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Stand-level factors associated with resurging mortality from eastern larch beetle (*Dendroctonus simplex* LeConte)

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ABSTRACT

The current outbreak of eastern larch beetle (*Dendroctonus simplex* LeConte) in Minnesota, USA, ongoing since 2000, has been characterized with a severity and duration unprecedented in previous outbreaks within the state. This study investigates the relationship between tamarack mortality due to eastern larch beetle and extant stand and site characteristics. Observations of tree attribute information and site condition collected over the course of the outbreak from nearly 15,000 tamarack trees in three different ecological regions of Minnesota were modeled using linear regression. Increasing tree diameter was the best indicator of tamarack mortality within the northern limits of the state's tamarack range and during the later portion of the outbreak. Tamarack density was negatively related to tree mortality in the north-central region during the later outbreak, while the density of co-located non-host gymnosperms was positively related to tree mortality in areas of marginal host distribution. A temporal change in the importance of predictor variables suggests that the influence of tree and site characteristics evolved as the outbreak progressed and subsequent mortality increased. A greater understanding of the factors associated with tamarack mortality and how the those factors change over time and space will help to inform management practices and mitigate the impacts of this bark beetle on the tamarack resource in Minnesota.

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1. Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) play an intrinsic role in North American coniferous forests as key drivers of natural disturbance (Bentz et al., 2010; Hicke et al., 2012). Generally regarded as the most significant biotic agents of mortality within forested ecosystems, some species of bark beetles develop landscape-level outbreaks that can alter biomes by eliciting changes in hydrology, nutrient cycling, and fire regimes (Raffa et al., 2008; Weed et al., 2013). Disturbances by bark beetles have resulted in significant tree mortality across a range of forest ecosystems, including but not limited to occurrences in the forests of ponderosa (*Pinus ponderosa* Lawson & C. Lawson), lodgepole (*Pinus contorta* Douglas ex Loudon), and whitebark (*Pinus albacaulis* Engelm.) pines in the Rocky Mountains (Aukema et al., 2006; Logan et al., 2010; Chapman et al., 2012); spruces (*Picea* spp.) in south-central Alaska (Berg et al., 2006; Sherriff et al., 2011); and loblolly (*Pinus taeda* L.) and shortleaf (*Pinus echinata* Mill.) pines in the southeastern portion of the USA (Duehl et al., 2011; Weed et al., 2013). Over the past few decades, many bark beetle outbreaks have been increasing in frequency, size, and severity (Raffa et al., 2008; Bentz et al., 2010).

Eastern larch or tamarack (*Larix laricina* (Du Roi) K. Koch) is a deciduous conifer that extends across northern North America with only a small break in western Yukon, Canada (Fig. 1) (Little, 1971). The range of tamarack is concomitant with that of eastern larch beetle (*Dendroctonus simplex* LeConte), the only tree-killing bark beetle associated with this host. Sporadic episodes of tree-killing activity by this native insect have been recorded in North America for over 125 years (Langor and Raske, 1988). Landscape-level outbreaks of eastern larch beetles were not observed until the mid-1970s, however, when large outbreaks occurred in Alaska, eastern Canada, and the northeastern part of the USA (Werner, 1986; Langor and Raske, 1989a). Each of these outbreaks, which lasted up to six years, were preceded by large-scale defoliation events by spruce budworm (*Choristoneura fumiferana* (Clemens)), larch sawfly (*Pristiphora erichsonii* (Hartig)), larch budmoth (*Zeiraphera* spp. Treitschke), or larch casebearer (*Coleophora laricella* (Hübner)) (Werner, 1986; Langor and Raske, 1989a,

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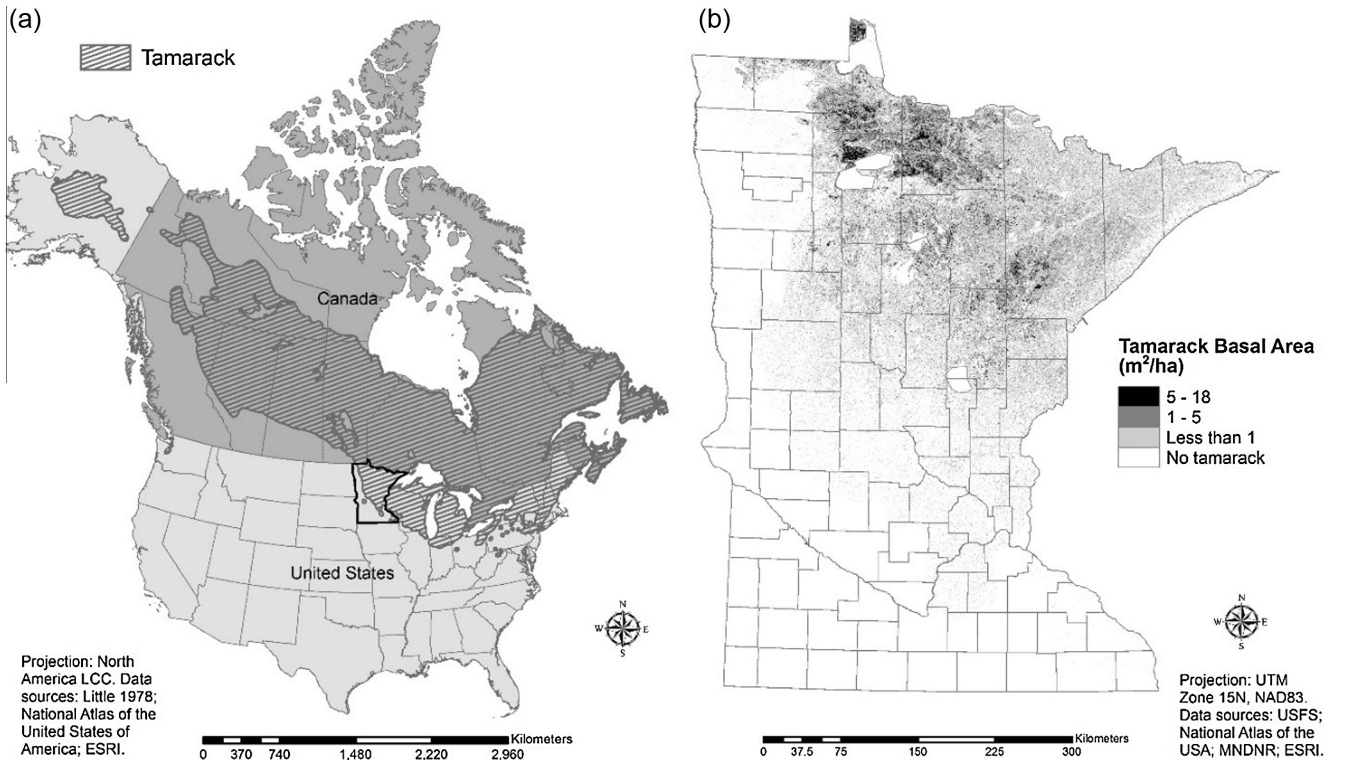

Fig. 1. Distribution of tamarack, *Larix laricina*: (a) range in North America, and (b) density in Minnesota. Digital vector data for the range of tamarack was adapted from Little (1971) and raster data describing tamarack basal area was derived using a k-nearest neighbor imputation approach developed by Wilson et al. (2012).

1989b). Feeding by defoliators may predispose tamarack to attack by eastern larch beetles (Swaine, 1918).

The states of Minnesota, Wisconsin, and Michigan represent the southwestern extent of the range of tamarack in the Great Lakes region of the USA, where tamarack functions as an important pioneer species, especially on hydric sites (Duncan, 1954; Seybold et al., 2002). Where not growing in pure stands, tamarack mixes with black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), balsam fir (*Abies balsamea* (L.) Mill), northern white-cedar (*Thuja occidentalis* L.), black ash (*Fraxinus nigra* Marshall), red maple (*Acer rubrum* Marshall), and paper birch (*Betula papyrifera* Marshall), especially on mesic sites (Duncan, 1954; Burns and Honkala, 1990). Estimates of the extent tamarack in Minnesota at the time of European settlement are difficult to ascertain; however, tamarack was the most frequently occurring species in the Public Land Survey (PLS) conducted between 1847 and 1908, where it accounted for 16.9% of bearing trees used to navigate to survey corners (Almendinger, 1997). Inventory data collected by the US Department of Agriculture (USDA), Forest Service during Minnesota's first forest inventory, conducted in 1936, estimated the area of tamarack at approximately 265,000 ha (Stone, 1966). While the total area of tamarack forests grew to nearly 444,000 ha by 2014, analysis of changes in species composition since the PLS have indicated a decrease in tamarack abundance from 23% to 6% by 2014 (Fig. 1) (Hanberry et al., 2013; Miles, 2015).

Compounding this long-term reduction in the tamarack cover type in the wake of European settlement has been a massive outbreak of eastern larch beetles throughout the Great Lakes region since 2000 (Graham and Storer, 2011; McKee and Aukema, 2015). This ongoing outbreak represents the longest continuous period of tree-killing activity by eastern larch beetle ever recorded in North America (Langor and Raske, 1988; Aukema et al., 2016). Over the course of more than a decade, the volume of dead tamarack in Minnesota due to eastern larch beetle rose from approximately 108,000 m^3 in 2003 to 426,000 m^3 by 2014, making eastern larch beetle the largest contributor (88%) to tamarack mortality in the state (Miles, 2015). As eastern larch beetles typically colonize trees that are weakened by local disturbance events such as defoliation from other insects, wind throw, ice damage, flooding, or timber harvesting activities (Langor and Raske, 1988; Langor and Raske, 1989a, 1989b), none of which have been readily apparent in the current outbreak, the reasons behind the deviation of eastern larch beetle activity from historic patterns is unclear (McKee, 2015).

Causal factors for outbreaks of eastern larch beetle are not well understood (Langor and Raske, 1989b; Seybold et al., 2002). Recent studies investigating the increasing progression of tamarack mortality from eastern larch beetle have focused largely on the insect. Eastern larch beetles typically overwinter as adults. They emerge in early spring and colonize tamaracks through a pheromone-mediated mass attack strategy common to many bark beetle species. After mating, females lay eggs along galleries bored underneath the bark, where the brood then develops. Some parental females will re-emerge from these trees to attack new trees, although these later sibling broods may not develop to cold-hardy adult stages by the fall, prior to overwintering (Langor and Raske, 1987a, 1987b). Recent laboratory and field studies on the development of eastern larch beetles suggest that extended growing seasons and/or elevated temperatures increase the likelihood that sibling broods will overwinter as adults, increasing insect numbers in subsequent years (McKee, 2015; McKee and Aukema, 2015). Additionally, warmer winter temperatures are projected to reduce the over-wintering mortality of eastern larch beetles and also contribute to the number of beetles surviving into the subsequent year (Venette and Walter, 2012).

Despite these new insights about the insect, little is known about site and stand conditions that are favorable for outbreaks of eastern larch beetles (Langor and Raske, 1987a; Langor, 1989;

Seybold et al., 2002). Identifying tree- or stand-level attributes associated with increased risk of mortality has been completed for many species of bark beetles such as the mountain pine beetle (*Dendroctonus ponderosae*, Hopkins), spruce beetle (*D. rufipennis* Kirby), Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), and European spruce bark beetle (*Ips typographus* (L.)) (Safranyik et al., 1975; Negron, 1998; Dutilleul et al., 2000; Eriksson et al., 2005; Safranyik, 2011). Subsequent knowledge of the profiles of forest stands at risk to beetle attack can be used to develop silvicultural guidelines to reduce pest damage (Shore et al., 2000; Fettig et al., 2007).

Characterizing relationships between tree mortality and stand conditions is the first step in developing silvicultural management tactics against eastern larch beetle, as none currently exist (Seybold et al., 2002). In this paper, we utilize a dataset of the USDA Forest Service, Forest Inventory and Analysis program (FIA), which represents a nationally consistent inventory of forests across all land ownerships. Analysis of nearly 15,000 tamarack trees measured on almost 1700 plots spanning three ecological regions of Minnesota, USA was collected over a 10-year period, ranging from 2005 to 2014. The specific aim was to elucidate the relationship between tree mortality from eastern larch beetles and various site, stand, and tree characteristics, and thus inform management strategies aimed at minimizing the impacts of this bark beetle.

2. Materials and methods

2.1. Sampling methods and forest inventory data

Field data collection is conducted in a consistent and systematic manner as part of a national inventory of US forests under the FIA program (Bechtold and Patterson, 2005). In accordance with the FIA definition, forest land must meet a minimum area of 0.4 ha, be at least 36.6 m wide, and have at least 10% canopy cover of live trees (Bechtold and Patterson, 2005). Plots consist of four 7.2 m fixed-radius circular subplot, each containing a 2.07 m microplot. All trees greater than 12.7 cm in diameter at breast height (d.b.h.) are measured on forested subplots; seedlings and trees with a d.b.h. between 2.5 and 12.7 cm are measured on the microplot (USDA Forest Service, 2014). Additionally, field crews record plot attributes (e.g., land cover, forest type, ownership) and tree measurements, including species, diameter, disturbance, and, whenever possible, presumed agent of mortality if the tree is dead. Trees colonized by eastern larch beetle are relatively easy to ascertain, as there are few bark beetles that feed on tamarack and eastern larch beetles etch characteristic gallery patterns under the bark (Dodge, 1938; Langor, 1991; McKee, 2015). Dead tamarack with field recorded insect damage or insect cause of death were classified as trees killed by eastern larch beetle (USDA Forest Service, 2015).

Data collection by the FIA program since 1998 is conducted on an annual basis, such that a percentage of inventory plots are visited each year over a variable period. In Minnesota, 20% of plots are collected annually reaching a completed inventory after a 5-year period. As a result, site- and tree-level observations were collected on 1696 plots inventoried in Minnesota over two inventory periods: 2005–2009 and 2010–2014 (Table 1). We designate these time periods as 'earlier' and 'later' as they span the early and late periods of the statewide eastern larch beetle outbreak that continues to the present (Fig. 2, Table 1). Each plot contained at least one tamarack tree greater than 12.7 cm d.b.h., and all plots containing tamarack were included in the analysis even if no mortality was noted. Eleven site-, stand-, and tree-level variables (of which 6 were continuous and 5 were categorical), collected for live and

Table 1
Summary of USDA Forest Service, Forest Inventory and Analysis data used to determine association of tamarack mortality with eastern larch beetle, 2005–2014, Minnesota, USA.

Ecological region	Number of observations			
	2005–2009		2010–2014	
	Plots	Trees	Plots	Trees
North-central	326	3324	344	3479
Superior	473	3691	507	4025
Oak savanna/Parkland	24	193	22	189

dead trees greater than 12.7 cm d.b.h., were considered as potential predictors of susceptibility to eastern larch beetle mortality (Table 2). Because tamarack grows across a wide range of edaphic conditions, the study area was divided into three regions: the North-central region of the state, a Superior region adjoining Lake Superior, and the Oak savanna/Parkland region, which extends the length of the state, running from the northwest to southeast (Fig. 2). These study regions were developed by aggregating formal ecological units constructed by the USDA Forest Service based on a national ecological classification system that considers criterion such as climate, native plant communities, and geology (McNab et al., 2007), and which is utilized by the US Environmental Protection Agency/Commission for Environmental Cooperation, the Minnesota Department of Natural Resources, and the World Wildlife Fund.

2.2. Statistical analysis

The relationship between identified tree-, stand-, and site-level variables (Table 2) and tamarack mortality due to eastern larch beetle was modeled using linear mixed effects models via the glmer function in the lme4 package in the R statistical environment (Bates et al., 2014). The binomial response was equal to one when mortality was due to eastern larch beetle and zero when mortality was absent or not due to eastern larch beetle and a logit link function was applied in the model. We approached this analysis in two ways. First, we explored the association of each of the candidate variables to explain tree mortality (Table 2) in separate regression models. A term for plot was fit as a random effect in each model. Analyses were conducted separately for two periods, earlier (2005–2009) and later (2010–2014), with no repeated measures of trees within each time period. Separate models were developed for each of the three regions for the earlier and later time periods, and resulted in 66 individual model runs. Second, best fit models were constructed for each region and for each time period using all available predictors. Correlation between pairs of variables was assessed prior to inclusion in a model in order to reduce inferential problems from multicollinearity. The two variables with the lowest P-values from the single predictor models were used for an initial fit, and a manual forward selection process was conducted to arrive at a best model, where all terms were significant using $\alpha = 0.05$.

3. Results

The tamarack forest type is most abundant in the North-central and Superior regions of Minnesota, where it covers approximately 208,000 ha and 229,000 ha, respectively. Within the Oak savanna/Parkland region, the tamarack forest type comprises nearly 6500 ha. Landscape-level mortality due to eastern larch beetle became evident in the plot data in 2003 (Fig. 3a and b). Peak outbreak mortality occurred in 2012 in both the North-central and Superior regions with volume losses of approximately 303,000 m^3 and 147,000 m^3, respectively. Peak mortality of

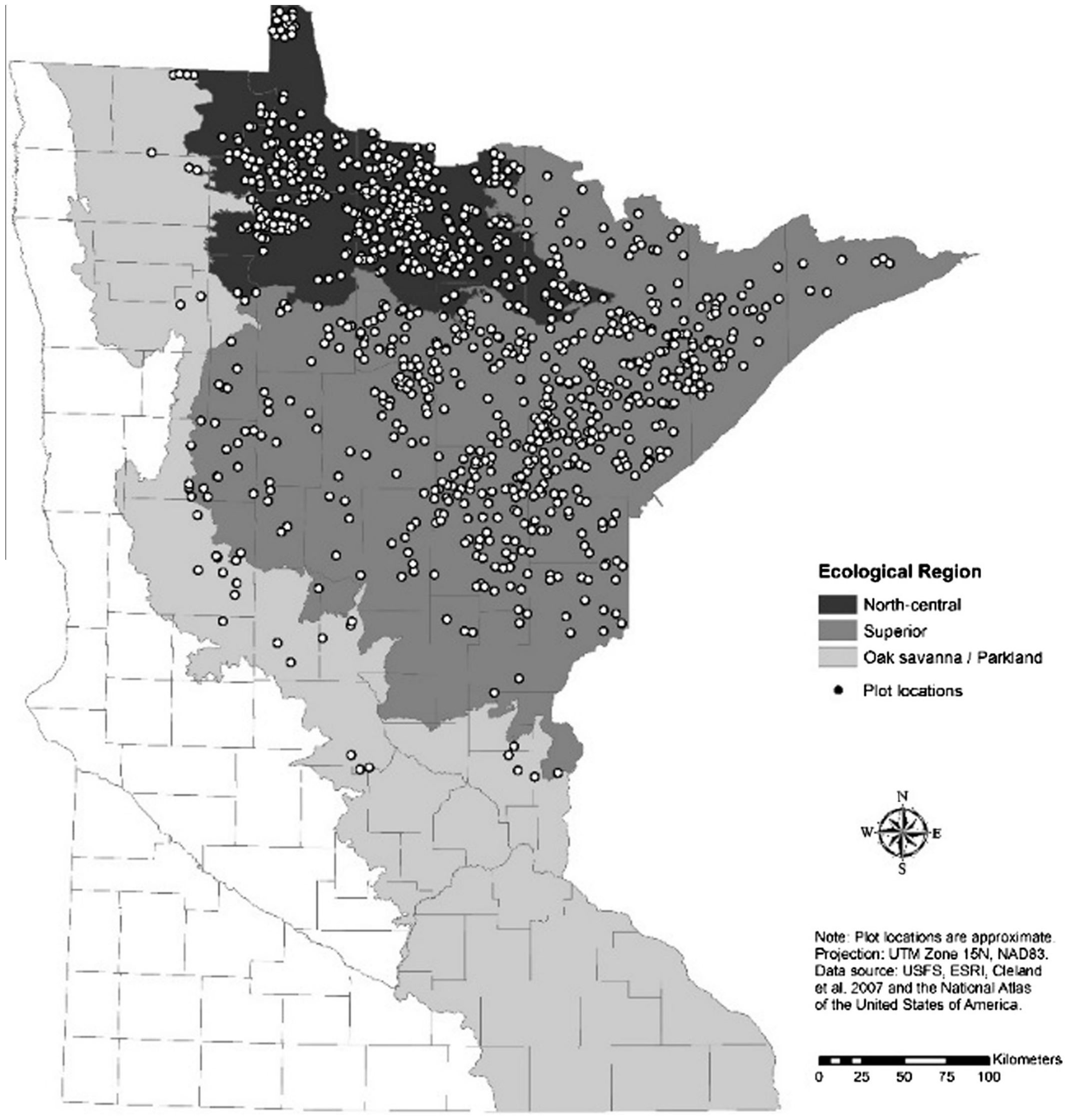

Fig. 2. Location of plots by ecological region: North-central (n = 670), Superior (n = 980), and Oak savanna/Parkland (n = 46), Minnesota, USA. Plot locations are approximate. (See above-mentioned references for further information.)

Table 2
Variables used to analyze association of tamarack mortality with eastern larch beetle in long-term FIA study plots, 2005–2014, Minnesota, USA. More detailed descriptions of FIA's inventory variables can be found in USDA Forest Service (2015). Summary statistics are provided for continuous variables where useful.

Variable	Description	Minimum	Mean	SE	Median	Maximum
Basal area of tamarack	Total tree basal area due to live tamarack on the plot (m^2)	0	0.56	0.0036	0.45	2.53
Basal area of non-hosts	Total tree basal area due to live non-host species on the plot (m^2)	0	0.28	0.0031	0.12	4.36
Basal area of non-hosts gymnosperms	Total tree basal area due to live non-host gymnosperms on the plot (m^2)	0	0.23	0.0029	0.07	4.33
Basal area of angiosperms	Total tree basal area due to live angiosperms on the plot (m^2)	0	0.05	0.0012	0	1.39
Diameter (cm)	Tree diameter at breast height (1.4 m)	12.70	18.43	0.0441	17.02	61.21
Distance to road	Distance of plot to nearest improved road (0 = ⩽91.4 m; 1 = >91.4 m)	–	–	–	–	–
Inventory year	Year observations were collected	–	–	–	–	–
Physiographic class	Physiographic status determined by landform, topography, and soils (0 = non-hydric; 1 = hydric)	–	–	–	–	–
Site class	Site productivity (0 = ⩽3.4 m^3/ha/yr; 1 = >3.4 m^3/ha/yr)	–	–	–	–	–
Site index (m)	Average total height that dominant and co-dominant trees in full-stocked, even-aged stands will obtain at key ages; a measure of stand productivity	4.27	13.12	0.0298	12.80	27.43
Water	Presence of water on a plot, e.g., streams, bogs, and flood zones (0 = no, 1 = yes). May be temporary or permanent but is <0.41 ha in size or <9.14 m wide	–	–	–	–	–

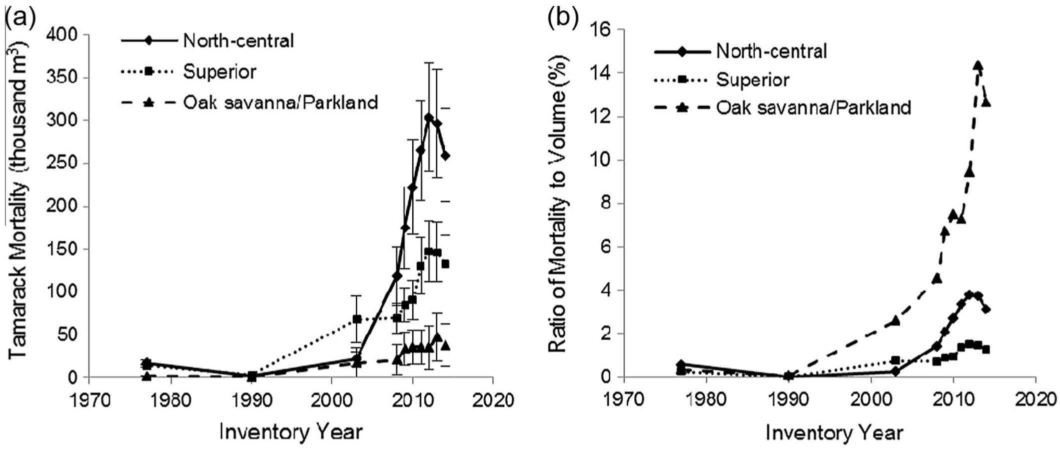

Fig. 3. Annual volume of tamarack lost to eastern larch beetle in Minnesota, 1977–2014, detected from FIA plots by ecological region: (a) thousands of cubic meters and (b) percent of total live volume of tamarack, 1977–2014. Error bars represent a 68% confidence interval and are unavailable for inventory years prior to 2003 and for ratio estimates.

tamarack in the Oak savanna/Parkland region of Minnesota occurred in 2013, with a loss of 47,000 m^3 of tamarack volume (Fig. 3a). Within the North-central and Superior regions, the rate of tamarack mortality, as a function of live tree volume, remained relatively low, with peak mortality rates of 3.78% and 1.51%, respectively (Fig. 3b). Conversely, while total mortality was low in the Oak savanna/Parkland region, the rate of mortality was consistently the highest throughout the course of the outbreak, reaching a peak rate of 14.38%. Across all 3 regions, the rate of mortality increased as the outbreak progressed, indicating subsequent annual losses in tamarack volume that were greatest in the Oak savanna/Parkland.

The significance of tree- and stand-level variables on the probability of tamarack mortality due to eastern larch beetle varied both regionally and temporally (Tables 3 and 4). In the early stages of the outbreak (Table 3), the only variables that explain the likelihood of tree mortality occurred within the North-central region, where the probability of mortality increased with increasing tree diameter and the presence of water (Table 3). The 50% response point on a logistic regression can be determined by dividing the intercept by the slope coefficient. Examining the effect of tree diameter, the plot data showed that tamaracks greater than 32 cm in diameter (i.e., −15.13/0.47 in Table 3) were more than 50% likely to be killed by eastern larch beetle in the early stages of the outbreak in the North-central region of the state. In the later stages of the outbreak, increased likelihood of tree mortality was again positively associated with diameter in the North-central region, and also in the Superior region (Table 4). Here, the beetles again appeared to be killing the largest diameter trees, with trees larger than 48 cm (North-central region) and 54 cm (Superior region) more than 50% likely to have been killed by eastern larch beetle. In the Oak savanna/Parkland region, we noted that increasing basal area of non-host gymnosperms was positively related to eastern larch beetle mortality during the later stages of the outbreak (Table 4).

When explanatory variables were examined in multiple regressions, again, tree diameter and presence of water were positively related to the probability of tamarack mortality due to eastern larch beetle in the North-central region in the early years of the outbreak (Table 5). Among the models produced for the later years, the best model for the North-central region included positive terms for tree diameter and site index as a measure of stand productivity, and a negative term for tamarack basal area (Table 6). We did not find that the addition of any variables to the model with tree diameter improved that model. The probability of eastern larch beetle mortality in the Oak savanna/Parkland region was positively related to non-host gymnosperm basal area and tree diameter.

Table 3
Effects of various tree- and stand-level variables on mortality of tamarack from eastern larch beetle, measured in long-term FIA study plots, 2005–2009, Minnesota, USA. Table reflects single-variable logistic regressions, separately for each region. For example, estimating effect of tree diameter on probability of mortality in the Superior region can be calculated P(tamarack is dead) = $1/1 + e^{-(-13.67+0.11*\text{diameter})}$. Estimates listed in bold are statistically significant ($\alpha = 0.05$). Estimates listed as NA contain insufficient sample sizes.

Variable [a]	North-central		Superior		Oak savanna/Parkland	
	Intercept	Slope	Intercept	Slope	Intercept	Slope
Basal area of tamarack	**−10.03 (<0.01)**	−0.10 (0.53)	**−12.12 (<0.01)**	−0.17 (0.62)	**−10.71 (0.02)**	0.10 (0.88)
Basal area of non-hosts	**−10.50 (<0.01)**	−0.02 (0.89)	**−12.57 (<0.01)**	−0.15 (0.76)	**−9.78 (0.01)**	−0.61 (0.86)
Basal area of non-host gymnosperms	**−10.32 (<0.01)**	−0.08 (0.67)	**−11.84 (<0.01)**	−1.35 (0.59)	NA	NA
Basal area of angiosperms	**−10.64 (<0.01)**	0.25 (0.41)	**−13.01 (<0.01)**	0.10 (0.82)	**−9.88 (0.01)**	−0.48 (0.87)
Diameter	**−15.13 (<0.01)**	**0.47 (<0.01)**	**−13.67 (<0.01)**	0.11 (0.39)	**−11.19 (<0.01)**	0.11 (0.51)
Distance to roads	NA	NA	**−12.08 (<0.01)**	−0.90 (0.82)	NA	NA
Inventory year	**−11.94 (<0.01)**	0.48 (0.33)	**−13.21 (<0.01)**	0.10 (0.90)	**−10.17 (0.03)**	−0.05 (0.97)
Physiographic class	**−10.14 (<0.01)**	−0.45 (0.85)	NA	NA	NA	NA
Site class	**−10.83 (<0.01)**	0.93 (0.46)	**−12.98 (<0.01)**	0.21 (0.93)	NA	NA
Site index	**−10.51 (<0.01)**	0.55 (0.35)	**−15.07 (<0.01)**	0.05 (0.63)	−8.92 (0.36)	−0.03 (0.89)
Water	**−10.85 (<0.01)**	**2.53 (0.04)**	**−13.13 (<0.01)**	1.17 (0.64)	NA	NA

[a] Variable descriptions are provided in Table 2.

Table 4
Effects of various tree- and stand-level variables on mortality of tamarack from eastern larch beetle, measured in long-term FIA study plots, 2010–2014, Minnesota, USA. Table reflects single-variable logistic regressions, separately for each region. For example, estimating effect of tree diameter on probability of mortality in the Superior region can be calculated P(tamarack is dead) = $1/1 + e^{-(-11.92+0.22*\text{diameter})}$. Estimates listed in bold are statistically significant ($\alpha = 0.05$). Estimates listed as NA contain insufficient sample sizes.

Variable [a]	North-central		Superior		Oak savanna/Parkland	
	Intercept	Slope	Intercept	Slope	Intercept	Slope
Basal area of tamarack	**−8.40 (<0.01)**	−0.28 (0.08)	**−9.57 (<0.01)**	−0.13 (0.36)	**−6.41 (0.02)**	−0.83 (0.46)
Basal area of non-hosts	**−9.61 (<0.01)**	1.1×10^{-3} (0.99)	**−10.33 (<0.01)**	0.03 (0.72)	**−8.72 (<0.01)**	0.18 (0.64)
Basal area of non-host gymnosperms	**−9.54 (<0.01)**	−0.02 (0.85)	**−10.20 (<0.01)**	1.2×10^{-4} (1.00)	**−8.51 (<0.01)**	**3.80 (0.03)**
Basal area of angiosperms	**−9.67 (<0.01)**	0.19 (0.50)	**−10.31 (<0.01)**	0.12 (0.46)	**−8.51 (<0.01)**	0.11 (0.79)
Diameter	**−11.56 (<0.01)**	**0.24 (<0.01)**	**−11.92 (<0.01)**	**0.22 (<0.01)**	NA	NA
Distance to roads	**−9.17 (<0.01)**	−0.45 (0.86)	**−8.59 (<0.01)**	−1.66 (0.26)	NA	NA
Inventory year	**−8.85 (<0.01)**	−0.19 (0.52)	**−9.75 (<0.01)**	−0.12 (0.73)	−6.05 (0.20)	−0.51 (0.62)
Physiographic class	**−9.10 (<0.01)**	−0.53 (0.76)	**−9.25 (<0.01)**	−1.02 (0.47)	**−7.74 (0.04)**	−0.59 (0.87)
Site class	**−9.91 (<0.01)**	1.78 (0.06)	**−10.39 (<0.01)**	0.88 (0.40)	**−7.58 (0.01)**	−1.28 (0.70)
Site index	**−9.34 (<0.01)**	0.89 (0.08)	**−11.60 (<0.01)**	0.03 (0.45)	−5.95 (0.36)	−0.05 (0.73)
Water	**−9.34 (<0.01)**	−0.32 (0.78)	**−9.62 (<0.01)**	−0.68 (0.57)	**−8.08 (0.04)**	−0.16 (0.97)

[a] Variable descriptions are provided in Table 2.

Table 5
Results of logistic multiple regression models effects of various tree- and stand-level variables on mortality of tamarack from eastern larch beetle, measured in long-term FIA study plots, 2005–2009, Minnesota, USA.

Region[a]	Variable	Estimate	SE	*Z*-value	*p*-value
North-central	Intercept	−15.48	1.59	−9.73	<0.01
	Diameter	0.47	0.08	6.00	<0.01
	Water	2.87	1.40	2.05	0.04

[a] No significant models were found in the Superior and Oak savanna/Parkland regions.

Table 6
Results of logistic multiple regression models effects of various tree- and stand-level variables on mortality of tamarack from eastern larch beetle, measured in long-term FIA study plots, 2010–2014, Minnesota, USA.

Region	Variable	Estimate	SE	*Z*-value	*p*-value
North-central	Intercept	−12.54	1.66	−7.53	<0.01
	Diameter	0.24	0.05	4.41	<0.01
	Site index	0.06	0.03	2.01	0.05
	Basal area of tamarack	−0.34	0.16	−2.10	0.04
Superior	Intercept	−11.92	1.06	−11.24	<0.01
	Diameter	0.22	0.07	3.38	<0.01
Oak savanna/ Parkland	Intercept	−31.59	9.26	−3.41	<0.01
	Basal area of non-host gymnosperms	6.32	2.48	2.55	0.01
	Diameter	1.58	0.44	3.62	<0.01

4. Discussion

Tree- and stand-level conditions had a considerable impact on tamarack mortality caused by eastern larch beetle during the current outbreak in Minnesota. The degree to which these conditions affected mortality reflected regional variation in host attributes across the study area, as well as temporal variation over the course of the outbreak. Notably, we observed that eastern larch beetle colonizes the largest diameter trees in a stand during epidemic phases, which is consistent with behavior noted in other bark beetle systems such as spruce beetle, Douglas-fir beetle, mountain pine beetle, and western balsam beetle (*Dryocoetes confusus*) (Allen et al., 2006; Fettig et al., 2007; Klutsch et al., 2009; Johnson et al., 2014). Preference for large diameter trees was initially observed in the North-central region (Tables 3 and 5), i.e., the outbreak epicenter, and subsequently intensified as eastern larch beetle populations spread across the region (Tables 4 and 6). In the absence of inciting factors typical of historic outbreaks, such as large-scale defoliation, large diameter trees may increase the likelihood of attack by eastern larch beetle, particularly in areas where tamarack growth is not limited by marginal growing conditions (Langor and Raske, 1989b; Jenkins et al., 2008).

While the importance of diameter as a predictor of tamarack mortality increased over time, the effect of diameter in the later outbreak, while still significant, shows a slight reduction, which may indicate that once large-diameter trees have been preferentially attacked, selection of slightly smaller diameter trees becomes necessary to maintain beetle population growth. Field observations indicate that eastern larch beetles do not prefer to attack tamarack trees less than 12.7 cm in diameter (McKee, 2015). We note that removal of small diameter trees from our data did not impact the relationship between diameter and mortality due to eastern larch beetle. Further, a reduction in the availability of large diameter preferred hosts may help explain the negative relationship between host density and tamarack mortality due to eastern larch beetle in the North-central region found in the later outbreak. Of the remaining tamarack trees, it is possible that the largest were more likely to be found in stands where the density of tamarack was lower and trees were more dispersed, thus allowing for trees to grow in size in the absence of competition for available resources.

Landscape-level bark beetle outbreaks often encompass a range of ecological and forest conditions that influence tree distribution and growth. The Oak savanna/Parkland region represents the extreme margin of the range of tamarack in Minnesota and the lower limits of successful growing conditions for the species. As a pioneer species, tamarack is among the first to colonize a site, until lack of shade tolerance leads tamarack to be outcompeted by shade tolerant species (Duncan, 1954; Burns and Honkala, 1990). We observe that basal area of non-host gymnosperms was positively associated to tamarack mortality due to eastern larch beetle within the Oak Savanna/Parkland region during the later outbreak. One possible explanation is that eastern larch beetles in this region may be killing tamarack that are stressed due competition from shade tolerant gymnosperms. Stress on tamarack may be further exacerbated by warming climate conditions which have occurred in Minnesota over recent decades; these changes in climate have also been projected to contract the range of tamarack farther northward (Woodall et al., 2009; Zhu et al., 2012).

Several significant droughts occurred across much of the range of tamarack in Minnesota in 2003, 2006, and again in 2011. While the presence of water was associated with an increased probability of mortality in the North-central region in the early time period (Tables 3 and 5), its importance waned in the later period (Tables 4 and 6). Due to variability in the timing of plot visits, it is difficult to ascertain the causes of standing water and the timing of accumulation, whether before or after individual trees were killed by eastern larch beetles. The presence of water may be an indication of localized flooding contributing to tamarack mortality, or potentially a symptom of eastern larch beetle attack. Increasing beetle-induced tamarack mortality could have led to reduced evapotranspiration on hydric sites and a subsequent rise in the water table similar to altered site hydrologies following outbreaks of mountain pine beetle (Hubbard et al., 2013; Mikkelson et al., 2013). Furthermore, the spatial variability typically associated with drought was likely partially explained by the random intercept in our models. It is therefore difficult to draw strong conclusions about the role of drought from observations of water at tamarack sites.

While retrospective inventory data is well suited for examining the effects of tree-killing agents that etch distinctive galleries such as bark beetles, it is less well suited to examine other biotic factors that may be important to the vigor of tamarack. The extent to which defoliation by larch casebearer (*C. laricella* (Hübner)) predisposed tamarack to mortality from eastern larch beetle is not well differentiated, for example. Populations of larch casebearer have been increasing across the range of tamarack in the state of Minnesota over the last decade and is an area of current study.

The analysis of such a large number of observations coincident with a major bark beetle outbreak represents an opportunity to better understand factors that make trees more susceptible to mortality on a landscape-scale. Because these relationships are complex, considering them in isolation can lead to poor inference. While this study is based on data collected from the state of Minnesota, the results are relevant to eastern larch beetle outbreaks that have occurred throughout the USA, including Alaska, Wisconsin, Michigan, New York and Maine (Werner, 1986; Langor and Raske, 1989b). We have attempted to include a multitude of factors in a robust framework in order to shed light on these relationships and to inform mitigation activities. Though results may vary for other bark beetles, the approach used to analyze such factors could be replicated with other host tree species using a large volume of national forest inventory data.

5. Conclusions

Based on models built using nearly 15,000 observations of individual tamarack trees, mortality due to eastern larch beetle is related to tree- and site-level variables, including tree diameter, the presence of water on a site, site index, and the density of non-host gymnosperms with regional variation. Understanding the tree and site characteristics that make tamarack trees more susceptible to mortality from eastern larch beetle will provide knowledge that informs land management strategies. As preference for large diameter trees was consistent across space and time, management efforts aimed at reductions of preferred host abundance may help to minimize the impacts of eastern larch beetles on tamarack resources. While the mechanisms for reducing bark beetle populations and subsequent tree mortality vary by beetle species and forest type, landscape-level efforts to reduce host susceptibility and outbreak conditions should also broadly consider the impacts of forest heterogeneity on beetle population growth (Fettig et al., 2007). Further investigation will include spatial and temporal analysis of climate variables to assess their influence on tamarack mortality due to eastern larch beetle, as well as the use of aerial survey data to identify the extent to which larch casebearer defoliation predisposes tamarack to mortality by eastern larch beetle.

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