Assessing the Threat Posed by Indigenous Exotics: A Case Study of Two North American Bark Beetle Species

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Ann. Entomol. Soc. Am. 103(1): 39–49 (2010)

ABSTRACT The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, was detected in 2001 in northern Minnesota outside its natural range and the range of its native hosts, Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, and western larch, *Larix occidentalis* Nutt. Consecutive years of detection indicated that *D. pseudotsugae* may have been established in a new environment and provided a possible example of an indigenous exotic species in North America. Pheromone-baited logs of *P. menziesii* and tamarack, *Larix laricina* (Du Roi) K. Koch. were placed at four sites in northern Minnesota in an attempt to detect this indigenous exotic. Bark was removed from one half of logs and checked for *D. pseudotsugae* galleries. The remaining logs were left intact and reared to collect adult beetles the following spring. No *D. pseudotsugae* galleries were identified and no adults of the indigenous exotic were located. Along with the eastern larch beetle, *Dendroctonus simplex* LeConte, native Minnesota populations of *Polygraphus rufipennis* (Kirby) and *Dryocoetes autographus* (Ratzeburg) colonized *P. menziesii* logs. The reciprocal study was conducted in Montana, primarily to determine whether *D. pseudotsugae* would attack pheromone-baited logs of *L. laricina*. Logs from the Minnesota and Montana experiments were used to estimate the success of *D. simplex* and *D. pseudotsugae* in the non-native hosts *P. menziesii* and *L. laricina*, respectively. Both *D. simplex* and *D. pseudotsugae* successfully colonized and reproduced in non-native logs in the field, albeit at low numbers. The potential threat of indigenous exotic species to North American forests also is discussed.

KEY WORDS *Dendroctonus pseudotsugae*, *Dendroctonus simplex*, exotic species, brood production, Scolytidae

Much attention has been paid to the global movement of commodities and the threat posed by introducing nonindigenous insects and other organisms into new areas of the world via this pathway (USDA 2000, FAO 2002, Kliejunas et al. 2006). On a global scale, this pathway is well documented as a threat to forest ecosystem health, and numerous nonindigenous species have been introduced into new habitats via solid wood packing or other materials (Kobayashi 1988, Mota et al. 1999, Allen and Humble 2002, Haugen and Hoebeke 2005, Work et al. 2005, Yan et al. 2005, Brockerhoff et al. 2006a, Haack 2006, Humble and Allen 2006, Poland and McCullough 2006, Lee et al. 2007, Langor et al. 2009). The occurrences have become so frequent that new invasives are displacing previously introduced species (Bybee et al. 2004, Lee et al. 2009). Although not all introductions result in serious economic or ecological impacts, invasive populations of *Agrilus planipennis* in North America (Poland and McCullough 2006) and *Dendroctonus valens* in China (Yan et al. 2005) have caused considerable losses in regional forests.

Although threats posed by non-native insects are often well documented, a less discussed threat to native ecosystems is the intra-continental movement of indigenous insects. Movement of indigenous species into ecosystems outside their natural range, i.e., indigenous exotics, could result in established insect populations on new host tree species in new ecosystems. For example, *Ips calligraphus* (Germar) is now established in California and probably resulted from an introduced population (Wood and Stark 1968). *Agrilus anxius* Gory (Coleoptera: Buprestidae) also has expanded its range in the western United States where it was not found previously (Carlos et al. 2002). The North American range of *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae) has expanded, and it has been speculated that this was aided by anthropogenic means (Gall 1992). In Europe, *Dendroctonus micans* (Kugelann) has probably been aided in an expansion of its distribution by anthropogenic movement of infested materials (Grégoire 1988). As large-scale exotic species detection efforts expand (e.g., USDA–APHIS Cooperative Agriculture Pest

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Survey, USDA Forest Service Early Detection Rapid Response Survey, Canadian Food Inspection Agency, Brockerhoff et al. 2006b) and other surveys are conducted, more indigenous exotics are being identified in areas outside their native ranges (Humble et al. 1997, Rabaglia and Williams 2002, Dodds et al. 2004, LaBonte et al., 2005). Consequently, it is prudent to begin considering threats posed by intra-continental movement of wood material and the potential indigenous exotic insects and microorganisms carried along with this material. Numerous pathways exist for intracontinental movement of wood, including firewood, salvaged logged trees, logs for home construction, and nursery stock.

Bark beetles [Coleoptera: Scolytidae, sensu Wood (2007)] are a group of cryptic insects that can easily be transported to new environments in whole logs or packing material. Large-scale or regional outbreaks are frequently documented for many bark beetle species and many of these insects are also found in fire-damaged trees that are eventually salvage logged. Consequently, bark beetles and associated organisms are likely candidates for intracontinental movement. Bark beetles with wide (>5 species) host ranges [e.g., mountain pine beetle, *Dendroctonus ponderosae* Hopkins, pine engraver, *Ips pini* (Say), and the California fivespined ips, *Ips paraconfusus* Lanier, in North America; and the Eurasian spruce engraver, *Ips typographus* (L.), *Tomicus minor* (Hartig), and *Tomicus piniperda* (L.) in Europe] are of particular concern, as they are more likely to encounter a suitable host in an adventive habitat than a bark beetle with a limited (one to two species) host range [e.g., Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, or western pine beetle, *Dendroctonus brevicomis* LeConte]. However, host specificity is not the only consideration as beetles that can exploit downed or weakened tree material (e.g., *Ips* spp., *D. pseudotsugae*) may be more successful colonizers because of their ability to use and establish populations in a wider range of host material. Founder populations of these species may not need to be as large as those of more aggressive bark beetles that exploit living trees and use aggregation as a strategy to overcome host defenses.

Case Study in North America. As an example of the intracontinental movement of a species to an area outside of its natural range, *D. pseudotsugae* was collected in 2001 and 2002 in multiple-funnel traps baited with pheromones targeting the eastern larch beetle, *Dendroctonus simplex* LeConte, in north central Minnesota (Dodds et al. 2004). *D. pseudotsugae* is native to western North America (Fig. 1) where it successfully colonizes living or dead Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, and dead western larch trees, *Larix occidentalis* Nutt. (Schmitz and Gibson 1996). Although *P. menziesii* is its primary host and the only living tree species successfully colonized, *D. pseudotsugae* also can reproduce in dead *L. occidentalis* (Ross 1967, Furniss 1976, Schmitz and Gibson 1996). *P. menziesii* and *L. occidentalis* are both found in western North America and are not native to Minnesota forests (Fig. 2). Consequently, detecting this beetle in pheromone-baited traps in Minnesota was unexpected. Subsequent research on log imports into Minnesota identified a company importing salvage-logged *L. occidentalis* from western Montana. Investigation of this log facility determined the *D. pseudotsugae* pathway into Minnesota. Subsequent rearing from *L. occidentalis* taken from the log facility resulted in the identification of 16 species of insects (indigenous exotic and indigenous species) and two species of fungi not recorded previously in Minnesota (Dodds et al. 2004).

Although the natural distribution of *D. pseudotsugae* does not include Minnesota, the closely related *D. simplex* is found frequently in this state infesting its primary host tamarack, *Larix laricina* (Du Roi) K. Koch. (Fig. 1). *D. simplex* is found wherever *L. laricina* grows (Fig. 2) and ranges from northeastern North America west through Canada and to Alaska (Seybold et al. 2002). *D. simplex* also has been reported infesting red spruce, *Picea rubens* Sarg., in Maine (Baker 1972) and black spruce, *Picea mariana* (Mill.) B.S.P., in Minnesota (S.J.S. and M. A. Albers, unpublished).

D. pseudotsugae and *D. simplex* are considered relatively host-specific, successfully reproducing in only a few tree species (Wood 1982). However, during a laboratory study *D. pseudotsugae* successfully reproduced at low numbers in *L. laricina* (Furniss 1976). In the same study, *D. simplex* did not successfully reproduce in *P. menziesii* but it did reproduce in *L. occidentalis* (Furniss 1976). The geographic ranges of *P. menziesii* and *L. laricina* do not overlap in North America (Burns and Honkala 1990) (Fig. 2); thus, *D. pseudotsugae* and *D. simplex* populations do not interact. Wood (1963) treated *D. pseudotsugae* and *D. simplex* as a species pair with the highest degree of specialization among the *Dendroctonus* and suggested that *D. pseudotsugae* and *D. simplex* were "geographical replacements of one another that developed in comparatively recent geological time." Thus, they probably had a common progenitor whose populations may have been isolated in the eastern and western portions of North America during glaciation (Furniss 1976). During the Wisconsin period of glaciation, the isolated populations evolved measurable differences in physical size, form, and host preferences from each other, and probably from their progenitor (Furniss 1976).

We conducted reciprocal field studies in Minnesota and Montana to investigate the relative potential of *D. simplex* and *D. pseudotsugae* to colonize *P. menziesii* and *L. laricina*, respectively. Because a population of *D. pseudotsugae* had already been detected in Minnesota, the focus of the research was on the behavior of *D. pseudotsugae* as a potential indigenous exotic in Minnesota. Specifically, we hoped to confirm the presence of an established *D. pseudotsugae* population in Minnesota and determine the local host. Further studies were conducted to more thoroughly investigate the establishment potential of *D. simplex* and *D. pseudotsugae* on non-native hosts under field conditions. To this end, *P. menziesii* and *L. laricina* logs were placed in Minnesota and Montana to determine whether native bark beetles would colonize and re-

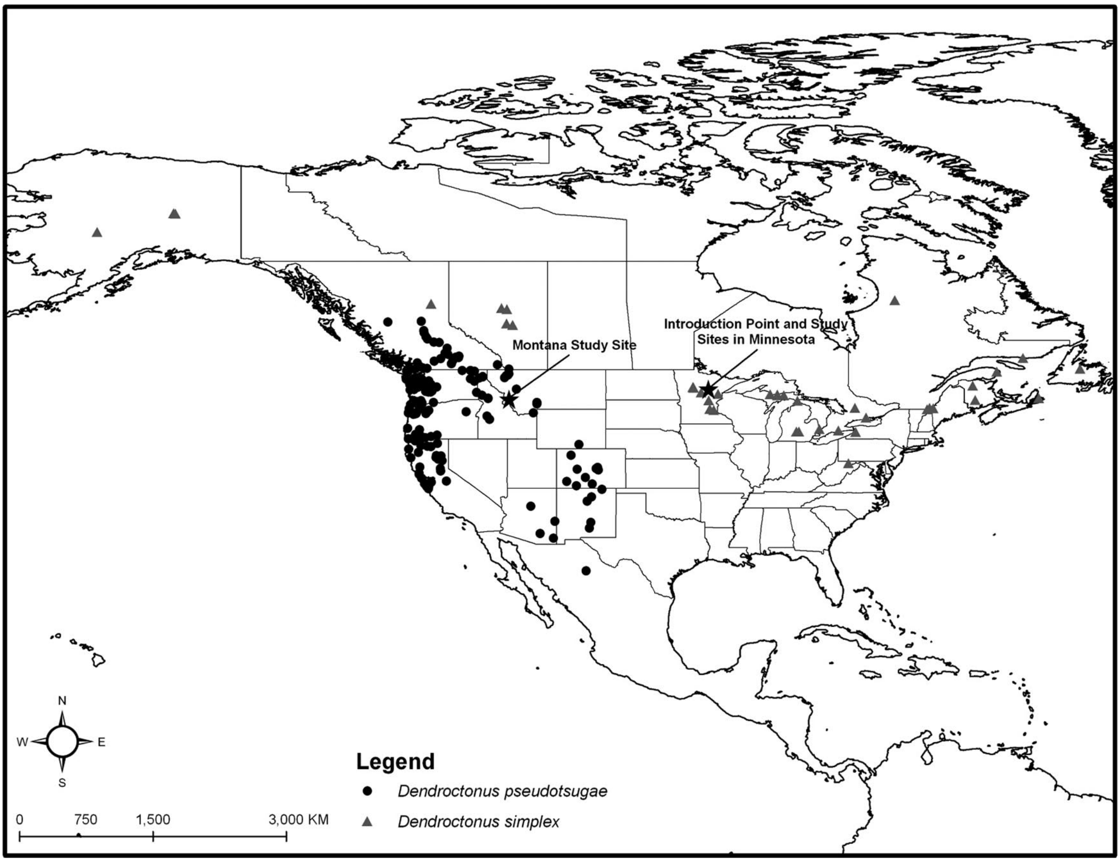

Fig. 1. Distributions of *D. pseudotsugae* and *D. simplex* in North America and the locations of study sites in Minnesota and Montana. *D. pseudotsugae* was inadvertently introduced into Minnesota in salvaged logged *L. occidentalis*. Locality data for *D. pseudotsugae* and *D. simplex* were taken from Wood (1982).

produce in the non-native host trees. In addition, two *D. pseudotsugae* pheromone blends were tested for their effectiveness on trapping *D. simplex* and *D. pseudotsugae.*

Materials and Methods

Study Sites. Four sites were chosen to survey for *D. pseudotsugae* within 8.5 km of Grand Rapids, MN (Table 1). Sites were selected because of their proximity to the probable *D. pseudotsugae* introduction site or because *D. pseudotsugae* had been captured there in pheromone-baited traps in previous years. The sites in Arbo, Cohasset, Grand Rapids, and Sugar Lake (elevation, 410–440 m) encompassed multiple cover types that included various tree species (Table 1).

To investigate whether or not *D. pseudotsugae* would use *L. laricina* as a host, a single site was chosen in the Bitteroot National Forest (45.91468° N, 113.82510° W) in western Montana. This site was located in an area that had recent *D. pseudotsugae* activity and tree mortality was expected to continue through the study period. The area was dominated by *P. menziesii* but also had *Tsuga heterophylla* (Raf.) Sarg. and *Picea engelmannii* Parry ex Engelm. present. Elevation was ≈1,770 m.

Detecting *D. pseudotsugae* in Minnesota. At each of the four sites in Minnesota, nine pairs of 1-m-long *P. menziesii* and *L. laricina* logs were placed in a systematic grid pattern with at least 150 m between pairs. Thus, there were 36 pairs of logs in this experiment. *P. menziesii* and *L. laricina* logs were placed 2 m apart in each pair, in a vertical position and fixed in place with wooden stakes and nylon wire ties. *D. pseudotsugae* pheromone attractants were tied to a wooden stake located equidistant between the logs in each pair. Two pheromone combinations were used: 1) frontalin (8.4 mg/d), seudenol (2.2 mg/d), and ethanol (30 mg/d) (Ross and Daterman 1995); and 2) a commercial formulation (Pherotech International [now Contech] Inc., Delta, BC, Canada) of frontalin (2.8 mg/d), methylcyclohexenol (MCOL) (1.5 mg/d), and ethanol (30 mg/d). All release rates were provided by the vendor and were measured at 20°C. Only one bait of either type was used for each pair of logs. Baits were placed in the field on 30 April and 1 May 2004. Logs were left out on field sites from 29 April, 2004 through 22 June 2004. *P. menziesii* logs were obtained from the

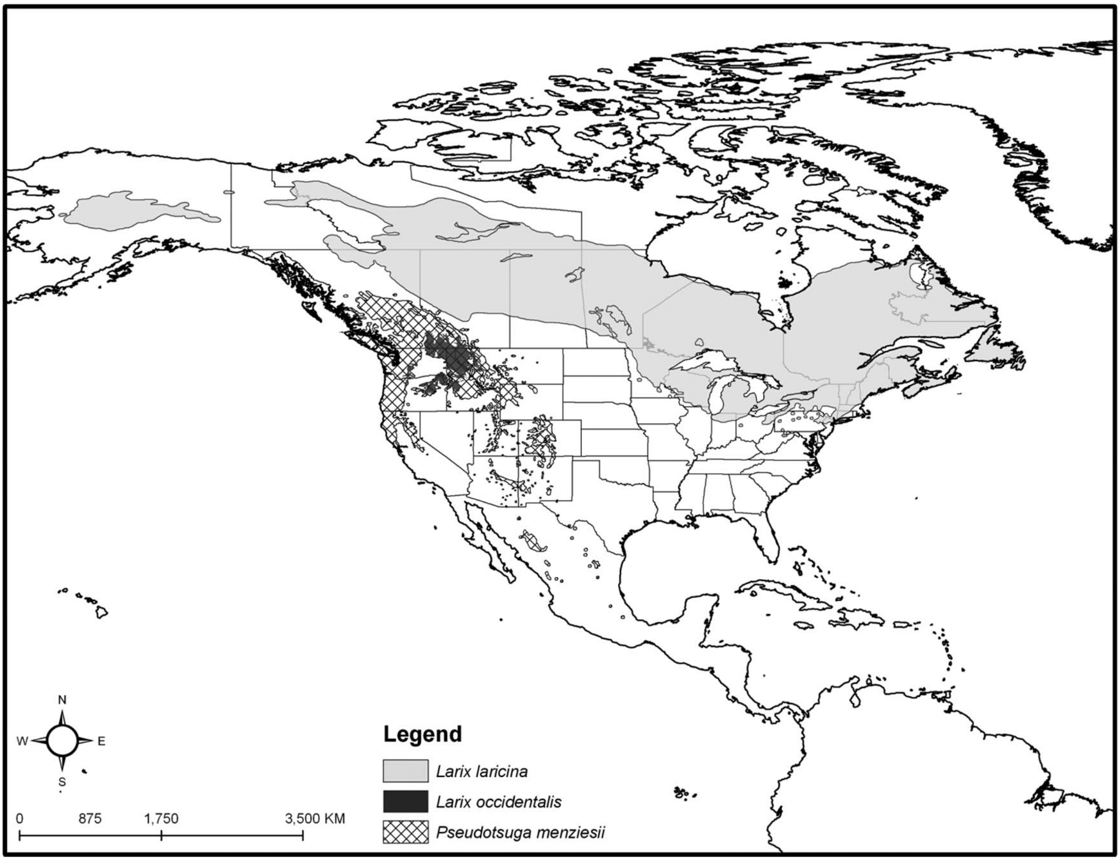

Fig. 2. Distributions of *P. menziesii*, *L. occidentalis*, and *L. laricina* in North America (data from USGS 1999).

Bighorn National Forest, Bighorn County, WY, and felled in early April. Uninfested *P. menziesii* with diameters between 29 and 35 cm were selected, cut into ≈1-m logs, and transported immediately in cold weather by truck to Minnesota for use in experiments. Uninfested *L. laricina* with diameters between 28 and 34 cm were cut from stands on the University of Minnesota Northern Central Research and Outreach Center (NCROC) in Grand Rapids, MN, and also felled in early April.

After removal from the field, logs were brought back to the NCROC where each log was cut into two equal length sections (i.e., 0.5 m). One half of each log was randomly chosen and bark was removed to examine the phloem and xylem surface for galleries of either *D. pseudotsugae* or *D. simplex.* There are subtle differences between *D. pseudotsugae* and *D. simplex* galleries and with careful dissection, galleries can be differentiated. The *D. pseudotsugae* egg gallery is straight and can range from 12 to 30 cm, but some may be as long as 90 cm (Wood 1982). Eggs are laid in groups at alternating positions along the length of the egg gallery. In comparison, *D. simplex* galleries are slightly sinuate with eggs laid in groups of three to six that are typically adjacent to one another (Wood 1982, Seybold et al. 2002). Brood adults were also collected from galleries for species identification. The other 0.5-m log section was held over winter in a sealed aluminum screen bag that served as a rearing cage. Emerged insects were collected in July 2005 and samples were checked for the presence of *D. pseudotsugae.* All bark beetles that emerged from logs were identified to species.

Table 1. Geographical locations and descriptions of study sites in Minnesota

Site	Location[a]	Forest type present
Arbo	47.34918° N, 93.57278° W	*L. laricina*, *Populus* spp.
Cohasset	47.26615° N, 93.65026° W	*L. laricina*, *Populus* spp., open areas
Grand Rapids	47.24805° N, 93.49666° W	*L. laricina*, *Pinus resinosa* Sol. ex Aiton, *Populus* spp.
Sugar Lake	47.20568° N, 93.66488° W	Commercial stand of *P. glauca*

[a] Elevation of study sites ranged from 410 to 440 m.

Colonization of Non-Native Host Logs by *D. simplex* and *D. pseudotsugae*. Logs from the *D. pseudotsugae* detection test also were used to assess the suitability of *P. menziesii* as a host for *D. simplex.* A companion study was conducted in Montana to assess whether *L. laricina* was a suitable host for *D. pseudotsugae.* In the

Montana study, 20 pairs of 1-m-long *P. menziesii* and *L. laricina* logs were placed along an access road in a *D. pseudotsugae*-infested area. Log pairs were separated by at least 50 m and spread throughout the area of *D. pseudotsugae* activity. This design differed from the Minnesota installation because we were not attempting to detect a newly established population; thus, the survey/sampling intensity was lower on a landscape level.

The *P. menziesii* logs in Montana were cut from live trees on 7 April 2005 from state forest lands adjacent to the Bitterroot National Forest. *L. laricina* logs were cut from live trees in Warba, MN (47.08898° N, 93.30823° W) during the last two weeks of March 2005 and stored frozen outdoors. The 1 m long logs of each species were placed and baited identically as they were in the Minnesota installation. Logs and baits were placed in the field on 8 April 2005 and collected on 15 June 2005.

Log Sampling. *Minnesota.* The 0.5-m-log section that was debarked to determine the presence of *D. pseudotsugae* galleries also was sampled to estimate *D. simplex* reproductive parameters in the logs from the two tree species. The number of *D. simplex* attacks, number of successful parent galleries, and the number of unsuccessful parent galleries were counted on each log section. Numbers of four-eyed spruce beetle, *Polygraphus rufipennis* (Kirby) (Coleoptera: Scolytidae), nuptial chambers also were counted over the entire log section. A 232-cm^2 sampling area was marked on a clear piece of acetate and used to define a subsampling area on log sections. Three randomly placed subsamples were taken on each log, with total length of parent galleries and total number of larval galleries recorded for each sample. The number of adults that emerged from the log section placed in screen bags was used to estimate adult emergence. The surface area for each log section was estimated by using the formula $(2\pi\, r) \times h$, and all variables were expanded to a per square meter basis.

Montana. After removal from the field, logs were brought back to the Bitterroot National Forest Sula Ranger District headquarters for destructive sampling and rearing. As was the case for the logs in Minnesota, one half of each log (top or bottom) was randomly selected for destructive sampling. The other half of the log was placed in a sealed screen bag that served as a rearing cage to estimate adult emergence and stored over the winter at the USDA Forest Service Chemical Ecology of Forest Insects Laboratory in Davis, CA.

Log sampling occurred earlier in the season compared with the previous year *D. simplex* log dissections in Minnesota, thus different colonization parameters were estimated. Visual inspection of the logs indicated that *D. pseudotsugae* had colonized the *P. menziesii* at a higher rate than *L. laricina.* Because of this, a slightly different sampling protocol was used for each tree species. A subsample of each *P. menziesii* log was taken, whereas the entire *L. laricina* log was sampled as described below. Three 232-cm^2 subsamples to estimate attacks, number and length of parent galleries, and number of eggs were taken from each *P. menziesii* log. Outer and inner bark was carefully removed down to the xylem surface. The sample was gently removed and all parent galleries were tallied. Additional bark was removed to trace and measure the entire length of each egg gallery. For each one-half meter log, attack density, gallery density, and egg density were calculated.

Because of the relatively lower attack rate on *L. laricina* logs, the half-meter logs were sampled entirely to estimate *D. pseudotsugae* colonization and colonization parameters. All bark was carefully removed from each log and all attacks, number and length of parent galleries, and number of eggs were counted or measured. For each one-half meter log, attack density, gallery density, and egg density were calculated. All estimates were expanded to a per square meter basis.

Data Analyses. Nonpaired *t*-tests were used to test for differences between surface areas of experimental logs. Analysis of variance (ANOVA) was used to test for differences between number of attacks, number of successful and unsuccessful parent galleries, parent gallery length, number of larval galleries, number of *P. rufipennis* nuptial chambers, and number of adults emerged from experimental logs in Minnesota. Log species and pheromone type were main effects, and interactions among site, log species, and pheromone were tested. ANOVA also was used to test for differences between the pheromone types. The four sites in Minnesota served as blocks. For the Montana experiment, number of attacks, number of parent galleries, parent gallery length, number of eggs, and number of adults emerged were tested with ANOVA. Because only one large area was used for the Montana experiment, no blocking was needed. To meet the assumptions of ANOVA, all data were checked for normality and homogeneity of variances. Because all data were normal and variances were homogenous, no transformations were necessary.

Results

Detecting *D. pseudotsugae* in Minnesota. Only three species of scolytids [*D. simplex*, *P. rufipennis*, and *Dryocoetes autographus* (Ratzeburg)] emerged from *L. laricina* and *P. menziesii* logs. In total, three *D. autographus* emerged from *P. menziesii* logs. No signs of *D. pseudotsugae* were found in any trap logs from the Minnesota sites. Every *Dendroctonus* spp. parent gallery located on *P. menziesii* and *L. laricina* logs was identified as belonging to *D. simplex.* In addition, brood adults collected during the bark sampling were all identified as *D. simplex.*

Colonization of Non-Native Host Trees by *D. pseudotsugae* and *D. simplex.* *D. simplex Log Colonization.* In Minnesota, *L. laricina* and *P. menziesii* logs had equal surface areas available for bark beetle colonization ($t = -0.97$, df = 70, $P = 0.34$). There were no significant interactions among the factors site, log species, and pheromone type for any of the variables tested (P values ranged from 0.07 to 0.97). There were no significant differences in *D. simplex* attacks on logs among the four sites used in this study ($F = 3.5$; df =

Table 2. *D. simplex* colonization and reproductive parameters on *L. laricina* and *P. menziesii* logs placed at four locations in northern Minnesota

Variable	Species of log[a,b]	
	L. laricina	*P. menziesii*
Attacks	7.23 ± 1.33a	2.06 ± 0.89b
Successful parent galleries	20.8 ± 3.16a	4.52 ± 1.63b
Unsuccessful parent galleries	0.24 ± 0.12a	0.48 ± 0.26a
Parent gallery length (cm)	209.89 ± 28.82a	110.19 ± 41.74a
Total larval galleries	1145.83 ± 126.98a	290.95 ± 99.43b
Adults	362.1 ± 64.57a	26.08 ± 7.19b
P. rufipennis galleries	3.37 ± 1.69a	13.73 ± 2.94b

[a] All estimates are per square meter of surface area. $N = 36$ for *L. laricina* and $N = 36$ for *P. menziesii* logs.

[b] Rows with the same letter are not significantly different ($P > 0.05$).

Table 3. *D. pseudotsugae* colonization and reproductive parameters on *L. laricina* and *P. menziesii* logs placed at one location in western Montana

Variable	Species of log[a,b]	
	L. laricina	*P. menziesii*
Attacks	5.07 ± 1.66a	4.97 ± 1.29a
Successful parent galleries	13.06 ± 3.40a	10.33 ± 2.13a
Parent gallery length (cm)	63.99 ± 23.32a	430.13 ± 99.70b
Eggs	55.69 ± 23.33a	112.4 ± 36.31a
Adults	28.5 ± 10.86a	58.11 ± 12.81b

[a] All estimates are per square meter of surface area. $N = 20$ for *L. laricina* and $N = 20$ for *P. menziesii* logs.

[b] Rows with the same letter are not significantly different ($P > 0.05$).

3, 56; $P = 0.48$). *D. simplex* attacks in *L. laricina* (7.23 ± 1.33) were significantly higher than in *P. menziesii* logs (2.06 ± 0.89) ($F = 9.88$; df = 1, 56; $P = 0.003$) (Table 2). There were significantly more *D. simplex* attacks on logs in the vicinity of the commercial bait that contained MCOL (6.54 ± 1.13) than the bait that contained seudenol (2.67 ± 1.19) ($F = 5.15$; df = 1, 56; $P = 0.03$). Although *D. simplex* successfully constructed significantly more parent galleries in *L. laricina* (20.8 ± 2.48) than in *P. menziesii* (4.52 ± 2.48) ($F = 21.65$; df = 1, 56; $P < 0.001$), there was no significant difference between tree species in the number of unsuccessful parent galleries ($F = 0.46$; df = 1, 56; $P = 0.5$). Length of parent galleries did not differ significantly between logs of the two tree species ($F = 3.30$; df = 1, 56; $P = 0.07$). Number of larval galleries was also significantly higher in *L. laricina* (1,145.83 ± 126.98) than in *P. menziesii* (290.95 ± 99.43) ($F = 28.82$; df = 1, 56; $P < 0.001$). The number of adults reared from *L. laricina* (362.1 ± 64.57) was significantly higher than from *P. menziesii* (26.08 ± 7.19) ($F = 35.62$; df = 1, 56; $P < 0.001$).

There was no interaction among site, pheromone, and log species and the response of *P. rufipennis* ($F = 0.23$; df = 1, 56; $P = 0.87$). There was no difference in response of *P. rufipennis* to either pheromone ($F = 1.08$; df = 1, 56; $P = 0.30$); however, this bark beetle was found significantly more often in logs of *P. menziesii* than *L. laricina* ($F = 8.47$; df = 1, 56; $P = 0.005$) (Table 2).

***D. pseudotsugae* Log Colonization.** In Montana, *L. laricina* and *P. menziesii* logs had equal surface area available for bark beetle colonization ($t = -0.87$, df = 38, $P = 0.39$). There were significantly more attacks on logs in the vicinity of the commercial bait that contained MCOL (8.99 ± 1.6) than the bait that contained seudenol (1.06 ± 0.47) ($F = 21.41$, df = 1, 36; $P < 0.001$). However, there was no significant difference between attack density ($F = 0.004$, df = 1, 36; $P = 0.95$), number of successful parent galleries ($F = 0.51$, df = 1, 36; $P = 0.47$), or the number of eggs ($F = 2.46$, df = 1, 36; $P = 0.13$) on *P. menziesii* or *L. laricina* logs (Table 3). Lengths of parent galleries were significantly longer in *P. menziesii* than in *L. laricina* logs ($F = 28.78$, df = 1, 36; $P < 0.001$). Adult emergence was significantly higher from *P. menziesii* than from *L. laricina* ($F = 9.03$, df = 1, 36; $P < 0.001$).

Discussion

Detecting *D. pseudotsugae* in Minnesota. Detecting a low-level population of a newly established insect is often a challenging task. Unlike many exotic species introductions, current pheromone technology (Ross and Daterman 1995) was available for detecting *D. pseudotsugae* in a new environment. The combination of a native host trap log (i.e., *P. menziesii*) and powerful pheromone attractants provided a strong survey tool for *D. pseudotsugae* in Minnesota. *D. pseudotsugae* responds strongly to pheromone blends of frontalin and ethanol along with either seudenol or MCOL, the two blends used in this study (Ross and Daterman 1995). Although attraction distances are unknown for the bait incorporating MCOL, the lure with seudenol attracts *D. pseudotsugae* from at least 200 m (Dodds and Ross 2002). Consequently, we estimated that we covered an area of ≈50 ha with pheromones and trap logs at each site. With ≈200 ha of mixed hardwood–conifer forests covered with pheromones in a landscape dominated by hardwoods, and targeting areas near the introduction point, we feel strongly that detection efforts were optimized. If *D. pseudotsugae* was in the area, we believe we likely would have detected the population through either log dissections to identify parent galleries or rearing of adults from infested logs. Neither *D. pseudotsugae* parent galleries nor adults were found in *P. menziesii* or *L. laricina* logs in Minnesota.

Although we did not detect *D. pseudotsugae* in any trap logs, we cannot entirely rule out the possibility that *D. pseudotsugae* has established populations in northern Minnesota, and we were unable to attract it to our logs. Alternatively, it is possible that *D. pseudotsugae* populations were never established and the trap catches in 2001 and 2002 were a result of multiple introduction events, even though pheromone-baited trap collections in 2002 came from as far away as 17 km from the point of introduction. Salvage-logged trees with bark were imported into Minnesota for at least three consecutive years. In addition to our detection efforts, a limited number of pheromone-baited traps not involved in this study were placed by several agencies throughout the original detection area. These traps captured only one adult in 2003 (14 traps) and two adults in 2005 (10 traps). No adults were captured in 2004 (125 traps), 2006 (six traps), or 2007 (nine traps) (M. A. Albers, personal communication). During outbreaks in its native range, *D. pseudotsugae* populations are often found relatively close to previous year infestations, whereas endemic populations are more dispersed (Dodds et al. 2006). If this spatial pattern was similar for introduced populations, detection would have been more difficult as populations may have spread further distances from the introduction point. In seeking suitable host material, *D. pseudotsugae* may have dispersed beyond the area covered by our detection study.

Colonization of Non-Native Logs by *D. simplex* and *D. pseudotsugae*. *D. simplex* and *D. pseudotsugae* were capable of completing development in logs of non-native tree species that they do not encounter in their native ranges. Although successful reproduction occurred in both cases, numbers of emerging adults were significantly lower in non-native logs. In studies investigating colonization success in different host and nonhost species, bark beetles either do not colonize or have lower success in nonhost logs than host logs (Elkinton and Wood 1980, Safranyik and Linton 1983, Wainhouse and Beech-Garwood 1994). However, in some cases beetles successfully colonize previously unreported hosts (Furniss and Schenk 1969, Safranyik and Linton 1982, Lee et al. 2008).

D. simplex attacked *L. laricina* logs at a rate 3 times higher than *P. menziesii,* indicating that this bark beetle clearly preferred its native host. However, *D. simplex* successfully created parent galleries and larvae initiated feeding in *P. menziesii* logs. The presence of *D. simplex* larvae in *P. menziesii* logs indicated that inside non-native logs, eggs hatched, larval feeding was initiated, and some level of development occurred. Although *D. simplex* was able to successfully reproduce within *P. menziesii,* only a fraction of adults were produced from the non-native logs compared with the native *L. laricina* logs.

D. simplex is recorded in only a few hosts (Wood 1982, Seybold et al. 2002) and did not successfully reproduce in *P. menziesii* logs in a laboratory experiment where entrance into logs was forced (Furniss 1976). It is unknown why *D. simplex* successfully colonized *P. menziesii* logs in the current field-based study and did not successfully reproduce in the previous laboratory study. The current study had more host material in the field, a large plume of pheromones, and a large source of local *D. simplex* to attack logs. Colonization of *P. menziesii* logs could have been a result of "spill-over" attacks from the *L. laricina* logs or the result of directed landing on the nonhost log. However, we saw no evidence of a temporal pattern of *L. laricina* logs attacked first and then a shift to *P. menziesii.*

The comparison of developmental variables in non-native and native logs was not as striking for *D. pseudotsugae* in Montana as it was for *D. simplex* in Minnesota. *D. pseudotsugae* attacked and initiated successful parent galleries equally well in *L. laricina* and *P. menziesii* in Montana, suggesting that at least in the presence of pheromone, *D. pseudotsugae* did not differentiate between a native and non-native log in pre- or postlanding assessment, or after penetrating the bark and entering the phloem of the non-native log. Although attacks and parent galleries were similar between the logs, twice the numbers of eggs were laid by *D. pseudotsugae* in its native host *P. menziesii.* The lower number of eggs laid in *L. laricina* could be explained by the effects of ovipositing and feeding in a tree species with thinner phloem (Haack et al. 1984a). Bark and phloem was not measured in the current study, but observations on *P. menziesii* suggest that this species had much thicker bark and phloem than that found on *L. laricina* logs. Although thinner phloem may explain reduced oviposition in *L. laricina* logs, the overall lower success of *D. pseudotsugae* in *L. laricina* might also be attributed to monoterpene content of logs. In *L. occidentalis, D. pseudotsugae* can only successfully complete development in downed trees and the monoterpene Δ^3-carene has been suggested as the causal agent for this (Reed et al. 1986). *Larix laricina* has almost the same relative content of Δ^3-carene as *L. occidentalis* (Stairs 1967), although the rate of volatilization from cut logs is unknown.

Both *D. simplex* and *D. pseudotsugae* readily attacked non-native logs in this study. Host volatiles are important components of host selection by bark beetles (McMullen and Atkins 1962, Byers 1995, Kohnle 2004, Pureswaran and Borden 2005, Seybold et al. 2006), but pheromones used in the study may have overwhelmed this attraction and led to the bark beetles attacking both hosts in these studies. Although this would explain the landing on non-native logs, it would not explain the initiation of parent galleries and even subsequent oviposition and development in those logs. Some bark beetle species use postlanding cues to assess host suitability (Elkinton and Wood 1980, Hynum and Berryman 1980, Witanachi and Morgan 1981, Moeck et al. 1981, Raffa and Berryman 1982, Wallin and Raffa 2000), but *D. simplex* and *D. pseudotsugae* may not behave in the same manner. Once inside the phloem of a log, colonizing *D. simplex* and *D. pseudotsugae* would be faced with other obstacles to successful reproduction. The cause of high mortality to *D. simplex* and *D. pseudotsugae* brood developing in non-native logs is unknown, but various mechanisms affect colonizing bark beetles. Resin chemistry (Raffa et al. 1985, Seybold et al. 2006), lignin chemistry (Wainhouse et al. 1990), associated fungal success rate (Neal and Ross 1999), and physical properties of resin (exudation pressure, rate of flow, rate of crystallization) and phloem (moisture and thickness) (Cobb et al. 1968, Amman 1972, Haack et al. 1984b) have all been suggested as potential limits to bark beetle colonization success. These or other mechanisms could impact developing brood. Nonetheless, the capacity of each bark beetle species to exercise the full sequence of behaviors from host selection to development and emergence in the non-native logs suggests that an ancestral pattern still exists that links *D. simplex* and *D. pseudotsugae* to their common progenitor. This relictual or lateral host recognition is similar to that hypothesized by other workers to explain the colonization by European phytophagous insects of tree genera in North America that have been extinct in Europe since the Pleistocene (Niemelä and Mattson 1996, Langor et al. 2009).

Are Indigenous Exotics a Threat? Predicting the likelihood of establishment of a nonindigenous organism is a difficult challenge and many factors must be considered, including life-history characteristics and size of the invading population (Kolar and Lodge 2001, Taylor and Hastings 2005). In the case of bark beetles, life-history characteristics (e.g., cold tolerance, host range, dispersal potential, reproductive potential, aggressive or opportunistic colonization behavior) are important considerations in determining the risk that a given species presents to a new ecosystem. For example, although *D. simplex* and *D. pseudotsugae* have the ability to exploit weakened material as a reproductive substrate, they both have a restricted host range. The ability of a bark beetle to exploit downed or recently dead material likely increases its ability to become established in a new environment because the invading population does not need to aggregate to overcome defenses of living host trees. Conversely, a monophagous species may have a more difficult transition onto a new host. A polyphagous secondary species probably has the highest probability of becoming established in a new environment. Finally, a more aggressive beetle like *D. ponderosae* would probably need to be introduced in large numbers to become established in a new environment. Given the current example of *D. pseudotsugae* in Minnesota, it is evident that pathways exist to move large numbers of beetles over large distances intracontinentally and into new environments.

The destructive capacity of bark beetles is not limited to an established population outright killing trees. Introduction of pathogenic fungi into new systems can be as deleterious as an introduced insect (Gordon et al. 2001). This is especially true if native insects are effective vectors of the pathogen. Because *D. pseudotsugae* and *D. simplex* can successfully hybridize (Furniss 1976) it seems possible that microorganismal fauna could interact in host trees and become established, with or without successful colonization by the invading bark beetle. Both bark beetles responded to pheromone combinations used in this study and share seudenol as a common attractant (Rudinsky et al. 1974, Werner et al. 1981), so *D. simplex* attacked trees would probably be attractive to *D. pseudotsugae* in a natural setting. Temporal overlap in flight also would be conducive for interactions in attacked trees and increase the chances of horizontal transmission of microorganisms.

Of the western North American *Dendroctonus* spp., *D. pseudotsugae* may be one of the most unlikely species to become established in a new environment. If *L. laricina* were not an acceptable host for *D. pseudotsugae*, it is unlikely it would establish on other trees present in Minnesota forests. *D. simplex*, another monophagous bark beetle, also would only be a limited threat to *P. menziesii* in western forests. However, we did not investigate *D. simplex*'s success rate in *L. occidentalis*, a species that it has successfully colonized in the laboratory (Furniss 1976).

The sibling species *D. pseudotsugae* and *D. simplex* present an example of geographically isolated entities where pre- and postmating barriers seem to be absent. Other North American bark beetles with related substructuring of populations include eastern and western populations of *I. pini* where a premating barrier is present but a postmating barrier is absent (Lanier 1972, Seybold et al. 1995, Domingue and Teale 2007); eastern and western populations of *Dendroctonus valens* LeConte and eastern populations of *Dendroctonus terebrans* (Olivier) where the status of a premating barrier is unclear, but a postmating barrier is present (Pajares and Lanier 1990); and a subset of the *grandicollis* species group of *Ips* (*confusus, hoppingi, paraconfusus*) in which a premating barrier is absent, but a postmating barrier is present (Merrill 1991, reviewed in Seybold 1993). Most of these taxa are highly polyphagous (Wood 1982), and those that are monophagous or oligophagous (*I. confusus* and *I. hoppingi*) will develop in a wider range of hosts in the laboratory (Merrill 1991). Although there has been considerable opportunity for humans to integrate these populations or for the populations to interact in zones of sympatry or through dispersal from nearby zones of allopatry, they seem to have remained segregated. Thus, intracontinental blending of some North American bark beetle populations seems to have occurred with low frequency.

Nonetheless, several indigenous exotic species have become established outside their natural ranges in North America (Wood and Stark 1968, Gall 1992), and this is probably the case in Europe and other fauna-rich places that have significant intracontinental movement of wood products. Although predicting the effects of these introductions is difficult, potential impacts should be considered when moving material intracontinentally. Although *D. pseudotsugae* does not seem to be established in Minnesota, its introduction still illustrates the potential for indigenous insects being introduced into new environments in large numbers. Aggressive bark beetles, or species with a wider host breadth, could pose significant threats to native ecosystems and given an extremely large founder population, could have a better chance of establishing populations. Wood products resulting from the current unprecedented *D. ponderosae* outbreak in western Canada raise serious concerns as a source of infested material that could be transported, along with other organisms, into new environments (Allen et al. 2003).

Acknowledgments

We thank Mike Albers (Minnesota Department of Natural Resources); Kurt Allen and Dan Long (USDA Forest Service, Forest Health Protection, Region 2, Rapid City Service Center); Kurt Gelderman (Montana Department of Natural Resources and Conservation); Ken Gibson (USDA Forest Service, Forest Health Protection, Region 1, Missoula), Allison Hanson (University of California–Riverside); Scott Hill (USDA Forest Service, Bighorn National Forest); Brad Jones (Itasca County Land Department); Jim Lind, Kamal Gandhi, and Tim O'Brien (University of Minnesota); Sheryl Meekin (USDA Forest Service, Bitteroot National Forest, Sula Ranger District); and Scott Pitak (Pitak Logging) for logistical support and field assistance. Larex Incorporated, Minnesota Power, and Blandin Paper Company allowed access to study sites in Minnesota. Funding was provided by the USDA Forest Service, Forest Health Protection, Northeastern Area Office; the USDA Forest Service Pacific Southwest Research Station; and the Department of Forest Resources, University of Minnesota.

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Received 3 May 2009; accepted 21 October 2009.