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Variation in occurrence and extent of internal stem decay in standing trees across the eastern US and Canada: evaluation of alternative modelling approaches and influential factors

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The occurrence (probability) and extent (proportion) of tree internal stem decay are important attributes influencing potential wood quality and value, but variation in decay by species, tree size and geographic range are rarely evaluated and modelled. In this analysis, we used 1246 destructively sampled trees across 33 species in the northeastern United States and New Brunswick, Canada to determine the factors influencing the combined probability and proportion of decay. In the process, we evaluated three modelling approaches including a two-part conditional model, multinomial model and generalized additive model for location, scale and shape (gamlss) that simultaneously predicted both probability and proportion of decay. Predictive capability for all three methods were nearly identical when classifying decay occurrence. Compared with the other methods, the gamlss model had a lower mean bias and root mean square error (RMSE) when predicting decay extent. Tree diameter to height ratio (ratio of diameter at breast height to total height), height, crown ratio, species tolerance to flooding and drought, leaf longevity, and an assessment of perceived tree risk of mortality (risk class) were selected as predictors in the best overall model for decay occurrence. For predicting decay extent, the best model included risk class, crown ratio and the last freezing date of spring. Further analysis identified significant species differences, which we used to develop functional species groupings based on decay occurrence and extent. Despite these observed relationships, a high degree of unexplained variation remained, highlighting the challenges of modelling decay in trees of different species across a range of growing environments.

Introduction

Degradation of xylem cell walls due to microbial activity, also known as decay or heart rot, can be classified into two primary stages: (1) incipient decay, where wood is discoloured (or stained), but there is little or no loss in physical character and (2) advanced decay, where there is an evident loss of wood density or mass for a given volume (Wagener and Davidson, 1954). Once decay is advanced, its influence on wood properties is strong. Wilcox (1978) found that decreases of one and nine per cent of wood mass could result in impact bending strength reductions as great as 20 per cent and 80 per cent, respectively. From a wood products perspective, predicting the occurrence, amount and location of decay in trees is of interest because the degradation in mechanical properties (e.g. bending strength) results in downgrades of saw timber quality sections to pulp or cull. In addition, quantifying the amount of decay is important in national biomass inventories (Woodall *et al.*, 2011), as it is used to discount gross wood volume and ultimately estimate biomass and carbon. Consequently, accurate estimates of sound volume and other wood properties such as wood density (Miles and Smith, 2009) play a key role in accounting for biomass and carbon across large spatial scales (Woodall *et al.*, 2011). Despite its importance, there has been insufficient research conducted to quantify the occurrence and extent of decay in many tree species (Defo *et al.*, 2015).

Decay occurrence is generally expressed as a probability, while decay extent is often quantified as a proportion (or percentage) of decay when it occurs (e.g. Schneider *et al.*, 2008). In addition, decay can be viewed as a proportion including zero values or the product of occurrence (probability) and extent (proportion), which we refer to here as decay prevalence.

Species-level differences in the occurrence and extent of decay have been attributed to diverse factors, including species traits, such as wood physiology or wood structure. More rapid decay propagation in flowering *vs* coniferous species is sometimes attributed to the higher amounts of decay-resistant chemical compounds found in the latter (Scheffer and Cowling, 1966). In addition to wood chemistry, wood mechanical properties such as modulus of elasticity (MOE) or modulus of rupture (MOR; Alden, 1995, 1997) describe how much stress wood can withstand without breaking, thereby preventing branch wounds and vectors for microorganisms (Shigo and Hillis, 1973). Both are positively correlated with wood density, a metric that is often more readily available for a broader range of species. Increasing decay rates were correlated with lower wood density in flowering, but not coniferous species across 816 species, worldwide (Chave *et al*., 2009). In addition, wood density was inversely correlated with decay in Scotch pine (*Pinus sylvestris* L.; Harju and Venäläinen, 2002). However, other studies found no such relationship (e.g. Wagener and Davidson, 1954) or that the relationship between decay and density within a species differed depending on the type of decay (i.e. white or brown rot; Yu *et al*., 2003).

Aside from the more obvious relationship between chemistry or wood mechanical properties and decay resistance, causative relationships between species traits and decay occurrence and extent are more difficult to understand. Loehle (1988) found that decay resistance significantly affects longevity and that long-lived conifers are slow grown and shade tolerant. Considering this, species-level tolerance to other environmental conditions (Niinemets and Valladares, 2006) such as drought and flooding may also be linked to decay. Conversely, a species that exhibits one tolerance trait may not exhibit another, and decay resistance (or tolerance) may be at the cost of another trait (e.g. flood, shade or drought tolerance). Finally, these ecological traits may serve as proxies for specific site conditions that are conducive to the growth of fungal pathogens.

Decay resistance, defined as a tree species' ability to deter microbial organisms when they are introduced, is frequently measured in a controlled laboratory setting or by exposing wooden stakes to field conditions (Scheffer and Cowling, 1966). However, for standing trees in a natural environment, decay resistance is extremely difficult to test as decay inception is generally unknown and assessment is problematic. When decay rates are assessed in natural environments, studies often focus on downed logs (Russell *et al*., 2014), whereas decay rates in standing trees are difficult to measure without expensive technology such as tomography (e.g. Brazee *et al*., 2011). More simply, the occurrence and extent of decay can be measured at the time a tree is felled. This is important to note because the actual amount of decay in a standing tree would not only be dictated by a species' decay resistance, but also its likelihood of occurrence. This likelihood should be affected by a suite of stand and environmental factors that could be used to assess a species' decay prevalence in a complex and competitive environment. Consequently, it may also be useful to group species together according to both observed decay occurrence and extent. To our knowledge, no comprehensive study has assessed whether such species groupings are statistically warranted for standing trees.

Recent literature pertaining to decay in standing trees tends to focus on examination of incipient decay responses, such as red heartwood and other discoloured wood (Baral *et al*., 2013; Havreljuk *et al*., 2013). However, incipient decay responses are also generally assumed to be a function of microbial organisms and should correlate with advanced decay, which can be effectively described by similar site- and tree-level factors. Across larger spatial scales, various edaphic (Horsley *et al*., 2002; Yanai *et al*., 2009), climatic (Havreljuk *et al*., 2013) and silvicultural factors (Erickson *et al*., 1992) have been thought to influence decay formation or incipient decay. At the tree-level, numerous morphological factors have been shown to influence the prevalence of decay including diameter at breast height (DBH; Drouin *et al*., 2010), tree age (Kadunc, 2007; Giroud *et al*., 2008), total tree height (e.g. Giroud *et al*., 2008; Schneider *et al*., 2008) and crown ratio (Westfall, 2013). The presence of external stem defects, such as scars, forks and burls, has also served as an effective indicator of decay; more specifically, the frequency (Knoke, 2003), location and size of defects (Belleville *et al*., 2011) have proven to be useful variables for predicting decay probability. However, most of these previous studies focused on either product grade or red heartwood as responses, sampled the tree only at DBH and lower, were limited to one or two species, and covered a geographic span of less than two degrees of latitude.

While external tree defects have been shown to be effective indicators of internal stem decay, rigorous enumeration of individual defects may not be practical during a typical standing tree inventory due to time and logistical constraints. An alternative method for assessing stem quality and vigour is using classification systems that assign trees to different categories based on the presence and severity of observable external defects (e.g. Boulet, 2007). However, studies that have examined the ability of these classifications to predict the extent of discoloured wood have presented both positive (Drouin *et al*., 2010; Baral *et al*., 2013) and negative results (Belleville *et al*., 2011). Recently, the Northern Hardwoods Research Institute (NHRI) developed a tree classification system which assesses (1) tree form class (FC) based on fork height, lean and sweep and (2) risk class (RC), an assessment based on external signs and symptoms (e.g. fruiting bodies, large holes, animal damage or mechanical damage) that may indicate a reduction in tree value and health or increase in mortality (Pelletier *et al*., 2013). This classification system has performed well when assessing saw log product recovery from (Castle *et al*., 2017) and diameter growth (Castle, 2017) of hardwood species, but additional work is warranted to examine if risk and form classifications can improve predictions of decay occurrence and extent.

From a statistical perspective, modelling the proportion of tree decay is challenging for three primary reasons. First, decay is highly variable within and among trees. Second, data distributions are zero-inflated due to a high frequency of trees with no decay. Finally, decay proportions are constrained between zero and one. Common statistical approaches, which generally assume a normal distribution, are inappropriate for these data and can result in biased parameter estimates and standard errors (Fortin *et al*., 2009; Zuur *et al*., 2009). To address the problem of zero-inflation, a two-part conditional model has often been used to predict the proportion of decay (Schneider *et al*., 2008; Fortin *et al*., 2009). This approach first predicts the presence and absence of decay using binary logistic regression and a second regression model to predict the proportion of decay

when it occurs. Similarly, multinomial logistic regression (Westfall, 2013) can be used to predict various classes of decay given its inherently high variability. Generalized additive models for location, scale, and shape (gamlss; e.g. Stasinopoulos and Rigby, 2007) may provide a flexible modelling framework, where the probability of occurrence and proportion of decay can be modelled simultaneously, while accounting for the zero-inflated beta-distribution. In forestry, gamlss has not been widely used, but recently it was implemented to model beta-inflated data to predict the likelihood that a given species would dominate a stand (Guay-Picard *et al.*, 2015) and mortality (Schwantes *et al.*, 2016). It may also provide an alternative to the more commonly used two-part framework for modelling decay occurrence and extent.

The overall goal of this study was to improve understanding of how various factors influence decay occurrence and extent across a broad range of common coniferous and flowering tree species in eastern North America. Specific objectives were to: (1) compare the efficacy of three different modelling approaches to estimate the occurrence and extent of decay including a zero-inflated conditional approach, multinomial logistic regression and gamlss regression; (2) determine the most influential common tree- and site-level attributes including size, diameter–height ratio, crown ratio, species or species traits, and climate, for predicting a tree's decay occurrence and extent and (3) assess whether a recently developed risk of mortality classification system (risk class; Pelletier *et al.*, 2013) could improve predictions of decay occurrence and extent after selecting the best modelling approach and most influential factors. It was expected that the more flexible gamlss approach would give more robust and reliable parameter estimates and its simultaneous prediction would provide more stable standard error estimates as well as predictions by accounting for the relationship between probability and proportion of decay. In addition, we expected that tree size would be the most important factor and that species differences in decay occurrence and extent would be better explained by traits such as tolerance, wood density and broad taxonomic divisions (i.e. flowering or coniferous). Lastly, we expected that assessing tree risk class would improve prediction of decay occurrence and extent after accounting for other influential factors given that visual indicators of high risk are often linked to factors related to decay (e.g. stem damage, fruiting bodies).

Methods

Study area

The study area spanned the northeastern United States and New Brunswick (NB), Canada (Figure 1). Due to the wide range of ecological and climatic conditions, trees were assigned to three regions with similar climates: (1) Northeastern (Pennsylvania (PA), New Hampshire (NH), Maine (ME) and NB); (2) Southeastern (Virginia (VA)); and (3) Great Lakes (Minnesota (MN), Wisconsin (WI), and Michigan (MI)). Each region varied slightly in terms of soil, topography and climate (Crookston, 2016).

Within the northeast region, sites were concentrated within the Laurentian Mixed Forest Province (Bailey, 1983). Topography in the region contains gentle slopes, while the winters are moderately long and occasionally severe. Soils across the region are predominantly medium to highly basic alfisols inland, but vary widely in terms of texture with contrasting combinations of clay, silt, sand, coarse fragments and peat. Mean annual precipitation across all sites in this region was 1091 mm (1008–1151 mm), while mean annual temperature was 5.9°C (2.0–7.8°C).

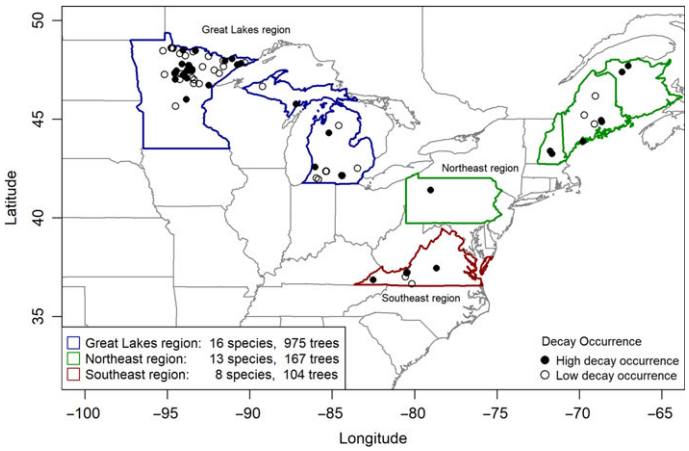

Figure 1 Study site locations used in this analysis with region (Northeast, Southeast, and Great Lakes) identified as well as the number of species and trees sampled in each region. Decay occurrence for each location is indicated as low or high as predicted by the location random effect after accounting for all significant variables. There were no obvious latitudinal or longitudinal trends observed in the data.

Stands were largely naturally regenerated, mixed-species stands that often displayed multi-aged structures.

Sites located in the Great Lakes region spanned the Eastern Deciduous Forest Province, and Laurentian Mixed Forest Province (Bailey, 1983). The Laurentian Mixed Forest Province overlaps between the northeast and Great Lakes, which suggested similar site conditions between the northeast and Great Lakes regions. However, sites within the northern extents of the Eastern Deciduous Forest Province were subjected to less rainfall and slightly cooler temperatures on average. Mean annual precipitation at the sites within the region was 760 mm (582–952 mm), while mean temperatures were 5.2°C (2.0–9.3°C). In general, soils in the Great Lakes are diverse and of complex glacial origin, which affects species distribution across the region (Dickmann, 2004).

The southeast region contained sites predominantly located within the Southern Mixed Forest Province. In contrast to the northern regions, sites in the southeast were subjected to longer growing seasons, and utisol soils dominated. Although there is a transition to southern pines in this region, most of the sites sampled in the southeast were also naturally regenerated mixed hardwood stands. Mean annual precipitation across sites in the region was 1043 mm (967–1273 mm), while mean temperatures were 11.0°C (7.4–13.1°C).

Data

Data were obtained from destructively sampled trees from four studies spanning a large geographic range, namely: (1) an ongoing collaborative biomass study between the United States Forest Service – Forest Inventory and Analysis Program (USFS-FIA) and several universities (Michigan State University, Virginia Tech and University of Maine (FIA-ME)); (2) Northern Hardwoods Research Institute (NHRI; Pelletier *et al.*, 2013); and (3, 4) two studies previously conducted by the USFS Northern Research Station in the north-central US ('Great Lakes') states (Schlaegel, 1975; Perala and Alban, 1994). These two studies were recently compiled as part of an ongoing effort to archive data pertaining to biomass, volume, and physical properties (Radtke et al., 2015). Across all datasets, trees were generally selected to represent the range of diameter classes of a given species. In most cases, trees were of good form and low risk of mortality. Due to the costly nature of destructive sampling, locations were often selected opportunistically; thus, the sample may not be entirely representative of the eastern US and Canada.

Table 1 Key attributes of the data by species group for diameter at breast height (cm), total height (m) and crown ratio (%)

Species group	DBH (cm)	Height (m)	Crown ratio (%)	Number of trees				
				Total	Decay observed	Northeast	Southeast	Great Lakes
Abies balsamea	16.2 (7.5) [4.9, 40.6]	12.9 (4.7) [3.4, 24.7]	69.1 (20.5) [23.5, 99.2]	87	25	30	0	57
Acer rubrum	24.2 (16.7) [3.0, 85.6]	18.4 (6.5) [6.5, 30.3]	66.5 (14.7) [26.2, 91.3]	107	52	31	23	53
Acer saccharum	18.9 (12.7) [3.3, 55.6]	15.8 (5.7) [5.0, 27.3]	61.7 (13.2) [42.5, 90.4]	55	23	18	1	36
Betula spp.	17.1 (8.3) [4.6, 36.0]	15.6 (4.6) [6.4, 23.1]	64.6 (14.3) [36.6, 89.2]	44	6	12	0	32
Fagus grandifolia	35.3 (22.8) [4.3, 79.8]	21.8 (8.6) [6.3, 33.7]	69.3 (18.9) [30.9, 93.7]	25	8	4	5	16
Fraxinus spp.	19.0 (17.5) [4.4, 81.8]	15.7 (5.6) [6.9, 25.5]	46.9 (14.0) [22.0, 84.0]	27	8	9	0	18
Juglans nigra	33.6 (21.4) [6.6, 71.4]	19.3 (8.2) [7.2, 30.5]	60.4 (12.7) [38.2, 88.0]	18	5	0	3	15
Lirodendron tulipifera	42.5 (23.8) [4.6, 80.5]	27.6 (9.5) [6.2, 37.3]	67.4 (11.1) [41.8, 84.7]	17	1	0	1	16
Other coniferous spp.	27.3 (14.9) [5.8, 54.9]	15.0 (5.0) [5.6, 25.6]	70.9 (16.0) [41.3, 95.2]	17	6	7	0	10
Other flowering spp.	12.7 (8.8) [4.5, 38.4]	12.2 (3.6) [7.1, 19.7]	63.0 (15.1) [42.1, 90.4]	21	3	2	2	17
Pinus spp.	32.6 (16.6) [5.5, 81.3]	20.4 (6.1) [5.0, 40.2]	54.1 (20.5) [6.3, 92.0]	118	17	35	32	51
Populus spp.	18.1 (8.1) [2.8, 49.5]	18.2 (5.0) [4.9, 28.3]	40.6 (11.3) [10.9, 93.8]	573	263	2	0	571
Quercus alba et al.	37.8 (23.1) [6.3, 87.6]	20.0 (6.6) [7.2, 33.3]	68.4 (17.1) [27.9, 93.6]	51	23	3	32	16
Quercus rubra et al.	32.9 (21.0) [4.8, 83.3]	20.8 (6.4) [8.0, 35.8]	60.2 (16.2) [26.4, 89.6]	47	12	13	3	31
Tilia americana	13.3 (7.7) [5.4, 37.8]	11.8 (3.2) [8.0, 20.6]	56.7 (14.2) [23.2, 76.4]	21	2	0	0	21
Tsuga heterophylla	44.7 (21.3) [12.4, 82.0]	20.0 (5.5) [9.9, 26.8]	74.1 (9.6) [55.2, 88.8]	18	7	1	2	15
All species	22.5 (15.2) [2.8, 87.6]	18.0 (6.1) [3.4, 40.2]	52.3 (18.8) [6.3, 99.2]	1246	461	167	104	975

Standard deviation is shown in parentheses and minimum and maximum values are given in brackets. The total number of trees, total number with decay observed and total number by region are also shown here.

Risk and form class (Pelletier *et al.*, 2013) was assessed on trees sampled by NHRI, FIA-ME and Schlaegel (1975). The NHRI protocol assigns four risk classes and eight form classes, which we collapsed into two of each for this analysis: low risk/high risk and ideal form/non-ideal form. In our analysis, low risk trees (healthy or vigorous) were described as being unlikely to have reduced vigour, value or products over the next cutting cycle and a low probability of dying over the next 25 years. High risk trees were defined otherwise. Due to the subjective nature of predicting mortality, a tree was categorized as high-risk when evidenced by fungal pathogens (e.g. hypoxylon canker in aspen), cavities, cracks, scars and open wounds, which could serve as potential entry points for microorganisms. Ideally formed trees were free of sweep, inclined less than 15°, and did not have a fork below 5 m. Since this dataset contained very few non-ideal trees, it was not feasible to examine the influence of form class.

In all cases, DBH (diameter generally 1.37 m above ground, but 1.30 m above ground for NB trees) was measured before felling and total tree height (HT) was determined after felling. For each study, disks were removed from the stems at pre-determined intervals, though this varied between and within a given study. On each disk, advanced decay was measured; except for some white pine trees in NH this decay was always present in the heartwood, rather than the sapwood. Since the proportion of disk decay could vary considerably within a tree (i.e. decay proportion decreased from base to tip), we conducted a preliminary examination using trees with at least 12 disks sampled and an average section length of <2 m. This preliminary analysis suggested that unbiased estimates of decay proportion required a minimum of four disks with an average maximum log length of 4 m. After removing trees that did not meet these criteria, the total sample size was 1 246 trees (Table 1).

A total of 33 coniferous and flowering species over all four studies were included in this analysis. The most abundant were flowering species such as quaking aspen (*Populus tremuloides* Michx.) and red maple (*Acer rubrum* L.), while balsam fir (*Abies balsamea* L.) was the most common coniferous species (see Supplemental Table S1 for all common and scientific names). Due to their small sample size, some species were combined based on taxonomy into 16 preliminary species/species groups for analysis (Table 1). The pines (*Pinus* spp.) primarily included red pine (*Pinus resinosa* Ait.) and white pine (*Pinus strobus* L.), while the other coniferous species included northern white-cedar (*Thuja occidentalis* L.) and red spruce (*Picea rubens* Sarg.). American hornbeam (*Carpinus caroliniana* Walt.) and American elm (*Ulmus americana* L.) largely dominated the other flowering species. The aspens (*Populus* spp.) contained bigtooth aspen (*Populus grandidentata* Michx.), quaking aspen, and cottonwood (*Populus deltoides* Bartr. ex Marsh.). Red oaks (*Quercus rubra et al.*) included northern red oak (*Quercus rubra* L.) and scarlet oak (*Quercus coccinea* Muenchh.), while white oak (*Quercus alba* L.) and chestnut oak (*Quercus prinus* L.) were termed white oaks (*Quercus alba et al.*). All other species were treated individually. Data for each species/species group were summarized by key tree-level variables and total number of trees by region (Table 1).

The next step was to compute the decay proportion for trees with decay. For all studies, the diameter was measured in two dimensions across the area identified as decayed on each disk, which was generally observed in the heartwood of the stem. From that, we calculated each tree's weighted decay proportion ($Decay_{prop}$) on an area basis by summing across all disks (1 to n_j) in tree j:

$$Decay_{prop_j} = \frac{\sum_1^{nj} \text{decay area } ij}{\sum_1^{nj} \text{wood area } ij} \quad (1)$$

where decay and wood areas for disk i within tree j are the respective areas measured as ellipses. Given that crown ratio and risk class were not measured on all trees, the initial dataset (n = 1246 trees) was divided into two datasets. The first dataset had crown ratio measurements for all trees (n = 1199, hereafter dataset 1), while the second dataset consisted of 557, predominantly flowering, trees with risk classifications (hereafter dataset 2; Table 2).

Table 2 Summary statistics across key variables used in dataset 1 (where crown ratio was available for all trees) and dataset 2 (where risk class, a visual assessment of a tree's risk of mortality, was available for all trees) by taxonomic division and species group, respectively

Species group	Risk class	Number of trees		Height (m)	Crown ratio (%)	DBH/HT (cm/m)	Leaf longevity (mo.)	Drought tolerance	Flood tolerance	Decay probability	Decay proportion
		Total	Decay observed								
	Dataset 1										
Coniferous	–	231	55	17.1 (6.6) [3.4, 40.2]	62.5 (21.1) [6.3, 99.2]	1.5 (0.5) [0.7, 3.3]	32.9 (11.3) [21.0, 60.0]	1.9 (1.0) [1.0, 4.0]	1.5 (0.5) [1.0, 2.0]	0.238	0.013 (0.050) [0.000, 0.384]
Flowering	–	968	380	18.1 (6.0) [4.9, 37.3]	49.8 (17.4) [10.9, 93.8]	1.1 (0.4) [0.4, 3.5]	5.3 (0.3) [5.0, 6.0]	2.0 (0.5) [1.5, 3.8]	1.8 (0.5) [1.0, 3.0]	0.393	0.014 (0.045) [0.000, 0.594]
	Dataset 2										
Populus spp.	Low	292	105	18.0 (4.8) [5.2, 27.3]	–	0.9 (0.2) [0.5, 1.9]	5.0 (0.0) [5.0, 5.0]	1.7 (0.1) [1.7, 2.5]	1.7 (0.0) [1.7, 2.0]	0.360	0.004 (0.014) [0.000, 0.140]
Other flowering	Low	30	19	18.9 (4.9) [5.0, 27.3]	–	1.2 (0.5) [0.6, 2.2]	5.7 (0.2) [5.5, 6.0]	2.4 (0.5) [1.5, 3.8]	1.8 (0.9) [1.0, 3.0]	0.633	0.009 (0.018) [0.000, 0.075]
Coniferous	Low	16	7	22.6 (4.5) [10.5, 29.4]	–	1.3 (0.3) [0.8, 1.9]	27.6 (14.3) [21.0, 60.0]	2.3 (0.2) [2.2, 2.7]	1.1 (0.3) [1.0, 2.0]	0.438	0.002 (0.003) [0.000, 0.010]
Populus spp.	High	159	101	18.7 (4.5) [5.4, 27.3]	–	0.9 (0.2) [0.5, 1.6]	5.0 (0.0) [5.0, 5.0]	1.7 (0.1) [1.7, 2.5]	1.7 (0.0) [1.7, 2.0]	0.635	0.029 (0.050) [0.000, 0.258]
Other flowering	High	44	32	17.6 (3.7) [10.4, 25.7]	–	1.5 (0.5) [0.6, 2.8]	5.6 (0.2) [5.5, 6.0]	2.2 (0.5) [1.5, 3.5]	1.9 (0.9) [1.0, 3.0]	0.727	0.027 (0.042) [0.000, 0.187]
Coniferous	High	16	7	21.3 (2.4) [16.2, 24.9]	–	1.1 (0.2) [0.9, 1.4]	21.7 (2.8) [21.0, 32.3]	2.1 (0.3) [1.0, 2.2]	1.1 (0.2) [1.0, 2.0]	0.438	0.010 (0.018) [0.000, 0.057]

Standard deviation is shown in parentheses; minimum and maximum values are given in brackets.

Variable selection

The explanatory variables that we examined in this analysis included tree-level, species-level and climatic variables. We tested the following measured and calculated variables (see Supplemental Table S2 for all tested variables and their abbreviations): DBH (cm), crown ratio (CR, %), height (HT, m), diameter–height ratio (DBH/HT) and NHRI risk class (RC). Risk class was only available in dataset 2, while crown ratio was only examined in dataset 1. Since there were 16 species groups with varying sample sizes, across numerous locations in this analysis and it was of interest to explore a meaningful basis for grouping species, we tested several different species traits to model decay occurrence and extent. These included (1) two broad taxonomic divisions separating flowering and coniferous species; (2) leaf longevity (LL; i.e. the leaf life span in months for a given species; Reich *et al.*, 1999); (3) tolerance to shade (ST), flood (FT) and drought (DT) (Niinemets and Valladares, 2006; see Table 2); (4) wood density expressed as wood specific gravity (Miles and Smith, 2009; see Supplemental Table S1); (5) wood mechanical properties such as modulus of elasticity (MOE), modulus of rupture (MOR), maximum crushing strength (C_{II}), stress at proportional limit (C_I), work to maximum load (WML), hardness and shear parallel to the grain ($shear_{II}$; Alden, 1995, 1997); (6) downed woody debris decay rate (k; Russell *et al.*, 2014); and (7) Scheffer and Cowling (1966) decay resistance (or resistance to microbial deterioration) classification. We grouped trees as 'low' resistance (Scheffer and Cowling non-resistant) and 'high' resistance (Scheffer and Cowling slight to very resistant, see Table 6). Flowering and coniferous was chosen as a more precise division based on taxonomy, but the division is nearly equivalent to dichotomies such as hardwood/softwood and deciduous/evergreen, which are more commonly used. As such, flowering plants generally have higher wood density and shorter leaf longevity than coniferous plants, but there are exceptions. Leaf longevity data were available for 13 species at the species-level and 14 species by genera. For the remaining six species, leaf longevity was estimated using other species in the same division (see Supplemental Table S1). The relatively high influence of location in preliminary analyses, suggested that variables related to site such as soil, competition and climate may influence occurrence and extent of decay. While the first two variables were not available, we used climate normals derived from 1961 to 1990 for 24 variables pertaining to temperature and precipitation (Crookston, 2016).

We used boosted regression trees to assess the contribution (i.e. relative influence) of all variables prior to modelling in a (semi-) parametric framework. Boosted regression trees offer several advantages over parametric models in that they are robust to influential observations, do not require variable transformations, and can easily examine numerous interactions (Elith *et al.*, 2008). Following recommendations described in Elith and Leathwick (2017), we used the R package dismo (Hijmans *et al.*, 2017) to determine the optimal number of trees and rank each variable by relative influence for occurrence (Supplemental Table S2) and extent (Supplemental Table S3). As suggested by Müller *et al.* (2013), we considered a variable influential and used it in model selection by AIC when the relative influence was greater than that due to chance (i.e. relative influence > total influence/no. of parameters). For predicting occurrence, we observed that after excluding the location variable, the threshold where relative influence was greater than chance was 0.697 and eight additional variables were suitable for model development (Supplemental Table S2).

Model development

Because decay proportion is highly variable, zero-inflated and constrained between zero and one, three alternative modelling approaches were evaluated to aptly predict the probability of occurrence and proportion of decay in individual trees: (1) a two-part, zero-inflated conditional model similar to previous decay analyses (Giroud *et al.*, 2008; Schneider *et al.*, 2008); (2) a multinomial regression model similar to Westfall (2013); and (3) a semi-parametric, zero-inflated generalized

Table 3 Full (F), reduced (R) and species (SPP) models for datasets 1 and 2, where Y_{occ1} and Y_{occ2} represent the logit-transformed response for the probability of decay occurring (in the two-part conditional framework), not occurring (in the generalized additive models for location scale and shape (gamlss) framework), or occurring in a particular severity group (in the multinomial framework), Y_{ext1} and Y_{ext2} represent the logit-transformed response predicting the extent of decay for datasets 1 and 2, respectively, for the two-part conditional and gamlss frameworks, and $Y_{\sigma 1}$ and $Y_{\sigma 2}$ represent the sigma (scale parameter) formulation for the gamlss model for datasets 1 and 2, respectively

Response	Dataset	Model description	Predictive model (right hand side)	Model no.
Y_{occ1F}	1	Full occurrence	$b_0 + b_1 \ln(HT) + b_2 DBH/HT + b_3 LL^{-1} + b_4 CR^{-0.5} + b_5 \ln(\text{FT}) + b_6(\text{DT})$	6
Y_{occ1R}	1	Reduced occurrence	$b_0 + b_1 \ln(HT) + b_2 DBH/HT + b_3 LL^{-1}$	7
Y_{ext1F}	1	Full extent	$b_0 + b_1 sday + b_2 CR + b_3 \ln(CR)$	8
Y_{ext1R}	1	Reduced extent	$b_0 + b_1 sday$	9
$Y_{\sigma 1F}$	1	Full sigma	$b_0 + b_1 CR + b_2 sday$	10
$Y_{occ1SPP}$	1	Full species occurrence	$b_0 + b_1 ln(HT) + b_2 DBH/HT + b_3 SPP + b_4 CR^{-0.5}$	11
$Y_{ext1SPP}$	1	Full species extent	$b_0 + b_1 sday + b_2 CR + b_3 \ln(CR) + b_4 SPP$	12
Y_{occ2F}	2	Full occurrence	$b_0 + b_1 DBH/HT + b_2 RC$	13
Y_{occ2R}	2	Reduced occurrence	$b_0 + b_1 DBH/HT$	14
Y_{ext2F}	2	Full extent	$b_0 + b_1 sday + b_2 RC$	15
Y_{ext2R}	2	Reduced extent	$b_0 + b_1 sday$	16
$Y_{\sigma 2F}$	2	Full sigma	$b_0 + b_1 sday + b_2 RC$	17
$Y_{\sigma 2R}$	2	Reduced sigma	$b_0 + b_1 sday$	18

For convenience, we present only the fixed effects portion of all models. Predictor variables are as follows: tree height (HT); diameter–height ratio (DBH/HT); crown ratio (CR-%); leaf longevity (LL); flood tolerance (FT); drought tolerance (DT); Julian date of the last freezing date of spring (sday); species (SPP) and classification of risk of mortality (RC).

additive model accounting for location, scale, and shape parameters (gamlss, Stasinopoulos and Rigby, 2007). Each method is described in detail below.

Two-part conditional model

In the two-part conditional model, we first predicted the presence of decay as a binary response variable (i.e. decay = 1, no decay = 0). A binomial logistic regression model was used to predict the probability that a tree had decay:

$$\Pr(\text{decay}) = \exp(Y_{occd} + Zb)(1 + \exp(Y_{occd} + Zb))^{-1} + \mathcal{E}, \quad (2)$$

where Pr(decay) is the probability that a tree demonstrated decay. The logit-transformed probability of decay occurring for dataset *d* Y_{occd} was calculated based on models 6, 7, 11, 13 and 14 (Table 3), Z is the design matrix for the random effect covariates, *b* is the vector of random effect parameter coefficients and ε is a random error component. The binomial model was fit with the lme4 package (Bates *et al.*, 2015) in R version 3.2.5 (R Core Team, 2016). Parameter estimates were derived using maximum likelihood estimation (ML).

For trees that demonstrated presence of decay (i.e. decay proportion > 0), we then predicted the decay extent. Since decay extent was measured as a proportion and constrained between 0 and 1, beta regression was used to quantify the response. As in the binomial model above, a logit link function was chosen to model the mean proportion of decay in individual trees also requiring an inverse logit transformation to calculate the decay proportion such that

$$\text{Decay}_{prop} = \exp(Y_{extd} + Zb)(1 + \exp(Y_{extd} + Zb))^{-1} + \mathcal{E} \quad (3)$$

where Decay_{prop} was the proportion of decay for an individual tree, Y_{extd} was the logit-transformed response based on models 8, 9, 12, 15 and 16 (Table 3) for a particular dataset. The model parameters were estimated using ML in the glmmADMB package (Skaug *et al.*, 2016) in R.

Multinomial regression

Given the high variability in decay occurrence and extent, a more effective method may be to classify trees into several decay severity groups such as high, low and none. For example, Westfall (2013) found a multinomial approach to be effective when examining the extent of tree defect in standing trees using three classifications of cull. In this analysis, three classes were also used to characterize decay severity groups (DecaySeverityGroup) based on a tree's proportion of stem decay and the observed data: (1) trees with no decay (0 per cent decay), (2) low decay (>0–1.2 per cent decay) and (3) high decay (>1.2 per cent). The median breakpoint of 1.2 per cent was selected to maintain a sufficient sample size in each class for trees demonstrating internal stem decay. Using this framework, the occurrence of decay was expressed as three underlying logit models using the following model form:

$$\Pr(\text{DecaySeverityGroup}_k) = \exp(Y_{occdk})(1 + \exp(Y_{occdk}))^{-1} + \mathcal{E}, \quad (4a)$$

where $\Pr(\text{DecaySeverityGroup}_k)$ is the predicted probability of decay occurring for the *k*th decay severity group (none and low). The multinomial model was fit in R using the nnet package (Venables and Ripley, 2002), which did not allow the inclusion of random effects. All parameter estimates were derived using ML. As with the previous model, Y_{occd} represents the logit-transformed probability of decay occurring; however, the interpretation differs from the two-part conditional model, as separate parameter estimates were given for the none and low severity groups. The high severity group was calculated as

$$Pr(\text{DecaySeverityGroup}_{\text{High}}) = 1 - Pr(\text{DecaySeverityGroup}_{\text{Low+None}}) \quad (4b)$$

Since random effects could not be specified when using the multinomial approach, all comparisons between it and other modelling frameworks were performed using only the fixed effects.

Generalized additive models for location, scale and shape

Generalized additive modelling for location, scale and shape (gamlss) is a semi-parametric approach and can simultaneously estimate four parameters, namely location or mean (μ), scale or dispersion (σ) and shape, which represented the probability that decay did not occur (ν) or that the tree was entirely decayed (τ). This allows for a highly flexible model form, which can accommodate highly skewed, kurtotic and non-normally distributed data (Stasinopoulos and Rigby, 2007). It was assumed that the probability of occurrence and proportion of decay were correlated, and that simultaneously modelling these responses would provide more reliable standard error estimates and potentially improve overall prediction. For this analysis, a zero-inflated beta distribution was used, which constrains the predictions from zero to one. The response and shape parameter (ν) estimates given by gamlss were of opposite signs for model coefficients of those given by the two-part conditional model and represented the probability that decay did not occur. As such, the probability of decay occurring was calculated as follows:

$$Pr(\text{decay}) = 1 - \exp(Y_{occd} + Zb)(1 + \exp(Y_{occd} + Zb)) + \tau)^{-1} + \mathcal{E} \quad (5)$$

For a given tree, in the gamlss framework, the logit-transformed probability of decay not occurring for dataset d Y_{occd} was calculated based on parameters given in various full and reduced models (Table 3). The shape parameter (ν) was equivalent to $exp(Y_{occd} + Zb)$ and τ represented the probability that the tree was entirely decayed. Given the near impossibility of an entirely decayed live tree, τ was set to zero in this analysis. Our focus was on the probability of occurrence and mean decay extent, which were primarily reflected in the ν and μ parameters. However, preliminary analyses showed that the scale parameterization (σ) could influence the μ parameters so the scale parameter was included for comparison in some model formulations. The gamlss package (Stasinopoulos and Rigby, 2007) in R was used for model fitting.

Model selection and assessment

The first stage of model selection was done using the two-part conditional framework. The random effects structure (**Z***b*) with region and location was selected by Akaike Information Criteria (AIC) for both the null and full decay occurrence-models, but random effects were not selected in the decay extent models. The influential fixed effects variables (i.e. those regarded as influential when compared with all variables; Supplemental Table S2) that we tested for predicting occurrence in dataset 1 included height, DBH/HT, leaf longevity, crown ratio, DBH, flood tolerance, decay rate (Russell *et al.*, 2014), and drought tolerance, along with highly ranked interactions between DBH/HT and crown ratio, flood tolerance and height, and leaf longevity and crown ratio. High correlation between DBH and DBH/HT ($r = 0.88$), as well as between decay rate and leaf longevity and a high multi-variance inflation factor (vif > 5, as suggested in Guay-Picard *et al.*, 2015), suggested multicollinearity so DBH and decay rate were removed, reducing the highest variance inflation factor to 2.0.

For modelling decay extent, we tested influential variables (Supplemental Table S3) such as height, DBH/HT, crown ratio, work to maximum load, Julian date of the last freeze in spring (sday) and annual dryness index (adi). Two climate variables (summer precipitation balance (smrpb) and summer dryness index (sdi)), which were highly collinear (vif > 5) with sday, as well as DBH and wood density, which were collinear with DBH/HT and WML, respectively, were removed. For dataset 1, the best or full (F) models were selected based on AIC for occurrence (Table 3, model 6) and extent (Table 3, model 8). These models were then reduced by removing half of the parameters for occurrence and one-third of the parameters for extent using relative influence as a guide. Full models were compared with a null and reduced (R) model for occurrence (model 7) and extent (model 9). Once the best models were selected using the two-part conditional models, gamlss models were simultaneously fitted with and without random effects on the nu formulation, but only with fixed effects on the mu (μ) and sigma (σ) formulations (see full models 6 and 8 and reduced models 7 and 9). Though not shown in Table 3, the interactive model added highly ranked interactions to model 6.

The multinomial model used the same fixed effects forms described by models 6 and 7 to predict the probability of no and low rot. While all gamlss and two-part conditional models were examined with and without random effects for location and region, we could not examine the multinomial model in the mixed-effects framework so all comparisons between the multinomial model and the other two frameworks were made using the fixed effects only models.

To assess the influence of the scale parameter (σ), we tested highly influential extent variables to select the best σ formulation (model 10), while simultaneously accounting for the full occurrence and extent models. Finally, we developed a gamlss model that included the full μ, ν and σ formulations above and replaced species related variables such as leaf longevity, flood tolerance and drought tolerance with species (SPP) in the occurrence (model 11) and extent (model 12) formulations.

All model testing for dataset 2 was conducted using gamlss and we only tested variables that were included in the best model from the larger dataset. The full and reduced models for dataset 2 are also presented in Table 3.

Model verification

We verified our models in two stages, namely: (1) assess prediction of occurrence and (2) evaluate prediction of decay proportion (extent) for all non-zero values. Decay occurrence models were examined in terms of specificity, which is the ability of a model to correctly identify trees with decay (i.e. true positive rate) and sensitivity which is the ability of a model to correctly identify trees without decay (i.e. true negative rate). Goodness of fit was determined by calculating the area under a curve (AUC) (Hosmer *et al.*, 2013) which was derived by plotting the sensitivity *vs* 1 – specificity. AUC values range from 0.5 to 1.0 with higher scores indicating a model with greater capability of discriminating if a subject experienced the given outcome of interest.

The predictive capability of the decay occurrence models was also assessed by classification rate. The OptimalCutpoints package (López-Ratón *et al.*, 2014) in R can generate numerous cutpoints that optimize sensitivity and specificity. However, based on a preliminary analysis, we selected a cutpoint of 0.5, which showed greater overall classification rates and high specificity. In the case of the multinomial model, models predicted high, low and no decay probability and trees were classified according to the highest predicted probability. While volume under the surface (VUS) is generally used to evaluate multinomial models (Westfall, 2013), we simplified prediction in this analysis to a binomial response for stage one verification, but maintained all decay classes for stage two. For all models used to predict the proportion of decay, residual plots were examined to assess the assumptions of normality and constant variance of the error terms. In addition, the precision and accuracy of the models were evaluated by calculating root mean square error (RMSE) and mean bias (MB; predicted-observed) respectively, for all cases where decay was observed.

Given high variability and imbalance in the underlying data, bootstrapping was conducted using the gamlss model to ensure robustness against highly influential observations. For this, we sampled 500 and 250 trees from datasets 1 and 2, respectively, with replacement 500 times. This method was similar to boosted regression, but predictors were more limited, only additive effects were considered, and our criteria was not prediction error. Rather, we used bootstrapping to examine both the frequency that a variable was statistically significant and the frequency at which a variable was selected in the best model. For this analysis, we used AIC to determine the optimal model, while *P*-values

were used to interpret the statistical significance of a given variable to address the hypotheses described in our objectives.

Species decay groups

We developed final species occurrence and extent groups by ranking each species in terms of probability and proportion of decay. Both values were predicted for each species as a function of conditional (i.e. marginal) means (Lenth, 2016) after accounting for all other significant variables in the full occurrence (11) and extent models (12). Here, we preferred the two-part conditional approach because pairwise comparisons could be made between species in terms of decay occurrence and decay extent using a compact letter display (Hothorn *et al.*, 2016), which provides a means to assess statistically significantly different groups ($\alpha < 0.05$). While the occurrence model was specified as a binomial model as described above, the extent model was fit as a linear model without constraining the data to a beta distribution. In both cases, we specified a location random effect, which had a minimal influence in the extent model. Decay prevalence (decay proportion with 0 values) was calculated using conditional means estimated for probability and proportion of decay. By assessing natural breaks located near the mean in this ranked factor, species were classified into two primary species groups, namely high and low for occurrence, extent, and prevalence. Lastly, we ordered species in terms of decay tolerance, which was done by calculating and scaling the aforementioned factor of decay prevalence ($Decay_{prev}$) to a numeric value similar to Niinemets and Valladares (2006) as follows:

$$Decay_{Tol} = 5 - Decay_{prev} * 5/Decay_{prev\ max} + Decay_{prev\ min} \quad (19)$$

where $Decay_{Tol}$ is the numeric decay tolerance value, and $Decay_{prev\ min}$ and $Decay_{prev\ max}$ are the minimum and maximum factors of conditional means across all species measured here. In addition, we used the US Forest Service national FIA database (FIADB; O'Connell *et al.*, 2016) as a second source for comparing our species probability and proportion of decay. The FIADB proportions of decay/cull as summarized in Table 6 are visual estimates on standing trees and include trees with no decay (i.e. $Decay_{prop} = 0$). The cull estimates provided in the FIADB are used to estimate sound stem volume. We viewed these as approximate corollaries to our measurements of decay prevalence, and compared these in absolute terms by examining the difference between FIA cull and decay proportion (with 0 values) measured directly in this study.

Results

Comparison of modelling approaches

The gamlss and the two-part conditional decay occurrence models performed identically. For both frameworks, the AUC score for dataset 1 was 0.70 (Table 4; Supplemental Figure S1) and the

Table 4 Model fit statistics for the various modelling approaches and alternative formulations for predicting decay occurrence and decay extent

Formulation	Decay occurrence					Decay extent	
	Δ AIC	AUC	Sensitivity	Specificity	Classification rate	Mean bias	RMSE
Dataset 1: Two-part conditional models							
Null (fixed effects only)	246	0.50	0	100	64	0.0012	0.0698
Null w/ random effects	129	0.77	35	93	72	0.0012	0.0698
Full (fixed effects only)	107	0.70	33	86	67	0.0013	0.0688
Reduced w/ random effects	48	0.81	51	88	75	0.0013	0.0695
Full w/ random effects	0	0.83	57	86	75	0.0013	0.0688
Dataset 1: Generalized additive models for location, scale and shape (gamlss)							
Null (fixed effects only)	305	0.50	0	100	64	0.0013	0.0698
Full (fixed effects only)	156	0.70	33	86	67	0.0013	0.0688
Null w/ random effects	142	0.77	35	93	72	0.0013	0.0698
Reduced w/ random effects(σ)	51	0.81	51	88	74	0.0003	0.0694
Full w/ random effects (σ) species	17	0.84	58	85	76	0.0010	0.0682
Interactive w/ random effects	4	0.83	57	86	75	0.0013	0.0688
Full w/ random effects	0	0.83	57	86	75	0.0013	0.0688
Full w/ random effects (σ)	−7	0.83	57	86	75	0.0009	0.0682
Dataset 1: Multinomial models							
Null (fixed effects only)	123	0.50	0	100	64	−0.0354	0.0783
Reduced (fixed effects only)	53	0.55	17	93	65	−0.0065	0.0724
Full (fixed effects only)	0	0.59	32	86	66	−0.0011	0.0735
Dataset 2: Gamlss with sigma (σ)							
Null (fixed effects only)	149	0.50	0	100	51	0.0003	0.0437
Null w/random effects	79	0.79	59	81	70	0.0003	0.0437
Reduced w/random effects	78	0.78	63	77	70	0.0003	0.0435
Full (fixed effects only)	49	0.66	56	68	62	0.0002	0.0409
Full w/random effects	0	0.81	68	74	71	0.0002	0.0409

The fit statistics were the change in Akaike Information Criteria from the full model (ΔAIC which is presented for the combined occurrence and extent model in gamlss and for occurrence only in the other two frameworks), area under the curve (AUC), sensitivity (% true positives), specificity (% true negatives), classification rate, mean bias (pred. – obs.), and root mean square error (RMSE). The mean decay proportion was 0.0391 for dataset 1 and 0.0275 for dataset 2. Random effects were specified only on the occurrence models.

classification rate was 67 per cent for predicting decay occurrence for both of the full models without random effects. An AUC score of 0.70 is generally considered acceptable discrimination (Hosmer *et al.*, 2013). Overall, the gamlss and two-part conditional occurrence models outperformed the multinomial model. As evidenced by comparing the full fixed effects only models, the multinomial model had lower AUC, sensitivity and a lower classification rate.

We observed no obvious latitudinal, longitudinal, or regional differences in decay occurrence (Figure 1), and the region random effect added little to overall model performance. However, adding a location random effect substantially reduced AIC as well as increased AUC (0.83) and classification rates (75 per cent) for predicting decay occurrence. In gamlss, the null random effects model outperformed the full fixed effects model in terms of AIC, AUC and classification rate (Table 4), affirming there was still a large amount of variation related to site.

When predicting extent, no random effects were selected in the best model. A comparison of full fixed effects models without the scale parameter (σ) in gamlss revealed that the multinomial model performed best in terms of mean bias, but not in terms of RMSE. The gamlss approach proved best in terms of RMSE (0.0682) after incorporating the σ parameter (Table 4), while the reduced model with σ demonstrated the lowest mean bias overall (0.0003). However, the high dispersion made it difficult to predict decay in any given tree consistently as evidenced by relatively high RMSE. The results suggested that the random effects two-part conditional and gamlss approaches were equally suited for predicting occurrence and depicting trends for both datasets; however, the gamlss model was superior when predicting decay extent. Consequently, gamlss was used to present all trends (Figure 2).

Influential factors and trends

In all cases, the best models were additive (i.e. they did not contain two-way interactions; see 'Interactive w/ random' formulation Table 4). The most important factors for predicting decay occurrence (determined by AIC) were log-transformed height, DBH/HT, leaf longevity^{-1}, crown ratio (%), log-transformed flood tolerance (FT), drought tolerance (DT) and risk class (RC, Table 5). For dataset 1, the comparison between full and reduced gamlss occurrence models with random effects indicated that the additional predictors (drought tolerance, flood tolerance, and crown ratio) improved AIC, AUC, and classification rate (Table 4). Our models indicated that decay occurrence increased with increasing DBH/HT and decreased with increasing crown ratio (Figure 2). When predicting decay occurrence with respect to DBH/HT, we observed that the full random effects model was more sigmoidal and the full model predicted higher than the reduced model (Figure 2).

In addition to Julian date of the last freeze in spring (sday), crown ratio and log (crown ratio) were chosen in our best decay

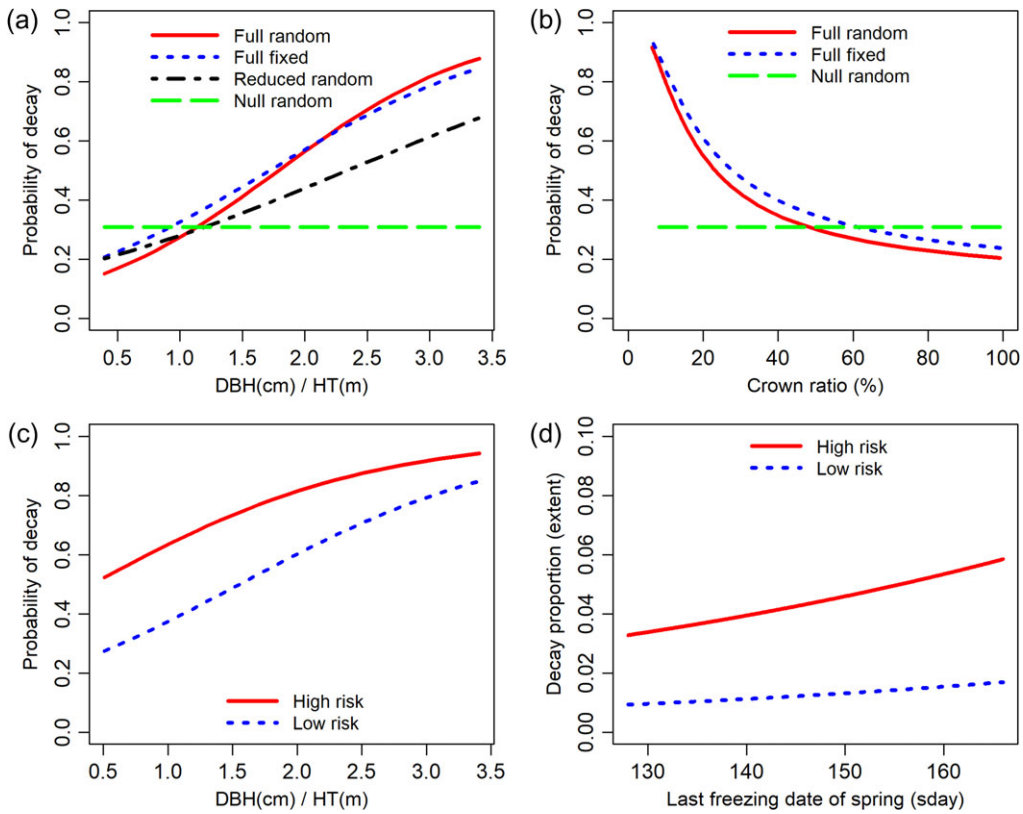

Figure 2 Probability of decay occurrence as a function of diameter to height ratio (DBH/HT) and crown ratio (CR-%) for four different model types (dataset 1: panels a and b); DBH/HT and risk classification (high/low) based on external symptoms which may lead to loss in value or increase in mortality (dataset 2: panel c); and decay proportion based on risk class and the Julian date of the last freezing day in spring (dataset 2: panel d). All lines were projected using fixed effects only, but models were constructed with and without random effects.

Table 5 Mean generalized additive models for location, scale and shape (gamlss) bootstrapped coefficients with full gamlss model parameter estimate (fit with random effects), standard error and associated *P*-value by attribute and dataset

Variable	Model	Full model estimates			Bootstrap estimates			
		Parameter estimate	Standard error	*P*-value	Coefficient average	Significance proportion	AIC proportion	Relative influence
Dataset 1								
Intercept	Extent	−4.050	1.370	0.003	−4.078	0.476	–	–
sday	Extent	0.027	0.005	0.000	0.029	0.834	0.790	13.260
Crown ratio	Extent	0.038	0.009	0.000	0.041	0.826	0.974	15.682
log(Crown ratio)	Extent	−1.236	0.417	0.003	−1.368	0.540	0.832	–
Intercept	Occurrence	7.891	0.757	0.000	7.408	1.000	–	–
log(Height)	Occurrence	−0.782	0.245	0.001	−0.727	0.463	0.726	7.105
DBH/HT	Occurrence	−1.231	0.212	0.000	−1.216	0.982	0.996	7.091
Leaf Longevity^{-1}	Occurrence	−11.028	1.425	0.000	−9.775	0.998	1.000	5.021
Crown ratio$^{-0.5}$	Occurrence	−12.673	2.690	0.000	−13.495	0.942	0.960	3.720
log(FT)	Occurrence	−1.387	0.282	0.000	−1.257	0.870	0.978	2.931
DT	Occurrence	0.470	0.133	0.000	0.522	0.778	0.772	2.637
Dataset 2								
(Intercept)	Extent	−5.412	0.902	0.000	−5.289	0.880	–	–
sday	Extent	0.016	0.006	0.011	0.015	0.365	0.326	14.285
Risk class (RC)	Extent	−1.279	0.111	0.000	−1.302	1.000	1.000	20.177
Intercept	Occurrence	0.377	0.360	0.294	0.598	0.122	–	–
DBH/HT	Occurrence	−0.928	0.327	0.005	−1.160	0.543	0.580	7.772
Risk class	Occurrence	1.064	0.193	0.000	1.057	0.954	0.994	6.140

Significance was the proportion of times a variable was statistically significant ($P < 0.05$) after 500 bootstrapped samples with 250 sample trees selected with replacement. Variables were Julian date of the last freezing date of spring (sday), flood tolerance (FT), drought tolerance (DT), tree height (HT) and risk class (RC), which is a visual assessment of a tree's risk of mortality.

extent model using dataset 1. However, Δ AIC was less than 10 between the null and full (best) model suggesting that the null model is not entirely without support (Burnham and Anderson, 2004). Log-transformed crown ratio suggested that extent decreased to a minimum then increased across crown ratio, which seemed biologically unlikely. While log (crown ratio) was commonly selected in our best model (83 per cent), it was statistically significant only 54 per cent of the time in the bootstrapping analysis suggesting that this relationship was highly influenced by a small number of observations in the data (Table 5). Decay extent was higher in trees with a higher risk class and increased with a later freeze date (sday) (Figure 2). However, while sday was robust to bootstrapping in dataset 1 (83 per cent significant), it was not when using dataset 2 (37 per cent significant). With the exception of log transformed height and drought tolerance, all variables in the occurrence model were robust to bootstrapping in terms of AIC (>95 per cent) and statistical significance (>85 per cent). Despite having lower significance and AIC proportions, all variables such as log transformed height and drought tolerance were left in the models since the relationships were biologically reasonable.

Dataset 2 was a reduced dataset and used to examine the efficacy of the risk classification system. The reduced model for dataset 2 included only DBH/HT in the occurrence model (Table 3, Model 14) and sday in the extent model (Table 3, Model 16). Including a risk classification marginally improved AUC, classification rate and mean bias, but significantly reduced RMSE (Table 4). Decay was 1.8 times more likely to occur in a tree perceived to be at high risk of mortality ($P < 0.001$, $\alpha = 0.05$, Table 5, Figure 2c). Similarly, a high risk tree exhibited 2.1 times more decay extent, on average, than a low risk tree ($P < 0.001$, $\alpha = 0.05$, Table 5, Figure 2d).

At the species level, decay occurrence increased as flood tolerance increased and decreased as leaf longevity and drought tolerance increased (Figure 3). However, these trends do not hold across all species. In particular, anomalies (e.g. sugar maple (*Acer saccharum* Marsh.) and American basswood (*Tilia Americana* L.) with regard to flood tolerance; balsam fir and white oaks with regard to leaf longevity, etc.) suggest that the existing species traits do not entirely describe species-level decay occurrence.

Species decay tolerance

We looked at several criteria to rank or group species based on their probability and proportion of decay after accounting for other significant factors using conditional means (Table 6). High occurrence and extent were marked at 30 per cent and 4 per cent, respectively. With regard to decay tolerance, we described high tolerance here as over 2.5, which would equate to low decay prevalence (<1.2 per cent). This divided our sampled

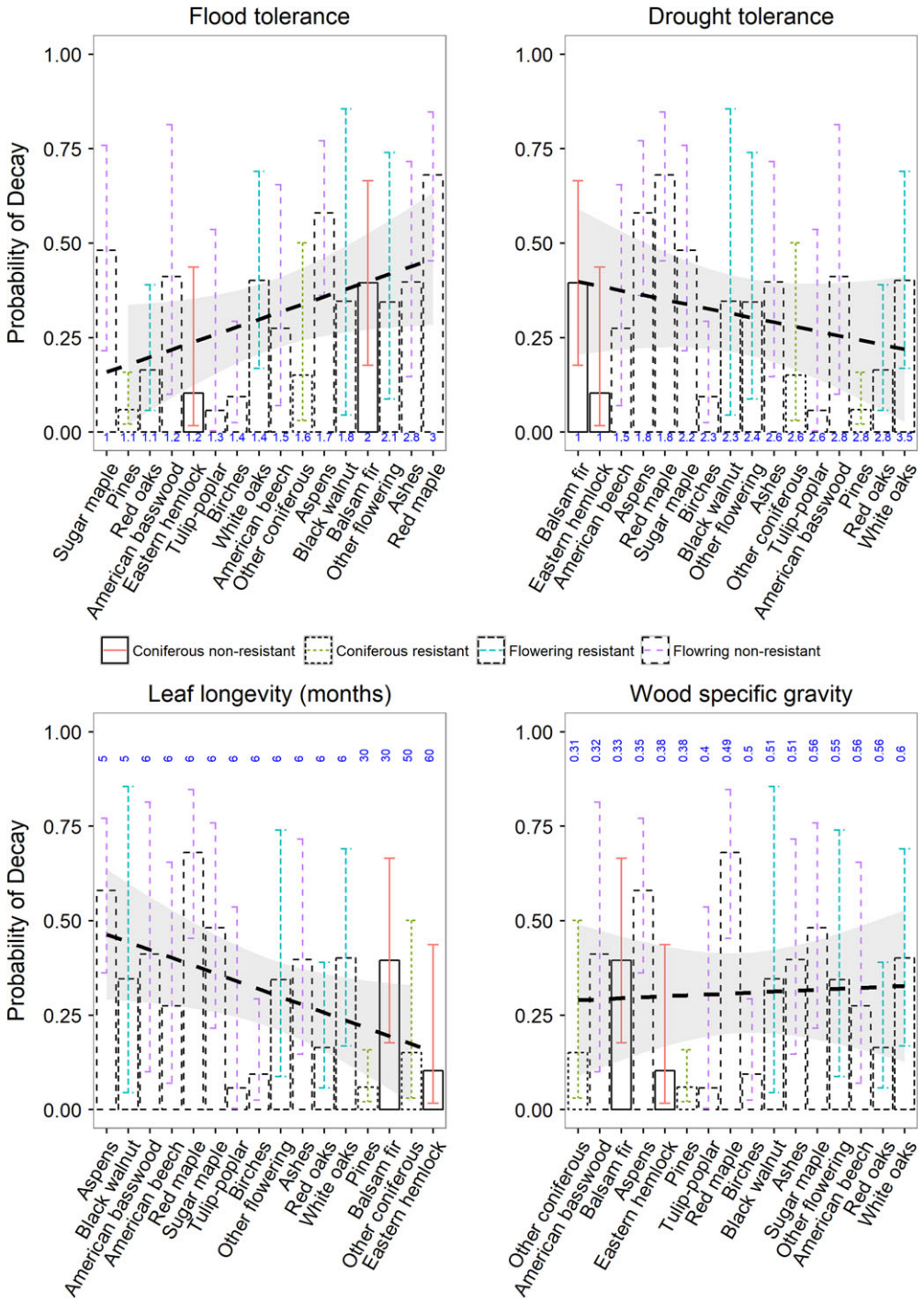

Figure 3 Predicted mean and 95 per cent confidence interval for decay occurrence probability for all species for each of the following traits: flood tolerance, drought tolerance, leaf longevity, and wood specific gravity. Species are also grouped according to decay resistance class (Scheffer and Cowling, 1966) and taxonomy. All means are least square means after accounting for risk class (risk of mortality), crown ratio, tree diameter to height ratio (DBH/HT), region and location. Species flood tolerance, drought tolerance, wood specific gravity and leaf longevity are presented as blue indexed values. General relationships between each trait and decay occurrence are presented as a linear (dashed) trendline with a 95 per cent confidence interval (shaded). Given a lack of continuity across species, trendlines are not to scale.

species in half and was the midpoint of the potential range of tolerances, which we scaled between 0 and 5. Overall, the least tolerant species groups were aspens, red maple and balsam fir, while the most tolerant were tulip-poplar, pines, birches and red oaks. In general, species decay tolerance rankings were consistent with both occurrence and extent groupings (Table 6), but

Table 6 Observed mean and upper and lower 95 per cent confidence interval values for decay occurrence (probability), extent and decay prevalence (proportion with zero values) after accounting for other factors using conditional means (presented as percentages here)

Species	Taxonomic division	Decay occurrence (probability, %)		Decay extent (%)		Decay prevalence (with 0 values, %)	Compact letter display	Decay tolerance	Decay resist.	FIA cull (%)
Populus spp.	Flowering	**58.0**	**[36.2, 77.1]**	**4.4**	**[3.3, 5.7]**	**2.5**	C	0.002	Non	1.3
Acer rubrum	Flowering	**68.1**	**[45.3, 84.6]**	3.7	[2.0, 6.5]	**2.5**	C	0.083	Non	3.0
Abies balsamea	Coniferous	**39.5**	**[17.7, 66.5]**	**6.0**	**[2.7, 13.0]**	**2.3**	BC	0.322	–	0.3
Acer saccharum	Flowering	**48.1**	**[21.5, 75.9]**	3.6	[1.3, 9.6]	**1.8**	BC	1.611	Non	1.9
Quercus alba et al.	Flowering	**40.2**	**[16.8, 69.0]**	**4.2**	**[1.8, 9.6]**	**1.7**	BC	1.694	Very	1.2
Tilia americana	Flowering	**41.1**	**[10.0, 81.4]**	**4.1**	**[0.5, 27.3]**	**1.7**	ABC	1.696	Non	1.4
Juglans nigra	Flowering	**34.7**	**[4.5, 85.5]**	**4.7**	**[0.9, 21.9]**	**1.6**	ABC	1.786	Very	3.4
Other flowering spp.	Flowering	**34.4**	**[8.8, 74.0]**	**4.7**	**[0.8, 22.4]**	**1.6**	ABC	1.828	N–V	2.6
Fagus grandifolia	Flowering	27.5	[7.0, 65.4]	3.8	[0.9, 14.5]	1.0	ABC	2.938	Non	5.2
Fraxinus spp.	Flowering	**39.7**	**[14.6, 71.6]**	2.6	[0.8, 8.0]	1.0	ABC	2.977	Non	1.5
Other coniferous spp.	Coniferous	15.1	[3.1, 50.1]	**4.8**	**[1.0, 19.0]**	0.7	ABC	3.590	N-V	1.7
Tsuga heterophylla	Coniferous	10.4	[1.7, 43.7]	**6.1**	**[1.4, 23.1]**	0.6	ABC	3.765	Non	0.6
Quercus rubra et al.	Flowering	16.4	[5.7, 38.9]	3.2	[1.2, 8.4]	0.5	AB	3.975	Slight	1.1
Betula spp.	Flowering	9.3	[2.5, 29.4]	2.9	[0.6, 12.4]	0.3	AB	4.465	Non	1.7
Pinus spp.	Coniferous	5.9	[2.1, 15.8]	3.5	[1.5, 8.0]	0.2	A	4.599	Slight	0.2
Liriodendron tulipifera	Flowering	5.7	[0.3, 53.6]	3.1	[0.1, 43.6]	0.2	ABC	4.651	Non	1.5

The compact letter display (CLD) depicts statistically distinct and overlapping species groups for decay occurrence. Decay tolerance used a continuous approach scaling prevalence similarly to other tolerance values examined in this study. For comparison, laboratory resistance groups (resist. – Scheffer and Cowling, 1966) are presented along with mean field cull calls available in the US Forest Service Forest Inventory and Analysis Program (FIA) database. The mean field cull calls are compared with decay proportion (including 0 values) for each species (species group). Flowering and coniferous spp. cover a range of resistance classes from non-resistant (Non) to very resistant (i.e. N–V). High probability and proportion are in bold.

there were some notable exceptions. Red maple had a fairly low tolerance (0.083) due to high occurrence, but was assigned to the 'low' decay extent group, while eastern hemlock (*Tsuga canadensis* (L.) Carr.) and the other coniferous species showed the reverse pattern. Though eastern hemlock exhibited relatively high extent, it was one of the least likely species to exhibit decay leading to an overall low decay occurrence and low decay prevalence (high tolerance). After accounting for other significant factors, the species with the lowest likelihood of occurrence were pines, which was evidenced by the conditional means comparisons illustrated by compact letter displays (Table 6) and graphically (Figure 3). Pines were significantly different than red maple, balsam fir, aspens, white oaks and sugar maple. Likewise, birches and red oaks showed significantly less decay occurrence than red maple and aspens. Tulip-poplar and eastern hemlock also showed low occurrence rates. The greatest extent of decay was observed in eastern hemlock, balsam fir, and other conifers, but there were no statistically significant differences between any species in terms of extent (Table 6).

In general, the lack of consistency of species importance was reflected in the statistical modelling and creating distinct groups across all species still proved difficult due to overlapping distributions. Inclusion of a species covariate had a significant effect on model fit (lower AIC, P-value < 0.001, $\alpha = 0.05$, Table 4); however, the average occurrence and extent of decay were not statistically different across all species (Table 6). Coniferous species were generally in the high tolerance grouping and a model that replaced flood tolerance, drought tolerance and leaf longevity with species increased the AIC value, suggesting that species traits effectively capture most of the species-level variation in these data (Table 5).

Species-level estimates of cull as measured in the FIADB were generally higher than those reported in this study for flowering species and often lower for coniferous species. Notable exceptions included aspens which were 1.2 per cent higher in our data and other coniferous species such as red spruce and northern white cedar which were 1.0 per cent lower in our data. The greatest differences were in American beech (*Fagus grandifolia* Ehrh.; i.e. FIADB estimates were 4.2 per cent higher than our data) and balsam fir (i.e. FIADB estimates were 2.3 per cent lower). Species (groups) such as pines, eastern hemlock, sugar maple and American basswood had the best agreement as differences were not more than 0.5 per cent.

Discussion

Our study took an empirically-based approach to examine the various factors (e.g. tree-level, geographic, environmental and species) that influence decay prevalence across a wide range of tree species. To our knowledge, this study is one of the few to examine such differences in advanced decay for standing trees across a wide geographic area and range of species (e.g. Basham, 1991). Prior studies have predominantly focused on incipient decay (e.g. red heartwood, Havreljuk *et al.*, 2013) and dead downed wood (e.g. Russell *et al.*, 2014). This analysis indicates that decay occurrence could be explained by tree form (namely DBH/HT), crown ratio, leaf longevity, tolerance to flooding and drought, and risk class. In addition, our results suggest that Julian date of the last freezing date of spring, crown ratio and risk classification may improve predictions of decay extent.

Challenges for modelling decay occurrence and extent

Due to the highly variable nature of the data, it was challenging to model both the occurrence and extent of decay. In addition, the available datasets used to develop the models were not representative samples and were highly unbalanced across species and sites. We tried to minimize these issues with the use of random effects and bootstrapping. However, the small sample sizes of some species did not allow for a more rigorous assessment of a species-specific effect as they were highly interactive with certain tree level covariates (i.e. tree size, risk class). For instance, it is possible that the inter-species effect of tree size on decay occurrence was more complex than that expressed by an additive term. The small residual sample sizes for trees with decay observed made modelling decay extent particularly difficult. The best extent models only improved AIC slightly (i.e. Δ AIC < 10), which suggests that the null model has some support as the best model (Burnham and Anderson, 2004). In addition, the occurrence and extent models shared crown ratio, DBH/HT, and height as influential variables (according to boosted regression); with additional data, we may expect to see decay extent models that support explanatory variables that align better with decay occurrence models.

The gamlss model improved predictions of decay extent when compared with the two-part conditional model. This improvement was likely due to the fitting of the additional σ parameter, which afforded a more flexible distribution. The fact that the semi-parametric gamlss model converged rapidly with no reduction in accuracy also made it ideal for bootstrapping. However, for utilizing random effects when predicting occurrence and making explicit comparisons between species and locations, the two-part conditional parametric model was preferred. Compared with the other two frameworks, the multinomial model classified nearly as well overall; mean bias was lower yet AUC scores were much lower and RMSE higher for this approach. In addition, the approach suffered from two drawbacks: (1) In contrast to Westfall (2013) where three distinct classes were evident when predicting cull (no cull, intermediate cull and entirely cull), we had no entirely decayed trees and no concrete way to separate high and low decay; and (2) we could not specify random effects. For these reasons, the multinomial approach was not used in further analysis here. Based on these findings, we propose that both the two-part conditional and gamlss models are more suitable for predicting occurrence and extent. Due to its accuracy and efficiency of estimation, gamlss is recommended for future analyses of this nature, particularly when the scale parameter can be determined.

Factors influencing decay occurrence and extent

Our initial expectation was that tree size (DBH and height) would offer the greatest explanatory power along with perceived risk to mortality. Decay occurrence increased until trees achieved 20 m in height and then remained consistent. The observed curvilinear relationship with height is supported in work by Knoke (2003) who found both height and height squared to be significant variables for predicting the occurrence of red heartwood in European beech (*Fagus sylvatica* L.). However, other studies have indicated that probability of decay declined with increasing height, likely indicating better site quality (Giroud *et al.*, 2008; Schneider *et al.*, 2008). Lastly, the assertion that the tallest trees would exhibit less decay may be supported by research that suppressed trees are more likely to exhibit external damage (Baral *et al.*, 2016) and that fast-growing trees heal over dead branches more rapidly (Dănescu *et al.*, 2015). After accounting for DBH/HT, flood tolerance, leaf longevity and drought tolerance in the best model, log transformed height was the least robust predictor across various subsets of data as indicated by the bootstrap analysis.

Although highly influential, DBH was not selected in the best AIC model due to multicollinearity with other covariates. Closer examination revealed that of the 10 largest trees (DBH > 79 cm), decay occurred in 60 per cent of them and that their average decay was less than the overall dataset. Giroud *et al.* (2008) concluded that short trees with larger DBH exhibited higher probabilities of red heartwood occurrence, which agreed with our finding that decay occurrence increased with tree DBH/HT (Figure 2). However, given that DBH and DBH/HT are highly correlated, this result is not entirely in opposition to previous studies, which suggested that increasing DBH resulted in greater discoloration (e.g. Drouin *et al.*, 2010) as well as higher cull proportion in standing trees (Westfall, 2013). Rather, DBH/HT may offer greater explanatory power as it is more closely related to other determinants of decay occurrence and extent such as competitive status within a stand (Rijal *et al.*, 2012), site factors like wind (Brüchert and Gardiner, 2006) and edaphic factors (Yanai *et al.*, 2009). Moreover, increasing DBH/HT is potentially correlated with age, and older trees could have been exposed to elements for longer periods of time, effectively increasing the likelihood that the tree may have developed broken branches or other wounds that may serve as entry points for decay organisms (Knoke, 2003; Giroud *et al.*, 2008).

Our findings showed an inverse relationship between tree internal decay occurrence and crown ratio, which is a result that may be related to the influence of crown size as an overall indicator of tree health and competitive status. For example, a larger crown may indicate competitive dominance and correlate with lower decay. In addition, trees with smaller crowns could indicate crown dieback and more dead branches (Westfall, 2013). Our results disagree with those of Kadunc (2007) who observed that larger crown lengths indicated trees with higher probability of decay, which was likely due to those trees having more significant forks. However, Kadunc (2007) only considered one flowering species in contrast to the large range of coniferous and flowering species examined in this analysis. This indicates that the influence of crown ratio on the relative likelihood of decay needs to be interpreted in terms of the overall physiological state of the trees being evaluated. Mäkelä and Valentine (2006) noted that the live crown ratio is proportional to the tapering of the stem due to crown rise, which occurs as lower branches are shed and dead, disused branches become incorporated in heartwood. The latter can help further explain our results, which suggest that for a given diameter a shorter tree with a relatively short crown has a high likelihood of containing decay (Figure 2).

The incorporation of risk classification into the model explained variation in both decay occurrence and extent, which is a result that could have important implications for future field assessments. In this study, risk was defined as the likelihood of future mortality in that higher risk trees were assumed more likely to experience mortality before the next cutting cycle.

Qualifiers for high risk trees share similarities between trees classified as having low vigour in other stem classification systems. For instance, Quebec's tree vigour assessment separates trees into four classes based on perceptions of tree mortality (Boulet, 2007). Given that low risk trees were less likely to exhibit decay, the current study adds to the existing literature that supports classifying trees based on perceived risk of mortality or vigour (e.g. Drouin *et al*., 2010; Baral *et al*., 2013; Castle, 2017; Castle *et al*., 2017).

Intra-specific variation and local effects on decay

The inability to find consistency between species in different decay assessments (i.e. laboratory-based, decaying logs, visual standing tree or felled) along with large overlap in occurrence of species groups and the inability to detect significant differences in extent within the felled tree dataset highlight the challenge of defining a species' response when there is likely a large number of historical/ environmental determinants of decay in trees. This supports a view that although some relevant differences in species exist, a high degree of intra-specific variation in decay within species/species-groups is still present (Figure 3; Table 6).

We hypothesized that climate may help explain some of this intra-specific variation. For example, Havreljuk *et al.* (2013) found that the proportion of red heartwood in sugar maple in Quebec may increase with lower annual daily minimum temperature, and they speculated that extreme freeze events could cause an increase in frost cracks leading to discoloration in this species. Given the more southerly latitudes explored in this analysis, we may not have had the ability to detect the effect of extreme freeze events. However, we did observe that decay extent increased with a later freezing date in spring, and would expect lower average minimum temperatures with later last freezing dates. Work by Burton *et al.* (2008) also suggests that sites with later freezing dates would also experience more frequent winter events, which would result in greater incidences of trees with broken branches and tops, splits, and cracks, increasing the number of entry points for damaging agents. Ultimately, a greater number of observations across a larger number of sites are likely needed to confirm these findings.

It should be noted that the climate data (1961–1990) was not entirely synchronized with the subject tree's growth period. However, we feel that more synchronous climate data would aid little in increasing these variables' explanatory power. Rather, the strong random effect of location suggested that much of the prevalence of decay may be explained by underlying site-specific factors such as: (1) edaphic factors; (2) management history; (3) competitive status; and (4) genetics. With regard to the first site-specific factor, Yanai *et al.* (2009) indicated that red heartwood size in sugar maple increased in more basic soils (higher pH) across several states in the northeastern US. In addition, stem decay may better be explained by soil drainage class (Hofmeyer *et al*., 2009). Second, management history may also be influential since trauma incurred during harvests could result in greater decay occurrence for residual trees on the harvest site (Erickson *et al*., 1992). In addition, practices such as high-grading in eastern hardwood forests may result in a landscape of genetically inferior, low vigour stock (Nyland, 1992), while commercial thinning in true fir stands can lead to losses of up to 1.7 per cent and 7.6 per cent of the cubic and merchantable board foot volume, respectively, due to wounds that lead to decay (Aho *et al*., 1989). However, partial harvesting may not necessarily result in increased damage as careful planning and operator experience has been shown to mitigate this effect (Cline *et al*., 1991). Third, a tree's competitive status may influence development of decay. For instance, Giroud *et al.* (2008) indicated paper birch (*Betula papyrifera* Marsh.) crowns that were exposed to the sun exhibited lower levels of red heartwood. Lastly, genetic variation within species may also have a role as several controlled studies have indicated that decay resistance can vary across different genetic families rather than location (Scheffer *et al*., 1949; Yu *et al*., 2003). In addition, Shigo and Marx (1977) suggested that compartmentalization rates are controlled by genetic factors. We could not examine these four factors in this study and consequently believe that future studies on stem decay are needed to better examine the influence of these factors and climate at a higher resolution.

Inter-specific variation and the value of functional groups for assessing decay potential

Although much of the variation remained unexplained and related to location, we observed that some species (species groups) such as pines (low decay occurrence) differed from red maple and aspens in terms of decay occurrence (Table 6). This was supported by other studies as laboratory resistance was higher in pines than in aspens and red maple (e.g. Scheffer and Cowling, 1966); pines also had lower observed field cull (FIADB), lower stem defect (i.e. advanced and incipient decay combined) in trees destructively sampled in Ontario (Basham, 1991), and a lower decay rate than red maple and aspens (Russell *et al*., 2014). Aspens were also described as 'poor wound compartmentalizers' by Shigo, which may partially explain the high decay prevalence seen in these species (Loehle, 1988). The observation for eastern hemlock that decay occurrence was low despite high extent was confirmed by research that suggests a low diversity of disease organisms that cause death or decay in living hemlock trees (Hough, 1960), and a low resistance after the wood is colonized (Scheffer and Cowling, 1966; Howard *et al*., 2000). However, our characterizations of species decay occurrence, extent and prevalence were often, but not always supported by previous research. Our finding of low occurrence and extent in birches was not supported in the existing literature as wounds in *Betula* species tend to develop into much larger columns of decayed wood (Shigo and Sharon, 1968 as cited in Blanchette, 1982). In addition, field cull observations were over five times higher and it was considered as non-resistant (Scheffer and Cowling, 1966). The largest discrepancy was observed for American beech (FIADB = 5.2 per cent vs. 1.0 per cent in our data, Table 6), and we surmise that this is due to the high prevalence of beech bark disease across the northeast (Morin *et al*., 2007), which was likely not well represented in the beech trees in this database. The relatively small sample size for American beech and some other species suggests caution when extrapolating predicted decay proportions to the greater population.

In addition to examining species differences, we wanted to further test this relationship by evaluating the effects of more general species characteristics. More specifically, we expected that wood density, taxonomic division and species' tolerance to various environmental factors such as shade, drought and flooding would explain decay prevalence. Chave *et al.* (2009), found that wood durability (i.e. a measure of wood resistance based on field or lab trials; Scheffer and Morrell, 1998) decreases as wood density increases, yet flowering plants (higher densities) have higher decomposition rates than conifers (e.g. Weedon *et al.*, 2009). Likewise, for all species examined here and for flowering species alone, we observed post-hoc that wood density was negatively correlated with durability, while there was a positive relationship between downed wood decay rates (Russell *et al.*, 2014) and wood specific gravity ($r = 0.23$). For the primary question at hand, we observed a slight increase in decay occurrence as specific gravity increased for all species (Figure 3). However, wood density was not selected for model testing since we only used variables that met the threshold defined by Müller *et al.* (2013). Rather, leaf longevity and a species' tolerance to flooding and drought were selected as the most influential species-level factors in addition to other tree-level metrics and location. While a model with wood density or drought tolerance and work to maximum load further reduced AIC by 6 and 13, respectively, the constraint imposed by the aforementioned threshold ensured that the model was not influenced by certain observations, while providing a more parsimonious model. As noted by Chave *et al.* (2009) with regard to decomposition, the ultimate facilitators of decay in standing trees remain unclear and correlated traits such as conduit (or pore) size may explain this relationship better than leaf longevity and wood density.

In terms of AIC, the traits-based model using leaf longevity, drought tolerance and flood tolerance was better than the species-based model suggesting that the original 16 species categorizations used in this analysis were likely excessive, which was also supported by conditional means comparisons. This finding would indicate that traits (rather than species) may help predict decay occurrence and should be explored in future analyses. Ultimately, species decay prevalence classifications and tolerance values similar to those presented in this analysis may prove useful.

Our results suggest that reducing the number of species groups on the basis of decay occurrence or prevalence would greatly reduce the number of parameters and simplify future analyses. They also indicate that treating species-level decay prevalence as a continuous variable ('decay tolerance') in a similar way as environmental tolerance (e.g. Niinemets and Valladares, 2006) may be a preferable alternative to dividing decay into discrete classes. However, both approaches have their strengths and weaknesses. Ideally, we would want to find a ranking that is consistent across the various ways of species groupings. In addition, future analyses would benefit from more observations of certain species to properly locate a species along a continuum.

Given the lack of an entirely representative sample, we note major inconsistencies among our study, prior analyses (e.g. Scheffer and Cowling, 1966) and existing datasets (e.g. FIADB), which illustrate the need for decay to be studied further. For example, birches and tulip-poplar exhibited high tolerance to decay, while white oaks and black walnut exhibited low tolerance in dataset 1, which was in contrast to the resistance classifications of Scheffer and Cowling (1966). Further, our study shows that grouping species by traits or risk might be more useful than trying to develop species-specific predictions, especially with limited and highly variable data. However, we acknowledge that species traits such as moisture tolerance are often naturally confounded with site-specific climate making it difficult to identify the actual biological mechanism. The Scheffer and Cowling (1966) decay resistance classification was of low relative influence. By itself, the variable was significant when predicting occurrence; however, it was not selected in a model that accounted for leaf longevity and environmental tolerance (i.e. flood and drought). Similarly, downed wood decay rates (Russell *et al.*, 2014) were not incorporated into models due to low relative influence. The fact that site and other tree- and species-level factors offered higher explanatory power, suggested that perceived decay resistance or prevalence may also vary depending on the test environment (e.g. laboratory, deadwood, standing live tree) and whether pathogens were naturally occurring or introduced to test resistance. This assumption may be further supported by conflicting relationships between wood density and wood durability as opposed to decomposition rates. Although we could not formally evaluate this here, we suggest that it is an important area for future research as assumptions about decay in one environment may lead to misinterpretation when predicting decay in another environment.

Conclusion

Overall, this study highlighted the tremendous within- and between-species variation in both stem decay occurrence and extent, while providing a solid statistical framework and potential covariates for future assessments. We observed strong empirical evidence that support the following conclusions: (1) gamlss was a flexible and robust modelling approach capable of handling difficult data like decay occurrence and extent; (2) increasing tree DBH/HT and decreasing crown ratio increased the likelihood of decay occurrence in a tree; (3) a classification system based on perceived risk of mortality can help improve estimates of both decay occurrence and extent; and (4) while differences between certain species were apparent (e.g. *Pinus spp.* vs. *Populus spp.* and *Acer rubrum*), species traits such as leaf longevity and environmental tolerance may better explain variation between species and may be used to group species to predict decay. However, as noted in Niinemets and Valladares (2006), species exist by making functional trade-offs so further exploration of inter-specific decay tolerance classification is warranted. Further sampling across a broader range of conditions will be needed to verify the results presented here and to better understand interactions between species traits and site-level factors. The small sample size of decayed trees made it especially difficult to predict and classify species by decay extent in this analysis. More controlled studies will be necessary to better understand how site, genetic, species traits and other stand-level factors may influence decay in standing trees across large spatial extents.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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