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Recovery potential for a green ash floodplain forest using various emerald ash borer management strategies in a population viability analysis

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ABSTRACT

The invasive emerald ash borer (*Agrilus planipennis* Fairmaire, EAB) has destroyed ash tree (*Fraxinus* spp.) populations across the US, but remnant populations including many small trees and, more rarely, larger trees remain after EAB had its first major impact across the landscape. The future survival of these remnant trees is critical to the viability of the ash species. Several different management options, including biocontrol, EAB-tolerant or resistant ash trees, and silvicultural strategies exist or are under development. Here we model changes that could occur in a preserve's remnant population of green ash (*Fraxinus pennsylvanica* Marsh.) after EAB peak mortality to assess management strategies. We used population viability analysis (PVA) and created a stage based model with baseline conditions and a model with recurrent catastrophes, where a catastrophe was defined as a year with reduced ash survival from an EAB outbreak. The catastrophes model had an increasing probability of a catastrophe occurring over ten years and included a gradual increase in ash survival (decline in EAB impacts) over the 9 years following a catastrophic event. We explored management scenarios for the catastrophes model including, 1) the reduction of future EAB induced mortality events to mimic possible effects of biological control or other environmental constraints; 2) addition of trees with increased survival to mimic restoration by planting ash trees with resistance to EAB, which are currently under development, or mimic clusters of trees with natural resistance to EAB created by natural selection. We also performed a sensitivity analysis to assess which size class impacted the population persistence the most over time and found that new seedlings were the most influential. There was no risk of extinction under the baseline model. The reduced catastrophe scenario was an improvement from the catastrophes model, reducing probability of extinction by 33%. Adding healthy ash improved population abundances over time and reduced the probability of extinction when there were repeated plantings. These scenarios relied on assumptions about how the population would react to management treatments, based on the scientific literature and cautious estimates. This approach provides a starting point for experiments testing individual management treatments to generate testable hypotheses, and the model may be readily updated with new data as it becomes available. Our PVA has revealed potential outcomes of alternative management practices and can increase our understanding of natural ash populations remaining after EAB introduction.

1. Introduction

When new pests, pathogens, or environmental conditions threaten the future of a species, models can be useful tools to predict and understand the impacts and to plan for conservation management strategies. Populations of North American ash (*Fraxinus* spp. (Oleaceae)) trees are threatened by an invasive insect, the emerald ash borer (*Agrilus planipennis* Fairmaire, EAB), which has caused escalating depletion of ash tree populations. EAB was accidentally imported from Asia in the mid-1990s and was first discovered in the Detroit, MI area in 2002 (Haack et al., 2002). The ash species threatened by EAB are important ecologically as a component of riparian forest ecosystems (Nisbet et al., 2015), linked to reduced crime and increased human health as urban trees (Kondo et al., 2017; Donovan et al., 2013), and are economically valuable timber (Gould et al., 2012).

The EAB life cycle is carried out on ash trees and generally results in up to 99% mortality of large host trees within a population (Knight et al., 2013; Cappaert et al., 2005). However, trees smaller than the preferred larger size classes (Klooster et al., 2014), sprouts of dead trees (Kashian, 2016), and rare surviving trees (Knight et al., 2012b) may

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remain after the majority of the larger reproductive mature ash trees are killed. In areas of Northwest Ohio where mature ash trees have died off, our continued data collection reveals that EAB are still present and infesting smaller trees, though in fewer numbers (Kappler, 2018). The future dynamics of EAB and remnant ash populations are unknown.

Management options for conservation of ash species in EAB infested areas include insecticide injections, parasitic wasp biocontrols, and development of EAB-resistant trees. While insecticide usage to protect individual ash trees is very effective, it is mostly used for high-value urban trees rather than forest trees due to the expense of continued treatment over time (Smitley et al., 2015). In contrast, wasp parasitoids are more readily used in natural settings. Wasp parasitoids (herein called parasitoids) directly attack and kill EAB eggs or larvae. They are species released as classical biological controls (biocontrols), including non-native *Oobius agrili* Zhang and Huang, *Spathius agrili* Yang, *Tetrasichus planipennisi* Yang (Gould et al., 2012), and *Spathius galinae* Belokoblyskij and Strazenac (Watt et al., 2016). Parasitism rates vary based on numerous factors and have been shown to increase ash sapling survival in Michigan (Duan et al., 2018; Kashian et al., 2018), although the long-term survival of these trees as they mature is unknown. Biocontrol parasitoid releases may be used alone or in concert with other management options.

Reintroduction of EAB-resistant ash trees may be a future option for ash-dominated forests where most of the ash have died. Research has demonstrated that some identified individual native ash trees can resist EAB significantly better than susceptible controls and efforts to identify and use such trees in a resistance breeding program to improve EAB resistance are ongoing (Koch et al., 2015). Rare surviving ash trees of both *F. americana* L. and *F. pennsylvanica* are currently being used in this program. In this resistance breeding program testing of F1 progeny trees show some trees are able to survive infestation and kill most of the EAB larvae that tried to feed on them (J. Koch, pers. comm.). Several examples of successful breeding programs to develop forest trees with resistance to invasive insects and diseases have been reviewed recently by Sniezko and Koch (2017). Despite these successes, little is known about potential population changes resulting from tree augmentation plantings of resistant trees, due to the long-term nature of experimental exploration in the field. However, clusters of trees with natural resistance to EAB may also be created by natural selection. Population viability analysis models can provide more immediate estimates related to these possibilities.

Population viability analysis (PVA) is an effective tool to estimate the population viability of a species under various environmental conditions and quickly identify factors that influence a population's viability (Akçakaya and Sjögren-Gulve, 2000; Morris and Doak, 2002; Caswell, 2001). Trees affected by pests and diseases, like whitebark pine (*Pinus albicaulis* Engelmann), have been evaluated with population models to help reveal that the native pests impacted the pine trees more than the invasive disease (Jules et al., 2016). Management actions are best conducted under circumstances where the affected species and its environment are heavily studied, but this is not always feasible. The potential changes from management can be added into models and evaluated for overall effectiveness in increasing population viability. For example, an individual based model was developed to examine how much harvest was detrimental to a big-leaf mahogany (*Swietenia macrophylla* King) population (Grogan et al., 2014). Models can also look at combinations of management strategies as well as individual ones to increase predictive power. For example, the endangered English yew tree (*Taxus baccata L.*), had management alternatives modeled to create a population viability risk management assessment to identify which management combinations were most beneficial (Dhar et al., 2008). EAB management options are continuously improving and will likely influence ash survival once implemented by land management authorities. Most augmentation predictions for forests are modelled in forest vegetation simulator (FVS), where forest stand growth and development are applied to ecosystem management (Dixon, 2002). The FVS program has successfully predicted short term changes (2 years) of reduced stem density and basal area for ash with EAB infestation (Levin-Nielsen and Rieske, 2015). Population viability analysis allows predictions to be projected for a longer period of time in a dynamic environment. The PVA provides a framework for evaluating potential outcomes for ash populations under specific conditions, while incorporating natural levels of environmental and demographic variation. By creating models for species in danger of decline we can better assess future scenarios, develop testable hypotheses, and potentially understand the underlying mechanisms driving changes in the populations.

The aim of this study was to compare, using PVA, the effects of simulated management interventions on the population persistence of a remnant green ash population after its initial decline from EAB. We modeled an extensively studied green ash population in Northwest Ohio that experienced > 97% mortality of larger trees from EAB by 2009 and in which surviving ash trees have been monitored and studied (Knight et al., 2012b; Kappler et al., 2018,2019). Green ash is a deciduous tree with a broad range in Canada and the eastern United States which has adapted to live in multiple habitats, as it is able to tolerate a variety of environmental stressors, e.g., high salinity, flooding, drought, and high alkalinity (Kennedy, 1990; MacFarlane and Meyer, 2005; Stewart and Krajicek, 1973). We created two models, one without further EAB impacts (baseline model) and one with EAB as a potentially reoccurring catastrophe (catastrophes model). We added management scenarios to the catastrophes model using a literature search for ash species to create estimates for parameters. Management strategies that we focused on were (1) reduced catastrophe, to simulate the release of biocontrols or other environmental constraints which improved ash survival by reducing catastrophe impacts; and (2) additional healthy ash added, simulating restoration where additional EAB-resistant ash individuals are planted and produce resistant offspring. We expected that the persistence of the green ash population in this natural floodplain would increase with increased survival and reproduction of mature ash trees. Using population models, we can evaluate the alternatives for management of this highly impacted population before their implementation.

2. Methods

2.1. Survey site

Our focal population was in Northwest Ohio, in the floodplain forest of Swan creek, located in the Oak Openings Preserve Metropark (Swanton, Ohio, USA). This area had a high infestation of EAB from 2004 to 2010, and almost all large ash trees were dead by 2009 (Knight et al., 2010). It holds a remnant population of green ash trees where EAB are still present in low numbers. A few larger trees in this population are lingering ash trees, which are either the last to be infested or have rare phenotypes conferring increased resistance to EAB (Koch et al., 2015). The model begins with the initial population of ash trees in all size classes currently present in this 1.23 km^2 site, as estimated from our extensive surveys (Kappler, 2018). Persistent sprouts from dead ash trees are uncommon at this site, consistent with the rarity of this phenomenon at > 150 long-term monitoring plots across Ohio (unpublished data). The Oak Openings Preserve is in the Oak Openings Region, which contains a mosaic of rare natural ecosystems surrounded by agriculture and urban/suburban areas. The floodplain forest of Swan creek contains green ash, cottonwood (*Populus tremuloides* Michx.), American elm (*Ulmus americana* L.), maple (*Acer* spp. (Sapindaceae)), oak (*Quercus spp*. (Fagaceae)), black walnut (*J uglans nigra* L.), black willow (*Salix nigra* Marsh.) and sycamore (*Platanus occidentalis* L.) species (Knight et al., 2012a).

2.2. Population monitoring

Purple panel sticky traps with lures have been set up yearly at this location since 2008 to survey for EAB presence (Knight et al., 2014). Each year, traps are set up in ash trees before EAB emergence and the number of EAB caught are counted at the middle and end of the summer. Trends in our data showed a decrease in EAB once large ash trees died, with a persistent reduced presence (< 25 per trap on average) over time (unpublished data K.S. Knight).

In this analysis the baseline model included data averages from focal ash population data collection after the peak EAB outbreak (2010–2017) to represent the aftermath forest (Table A1) (Kappler, 2018). From 2010 to 2014 yearly walking surveys of the floodplain were done to tag and collect data on ash trees > 12 cm dbh. Starting in 2015–2017 the surveys included tagging all ash trees taller than 1.37 m within 50 m of the east side of the creek edge, which included new ash sprouts from previously dead mature trees. New ash sprouts from dead mature trees made up 14% of the saplings in our survey. Ash seedlings were tagged and recorded from 2015 to 2017 in a total of 36 microplots within the floodplain. Oak Openings Preserve had nine plots spaced at least 50 m apart, and each plot was 400 m^2 with 4 m^2 microplots at cardinal directions, 6 m from plot center (Knight et al., 2014). From these 36 microplots we derived the survival of those < 1 cm dbh.

2.3. Population models

We constructed stage-based, stochastic population models, and explored a variety of scenarios. All models were developed in RAMAS® Metapop (Setakaut, NY, USA), and used the same stages (Fig. 1), simulation time (50 years), time intervals (1 year), replications (10,000), and model specifications in a female only population as in our previous work based on historic conditions and worst-case years of EAB infestation (2005–2008) (Kappler et al., 2019). For fecundity and first year growth we used pre-EAB estimates from our previous model (Kappler et al., 2019) which came from the literature (Table A2). To keep our model conservative, we did not extrapolate our seedling and sapling survey data, which represented only part of the entire floodplain area (Kappler, 2018), but estimated Year 1 abundance as 500 individuals. Our aftermath ash population initial abundance was 875 female individuals, which we distributed to start simulations at the stable stage distribution. We used peak infestation ash data for our EAB catastrophe impact parameters to create a worst case scenario, and we assessed management scenarios under these conditions.

We added catastrophe parameters in the baseline model to create the catastrophes model. The catastrophe simulates an increase in EAB which impacts our ash population similar to the initial infestation by reducing the ash survival rate. Outbreaks may occur as frequently as every 10 years, as that would be the amount of time it would take an ash cohort to grow into the size classes preferred by EAB based on the average stem diameter growth we observed of 1 cm dbh/year in our survey data. We assumed a greater chance of outbreak as available ash phloem volume increased and that the ash growth rate will remain the same over the time period of the model. In our model, we set the probability of occurrence of a catastrophe to increase linearly to 99% over 10 years (Table A3), and after an initial occurrence the probability restarted at zero. This created catastrophes that were more likely to occur the longer it had been since the last catastrophe. During the catastrophe year, we assumed EAB would impact ash survival exactly as it did during the initial peak EAB infestation to create a worst case scenario of reinfestation. We set the EAB catastrophe to reduce the survival rate by 90% for ash trees > 1 cm dbh, which was comparable to survival rates during peak EAB infestation. Our research and others have shown that ash > 1–2 cm dbh are damageable by EAB (Cappaert et al., 2005). After the initial outbreak year, most of the ash trees were dead and EAB populations typically decreased, so the impacts of EAB on remaining ash trees also decreased and those ash began to re-grow (KS Knight, unpublished data). Thus, after a catastrophe occurred, we reduced the catastrophe impact to survival by 10% per year over the following 8 years (Table A4). This simulated a slow recovery from the initial EAB impact for the focal population, which we assumed would occur every time the population had an EAB catastrophe as ash resources would run low for EAB when their beetle populations increased. This method allowed us to conservatively, with the fewest number of assumptions about recovery, simulate potential infestation oscillations that may occur in the field given the dearth of available data. Note, that the model assumed that there were no other impacts on the population other than the intermittent EAB catastrophe.

2.4. Management scenarios

We examined the potential effects of management strategies with various scenarios added to the catastrophes model, each had their own assumptions.

2.4.1. Reduced catastrophe scenario

We reduced the impact of the EAB catastrophe on the survival of the population, taking it from a 90% decrease to a 50% decrease in survival. After a catastrophe year had occurred, a reduction occurred in the catastrophe impact to survival of 5% per year over the following 8 years (Table A5). This simulated a successful introduction of biocontrol or the presence of other factors, such as woodpecker predation, that reduced the impact of EAB on ash populations in comparison to the first peak infestation. We based our 50% survival reduction on a study of ash saplings in an aftermath forests where parasitoid *T. planipennisi* killed 37–82% of the EAB larvae over 3 years (Duan et al., 2017), and on research indicating that woodpeckers (Picidae) prey on EAB in a density dependent pattern (Flower et al., 2014). Future EAB impacts could also be reduced for large ash due to lower relative density of EAB or natural selection for trees with greater resistance to EAB.

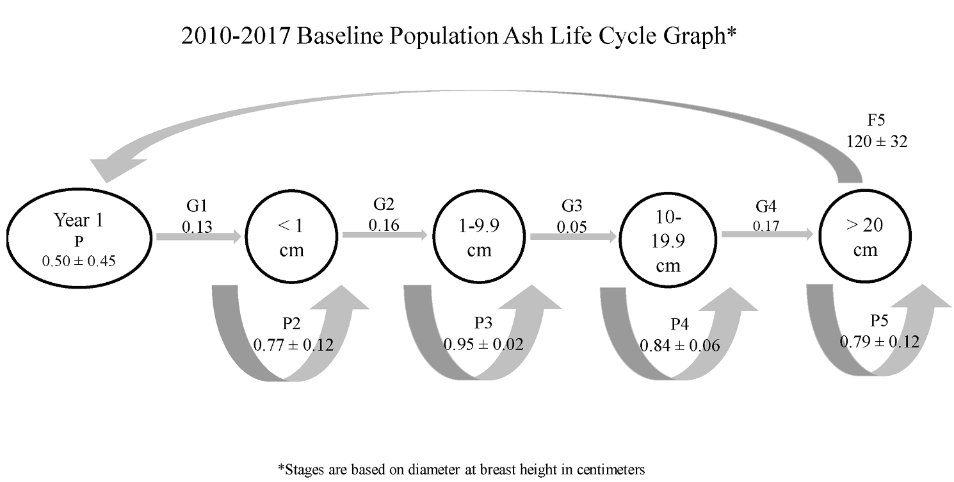


Fig. 1. For the population models the stages of the green ash tree are represented above by a circle which includes a range of sizes (cm, diameter at breast height). Arrows represent the probability of survival for each stage (P2-P5) with the standard deviation, and probability of growth into the next stage (G1-G5). F5 represents the ash fecundity with standard deviation. P, G, and F parameters are given for the baseline model.

Table 1
The results for models and scenarios (each with N = 10,000), for each of the scenarios we report the growth rate, final (Year 50) average total abundance, probability of a 50% decline in abundance, and probability of extinction.

	Stochastic Growth Rate (S.D.)	Year 50 Ave. Total Abundance (S.D.)	Prob. 50% Abundance Decline	Extinction Probability
Baseline Model	1.07 (0.08)	23,092 (7,060)	4%	0%
Catastrophes Model	1.01 (0.03)	1,686 (4,655)	90%	34%
Reduced Catastrophes	1.06 (0.04)	13,914 (10,013)	38%	1%
Additional Seedlings	1.02 (0.08)	4,079 (5,208)	48%	0%
Additional Saplings	1.02 (0.08)	5,246 (5,912)	44%	0%

2.4.2. Additional healthy trees scenarios

In the catastrophes model population we added an additional population of healthy ash trees to simulate restoration events with EAB resistant ash trees. This simulates the planting of trees bred for resistance to EAB (Koch et al., 2015), but could potentially occur through natural selection. We assumed the EAB resistant ash had survival rates of historic ash population dynamics found in the literature (Kappler, 2018) (Appendix Table 2). This changed survival for the population of planted resistant saplings (1–9.9 cm dbh) to 82% (S.D. 16), ash 10–19.9 cm dbh to 75% (S.D. 20), and mature ash (> 20 cm dbh) to 90% (S.D. 10). We arbitrarily selected an initial population size of 400, based on our previous tree planting efforts, which would translate to an additional 400 individuals added to the population once every five years to represent multiple plantings over time. This population of added trees did not have a catastrophe effect added to their simulation, as we assumed this resistant population would not be impacted by future EAB outbreaks. Thus, the catastrophe population and the planted resistant population were modeled with different parameters, but their population results were combined to represent the entire ash population. Two alternatives were created where all planted individuals were either in the stage class size 1–9.9 cm dbh or of stage size class < 1 cm dbh. Saplings used for restoration planting would likely be 1–2 cm dbh in size, but we assumed they would have the same survival chance from size 1–9.9 cm dbh. These scenarios represented multiple introductions of 400 saplings (size 1–9.9 cm dbh) or seedlings (< 1 cm dbh), respectively.

2.5. Model statistics

For this remnant population of surviving ash trees, we were interested in understanding whether the population was likely to persist, and how the different management scenarios affected that likelihood. Thus, for each model and scenario, we report the stochastic growth rate, average of the 10,000 replications for: abundances to the nearest whole number over time; total final abundance (Year 50); probability of extinction and the probability of a 50% abundance decline. In the baseline model we made four different sub-scenarios (dbh sizes < 1 cm, 1–9.9 cm, 10–19.9 cm, and > 20 cm, respectively), where the survival was increased to 99% for the focal stage and all other parameters remained unchanged. These scenarios function as a sensitivity analysis to identify the differential impacts on the outcome of changes to individual vital rates. Sensitivity to changes in specific vital rates can provide insight into the most effective targets for management. Interval extinction risk results, or the probability that the population abundance will fall below a range of abundances at least once during the 50 year interval, were tested between scenarios replicated 100 times instead of the original 10,000 times for significant differences with the nonparametric Kolmogorov-Smirnov test. The Kolmogorov-Smirnov D statistic was reported, which represents the maximum vertical deviation in the plotted probability curves, meaning the maximum difference in the probability of extinction between two models.

3. Results

Our results are from one of the larger remaining ash populations we have found in Ohio and the probability of extinction was of particular interest. We found significant differences ($p < 0.001$) in the interval extinction risk of this remnant population under multiple model scenarios. Final average total abundances varied, but the ash populations in all models and scenarios were predominantly smaller individuals at the end of the simulations (as is typical of tree populations). The model scenarios produced a variety of results that can be used as testable hypotheses for future work which can help refine the model.

For the baseline model, the stochastic population growth rate for the aftermath forest was 1.07 (± 0.08), and there was no risk of extinction (Table 1). All other model scenarios had a growth rate above 1 which indicates growth, which emphasizes that this population is essentially released from its limiting factors (e.g., competition) and can grow at its maximum rate. We observed that this floodplain forest did have an increase in canopy openness after EAB initially killed the mature ash as the ash were a dominant tree species (unpublished data). With additional catastrophes the abundances were reduced and the probability of a 50% decline and extinction rate increased (Table 1). In other words, the likelihood of persistence with a single EAB outbreak (e.g., baseline model) was considerably higher than with the possibility of recurring outbreaks (e.g., catastrophes model). The final average total abundances for all models and scenarios were varied from 1686 to 23,092 individuals, the largest occurring for the baseline model and the smallest for the catastrophes model (Table 1).

The reduced catastrophe scenario, meant to simulate the effects of biocontrol insects and woodpecker predation, produced an increase in the ash population, and the probability of decline was reduced by 52% when compared to the catastrophes model (Table 1). The additional healthy ash scenarios had simulated historic growth and survival of ash, but we found adding 400 individuals once was not enough to overcome the catastrophe impacts (unreported). With multiple additions of resistant trees every five years the overall population persisted with a reduced probability of 50% decline but a lower abundance at Year 50 than the reduced catastrophe scenario (Table 1). Although, adding EAB resistant ash saplings to the catastrophes population produced a complete reduction in the probability of extinction. The slight difference when we added resistant seedlings or saplings was a larger population abundance with added saplings (Table 1). Overall, all of the management interventions simulated produced a reduced risk of extinction, although the likelihood of a 50% population abundance decline was still present.

When we increased survival for only one stage of the population in our sensitivity analysis, results were significantly different with the youngest and largest stages (Table 2). There were high stochastic growth rates, with the lowest growth rate for the model at the 10–19.9 cm dbh stage. The model that increased year one (new germinated) ash had the highest growth rate indicating that this life stage had the most impact on improving the overall population persistence (Table 2).

The average abundance over time for the management scenarios reflected their expected performance, where reduced catastrophes improved abundance the most over the catastrophes model (Fig. 2), followed by addition of healthy ash trees (Fig. 3). Additional healthy ash scenarios improved the population abundance with repeated additions, and using saplings was an improvement over seedlings (Fig. 3). When final abundance at Year 50 is broken down into stage classes for each model, they are all heavily skewed towards younger individuals (Fig. 4a). Addition of saplings increased individuals in the younger stage classes more than addition of seedlings, although both more than

Table 2
Stochastic growth rates and standard deviations for baseline scenarios where the indicated stage had its survival increased to 99%.

	Year 1	< 1 cm	1–9.9 cm	10–19.9 cm	> 20 cm
Geometric Mean	1.0693	1.0668	1.0660	1.0576	1.0679
Standard Deviation	0.1718	0.0581	0.0456	0.0424	0.1090

doubled the abundance when added to the catastrophe population (Fig. 4b).

We found an 85% difference in the interval extinction risk between the baseline model and the catastrophes model, and a 66% difference between the catastrophe model and the reduced catastrophe scenario (Table 3). When we compared the catastrophes model to the additional healthy trees scenarios the populations' interval extinction risks were significantly different, where additional seedlings had a 78% difference in risk and additional saplings had a 76% difference. These results indicate that the models vital rate specifications were highly different even under stochastic conditions.

4. Discussion

Our baseline model results showed that if vital rates for the aftermath ash forest population remained the same without another EAB outbreak or other detrimental events or factors, the ash population would persist. This result occurred because at our site the mortality rates in surviving trees were found to be lower than the mortality rates at the peak of EAB infestation. The largest ash trees in the baseline model had fewer individuals to start with, but with an average survival of 79% for mature individuals the population approached carrying capacity over the 50 year timeline. In other words, the modeled ash population showed signs of recovery after a decade when the EAB catastrophe was assumed to be a single major bottleneck event. However, the EAB population may not remain low, and the assumptions of the baseline model, such as the historical fecundity expectation, may not hold. Thus, the results of the catastrophes model and its scenarios are important. In contrast to the baseline model, when we modeled scenarios where EAB repopulate and impact the ash population, there was no noticeable increase in abundance without intervention. Given the large bottleneck produced by the EAB outbreak, the results of our PVA suggest that the current ash population is vulnerable to repeated large impacts, regardless of the source, without interventions.

We modeled EAB as a recurring catastrophe that could occur at least once every 10 years but could also occur more often. Other invasive pests have been shown to exhibit cyclic outbreaks. For example, the gypsy moth (*Lymantria dispar* Linnaeus), was introduced to North America from Russia and spread along the east coast by 1990. The gypsy moth can have population fluctuations that cycle either every 4–5 years, or 9–10 years (Bjornstad et al., 2010). We hypothesize our local EAB population to cycle in 10 year periods, as we estimate it takes our ash 10 years for seedlings to grow into a tree > 3 cm dbh in their open canopy growing conditions. If cycles exist between EAB and ash, the cycle length will greatly affect the outcome of the models, especially if the cycles are long enough for seedlings to grow to maturity and reproduce. Our current stochastic models allow for variation in the number of years between catastrophe events, which we describe as being EAB impacts, but could also be attributed to any event(s) that reduce ash survival. Continued monitoring of EAB and ash populations are necessary to understand the length of any population cycles that may occur and assess if other threats are impacting ash persistence.

Under the catastrophes model, the extinction risk was 34% but could decrease to 1% if the catastrophe impact on survival was reduced to 50%. Management strategy scenarios that could achieve this change are variable. We assumed a reduced catastrophe simulated the release of biocontrols and natural woodpecker predation for the EAB population. With continued presence of EAB in our study population, we assume another EAB outbreak can occur and biocontrol use could be a productive solution. Some biocontrols are slightly susceptible to a fungus that kills EAB, whereas others are affected by different environmental factors which reduce their numbers (Dean et al., 2012). Success in reducing EAB with biocontrol occurred with repeated yearly *T. planipennisi* releases in Michigan over 7 years (Duan et al., 2015), and at a later date with ash saplings in S. Michigan aftermath forests where they killed 36–85% of EAB larvae on susceptible ash (Duan et al., 2017). Development of a population model for biocontrols would allow assessment of which species performs best, as others have done for mango mealy bug (*Rastrococcus invadens* Williams) parasitoids (Godfray and Waage, 1991). As for woodpecker predation, woodpecker hole surveys showed that after the EAB introduction there were significantly more holes on ash than

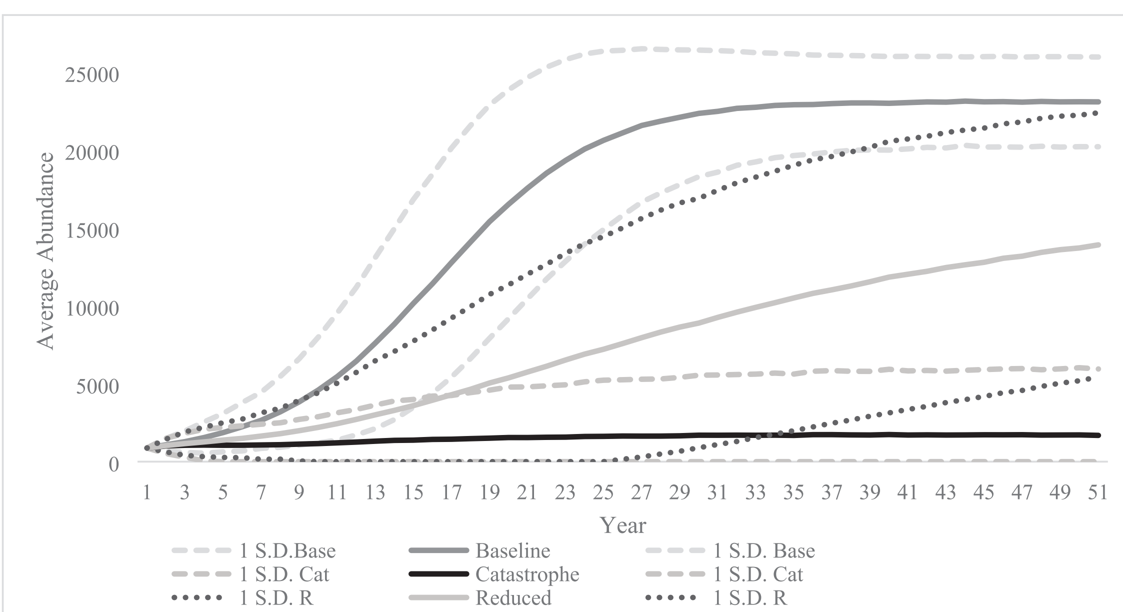


Fig. 2. The average abundance trajectory over time for the baseline (no catastophes) versus catastrophes and reduced catastrophes models (N = 10,000). All populations persist over time, but the catastrophes population does not increase. To view individual model trajectory examples see Fig. A1.

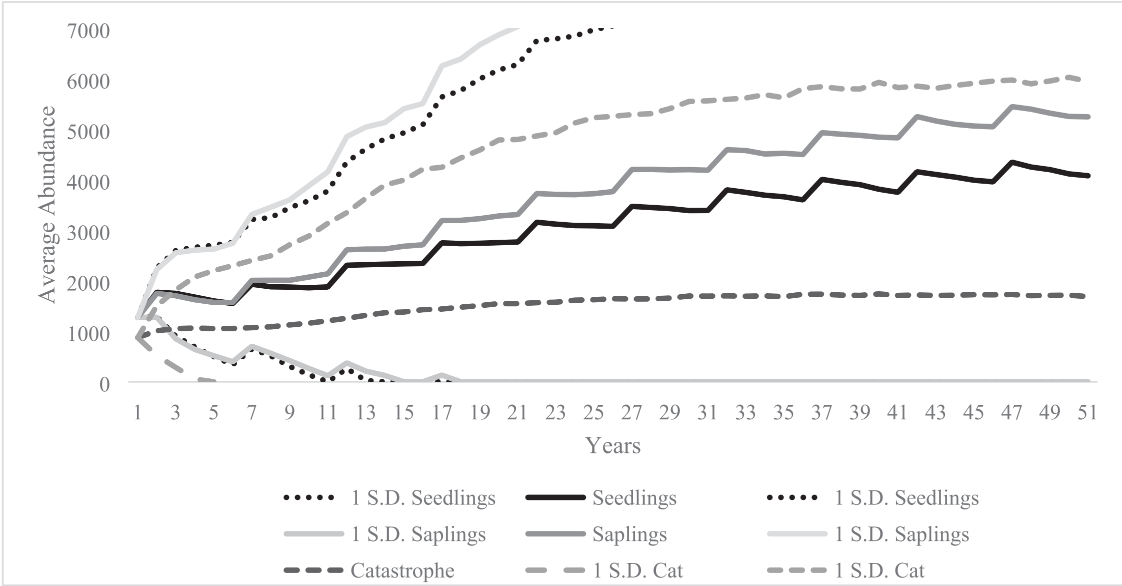


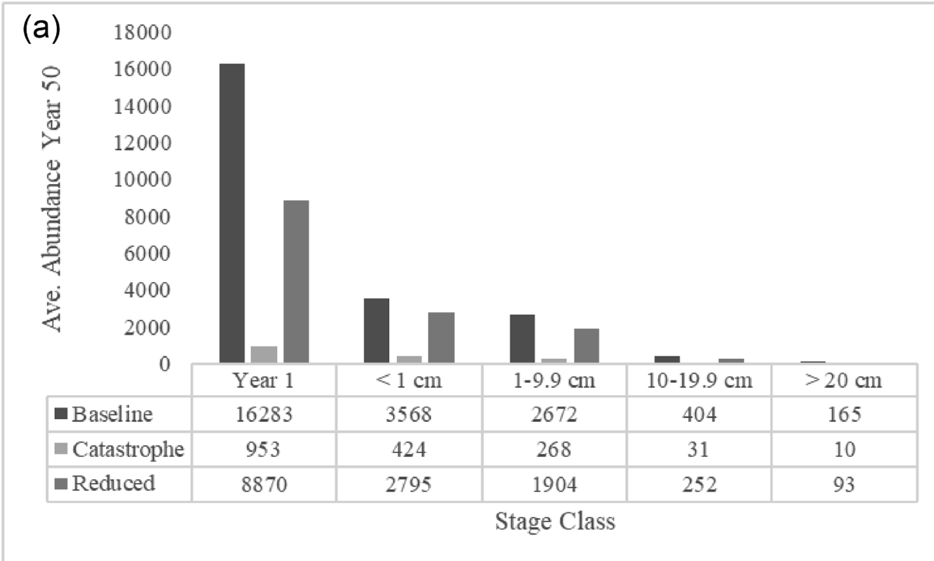
Fig. 3. The average abundance trajectories comparing the catastrophes model to a model that also included planting of resistant saplings and seedlings every 5 years (N = 10,000). The sapling restoration scenario is only slightly better at increasing the population abundance than the seedling restoration scenario.

non-ash tree species; and in trees that were cut down and surveyed, total predation rate on ash by birds was 37%. (Flower et al., 2014). Established woodpecker populations are necessary for these types of results and it is unknown whether assisting in their habitat needs could improve ash population success. Our focal population had an established woodpecker population and still had major ash mortality at the onset, but future research is needed in understanding woodpecker and ash survival in aftermath forest conditions. In areas where woodpeckers and biocontrols co-occur, predator interactions occur, where one predators' impact may reduce based on the presence of the other (Murphy et al., 2018, Jennings et al., 2013). Other natural factors may reduce the EAB catastrophe for our future scenario, such as increased EAB predators, e.g., native parasitoids (Duan et al., 2012) and changes in ash densities (Knight et al., 2013,2018).

In our models that simulated restoration of areas with resistant ash trees, adding individuals of stage 1–9.9 cm dbh had the best chance for prolonging the population persistence. The saplings and seedling restoration scenarios had different impacts, with added saplings producing higher final abundance values; likely this result is from reducing the time needed for resistant individuals to reach maturity. The use of this management technique depends on the production of EAB resistant ash trees through natural selection or ash resistance breeding programs. Replanting resistant trees has shown success for other species, and we can use these efforts as a template for the introduction of EAB resistant ash trees. For example, American elm trees with resistance to Dutch elm disease have been planted in multiple restoration plantings with early success (Knight et al., 2017). Other diseases like the chestnut blight also required the reintroduction of resistant trees, where crosses of Chinese chestnut (*Castanea mollissima* Blume) and American chestnut were then backcrossed multiple times with American chestnut and selected for resistance characteristics (Jacobs, 2007). These resistant trees thrived in areas with slow growing species like oaks and hickories (Schlarbaum et al., 1997). Testing of surviving ash trees and progeny for resistance using EAB egg assays have shown some ash individuals had a higher percentage of larval kills or slowed larval growth better than susceptible controls (Koch et al., 2015). If EAB resistant/tolerant ash trees can be bred for reintroductions our model results show a benefit when repeated additions occurred.

We used size class specific scenarios as a sensitivity analysis and suggest that the success of Year 1 seedlings and reproductively mature trees are very important to ash population persistence under continued EAB presence. The importance of the ash seedling and reproductive life stages in our models highlights the importance of land management actions which affect success of these life stages, including deer management, insecticide usage, and silvicultural interventions such as removal of competing trees. White-tailed deer (*Ododcoileus virginiana*) significantly impact tree seedling regeneration in multiple forest types (Rooney and Waller, 2003), including ash survival in bottomland forests (Rossell et al., 2005). Research on insecticide use for ash trees has shown that it is effective in protecting healthy mature trees from EAB (Herms et al., 2019). Research in natural habitats includes selective insecticide application for white ash stands to preserve genetic diversity, and strategies have been identified to increase conservation of genetic diversity through insecticide treatment (Flower et al., 2018). Results from Kappler et al. (2018) provided the first suggestion that silvicultural interventions may be useful for improving the survival of ash trees in remnant natural populations. Ash trees with healthy crowns had fewer ash neighbors (zero or one) within their 6 m radius when compared to less healthy ash trees (Kappler et al., 2018). This finding suggests that removal of neighboring unhealthy ash trees could be tested as a management option to increase survival of healthy reproductive ash trees. In a 35 year-long thinning experiment at slightly higher latitude (53°-56° N), European ash (*Fraxinus excelsior* L.) had a highly enhanced crown area and dbh with thinning that lasted 3–8 years, especially with younger stands (10–30 years-old) (Juodvalkis et al., 2005). Tree removal impacts sunlight acquisition for seedlings and competitive interactions for larger ash. Neighboring trees of other species may also inhibit the growth and survival of aftermath forest ash trees, as it has been shown that mature maples in forests with ash grew much faster after mature ash died during the first infestation of EAB (Costilow et al., 2017). Ash seedlings, like maple, survive in shaded areas and perform well under full sun (Kennedy, 1990), which allows them to increase growth and compete for canopy openings created within mixed deciduous forests (Gucker, 2005). Our model suggests that land management actions that affect seedling and reproductive life stages may be most beneficial for ash populations, especially when applying our results to similar forest types.

Management options for reducing ash damage from the invasive EAB include methods such as, utilizing insecticides, releasing parasitoids, as well as tree restoration. Each of the strategies associated with our management scenarios would have varying costs and benefits dependent on multiple variables. Some of the options, like using parasitoids, are currently supported by federal government programs (Gould



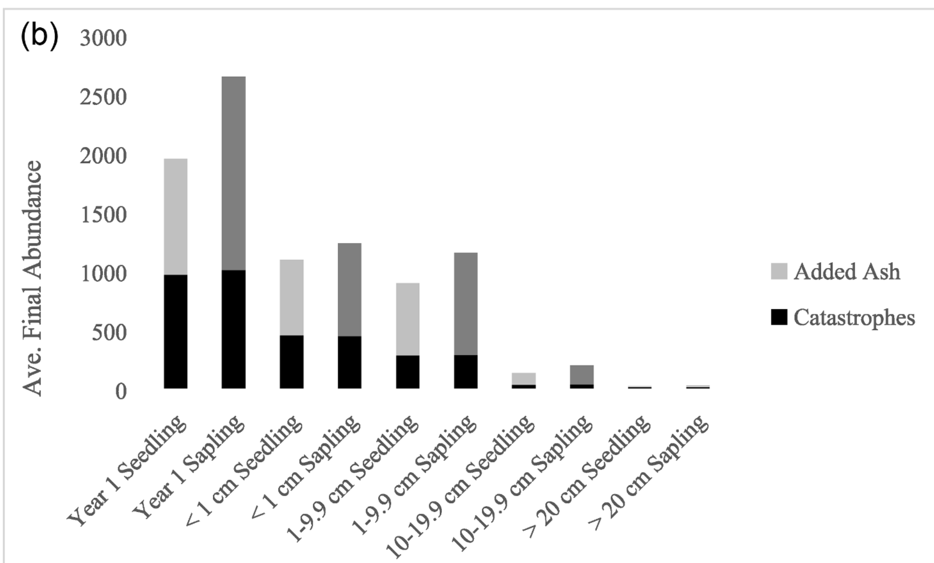


Fig. 4. a. The breakdown of the final Year 50 abundance averages by stage class for the baseline model, the catastrophes model, and the reduced catastrophes scenario. b. The breakdown by stage class of the catastrophes model abundance with the additional seedlings and additional saplings scenarios. The stacked bars show how many more trees are added to the population when adding seedling (grey) or saplings (dark grey) over time to the catastrophe population, which increases the overall population abundance.

Table 3
The results of the Kolmogorov-Smirnov test between models and scenarios. The D statistic represents the distribution difference between the two variables plotted curves. * denotes $p < 0.01$.

Scenario Comparisons	D statistic
Baseline vs. catastrophe	0.85*
Catastrophe vs. reduced catastrophe	0.66*
Catastrophe vs. sapling introductions	0.76*
Catastrophe vs. seedling introductions	0.78*

et al., 2012). Others, however, are not and would require other entities to pay associated costs. In forested locations, it may be cost prohibitive to use insecticides to protect the quantity of trees necessary to preserve ash forest ecosystems. Effective management may incorporate multiple strategies rather than relying on a single management tactic, potentially resulting in additive or synergistic benefits. In an adaptive integrated pest management plan, a greater chance of ash population persistence is likely if the plan is tailored to the specific population or environment. PVA allows for the exploration of additive effects that may be difficult to assess in the field and is a tool that can help assess integrated pest management plans. Of course, the management options presented could have unknown ecosystem and biological costs associated with them. Management options may be beneficial for the persistence of ash species even if most ash have already been killed by EAB as even just a small number of remaining trees or the next cohort could show partial EAB resistance/tolerance.

4.1. Conclusions

Green ash trees are an important species in floodplain forests and other areas, as they are tolerant of floods and help reduce erosion (Kennedy, 1990). Their importance in natural areas has become more apparent after losing many of them from EAB introductions. In our focal floodplain, the forest reverted to a more savanna-like state. While some forests may follow a similar trajectory, in others, non-ash trees may replace ash and maintain a closed-canopy forest. Models such as the ones described here report testable predictions and allow managers to understand possible scenarios that may occur. We found that a reduction in the impact of EAB on ash survival, which may be achieved through biocontrol or reintroduction of resistant ash trees, assisted the population recovery. Our model highlighted the importance of seedling and reproductive size classes to the persistence of the population. Utilizing resistance breeding for ash trees could increase survival of trees that could be reintroduced into natural areas and we show this strategy benefited the entire population. Combinations of strategies could show even greater promise. With continued monitoring during management, new data would allow for further validation and refinement of the models (Boyce, 1992). Adaptive management could be applied to this and other ash populations with the continued use of PVA and other management tools, to keep ash from extirpation and our forest more diverse.

CRediT authorship contribution statement

R.H. Kappler: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **K.S. Knight:** Data curation, Funding acquisition, Project administration, Resources, Supervision, Writing - review & editing. **R. Bienemann:** Data curation, Investigation, Writing - review & editing. **K.V. Root:** Conceptualization, Funding acquisition, Methodology, Project administration, Software, Supervision, Validation, Writing - review & editing.

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Appendix A

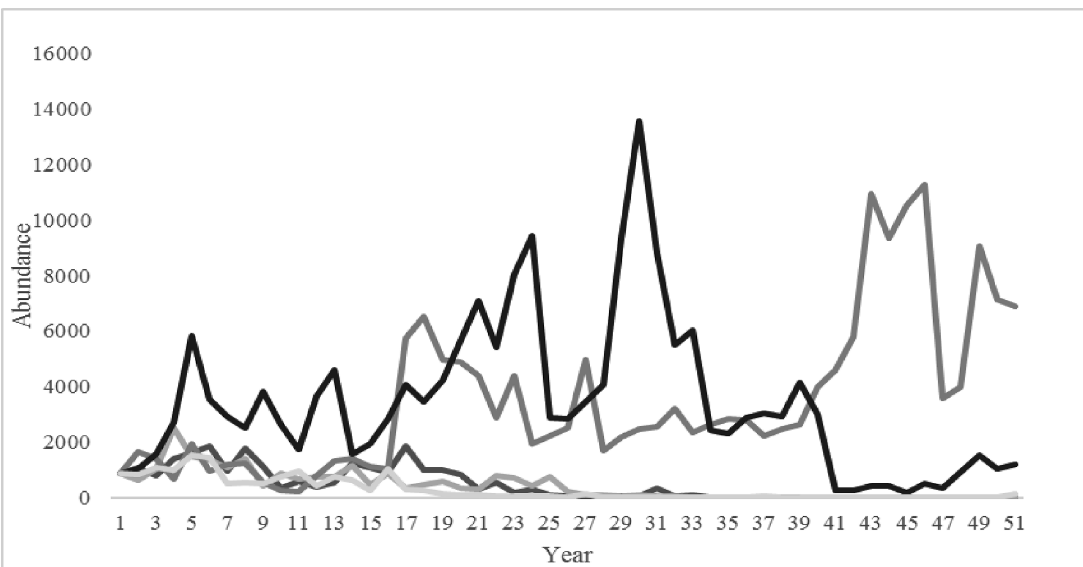

Fig. A1. An example of an ash population abundance trajectory for the catastrophes model with only five replications instead of the average of 10,000 as in Fig. 2. Variations of when the catastrophes occur creates a highly variable pattern of abundance that we expect may occur in nature.

Table A1
Summary of the data collected in Oak Openings Preserve for each size class over time. Yearly survival is reported along with mean survival and standard deviation for each size class.

	2010–2011	2011–12	2012–14	2014–15	2015–16	2016–17	Survival Mean	St. Deviation
< 1 Total					15	13		
< 1 dead					2	4		
< 1 Survival					0.87	0.69	0.77	0.09
1–9.9 Total					235	372		
1–9.9 dead					6	24		
1–9.9 Survival					0.97	0.94	0.95	0.02
10–19.9 Total	226	217	187	203	178	169		
10–19.9 dead	53	27	42	27	16	19		
10–19.9 Survival	0.77	0.88	0.78	0.87	0.91	0.89	0.84	0.06
> 20 Total	59	43	39	49	70	69		
> 20 dead	19	7	14	3	5	15		
> 20 Survival	0.66	0.84	0.64	0.94	0.93	0.78	0.79	0.12

Table A2
Table of parameters used in our models and scenarios. The probability of survival for each stage (P2-P5), probability of growth into the next stage (G1-G5), and fecundity F5 with the standard deviation is given along with citations of its origin and details of the data average.

Model	Parameter	Data Average (S.D.)	Citation	Details
Baseline	G1	0.13 (0.45)	Boerner and Brinkman (1996)	Average survival of new seedlings over 1 year
			Messaoud and Houle (2006)	Average new seedling survival from May to Sept.
	P2	0.77 (0.09)	Kappler (2018)	2015–2017 survival Oak Openings Preserve seedlings $<$ 1 cm
	G2	0.77ˆ7 (0)	Kappler (2018)	7 yrs of survival to grow into next size class
	P3	0.95 (0.02)	Kappler (2018)	Oak Openings Preserve data 2010–2017
	G3	0.05 (0)	Kappler (2018)	10 yrs of survival to grow into he next size class, 0.95ˆ10 too high to maintiain P3 + G3 = 1
	P4	0.84 (0.06)	Kappler (2018)	Oak Openings Preserve data 2010–2017
	G4	0.16 (0)	Kappler (2018)	10 yrs of survival to grow into he next size class
	P5	0.79 (0.12)	Kappler (2018)	Oak Openings Preserve data 2010–2017
	F5	120 (32)	Boerner and Brinkman (1996)	Average new seedling per year over ten years for ash spp.
Catastrophe	G1	–	–	Same as Baseline model
occurs only	P2	–	–	Same as Baseline model
during selected	G2	–	–	Same as Baseline model
years	P3	0.095	Kappler (2018)	90% reduction by multiplying by 0.1
	G3	0.005		90% reduction by multiplying by 0.1
	P4	0.084		90% reduction by multiplying by 0.1
	G4	0.016		90% reduction by multiplying by 0.1
	P5	0.079		90% reduction by multiplying by 0.1
	F5	12		90% reduction by multiplying by 0.1
Reduced Catastrophe	G1	–	–	Same as Baseline model
occurs only	P2	–	–	Same as Baseline model
during selected	G2	–	–	Same as Baseline model
years	P3	0.475	Duan et al. (2017)	50% reduction by multiplying by 0.5
	G3	0.03	Flower et al. (2014)	50% reduction by multiplying by 0.5
	P4	0.42		50% reduction by multiplying by 0.5
	G4	0.08		50% reduction by multiplying by 0.5
	P5	0.395		50% reduction by multiplying by 0.5
	F5	60		50% reduction by multiplying by 0.5
Added healthy ash	G1	–	–	Same as Baseline model
Applies only to added ash	P2	–	–	Same as Baseline model, no literature found for size class
	G2	–	–	Same as Baseline model, no literature found for size class
	P3	0.82 (0.16)	Krinard and Johnson (1981)	Survival for 3 years after planting
			Gardiner et al. (2009)	Green ash 3rd year survival after planting in floodplain
			Krinard and Kennedy (1995)	Survival of 3rd year planted floodplain trees
			Kolka et al. (1998)	Survival & growth 3 years after planting in river corridor
	G3	0.82ˆ16 (0)	Fitzgerald et al. (1975)	Growth of green ash historically took 16 years to gain 10 cm dbh
	P4	0.75 (0.20)	Krinard and Kennedy (1995)	Survival of 16th year planted floodplain trees
			Krinard (1989)	Suvival & growth of 11–15 yr old planted green ash trees
	G4	0.75ˆ16 (0)	Fitzgerald et al. (1975)	Growth of green ash historically took 16 years to gain 10 cm dbh
	P5	0.90 (0.10)	Marchin et al. (2008)	Common garden 30 yr survival
	F5	–	–	Same as Baseline model

Table A3
The probability change file for the catastrophes model. Where each row represents the next time step of the simulation and indicates the percent probability of a catastrophe event occurring in that time step.

% Chance
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0.99

Table A4
Matrix change file used to create the catastrophes model. It will multiply the baseline survival & fecundity rates by the corresponding numbers of the grid row, and continue the calculation where each row is the next year after the start of the catastrophe.

Y1	< 1 cm	1–9.9 cm	10–19.9 cm	> 20 cm
1.0	1.0	0.1	0.1	0.1
1.0	1.0	0.2	0.2	0.2
1.0	1.0	0.3	0.3	0.3
1.0	1.0	0.4	0.4	0.4
1.0	1.0	0.5	0.5	0.5
1.0	1.0	0.6	0.6	0.6
1.0	1.0	0.7	0.7	0.7
1.0	1.0	0.8	0.8	0.8
1.0	1.0	0.9	0.9	0.9

Table A5
Matrix change file for the reduced catastrophes scenario.

Y1	< 1	1–9.9	10–19.9	> 20
1.0	1.0	0.5	0.5	0.5
1.0	1.0	0.55	0.55	0.55
1.0	1.0	0.6	0.6	0.6
1.0	1.0	0.65	0.65	0.65
1.0	1.0	0.7	0.7	0.7
1.0	1.0	0.75	0.75	0.75
1.0	1.0	0.8	0.8	0.8
1.0	1.0	0.85	0.85	0.85
1.0	1.0	0.9	0.9	0.9

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117925.

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