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Transitional climate mortality: slower warming may result in increased climate-induced mortality in some systems

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Abstract. The potential for climate change to cause mass tree mortality in forested systems by pushing environmental conditions past physiological tolerance thresholds is well documented. Less well studied is damage and mortality associated with climatic transitions, where mortality is less on either side of the transition; the shift from freezing winter conditions to thawed winter conditions in temperate and high latitudes is a clear example. "Transitional climate mortality" is sporadic, but widespread, associated with exposure to mortality during these climatic transitions, and triggered by proximal weather events like a hard freeze after a period of above freezing temperatures. Interestingly, this suggests that slower warming could result in more intensive mortality because of extended exposure to potential mortality events. The concept is tested using a well-studied species (*Callitropsis nootkatensis*) on the US/Canadian Pacific coast. To identify the transitional mortality zone, statistical modeling combined with a current mortality map and bioclimatic variables was used. This process identified the −5° to 0°C zone (mean temperature of the coldest month) as particularly associated with transitional mortality. Weather station data from multiple locations were used to validate observations. Four GCMs (General Circulation Model) and two future warming scenarios (representative concentration pathway 2.6 and 8.5) were used to estimate time and spatial extent of exposure at broad scales; slower warming results in more intensive cumulative exposure than faster warming. Finally, by combining the observed mortality zone with weather station data a generalizable binomial model was tested as a means to estimate potential future mortality. This model is applicable to any system where the transitional mortality zone (e.g., temperature range) and the frequency of proximal mortality triggers are known. This type of mortality phenomena has been understudied but may be a large driver of future forest change, given the frequency of mortality events and the ubiquity of the freeze–thaw transition across temperate systems globally.

Key words: climate change; climate mortality; disturbance; emerging stressors; forest decline; freeze–thaw; snow loss; time series.

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Introduction

The rapid pace of climate change is expected to exceed the ability of many species to keep pace via migration (Loarie et al. 2009) or evolve tolerance to new conditions (Parmesan 2006, Hoffmann and Sgrò 2011). While some species may be able to survive, compete, or thrive in new conditions, others are likely to be more sensitive, either injured directly via climate shifts (Allen et al. 2010) or indirectly via reduced vigor relative to competitors (Buckley et al. 2011). This concern is especially relevant for sessile organisms such as long-lived plants, which cannot migrate and whose reproductive cycle may be exceptionally long (Fettig et al. 2013, Trumbore et al. 2015).

Understanding to what extent these organisms will be exposed to threatening conditions, and the likelihood of mortality given those conditions, is imperative to predicting the extent of climate-caused ecosystem disruptions.

The majority of research on climate-induced mortality is concerned with thresholds, points in climatic space beyond which mortality rapidly increases (Allen et al. 2010, Kreyling et al. 2014). Research has generally concluded that warming will result in increased mortality as these thresholds are crossed ("threshold responses," Allen et al. 2015). These thresholds are generally related to a physiological tolerance point past which a given species cannot survive, such as drought conditions beyond which xylem conductivity is disrupted, carbon starvation, or interactions with other disturbance agents (McDowell et al. 2008, Bentz et al. 2010, Urli et al. 2013, Anderegg et al. 2015*a*). These limits may cause mass plant mortality (Allen et al. 2015), and are of interest because they may constrict current species ranges, constrain future migration (Cavanaugh et al. 2015), and interact with other stressors (Anderegg et al. 2015*b*). In these cases, the threshold is a point beyond which conditions do not improve, and mortality is likely.

A fundamentally different type of climate-related mortality—here termed "transitional climate mortality"—is possible, though generally unexplored. Transitional climate mortality is associated with increased mortality around a particular climatic range, with lessened mortality on either side of the transitional zone; in essence, a spatiotemporal wave of mortality moves over the landscape, with potential survivors on both sides. The most obvious example is the freeze–thaw phase change associated with winter temperatures around 0°C. Below that temperature, conditions are generally frozen, a condition for which many species are well adapted. Above that average, winter conditions are reliably unfrozen, also tolerated by many species. However, at that threshold variability between frozen and thawed conditions within the same season may lead to significant physiological damage. Specifically, warm conditions rapidly followed by freezing have been implicated in a variety of climate-induced injury or mortality events in many locations worldwide, such as budbreak/freezing events (Gu et al. 2008, Augspurger 2009, 2013), low snow conditions and cold snaps leading to soil freezing (Groffman et al. 2001), aboveground mortality (Bourque et al. 2005), root mortality (Campbell et al. 2014), and altered nutrient cycling (Urakawa et al. 2014). Other impacts include changes to microbial biomass and nitrogen cycling (Larsen et al. 2002), mobilization of previously sequestered metal contaminants from soil colloids (Mohanty et al. 2014), and potential interactions with nitrogen pollution to increase vulnerability to mortality (McNulty et al. 2017). As climate warms, many areas currently below freezing in the winter will cross this temperate zone, potentially exposing species to mortality-causing conditions and novel stresses (Inouye 2000).

A second difference between transitional climate mortality and the more well-studied threshold-type mortality is that transitional mortality is sporadic; it is not a physiological threshold that causes mortality, but rather a climatic condition which may not present every year (e.g., relatively warm winter and no snow) that exposes individuals to mortality-causing weather events operating on a shorter timescale (Bourque et al. 2005, Gu et al. 2008, Augspurger 2013, Hennon et al. 2016). Thus, the transitional climate mortality zone is defined as when an area is exposed to potential mortality, given acute, mortality-causing events. This has been well documented via studies combining probability of short-term, mortality events (e.g., a cold snap after a growing period) with long-term trends in exposure like a loss of winter snowpack due to climate warming (Beier et al. 2008, Gu et al. 2008). While it is true that mass mortality-causing threshold responses (Allen et al. 2015) similarly do not occur every year, but rather in, for example, hot and dry years, the key difference between the two types of mortality drivers is the risk of transitional climate mortality is temporary assuming a continually warming climate (Fig. 1). Thus, there are two components to the concept of transitional climate mortality—geographic extent of exposure, associated with the area exposed to potential mortality, and the time of exposure associated with the potential for actual mortality.

An excellent study system for this phenomenon are the northern Pacific temperate rainforests, an area which is experiencing the most rapid loss of freezing conditions globally (Meehl et al. 2004). Rapid mortality of *Callitropsis nootkatensis*

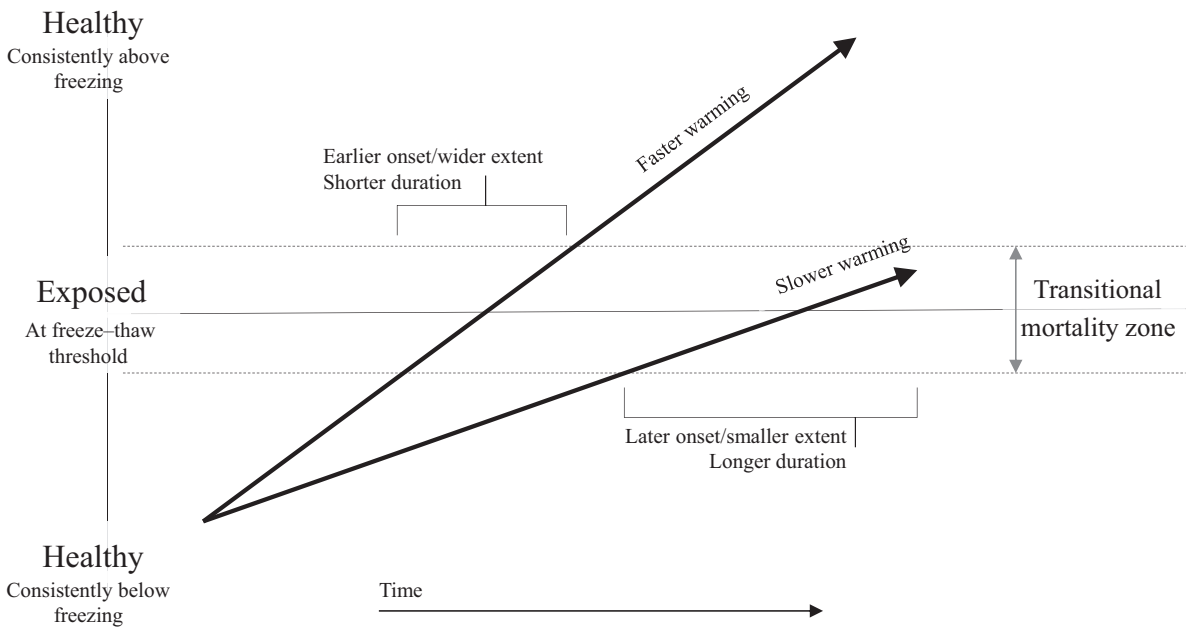

Fig. 1. The concept of transitional climate mortality. Faster warming scenarios result in earlier onset of exposure to mortality, and potentially more spatially extensive exposure, but slower warming scenarios result in longer times exposed to mortality-associated conditions.

(yellow-cedar) has been tied to climate and is relatively well studied (Hennon and Shaw 1994, Schaberg et al. 2005, Hennon et al. 2012, Oakes et al. 2014, Buma et al. 2017). The mortality is associated with a lack of winter snow driven by generally warming winter temperatures (exposure), which exposes soils to freezing during sporadic cold snaps in late spring, causing fine-root injury and occasionally death (proximal mortality events; Beier et al. 2008). Areas of shallow rooting, generally due to high water tables or shallow soils, are especially susceptible. Mortality can occur after a single freeze, though two or more events are sometimes required to kill mature trees as damage to root systems becomes progressively more severe. In affected areas, mortality is generally >70% of *C. nootkatensis* basal area (Hennon et al. 2016). *Callitropsis nootkatensis* is a useful test species for the new concept of transitional climate mortality because its range spans 20° of latitude, a variety of climatic conditions, and its healthy range and areas of mass mortality have been delineated for the entire range at a high resolution (Buma et al. 2017, Fig. 2). Generally, mortality does not seem to be tied to a threshold per se, but rather a climatic range of winter temperatures, below and above which there is little noted mortality. While plot-scale research has described the mechanistic mode of mortality (Hennon et al. 2012, 2016, Oakes et al. 2014), and the geographic range of mortality has been described (Buma et al. 2017), the rate of warming in relation to time of exposure, and the potential for a transitional climate mortality dynamic, has not been evaluated.

The purpose of this study was fourfold: (1) to determine whether observed mortality is consistent with the hypothesis of a climatic transition zone rather than a physiological threshold; (2) to estimate what proportion of the landscape exposed (i.e., in the climatic transition zone) experiences mortality; (3) to determine whether slower or faster climate warming, represented by a low-emission and high-emission representative concentration pathway (RCP), results in higher cumulative exposure or more spatially extensive exposure, respectively; and (4) to create a generalizable model to estimate the number of proximal events required to kill exposed individuals and one that can be applied to other transitional climate mortality settings.

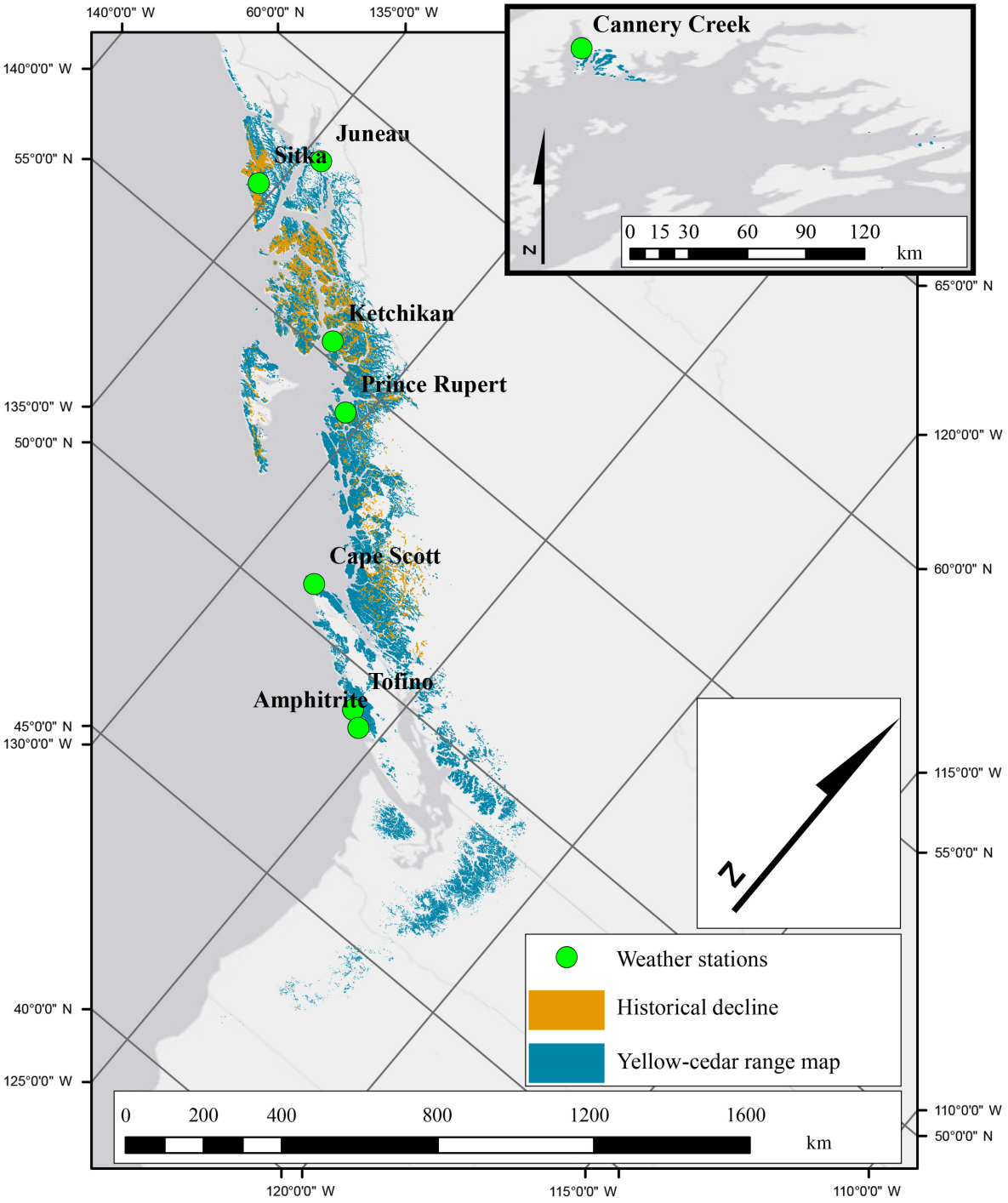

Fig. 2. Range and decline of *Callitropsis nootkatensis*. Locations refer to weather stations utilized in analyses. Note band of mortality with less/no decline noted in warmer areas to the south and colder areas to the north. Range and decline from Buma et al. (2017).

Materials and Methods

Map assessment and model building

The current areas of decline and healthy portions of the *Callitropsis nootkatensis* population were recently delineated within the entire range, which spans ~20° latitude and a variety of climates (Buma et al. 2017). This map of healthy and impacted populations was used as the basis for the climate and geographical analyses. Accuracy was assessed using 54 known decline points (mean 73.7% of *C. nootkatensis* basal area dead) and 47 healthy points (mean 8.4% dead) from Oakes et al. (2014), Krapek et al. (2017), and B. Buma, S. Bisbing, and A. L. Bidlack (*unpublished data*). These points span the entirety of southeast Alaska (total n = 101), where the majority of both healthy and dying populations are located (Buma et al. 2017). Because maps derived from models and aerial surveys, as in this case, are not expected to precisely align (Johnson and Ross 2008), several spatial lags were also tested: no lag (absolute spatial accuracy), and then 50, 100, 500, and 1000 m of buffer on the decline areas. For example, if a decline plot was 400 m from the actual mapped decline, it would be considered incorrect at the no lag, 50, and 100 m distance, but correct at the 500 and 1000 m distance (similar to methods applied to *Dendroctonus ponderosae* mortality mapping, see Johnson and Ross 2008).

A random sample of 10,000 points was taken from across the entire range. At each point, healthy or decline status was assessed/determined and recorded, and several climatic variables were sampled using the BioClim database (Hijmans et al. 2005, v1.4, updated to CMIP5 in 2017): mean annual temperature, max temperature of the warmest month, minimum temperature of the coldest month, mean temperature of the warmest quarter of the year, mean temperature of the coldest quarter of the year, annual precipitation, mean precipitation in the warmest quarter, and mean precipitation in the coldest quarter. These variables were chosen for their relevance to the freezing mechanism of *C. nootkatensis* decline (Hennon et al. 2016). Slope, elevation, and aspect were not found to be significant in initial testing (at the rangewide scale) and were excluded. Of this 10,000-point sample, 951 were in decline areas, so a subsample of 951 healthy points was randomly selected to create a balanced dataset with equal amounts of decline and non-decline sites (n = 1902). The sample was further subdivided into two random subsamples for model creation and independent validation.

A random forest classification model (Breiman 2001) was created using the R randomForest package (Liaw and Wiener 2002). Random forests are a "bagged" ensemble modeling method using regression trees; the method creates multiple trees from a random subset of variables. This method reduces overall model variance and is highly resistant to overfitting, important when modeling over a broad area (Breiman 2001). Two thousand trees were grown with a sampling size of 250 per class (decline/non-decline), which resulted in similar classwise error rates.

Transitional zone validation

To test that the transitional zone of mortality described by the model represented reality, the final model conditions were compared to historical climate data in both decline locations and points on either side of the hypothesized transitional zone (Fig. 2). Two locations are from areas of extensive historical decline (Sitka, Alaska, and Prince Rupert, BC) and two from warm locations where no mortality has been noted (Tofino and Amphitrite Point, BC). There are no long-term weather stations within the colder portions of the contiguous range, so two stations located at the extreme range edge were used. The Cannery Creek site is far from known decline locations. The Juneau weather station is located at the Juneau airport, and is lower in elevation and generally expected to be significantly warmer than actual populations in the area (Krapek et al. 2017). As a result, the data are provided as a geographical datapoint but not used in the formal analyses. Alaska data are from the NOAA Climate Data Online portal (www.ncdc.noaa.gov/cdo-web), using the Juneau airport reporting station and the Sitka Magnetic Observatory station (1899–1990) and the Sitka airport (1990–present). The two stations are both at sea level, separated by ~1.3 km, and have been used in combination for many historical climate reconstructions in the region (Wiles et al. 2014). Canadian data were obtained from Climate Canada (climate.weather.gc.ca) for the time period of 1963–1997 (the last point in which all three had data). Average daily temperature was calculated as the average of daily high and

low values (if only one was available, that day was omitted). Temperature of the coldest month was collected for each station, for each year of data.

In addition to climatic exposure (as captured by the model at a yearly resolution), the proximal trigger for mortality, warm periods followed by cold snaps were quantified. Daily data at each station were summarized similar to Beier et al. (2008): incidents of 7GD/3FD cold snaps (seven growing degree days [>5°C] followed by three freezing days [<0°C]), corresponding to severe, damage-causing events, were counted. Up to one day of "neutral" temperature (5–0°C) between the GD and FD events was allowed when counting.

Projections

This model was applied to the entire *C. nootkatensis* range using projected BioClim climate data (Hijmans et al. 2005, updated to CMIP5 projections) for both current and future conditions. Two RCPs reflecting low and high rates of radiative forcing/climate change (RCP 2.6 and 8.5) and four climate models (CNRM-CM5, GFDL-CM3, Hadley, and MIROC) for time periods (2050 and 2070) for a total of 16 scenarios in addition to current conditions. The models were chosen for their high accuracy in the region as previously evaluated by SNAP (2009). The end result for each scenario is a map of mortality exposure, visualized as either 0 (unsuitable, similar to areas of current high mortality) or 1 (suitable, similar to areas currently healthy).

Model outputs and analyses were limited to the current range of *C. nootkatensis*. While there is evidence that expansion is occurring on a multi-century timescale (Krapek et al. 2017), it is not likely to be relevant on the timescales under consideration here. Model results were summarized by latitudinal bands to evaluate mortality patterns and explore how mortality-associated climates vary as a function of geography. To assess whether slower warming results in longer-term exposure to potential mortality, the cumulative time of exposure to mortality-causing conditions was estimated by averaging across exposure, including current conditions, 2050, and 2070. Each time period was given equal weight. To assess whether the spatial extent of potential mortality is higher in faster warming scenarios, the total area exposed for at least one point in time in at least one of the models (current, 2050, or 2070) was calculated from the latitudinal data using area weighted means. In this case, the duration of exposure was not important.

To generalize the transitional exposure concept, the length of overall exposure can be linked to the probability of a proximal mortality event during those times via a simple binomial model, assuming year-to-year independence in the proximal mortality event. This gives the probability of a potential mortality event given time of exposure (expressed as percent, e.g., events per century, to normalize for differing weather station records) and likelihood of the proximal mortality driver, in the case of *C. nootkatensis*, the thaw/freeze frequency.

To test this idea, data from Kruzof Island, located by the Sitka, AK, weather station, Gravina Island, where the Ketchikan weather station is located, and Duke and Annette Islands (80 km north of the Prince Rupert station, Canada) were utilized together with modeled transition zone results. Kruzof Island has 15,997 ha of *C. nootkatensis*, of which 85% is considered medium or high risk due to shallow rooting and inadequate snow (modeled via topography and annual snow accumulation, respectively). A total of 10,821 ha on Kruzof has experienced mortality; that is, approximately 80% of susceptible populations have experienced decline. Gravina Island has 4582 ha, 72% at medium or high risk. A total of 1371 ha (42% of susceptible area) has experienced mortality. Duke/Annette Islands have 9912 ha, 75% at risk. A total of 843 ha has experienced mortality (11% of susceptible area). The Cannery Creek site has no documented decline and 0% at risk. The Juneau area was not utilized during this analysis because the weather station is located at a much lower, and warmer, elevation than the *C. nootkatensis* stands in the area (Krapek et al. 2017), and thus is not representative of actual thaw–freeze frequency experienced by current populations. Data on range, mortality, and susceptibility were taken from Hennon et al. (Table 24, 2016).

Results

Map accuracy

Generally, the model was quite accurate: 78% of the points were accurately identified as either exhibiting climate-induced mortality or healthy

with no lag (absolute spatial accuracy), and at 1000 m, the accuracy rate was 90% (Appendix S1: Fig. S1). Because the climate data utilized in the modeling are available at ~1 km^2 resolution (30 arc seconds), the map was considered accurate for the statistical analyses.

Model validity

The random forest model was successful in predicting decline/healthy status (accuracies ~75%), and when this model was tested against the independent validation dataset, accuracy remained at approximately 75%, with minimal variance (~2%) from run to run, and significantly better ($P < 0.001$) than random. For evaluating the entire range, the model was then rebuilt using the entire balanced dataset ($n = 1902$) with the same model parameters (Appendix S1: Fig. S2a); accuracy remained 75%.

Climate exposure was tightly correlated with observed mortality at the latitudinal scale ($r^2 = 0.94$; Appendix S1: Fig. S1), and the model did well distinguishing between mortality and non-mortality-associated climates at the 1 km scale. Overall, ~90% of areas in decline are located in exposed climate. Of the total exposed area, ~12% is (currently) experiencing mortality, compared to ~1% rate of mortality in the area considered climatically safe. In the most extensive decline areas (approximately 55.5–57.0° N), the proportion was 20–25%. Precipitation and temperature were both important in predicting the presence of current decline at the rangewide scale (Fig. 3). Summer precipitation and the minimum temperature in the coldest month were the most important climatic variable identified in predicting mass mortality, as was annual precipitation and mean winter (three coldest months) temperatures. Mortality is most constrained by temperatures in the coldest month of the year, generally in areas between approximately −5° and 0°C (Fig. 3). As is common in climate data, the

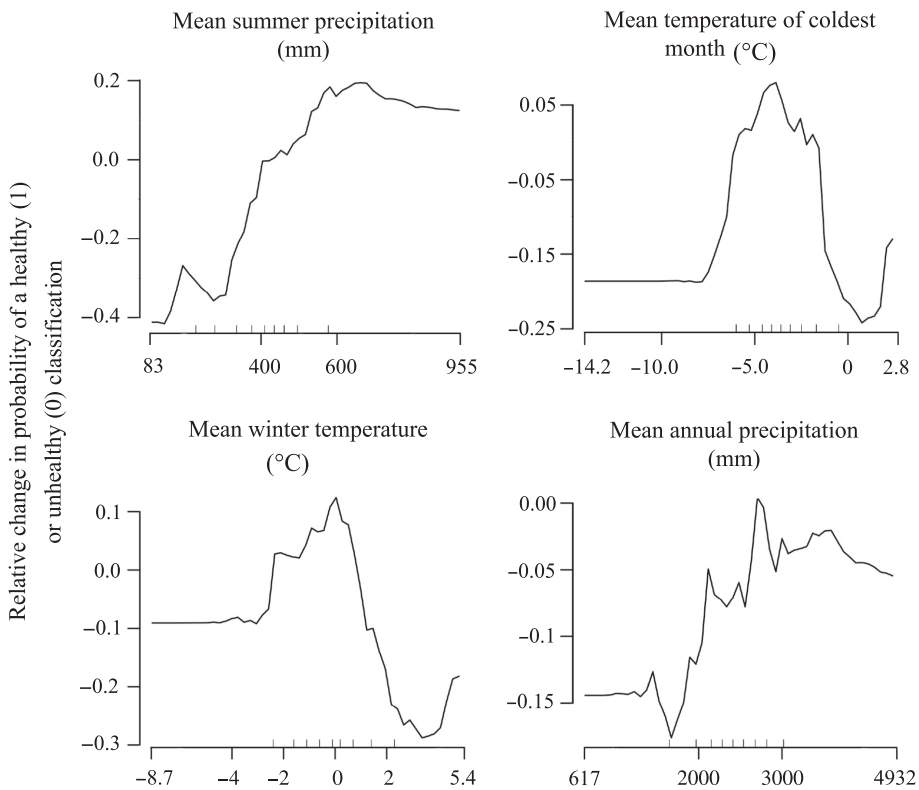

Fig. 3. Partial plots of the four top variables in the model creation process. *X*-axis range corresponds to the range of the variable in the input dataset; inner ticks correspond to their deciles. On the *y*-axis, higher/positive values mean a higher likelihood of mortality.

variables are somewhat correlated. However, although the two top variables (coldest month temperature and summer precipitation) were significantly correlated ($P < 0.05$), the correlation was weak ($r^2 = 0.11$; Appendix S1: Fig. S3).

There is evidence for a transitional zone of mortality, as areas on the cold end of the climatic spectrum for the species are generally unaffected, as are areas on the extreme warm end. At a broadscale mortality is confined to a band of similar climate stretching from sea level in the north to higher elevations in the middle of the range, healthy stands are found on both sides of that band (both warmer and colder) in the north and south.

Weather station data

The historical climate data analysis generally supports the model. The warmest locations (Tofino, Amphitrite Point, and Cape Scott, Canada) have reliably been above the exposure zone identified by the model (approximately −5° to 0°C, temperature of the coldest month; see Fig. 2), and the coldest locations (Juneau and Cannery Creek, Alaska, USA) have historically been below that level (Fig. 4). The areas of most extensive decline have historically been within that zone: Sitka (USA), Ketchikan (USA), and Prince Rupert (Canada; Table 1; Appendix S1: Fig. S2b). In general, the two sites with extensive mortality have also seen more long-duration/higher intensity cold snaps (7GD/3FD events) than the other sites.

Cumulative time of exposure

Populations in the extreme south (<45°), which are generally at high elevations, are expected to remain in benign climatic space, remaining cold enough to retain snow throughout the winter (Fig. 5A). Similarly, coastal areas in the south (~50°) are on the warm side of the transitional zone and are expected to remain so. In the heart of the species range, from approximately 50–60° north latitude, the average climate is generally unsuitable for the species/or unhealthy for the species, especially from ~56° north. Conditions remain poor under the slower-warming RCP2.6 emissions scenario compared to the RCP8.5 except in the extreme north. However, this portion of the range is only a very small fraction of the population (Fig. 5; current, 2050, and 2070 projections individually can be found in Appendix S1: Figs. S4, S5).

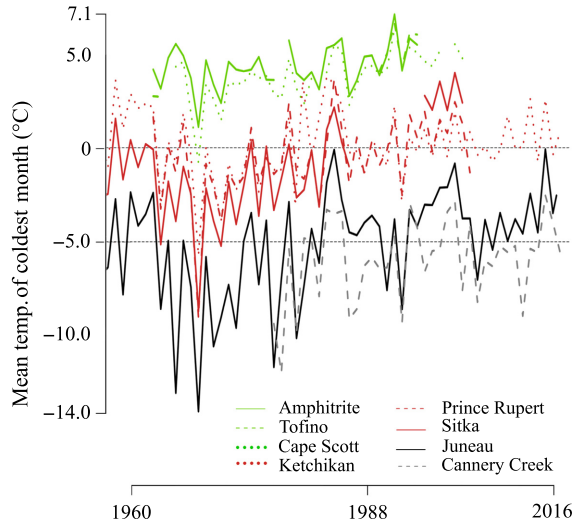

Fig. 4. Time series of weather stations described in Table 1 from 1960 to 2016. Lines are the mean temperature of the coldest month, with the transitional mortality zone (as suggested by model, see Fig. 3) marked by horizontal dashed lines.

The average score (1 healthy, 0 unhealthy) over all three time periods, and including current conditions, can be used as a proxy for cumulative time of exposure, with lower average scores associated with longer exposure to unhealthy, transitional mortality zone conditions. This score was lower (less healthy) for RCP 2.6 (70%) then 8.5 (75%) after weighing for the amount of area in each latitudinal band.

Cumulative extent of exposure

Over the entire time period, the majority of the range of *Callitropsis nootkatensis* will likely be exposed to mortality-causing conditions. The maximum proportion exposed is highest in the densest part of the range, where exposure is generally above 80% of the total range area, though most core portions of the range will potentially be exposed to substantial mortality (Fig. 5B). More area is likely to be exposed to potential mortality for some length of time in the faster warming scenarios. In RCP 8.5, the maximum extent of the areas exposed was slightly higher than RCP 2.6 at nearly all latitudinal bands, indicating that while the time of exposure may be brief, more area was potentially exposed under conditions fostered by the higher emission

Table 1. Weather stations spanning the transitional mortality zone.

Station	Time period	Duration (years)	Thaw–freeze events (%)	Proportion of susceptible area in decline‡	Annual precipitation (mm)	Years in −5° to 0°C zone (%)
Amphitrite	1963–1979, 1981–1999	37	1 (3)	No decline, unknown susceptible area	3062	0 (0)
Tofino	1963–1964, 1993–1998	8	0 (0)	No decline, unknown susceptible area	3422	0 (0)
Cape Scott	1966–1984, 1986–1996, 1997–2001, 2003–2004	36	0 (0)	No decline, unknown susceptible area	2675	1 (3)
Prince Rupert	1963–2005	43	1 (2)	11%§	2466	24 (55) (historically)
Ketchikan	1911–1942, 1948–1984, 1986–2016	101	3 (3)	42%	2748	52 (52) historically
Sitka	1899–1989, 1999–2004	93	6 (6)	80%	2410	52 (55) (historically)
Juneau¶	1941–2016	73	2 (2)	<1%	1844	41 (55) (recently)*
Cannery Creek	1979–2016	38	0 (0)	No susceptible area or decline	3130†	13 (34) (recently)

Notes: Amphitrite and Tofino sites have no decline, which are in warm locations. Prince Rupert, Ketchikan, and Sitka have extensive decline. Juneau has little historical decline, with scattered mortality noted in recent years. Cannery Creek has no decline. Trends for the 1960–2016 time period in Fig. 4.

† From wrcc.dri.edu.

‡ Calculated as area of *Callitropsis nootkatensis* in decline/(total *C. nootkatensis* area times vulnerable percentage [medium + high]). Original data from Hennon et al. (2016), see *Materials and methods* for details.

§ Data for Duke and Annette Islands, nearest site for which susceptibility data is available, located ~80 km away.

¶ Weather data from Juneau airport, which is lower in elevation than *C. nootkatensis* in the area; data shown as a geographic example only.

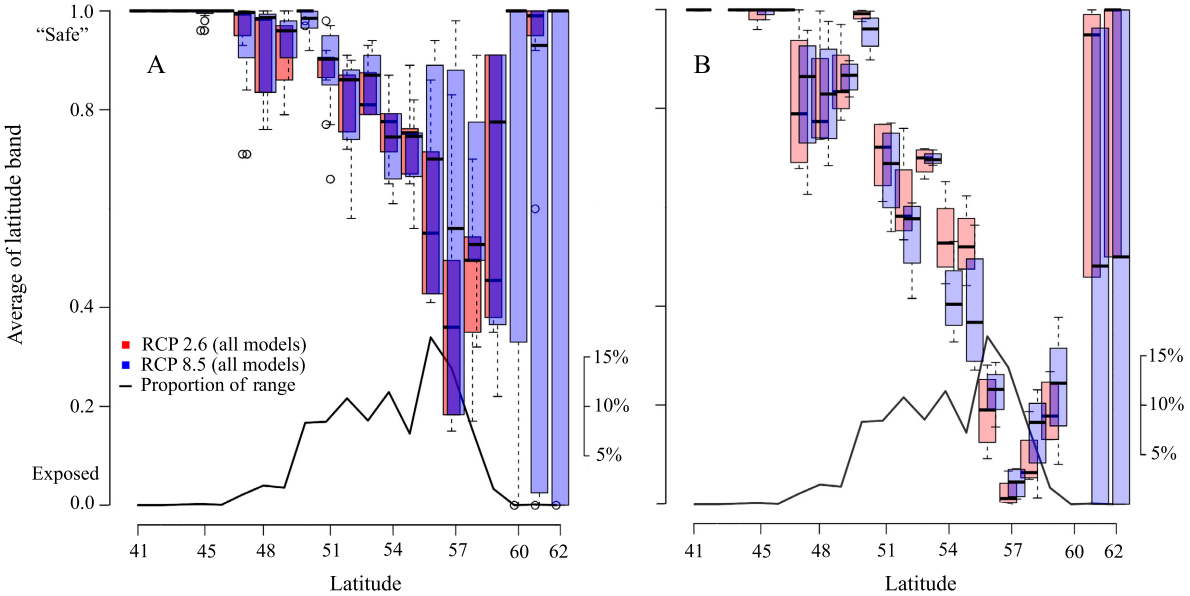

Fig. 5. (A) Average healthy score over all time periods and cumulative amount of range area by latitude. The lower emission scenario (representative concentration pathway [RCP] 2.6) results in slower warming than the higher emission scenario (RCP 8.5). Plots average across all four GCMs and three time periods (present, 2050, 2070). (B) Extent of exposure as a function of emission scenario. Data shown is the proportion of latitudinal band always in a healthy climate space during the current–2070 time period, across all climate models (i.e., if at any point in time the climate is unhealthy, the score is 0). The higher warming scenario results in slightly more spatially extensive exposure.

scenario (averaged across the four climate models, weighted average: RCP2.6: 54% exposed to mortality, RCP8.5: 57% exposed). Mean and minimum model outputs for each RCP are in Appendix S1: Fig. S6.

Binomial model

The binomial framework was successful in predicting approximate area dead in the two majorly impacted regions with available weather station data (Table 2). Comparing observed mortality on Gravina, Kruzof, and Duke/Annette Islands to nearby weather station data (Table 1) and the transitional mortality zone suggested by the model matches well if two to three events, on average, result in mortality of trees in susceptible areas (observed 42%, predicted 20–47% for Gravina; observed 80%, predicted 65–85% for Kruzof; observed 11%, predicted 10–30% for Duke/Annette; Table 2). All three locations have been exposed for considerable amounts of time (Fig. 4).

Discussion

Mortality patterns associated with *Callitropsis nootkatensis* die-off were assessed for their relationship to climate and evidence of transitional climate mortality.

Does the system exhibit signs of transitional climate mortality?

Callitropsis nootkatensis does exhibit the hypothesized transitional climate mortality pattern, with mass mortality associated with a significant climatic transition (snow to rain transition) but significantly less mortality at both higher and lower mean winter temperatures (Fig. 4). Mortality is centered around the −5° to 0°C coldest month temperature band, especially in areas of relatively high precipitation, whereas areas both warmer and colder than those temperatures appear healthy. This pattern was consistent across the entire range of the species, with mortality found at higher elevations in the south, tracking that elevational band (Buma et al. 2017). This is consistent with the current understanding of the decline, where exposure via warm winters (low snow cover and thus low thermal insulation for the soil) combines with occasional cold snaps to freeze soils to result in fine-root mortality (the proximal injury), which then limits the ability of individuals to uptake water and nutrients, resulting in whole-tree mortality (Hennon et al. 2012). The existence of healthy stands in relatively warm areas, however, provides important evidence for the transitional climate mortality concept. These areas are in the southern, coastal portions of the range, where conditions are generally warmer, outside the transitional mortality zone and where cold snaps are rare to non-existent (Buma et al. 2017, Figs. 3, 4, Table 1). In sum, there is a distinct transitional zone where mass mortality is found, as seen in Fig. 3.

High levels of exposure were tightly correlated with actual observed mortality (Fig. 2), further supporting the concept. The relationship was not expected to be 1:1 in this system, as the probability of mortality given exposure is also a function of (1) sporadic cold snaps (year-to-year weather variability, Beier et al. 2008, Barrett and Pattison 2016), with the scale of the region implying cold snaps, if they occur, do not occur in all places or at the same time, and (2) topographic variation in rooting depth, resulting in deeper rooted locations being more resistant to cold damage regardless of snow cover (Hennon et al. 2012). *Callitropsis nootkatensis* is most common in areas of poor drainage, where it is competitively dominant, but can occur in other locations.

Historical weather records generally support the model and the transitional climate mortality

Table 2. Observed mortality in susceptible areas compared to predicted mortality based on binomial model and number of proximal thaw/freeze events required for complete mortality.

Site|Weather station	Observed, %	1 Event, %	2 Events, %	3 Events, %
Duke/Annette Islands|Prince Rupert	11	67	30	10
Gravina|Ketchikan	42	79	46	20
Kruzof|Sitka	80	97	85	65
PWS West|Cannery Creek	0	0	0	0

Note: See *Materials and methods* for details.

concept. The areas with highest levels of historical decline, Prince Rupert and Sitka, have been considered exposed by the climate model for much of their instrumental record, as well as experienced a substantial number of freezing events (7GD/3FD). These sites have both since warmed beyond the average temperature zone associated with decline (Fig. 3). This corresponds to a noted reduction in mortality on USFS Forest Inventory Plots during the 1990–2000 time period, the spatial distribution of which generally covers the areas around those stations (Barrett and Pattison 2017). Recent mortality has continued, generally to the north compared to the Sitka or Prince Rupert areas (Oakes et al. 2014, Bidlack et al. 2017, USDA Forest Service Report: FS-R10-FHP 2017), as expected from the transitional model. Areas in climates generally considered safe have no noted mass mortality (Tofino, Amphitrite, and Cape Scott) and the colder areas in Alaska. The Cannery Creek site has recently warmed into the transitional mortality zone, but has not experienced the proximal freezing events that drive actual mortality.

The Juneau site is marginal, with recent temperatures transitioning into the transitional mortality zone as well as considerable amounts of minor, and to a lesser extent major, proximal freezing events (Table 1), yet mortality is, to date, low. This is a recent historical development, and the data used here cannot determine whether freezing events corresponded to low snow conditions (a freeze/thaw event while snow is still present would have little effect). Minor recent mortality has been noted in the area (~15 km distance; Buma et al. 2017). The largest natural populations closest to this site are at higher elevation/colder microclimates than the airport weather station (Krapek et al. 2017), so it is likely that the actual *C. nootkatensis* stands are colder on average than the weather station indicates, hence the limited decline to date (Buma et al. 2017). It is also possible that transitional mortality in Juneau, which should be likely, is precluding the expansion of local populations (which do not appear to be regenerating or expanding to fill potential habitat, Krapek and Buma 2017) to lower elevations. Supporting this hypothesis, seedling experiments in Juneau, near the weather station, have reported significant root damage over several years (Hennon et al. 2006, Schaberg et al. 2008).

How will climate change affect the species?

In the lower warming scenarios, generally healthy conditions are expected in the extreme north and south of the species range, but substantive additional exposure to mortality is expected in the central portions of the range, especially in the 2070 timeframe. The higher warming scenarios are similar, though less exposure is expected in the central portions by 2070 due to warm conditions pushing much of the landscape past the transitional mortality zone, and slightly more exposure is expected at the highest latitudes. Cumulatively, exposure (and subsequent mortality) is likely to be highest in the portions of the species range where it is currently most prevalent, likely leading to a substantial portion of the total species population declining. However, the geographic extent of the species appears more robust due to the extreme ends of the range remaining on either side of the transitional mortality zone. This may preserve important genetic variability within the species (Ritland et al. 2001).

There is an important caveat specific to this system. Because exposure is related to monthly/yearly climate, and the proximal freezing events which trigger mortality are driven by daily weather, the two may trend independently in the future. The one historical study conducted in the region (limited to southeast Alaska) found that the frequency of cold air outbreaks has not substantially declined despite the average temperature of the region warming over the mid-twentieth century (Beier et al. 2008), though the warm locations investigated here did show few cold snaps (Table 1). That could be due to their geographic location to the south and separated from cold air by multiple mountain ranges. It is possible that further north, where there are fewer barriers to cold interior air, that cold snaps will continue (Hennon et al. 2016). Thus, mortality may continue in areas like Sitka and Prince Rupert, in addition to expanding into currently colder areas. If that is the case, mortality will likely continue to accumulate beyond that expected from models based purely on annual and monthly means. In addition, this analysis was conducted at the rangewide scale. Investigations at finer scales may find other variables to be significant. More work modeling of weather variability, in particular cold air outbreaks at fine

spatial and temporal scales to reflect microclimate, and higher resolution climate products are necessary to further refine these predictions from a climate perspective.

The transitional zone mortality concept

The concept of transitional zone mortality centers around specific climatic zones that are associated with rapid mortality while a species is exposed, but lessened mortality once crossed. This phenomenon is likely most easily observed with the winter freezing threshold, as damage and mortality associated with freezing and thawing conditions in winter are well documented. Transitional zone mortality is generally a function of multiple variable factors interacting, such as snow loss and cold snaps in the *C. nootkatensis* system (here) and *Betula alleghaniensis* (Bourque et al. 2005). It is also consistent with patterns of mortality associated with long-term drought interacting with sporadic freeze–thaw events to increase mortality rates in *Pinus cembroides* and *Juniperus deppeana* (Polous 2014) and multiple co-existing *Juniperus* species due to xylem embolism (Willson and Jackson 2006). Because of this interaction between a background stressor (gradual loss of snow or occasional drought) and a sporadic weather event (in the examples, thaw and freezing events), this mortality is not expected every year. (This is also true for mortality associated with hard climate thresholds such as minimum precipitation and warm temperatures causing mass tree mortality.) Mortality then is not only a function of climate but also time of exposure.

Together with the reality of a directionally changing climate, the concept of transitional climate mortality leads to two generalized hypotheses: (1) Slower warming will result in any particular area being exposed to potential mortality for longer periods of time; and (2) more rapid warming will result in a broader extent of area exposed to mortality. Results supported these general hypotheses. The locations with the least exposure time have the least (or no) elevated mortality; similarly, the longer, historically exposed areas generally have higher mortality (Table 1). The slower warming scenario, coupled with observations that mortality is higher in areas that have been in that threshold zone longer (Beier et al. 2008, Hennon et al. 2012, Oakes et al. 2014), indicates that slower warming will result in longer exposure to adverse environmental conditions than faster warming scenarios, particularly in the center of the range of *C. nootkatensis*. The longer time in this mortality zone (indicated by lower average scores when averaged across all models and times, Fig. 5A) increases the chances of threshold mortality events, which requires the confluence of background warming and year-to-year weather (cold snaps).

In contrast, faster warming scenarios crossed those mortality-associated conditions faster, resulting in generally healthier average scores. This is due to the fact that while more area is exposed to the transitional mortality zone in higher warming scenarios (Fig. 5), the zone moves rapidly enough to expose any given area for only a short period of time. Because transitional zone mortality does not occur each year, this may result in less actual mortality if conditions become warm enough to preclude cold snaps. Faster warming overall, or tighter transitional mortality bands, would result in a larger difference between the scenarios in terms of extent.

The simple binomial framework approach suggested here seems successful and lends itself to incorporation into other systems. Four of the five cases here agreed well with predicted percentage of mortality, with two to three proximal mortality events required (on average) to kill an individual. In particular, the three sites which have been exposed the longest (Sitka, Ketchikan, and to a lesser extent Prince Rupert) were close to predicted values, as was the colder site (which has no susceptible areas or proximal events, and thus no predicted or observed mortality). The Juneau site currently shows less mortality than would be expected. However, *C. nootkatensis* populations in this area are generally higher in elevation and more northerly than the sea-level weather station (Krapek et al. 2017), so the actual conditions experienced by local populations are likely significantly colder than implied from Fig. 4 and Table 1. This would result in overprediction of retrospective mortality, because warming has not yet pushed the populations into the exposed climatic zones for as long as would be expected based on the weather station data.

That the binomial model worked for the three longer exposed regions, with higher mortality, suggests that it is a useful framework. If the time required to cross the transitional mortality zone

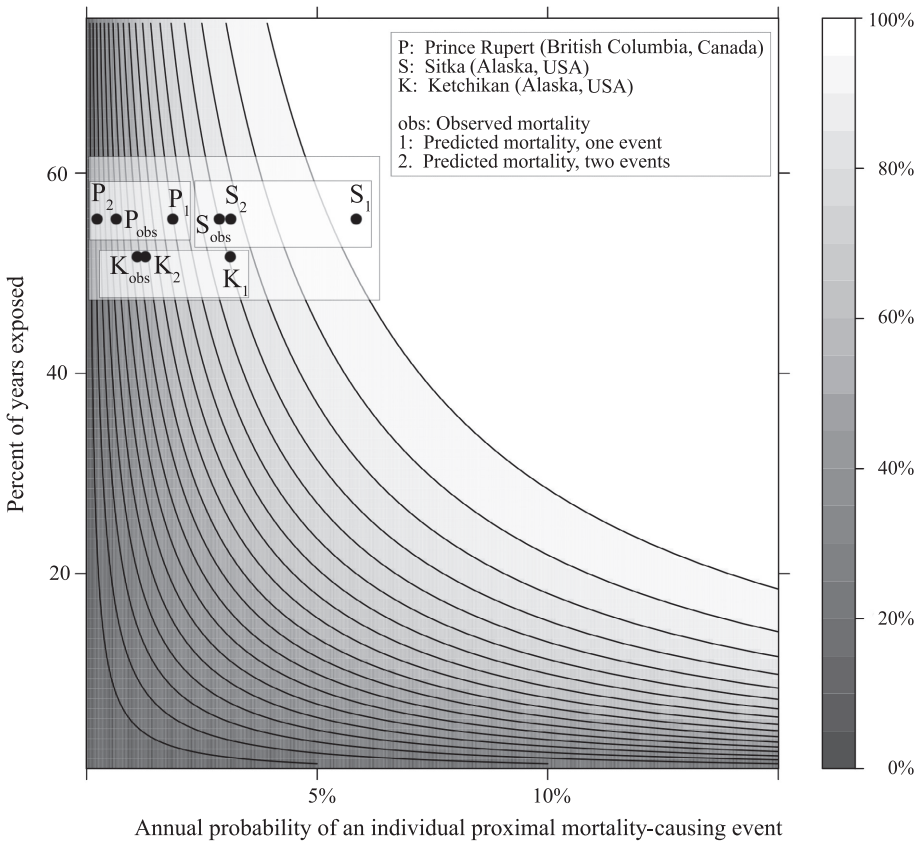

Fig. 6. Output space of the binomial model, with probability of a proximal mortality event on the *x*-axis and exposure time on the *y*-axis. Data points shown for the historically exposed sites (X_{obs}), including observed mortality (Table 1) and predicted mortality if one or two proximal events cause mortality on average (X_1, X_2; see Table 2). Cannery Creek had zero predicted and zero observed mortality, and so is not shown.

is modeled explicitly (exposure time), and probability of a proximal event during that time is known, then the expected overall mortality can be estimated based on Fig. 6. For example, if an exposure time of an additional 53 yr is expected for the Juneau area under the faster warming scenario (e.g., by 2070 the area is generally healthy; Appendix S1: Fig. S6), then final mortality would be estimated to be around 56% of susceptible areas, assuming approximately two thaw/freeze events are required, on average, for mortality (based on observations at the longer exposed sites). There are two significant, related assumptions: First, that the frequency of thaw/freeze events is random during the time of exposure. This appears to be true, at least for the northern portion of the study area (Beier et al. 2008). It also assumes that when the climate warms enough, thaw/freeze events will cease, as suggested by the sites in warmer locations (e.g., Cape Scott; Fig. 2). However, Beier et al. also found no trend in the frequency of thaw/freeze events over the 1950–2004 time period. Future work, therefore, must focus not only on higher resolution predictions of annual temperature to estimate exposure duration but also the short-term events which can trigger mortality events if exposed. This framework can be applied to any system where exposure conditions are known and the frequency of proximal events can be estimated. This approach is quite useful in emerging mortality associated with climate warming, where data or knowledge of mortality processes may be initially sparse.

Conclusions

Transitional zone mortality is a phenomenon where mortality is associated with a specific climatic transition, with less mortality on either side of that zone. The mortality process known as *Callitropsis nootkatensis* decline, caused by a loss of snow due to climatic warming and subsequent root freezing, is widespread and appears to represent a case of transitional zone mortality. Mortality is relatively high within a narrow temperature band associated with mean coldest temperatures near freezing (−5° to 0°C). Slower warming results in higher overall exposure to mortality, as more of the range area is within this temperature band for longer periods of time. Faster warming, in contrast, results in less overall exposure as a function of time, but more exposure as a function of extent. By combining both the time of exposure and the probability of a mortality event given exposure, the amount of a landscape affected can be predicted via a binomial statistical framework. This type of mortality phenomena has been understudied but may be a potentially large driver of future forest change, especially given the frequency of mortality events and the ubiquity of the freeze–thaw transition across mid- and high latitudes as well as elevations.

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Supporting Information

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