the majority of beetles travelled between 10 and 80 km. Because our study took place in the Southern Alps, a mountainous region with frequent strong winds, wind-aided dispersal is a likely mechanism that explains the detection of *H. ater* and *H. ligniperda* in remote river valleys.

Additional studies measuring long-distance dispersal have been conducted for bark beetles in the genus *Dendroctonus*. For example, Miller and Keen (1960) measured the dispersal of the western pine beetle *Dendroctonus brevicomis* LeConte from the natural pine forest edge to isolated patches of *Pinus ponderosa* Douglas ex. C. Lawson and concluded that beetles dispersed between 3.2 and 30 km. *Dendroctonus valens* LeConte, invasive in China, was recorded dispersing 20–35 km in the Luliang and Taihang mountains (Zhang *et al.*, 2002). In the United States, Smith (1971) reported *D. valens* flying distances of up to 16 km. Airborne mountain pine beetles (*Dendroctonus ponderosae* Hopkins) were found at 800 m above the forest canopy in

western Canada, and with wind assistance, were estimated to spread 30–110 km day⁻¹ (Jackson *et al.*, 2008). Flight mill studies conducted in laboratory settings have provided estimated flight distances of *Dendroctonus* and *Ips* bark beetles of up to 45 km (Atkins, 1961; Jactel & Gaillard, 1991; Byers, 2000).

Additionally, the movement of firewood and timber could explain the occurrence of *H. ater* and *H. ligniperda* in areas without host resources; it is a known pathway for the movement of other bark and wood-boring beetles (Haack *et al.*, 2010). *Pinus radiata* is commonly used for firewood throughout New Zealand and this may help explain the presence of *H. ligniperda* and *H. ater* in sites near backcountry homesteads. On Stewart Island, *Pinus* spp. firewood is commonly moved across Foveaux Strait from the South Island (Chase, pers. obs.), and we suspect this is the most likely pathway for the invasion of *H. ater* of Stewart Island.

After dispersal to a new area, beetles have to find and colonise suitable host material. This is a multistep process dependent on the physiological state of the beetle and local

environmental conditions (Wallin & Raffa, 2000; Raffa *et al.*, 2016). Both primary attraction and random landing are proposed as mechanisms of how a pioneer bark beetle finds a host (Person, 1931; Jactel *et al.*, 2001; Zhang & Schlyter, 2004; Saint-Germain *et al.*, 2007). For colonisation to occur, host material must be in a suitable physiological state (in this case, dying or dead pine materials). Additionally, because no sex pheromone which could cause aggregation has been detected for *H. ater* and *H. ligniperda*, it is also necessary for both a male and female to arrive to the same host at the same point time, reducing the chance of successful colonisation. However, there is evidence that *H. ligniperda* can mate with siblings before dispersal and, therefore, females may not need to find a mate upon arrival, increasing the probability of colonisation success. Establishing a continuing population in remote locations is dependent on availability of ephemeral hosts, the number of arriving beetles, and the ability to find both host and mate.

In scenarios where bark beetles disperse randomly and invade previously un-colonised suitable host-forest, establishment becomes dependent on both host density and propagule pressure (Lockwood *et al.*, 2005; Nowicki *et al.*, 2014). Additionally, as insects disperse across a landscape, the chances of population establishment decrease with increasing distance from source populations; Allee and stochastic effects may limit the capacity for low-density populations to establish (Tobin *et al.*, 2007; Kanarek *et al.*, 2013), leading to a ‘range-pinning’ effect (i.e. population establishment thresholds create an abrupt edge at the limit of a species’ spatial distribution) (Keitt *et al.*, 2001). However, it has recently been proposed that spread can still occur through a landscape if a portion of habitat patches have reduced Allee thresholds (Walter *et al.*, 2016). In the present study, we found that two highly successful saprophytic bark beetles were remarkably effective dispersers and their main limitation for range expansion appears to be the shortage of host material in areas away from large pine forests. That such small beetles appear to have very high dispersal capabilities is important both for understanding the processes determining which species are successful biological invaders and for designing effective biosecurity incursion response plans.

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and M.K.-F.B. analysed the data. K.D.C., D.K., A.M.L., E.G.B. wrote the manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12371

Appendix S1. R software code used to create weighted estimates of pine density with a distance decay function. For this example, random data was generated representing pine density.

References

- Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. *2nd International Symposium on Information Theory* (ed. by B. N. Petrov and F. Csadki), pp. 267–281. Akadémiai Kiadó, Budapest, Hungary.
- Atkins, M.D. (1961) A study of the flight of the Douglas-fir beetle *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae): III Flight capacity. *The Canadian Entomologist*, **93**, 467–474.
- Bain, J. (1977) *Hylurgus ligniperda* (Fabricius) (Coleoptera: Scolytidae). Forest and Timber Insects in New Zealand No. 18. Forest Research Institute, New Zealand Forest Service, Rotorua, New Zealand.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M. *et al.* (2012) Costs of dispersal. *Biological Reviews*, **87**, 290–312.
- Borden, J.H. (1989) Semiochemicals and bark beetle populations: exploitation of natural phenomena by pest management strategists. *Holarctic Ecology*, **12**, 501–510.
- Brockerhoff, E.G., Bain, J., Kimberley, M. & Knížek, M. (2006a) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Canadian Journal of Forest Research*, **36**, 289–298.
- Brockerhoff, E.G., Jones, D.C., Kimberley, M.O., Suckling, D.M. & Donaldson, T. (2006b) Nationwide survey for invasive wood-boring and bark beetles (Coleoptera) using traps baited with pheromones and kairomones. *Forest Ecology and Management*, **228**, 234–240.
- Brockerhoff, E.G., Kimberley, M., Liebhold, A.M., Haack, R.A. & Cavey, J.F. (2014) Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. *Ecology*, **95**, 594–601.
- Byers, J.A. (1996) An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling*, **91**, 231–243.
- Byers, J.A. (2000) Wind-aided dispersal of simulated bark beetles flying through forests. *Ecological Modelling*, **125**, 231–243.
- Chararas, C. (1962) *Etude biologique des scolytides des conifères*. P. Lechevalier, Paris, France.
- Chase, K.D., Gandhi, K.J.K. & Riggins, J.J. (2014) Effects of forest type and management on native wood wasp abundance (Hymenoptera: Siricidae) in Mississippi, United States. *Journal of Economic Entomology*, **107**, 1142–1149.
- Clark, A.F. (1932) The pine bark beetle, *Hylastes ater*, in New Zealand. *The New Zealand Journal of Science and Technology*, **14**, 1–20.
- Compton, S.G. (2002) Sailing with the wind: dispersal by small flying insects. *Dispersal Ecology* (ed. by J. M. Bullock, R. E. Kenward and R. Hails), pp. 113–133. Blackwell Science, Oxford, U.K.
- Costa, A., Boone, C.K., Kendrick, A.P., Murphy, R.J., Sharpee, W.C., Raffa, K.F. *et al.* (2013) Dispersal and edge behaviour of bark beetles

- and predators inhabiting red pine plantations. *Agricultural and Forest Entomology*, **15**, 1–11.
- Coulson, R.N. (1979) Population dynamics of bark beetles. *Annual Review of Entomology*, **24**, 417–447.
- Dobson, A.J. (2002) *Introduction to Generalized Linear Models*, 2nd edn. Chapman & Hall/CRC Press, London, U.K.
- Dytham, C. (2009) Evolved dispersal strategies at range margins. *Proceedings of the Royal Society of London B*, **276**, 1407–1413.
- ESRI (2011) *ArcGIS Desktop: Release 10*. Environmental Systems Research Institute, Redlands, California.
- Fox, J. (2002) *An R and S-Plus Companion to Applied Regression*. Sage Publications, Thousand Oaks, California.
- Google Earth (Version 7.1.4.1529) (2013) *Southern Alps, New Zealand* [WWW document]. URL <http://www.google.com/earth/index.html> [accessed on 15 October 2015].
- Gous, S., Raal, P. & Watt, M.S. (2014) Dense wilding conifer control with aerially applied herbicides in New Zealand. *New Zealand Journal of Forestry Science*, **44**, 1–5.
- Haack, R.A., Petrice, T.R. & Wiedenhoft, A.C. (2010) Incidence of bark- and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. *Journal of Economic Entomology*, **103**, 1682–1692.
- Haack, R.A., Britton, K.O., Brockerhoff, E.G., Cavey, J.F., Garrett, L.J., Kimberley, M. *et al.* (2014) Effectiveness of the international phytosanitary standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. *PLoS ONE*, **9**, e96611.
- Hayes, C.J., Fettig, C.J. & Merrill, L.D. (2009) Evaluation of multiple funnel traps and stand characteristics for estimating western pine beetle-caused tree mortality. *Journal of Economic Entomology*, **102**, 2170–2182.
- Hynum, B.G. & Berryman, A.A. (1980) *Dendroctonus ponderosae* (Coleoptera: Scolytidae): pre-aggregation landing and gallery initiation on lodgepole pine. *Canadian Entomologist*, **112**, 185–191.
- Informatics Team Landcare Research (2015) *LCDB v4.0 – Land cover database version 4* [WWW document]. URL <https://lris.scinfo.org.nz/layer/413-land-cover-database-lcdb-v40-change/metadata> [accessed on 9 September 2015].
- Jackson, P.L., Straussfogel, D., Lindgren, B.S., Mitchell, S. & Murphy, B. (2008) Radar observation and aerial capture of mountain pine beetle, *Dendroctonus ponderosae* Hopk. (Coleoptera: Scolytidae) in flight above the forest canopy. *Canadian Journal of Forest Research*, **38**, 2313–2327.
- Jactel, H. & Gaillard, J. (1991) A preliminary study of the dispersal potential of *Ips sexdentatus* (Boern) (Col., Scolytidae) with an automatically recording flight mill. *Journal of Applied Entomology*, **112**, 138–145.
- Jactel, H., Van Halder, I., Menassieu, P., Zhang, Q.H. & Schlyter, F. (2001) Non-host volatiles disrupt the response of the stenographer bark beetle, *Ips sexdentatus* (Coleoptera: Scolytidae), to pheromone baited traps and maritime pine logs. *Integrated Pest Management Reviews*, **6**, 197–207.
- Kanarek, A.R., Webb, C.T., Barfield, M. & Holt, R.D. (2013) Allee effects, aggregation, and invasion success. *Theoretical ecology*, **6**, 153–164.
- Kanarek, A.R., Webb, C.T., Barfield, M. & Holt, R.D. (2014) Allee effects, aggregation, and invasion success. *Theoretical Ecology*, **6**, 153–164.
- Keitt, T.H., Lewis, M.A. & Holt, R.D. (2001) Allee effects, invasion pinning, and species' borders. *The American Naturalist*, **157**, 203–216.
- Kerr, J.L., Kelly, D., Bader, M.K.-F. & Brockerhoff, E.G. (2016) Olfactory cues, visual cues, and semiochemical diversity interact during host location of invasive forest beetles. *Journal of Chemical Ecology*. DOI: 10.1007/s10886-016-0792-x.
- Kot, M., Lewis, M.A. & van den Driessche, P. (1996) Dispersal data and the spread of invading organisms. *Ecology*, **77**, 2027–2042.
- Ledgard, N. (2001) The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management*, **141**, 43–57.
- Liebholt, A.M. & Tobin, P.C. (2008) Population ecology of insect invasions and their management. *Annual Review of Entomology*, **53**, 387–408.
- Liebholt, A.M., Rossi, R.E. & Kemp, W.P. (1993) Geostatistics and geographic information systems in applied insect ecology. *Annual Review of Entomology*, **38**, 303–327.
- Liebholt, A.M., Brockerhoff, E.G., Garrett, L.J., Parke, J.L. & Britton, K.O. (2012) Live plant imports: the major pathway for forest insect and pathogen invasions of the US. *Frontiers in Ecology and the Environment*, **10**, 135–143.
- Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.
- Lu, G.Y. & Wong, D.W. (2008) An adaptive inverse-distance weighting spatial interpolation technique. *Computers and Geosciences*, **34**, 1044–1055.
- Mausel, D.L., Gara, R.I., Lanfranco, D., Ruiz, C., Ide, S. & Azat, R. (2007) The introduced bark beetles *Hylurgus ligniperda* and *Hylastes ater* (Coleoptera: Scolytidae) in Chile: seasonal flight and effect of *Pinus radiata* log placement on colonization. *Canadian Journal of Forest Research*, **37**, 156–169.
- McCarthy, J.K., Hood, I.A., Brockerhoff, E.G., Carlson, C.A., Pawson, S.M., Forward, M. *et al.* (2010) Predicting sapstain and degrade in fallen trees following storm damage in a *Pinus radiata* forest. *Forest Ecology and Management*, **260**, 1456–1466.
- McCarthy, J.K., Brockerhoff, E.G. & Didham, R.K. (2013) An experimental test of insect-mediated colonization of damaged *Pinus radiata* trees by sapstain fungi. *PLoS ONE*, **8**, e55692.
- Miller, D.R. (2006) Ethanol and (–)- α -pinene: attractant kairomones for some large wood-boring beetles in southeastern USA. *Journal of Chemical Ecology*, **32**, 779–794.
- Miller, J.M. & Keen, F.P. (1960) *Biology and Control of the Western Pine Beetle: A Summary of the First Fifty Years of Research*, Vol. **800**. US Department of Agriculture, Washington, District of Columbia.
- Moeck, H.A., Wood, D.L. & Lindahl, K.Q. Jr (1981) Host selection behaviour of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. *Journal of Chemical Ecology*, **7**, 49–83.
- Morgan, F.D. (1967) *Ips grandicollis* in South Australia. *Australian Forestry*, **31**, 137–155.
- Nathan, R., Perry, G., Cronin, J.T., Strand, A.E. & Cain, M.L. (2003) Methods for estimating long-distance dispersal. *Oikos*, **103**, 261–273.
- Nilssen, A.C. (1978) Development of a bark fauna in plantations of spruce (*Picea abies* (L.) Karst.) in North Norway. *Astarte*, **11**, 151–169.
- Nilssen, A.C. (1984) Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. *Annales Entomologici Fennici*, **50**, 37–42.
- Nowicki, P., Vrabec, V., Binzenhöfer, B., Feil, J., Zakšek, B., Hovestadt, T. *et al.* (2014) Butterfly dispersal in inhospitable matrix: rare, risky, but long-distance. *Landscape Ecology*, **29**, 401–412.
- NZFOA (New Zealand Forest Owners Association) (2014) *New Zealand plantation forestry industry: facts and figures* [WWW document]. URL http://www.nzfoa.org.nz/images/stories/pdfs/factsandfigures_2014_web.pdf [accessed on 20 November 2015].
- Person, H.L. (1931) Theory in explanation of the selection of certain trees by the western pine beetle. *Journal of Forestry*, **29**, 696–699.
- Perttunen, V. (1957) Reactions of two bark beetle species, *Hylurgus palliatus* Gyll. and *Hylastes ater* Payk. (Col., Scolytidae)

- to the terpene alpha-pinene. *Annales Entomologicae Fennicae*, **23**, 101–110.
- Petrice, T.R., Haack, R.A. & Poland, T.M. (2004) Evaluation of three trap types and five lures for monitoring *Hylurgus ligniperda* (Coleoptera: Scolytidae) and other local scolytids in New York. *The Great Lakes Entomologist*, **37**, 1–9.
- Phillips, T.W., Wilkening, A.J., Atkinson, T.H., Nation, J.L., Wilkinson, R.C. & Foltz, J.L. (1988) Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles (Coleoptera). *Environmental Entomology*, **17**, 456–462.
- Piel, F., Gilbert, M., De Cannière, C. & Grégoire, J.C. (2008) Coniferous round wood imports from Russia and Baltic countries to Belgium. A pathway analysis for assessing risks of exotic pest insect introductions. *Diversity and Distributions*, **14**, 318–328.
- Pureswaran, D.S., Gries, R. & Borden, J.H. (2004) Antennal responses of four species of tree-killing bark beetles (Coleoptera: Scolytidae) to volatiles collected from beetles, and their host and nonhost conifers. *Chemoecology*, **14**, 59–66.
- Rabaglia, R.J., Dole, S.A. & Cognato, A.I. (2006) Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. *Annals of the Entomological Society of America*, **99**, 1034–1056.
- Raffa, K.F. & Berryman, A.A. (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs*, **53**, 27–49.
- Raffa, K.F., Grégoire, J.-C. & Lindgren, B.S. (2016) Natural history and ecology of bark beetles. *Bark Beetles – Biology and Ecology of Native and Invasive Species* (ed. by F. E. Vega and R. W. Hofstetter), pp. 1–40. Elsevier, London, U.K.
- R Development Core Team, Version 3.2.3 (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. [WWW document]. URL <https://www.R-project.org/>.
- Reay, S.D. (2000) *Aspects of the ecology and behavior of Hylastes ater (Paykull) (Coleoptera: Scolytidae) in second rotation Pinus radiata forests in the central North Island, New Zealand, and options for control*. PhD thesis, University of Canterbury, New Zealand.
- Reay, S.D. & Walsh, P.J. (2001) Observations of the flight activity of *Hylastes ater* and *Hylurgus ligniperda* (Curculionidae: Scolytinae) in *Pinus radiata* forests in the central North Island, New Zealand. *New Zealand Entomologist*, **24**, 79–85.
- Reay, S.D. & Walsh, P.J. (2002) Relative attractiveness of some volatiles to the introduced pine bark beetles, *Hylastes ater* and *Hylurgus ligniperda* (Curculionidae: Scolytinae). *New Zealand Entomologist*, **25**, 51–56.
- Saint-Germain, M., Buddle, C.M. & Drapeau, P. (2007) Primary attraction and random landing in host-selection by wood-feeding insects: a matter of scale? *Agricultural and Forest Entomology*, **9**, 227–235.
- Saura, S., Bodin, Ö. & Fortin, M.-J. (2014) Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, **51**, 171–182.
- Shigesada, N., Kawasaki, K. & Takeda, Y. (1995) Modelling stratified diffusion in biological invasions. *The American Naturalist*, **146**, 229–251.
- Skarpaas, O. & Økland, B. (2009) Timber import and the risk of forest pest introductions. *Journal of Applied Ecology*, **46**, 55–63.
- Skellam, J.G. (1951) Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.
- Smith, R.H. (1971) *Red Turpentine Beetle*. US Department of Agriculture, Forest Pest Leaflet 55. Washington, District of Columbia.
- Solbreck, C. (1980) Dispersal distances of migrating pine weevils, *Hyllobius abietis*, Coleoptera: Curculionidae. *Entomologia Experimentalis et Applicata*, **28**, 123–131.
- Sopow, S.L., Bader, M.K. & Brockerhoff, E.G. (2015) Bark beetles attacking conifer seedlings: picking on the weakest or feasting upon the fittest? *Journal of Applied Ecology*, **52**, 220–227.
- Suarez, A.V., Holway, D.A. & Case, T.J. (2001) Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 1095–1100.
- Taylor, C.M. & Hastings, A. (2005) Allee effects in biological invasions. *Ecology Letters*, **8**, 895–908.
- Tobin, P.C., Whitmire, S.L., Johnson, D.M., Bjørnstad, O.N. & Liebhold, A.M. (2007) Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecology Letters*, **10**, 36–43.
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York, New York.
- Wallin, K.F. & Raffa, K.F. (2000) Influences of host chemicals and internal physiology on the multiple steps of postlanding host acceptance behavior of *Ips pini* (Coleoptera: Scolytidae). *Environmental Entomology*, **29**, 442–453.
- Wallin, K.F. & Raffa, K.F. (2002) Density-mediated responses of bark beetles to host allelochemicals: a link between individual behaviour and population dynamics. *Ecological Entomology*, **27**, 484–492.
- Walter, J.A., Johnson, D.M. & Haynes, K.J. (2016) Spatial variation in Allee effects influences patterns of range expansion. *Ecography*. DOI: 10.1111/ecog.01951.
- Webb, C.J., Sykes, W.R. & Garnock-Jones, P.J. (1988) *Flora of New Zealand. Naturalized Pteridophytes, Gymnosperms, Dicotyledons*, Vol. 4. Botany Division, DSIR, Christchurch, New Zealand.
- Williamson, M.H. (1996) *Biological Invasions*. Chapman & Hall, London, U.K.
- Wood, D.L. (1982) The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annual Reviews of Entomology*, **27**, 411–446.
- Yin, H.F. (2000) A synopsis of morphological and biological characters of *Dendroctonus valens* LeConte. *Acta Zootaxonomica Sinica*, **251**, 120 (in Chinese).
- Zausen, G.L., Kolb, T.E., Bailey, J.D. & Wagner, M.R. (2005) Long-term impacts of stand management on ponderosa pine physiology and bark beetle abundance in northern Arizona: a replicated landscape study. *Forest Ecology and Management*, **218**, 291–305.
- Zhang, Q.H. & Schlyter, F. (2004) Olfactory recognition and behavioural avoidance of angiosperm nonhost volatiles by conifer-inhabiting bark beetles. *Agricultural and Forest Entomology*, **6**, 1–20.
- Zhang, L., Chen, Q. & Zhang, X. (2002) Studies on the morphological characters and bionomics of *Dendroctonus valens* Leconte. *Scientia Silvae Sinicae*, **28**, 95–99.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, New York.

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