1 **Running header: Modeling forests under hemlock decline**

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3 **When a foundation crumbles: forecasting forest community dynamics**

4 **following the decline of the foundation species *Tsuga canadensis***

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12 ***Abstract.*** In the forests of northeastern North America, invasive insects and pathogens are

13 causing major declines in some tree species and a subsequent reorganization of associated forest

14 communities. Using observations and experiments to investigate the consequences of such

15 declines are hampered because trees are long-lived. Simulation models can provide a means to

16 forecast possible futures based on different scenarios of tree species decline, death, and removal.

17 Such modeling is particularly urgent for species such as eastern hemlock (*Tsuga canadensis*), a

18 foundation species in many northeast forest regions that is declining due to the hemlock woolly

19 adelgid (*Adelges tsugae*). Here, we used an individual-based forest simulator, SORTIE-ND, to

20 forecast changes in forest communities in central Massachusetts over the next 200 years under a

21 range of scenarios: a no-adelgid, status-quo scenario; partial resistance of hemlock to the adelgid;

22 adelgid irruption and total hemlock decline over 25 years, adelgid irruption and salvage logging

23 of hemlock trees; and two scenarios of preemptive logging of hemlock and hemlock/white pine.

24   We applied the model to six study plots comprising a range of initial species mixtures,

25   abundances, and levels of hemlock dominance. Simulations indicated that eastern white pine,

26   and to a lesser extent black birch and American beech, would gain most in relative abundance

27   and basal area following hemlock decline. The relative dominance of these species depended on

28   initial conditions and the amount of hemlock mortality, and their combined effect on

29   neighborhood-scale community dynamics. Simulated outcomes were little different whether

30   hemlock died out gradually due to the adelgid or disappeared rapidly following logging.

31   However, if eastern hemlock were to become partially resistant to the adelgid, hemlock would be

32   able to retain its dominance despite substantial losses of basal area. Our modeling highlights the

33   complexities associated with secondary forest succession due to ongoing hemlock decline and

34   loss. We emphasize the need both for a precautionary approach in deciding between management

35   intervention or simply doing nothing in these declining hemlock forests, and for clear aims and

36   understanding regarding desired community- and ecosystem-level outcomes.

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38   Keywords: Eastern hemlock, woolly adelgid, decline, northeastern forests, SORTIE-ND,

39   forecasting, simulation, resistance, preemptive logging, community dynamics, composition,

40   structure

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INTRODUCTION

44   A major challenge for ecologists is to study and forecast the dynamics of long-lived

45   species, the assemblages they form, and the ecosystems they inhabit. These challenges are

46   especially acute for studies of trees and forests, in which individuals can live for millennia and

47   for which rates of change of some ecosystem processes occur over centuries. In many cases,

48   researchers have used results from short-term observations and experiments to parameterize

49   simulation models (Scheller and Mladenoff 2007). Subsequent experiments with model

50   parameters inform research about, and suggest management strategies for, the emerging forests

51   of the future (e.g., Cyr et al. 2009, Fontes et al. 2010). Such studies increasingly are of critical

52   importance because many forests around the world are in decline (Butchart et al. 2010) and are

53   changing rapidly (Choat et al. 2012, Lindenmayer et al. 2012).

54   Perhaps nowhere are these changes more apparent than in northeastern North America,

55   where a number of tree species are declining due to irruptions of native and nonnative insects

56   and pathogens (Dukes et al. 2009). Of particular note is the rapid decline and disappearance of

57   the forest foundation species (*sensu* Ellison et al. 2005), eastern hemlock (*Tsuga canadensis* (L.)

58   Carr.), resulting from spread of a nonnative insect, the hemlock woolly adelgid (*Adelges tsugae*

59   Annand), along with the removal of this tree from forests by pre-emptive salvage logging (Orwig

60   and Kittredge 2005, Foster and Orwig 2006, Fajvan 2007, Ellison et al. 2010). Many researchers

61   have dedicated substantial time and effort in quantifying the pattern and rate of spread of the

62   adelgid (Preisser et al. 2008, Morin et al. 2009, Fitzpatrick et al. 2010, 2012, Gomez et al. 2015),

63   the rate and intensity of adelgid-related mortality for different demographic stages of hemlock

64 (Preisser et al. 2011), and the ultimate effects of hemlock mortality on forest ecosystem

65 properties and dynamics (Templer and McCann 2010, Block et al. 2012, Orwig et al. 2013).

66   Eastern hemlock is a long-lived, late-successional conifer species and, where it occurs,

67 often comprises a large proportion of overstorey basal area, either as pure stands, or as the

68 dominant species in mixed stands with other species such as eastern white pine (*Pinus strobus*

69 L.), red maple (*Acer rubrum* L.), birch species (*Betula* spp.), and oaks (*Quercus* spp.) (Orwig et

70 al. 2002). The loss of eastern hemlock from these forests results in the formation of new, multi-

71 sized canopy gaps, causing an associated increase of light into the heavily-shaded and generally

72 species-poor understory layer typical of hemlock stands (Ellison et al. 2010). Possible

73 successional pathways in response to this situation will be contingent largely on gap size, overall

74 site conditions, and the proximity, population structure, and life history attributes of the co-

75 occurring species in the community (Small et al. 2005, Eschtruth et al. 2006, Ellison et al. 2010,

76 Ford et al. 2012). Experimental (Ellison 2014) and observational studies (Small et al. 2005,

77 Eschtruth et al. 2013) have provided insights into possible trajectories of future forest

78 development following the loss of eastern hemlock, but these studies are of relatively short

79 duration (< 20 years). Process-based simulation models provide a means to explore a range of

80 scenarios associated with insect irruptions and subsequent changes in forest structure and

81 composition over a range of spatiotemporal extents and resolutions (Papaik et al. 2005, Cairns et

82 al. 2008).

83   Very few modeling studies have explored how forest ecosystem dynamics will change

84 following loss of eastern hemlock (Albani et al. 2010, Birt et al. 2014). Individual-based

85 modeling approaches should be particularly useful in exploring how tree- and neighborhood-

86 scale dynamics influence trajectories of species composition and structure under hemlock decline

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87   scenarios that are relevant to a specific forest area (Jenkins et al. 2000). Here we use an

88   individual-based forest simulator, SORTIE-ND (Pacala et al. 1993, 1996, Canham et al. 2004,

89   2006), parameterized for northeastern North American forests and initialized with tree-level data

90   from plots within the Harvard Forest in central Massachusetts, to model how forest stands

91   currently dominated by eastern hemlock may reorganize over the next 200 years under a range of

92   scenarios of hemlock woolly adelgid-related impacts. SORTIE-ND incorporates plant

93   demography, inter- and intraspecific interactions, and the effects of both natural and

94   anthropogenic disturbance in its forecasts of future forest structure. Our models address three key

95   questions: 1) what is the effect of adelgid-induced mortality on the next 200 years on structure

96   and species composition of New England (USA) forests; (2) how different will these impacts be

97   if partial resistance to the adelgid emerges in the next several decades; and (3) what are the

98   interactions between adelgid-induced mortality, pre-emptive salvage logging of eastern hemlock

99   by people, and background ("natural") rates of hemlock mortality?

100

101   **METHODS**

102   *Study area*

103   We modeled the future of forest stands in the "Transition Hardwoods-White Pine-

104   Hemlock" region (Westveld et al. 1956) of central Massachusetts. In many areas in northeastern

105   North America, including our study sites at Harvard Forest, eastern hemlock may account for >

106   70% of the basal area of the trees within any given forest stand (Ellison et al. 2010, Orwig et al.

107   2012). The forests in central Massachusetts are underlain by loamy soils derived from acidic,

108   glacial till; average annual temperatures are 7.1 ℃; and average annual precipitation ≈1,000 mm

109   (Greenland and Kittel 1997). Historically, much of the region was cleared for agriculture or

110   harvested for timber in the early-to-mid 1800s, and has been regenerating since then (Foster

111   1992).

112   The hemlock woolly adelgid arrived in Massachusetts in the first decade of the 21st

113   century (Preisser et al. 2008). The adelgid was introduced from Asia into eastern North America

114   (near Richmond, Virginia) in the early 1950s (Havill and Montgomery 2008). Since then, it has

115   spread rapidly and has established itself in forests from Georgia northward into Canada and west

116   into Michigan (Morin et al. 2009). The hemlock woolly adelgid in North America reproduces

117   asexually and kills trees of all sizes, ages, and stages (Orwig and Foster 1998). Tree morbidity

118   can occur within two years after adelgid establishment, and tree mortality follows in the next few

119   to 15 years (Orwig et al. 2002). Further, in anticipation of the arrival of the adelgid in a region,

120   people often log existing stands of eastern hemlock (Foster and Orwig 2006, Ellison et al. 2010).

121   Goals of this logging include: increasing the vigor and potential survivorship of remaining

122   eastern hemlock trees; redirecting succession and influencing future forest dynamics; and

123   realizing economic return from trees that will otherwise die (Orwig and Kittredge 2005, Fajvan

124   2007). Because eastern hemlock is of low commercial value, people often harvest other more

125   valuable species such as eastern white pine or red oak (*Quercus rubra* L.) at the same time as

126   they log eastern hemlock (Brooks 2004). Logging and the adelgid have different short-term

127   effects on forest succession and ecosystem dynamics because of differences rates of mortality

128   and biomass removal (fast *versus* slow) and subsequent dynamics (Kizlinski et al. 2002, Orwig et

129   al. 2013).

130

131   *SORTIE core parameterization*

132   SORTIE-ND is a spatially explicit forest simulator that includes effects of tree neighbors

133   on species-specific sapling and adult tree growth and mortality (Pacala et al. 1993, 1996,

134   Canham et al. 2004, Canham et al. 2006). SORTIE-ND tracks the fates of individual trees

135   located within a forest plot as the trees compete with neighboring trees for light and space. The

136   basic setup of the model requires parameterization of equations related to the generation of light

137   conditions across a given forest area, seed dispersal and seedling recruitment, and the growth,

138   mortality, senescence, and death of all seedlings, saplings and adults of each species (Table 1).

139   These equations include variables that characterize particular aspects of the life histories of

140   individual species, including how they respond to light conditions and the crowding and shading

141   effects of neighboring trees (Canham et al. 2006, Uriarte et al. 2009).

142   The functions that determine recruitment of tree seedlings in SORTIE-ND are derived

143   from field data describing seed production, dispersal, and establishment in a variety of soils

144   (Ribbens et al. 1994, LePage et al. 2000, Greene et al. 2004, Papaik et al. 2005, Papaik and

145   Canham 2006). In our implementation of SORTIE-ND, we used the "spatial disperse" option

146   that disperses seeds in each time step at random azimuth directions and distances away from

147   each tree of reproductive age or older. Dispersal distances follow a Weibull distribution, which

148   results in an inverse relationship between the number of dispersed seeds and distance from the

149   parent tree. Maximum fecundity for each species is based on the "standardized total recruits": the

150   total number of seeds produced by a 30-cm diameter parent tree, estimated as the average

151   number of viable seeds kg^{-1} of seed species^{-1} (Ribbens et al. 1994). Seeds can fall on six different

152   types of substrate: forest floor litter, moss, scarified soil, tip-up mounds, decayed logs, or fresh

153   logs. The distribution and availability of each of these substrates are represented as a regular $2 \times$

154   2-m grid across the simulation area, and are based on the number of dead trees that fall each time

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155   step, the direction of tree fall, decay rate of fallen dead trees, and proportion of fallen trees that

156   uproot and make tip-up mounds (Papaik et al. 2005). Successful seedling establishment in each

157   grid cell was determined by species-specific affinity for a particular substrate and relative seed

158   mass (Greene and Johnson 1998).

159   Seedling growth in SORTIE-ND uses a Michaelis-Menton function that increments

160   annual diameter growth as a species-specific function of light availability (Pacala et al. 1996),

161   computed within the 2×2-m grid cells. Available light is computed as a "global light index"

162   (GLI), an estimate of whole-season photosynthetically-active radiation conditional on the crown

163   geometry of individuals of each species, the location, size, and identity of nearby trees, and

164   species-specific light transmission coefficients (Canham 1988, Canham et al. 1994, 1999).

165   Species-specific seedling mortality was modeled as a function of the recent growth of each

166   seeding, its shade tolerance, and within-cell light availability (Kobe et al. 1995). We used

167   seedling growth and mortality parameters provided by C. Canham (*personal communication*)

168   based on previous studies of New England forests (e.g., Pacala et al. 1993, Pacala et al. 1996).

169   The growth and mortality of saplings and adults were modeled using neighborhood competition

170   index (NCI) functions (Canham et al. 2004, 2006, Canham and Murphy 2016). The NCI

171   functions adjust the maximum potential growth rate of each species by initial tree size, intra- and

172   interspecific competition, and within-cell environmental conditions. We used parameters for

173   sapling growth and mortality estimated as part of an analysis of Forest Service Forest Inventory

174   and Analysis (FIA) data, investigating the effects of climatic change on forests across the eastern

175   USA by Canham and Murphy (2016) and Canham (unpublished data).

176

177   *Model evaluation simulations*

178   To evaluate SORTIE's performance, we used 10 years of field observations on four plots within

179   the Harvard Forest Hemlock Removal Experiment (HF-HeRE, see Ellison et al. 2010 and 2014

180   for details), located in the Simes Tract of the Harvard Forest Long Term Experimental Research

181   (LTER) site (42.5°N, 72.2°W; mean elevation 250-m.a.s.l.; Fig. 1B). The HF-HeRE plots were

182   established in 2003 to study experimentally the effects of adelgid-related hemlock mortality and

183   preemptive salvage logging on forest structure and dynamics; post-treatment measurements of

184   tree seedlings, saplings, and trees were done in 2009 and 2014. Specifically, we used the

185   hemlock control plots numbers 3 and 6 (hereafter, "HeRE3-hemlock" and "HeRE6-hemlock")

186   and the two experimentally logged plots, plots 2 and 4 (hereafter, "HeRE2-logged" and "HeRE4-

187   logged"). For the logged plots, we compared observed and simulated changes that had occurred

188   after the 2005 logging operation. The application of SORTIE to the former two plots enabled us

189   to evaluate how well the model can reproduce observed forest dynamics under a scenario of

190   typical forest development without disturbance; the application to the latter two provided an

191   evaluation of the model under a scenario of post-preemptive-logging of hemlock that has

192   ostensibly occurred in advance of a catastrophic adelgid outbreak.

193

194   *Model forecasting simulations*

195   We simulated forest dynamics for 200 years under six scenarios aimed at answering our

196   main questions (Table 2). The first scenario, using the core parameterization of SORTIE

197   described above, included only background levels of natural mortality of eastern hemlock.

198   Scenarios 2 to 6 involved a range of hemlock mortality situations, via either adelgid-induced

199   mortality (Scenarios 2 and 3), salvage logging (Scenario 4), preemptive logging of hemlock

200   (Scenario 5), or logging of hemlock and merchantable pine (Scenario 6). These latter five

201   scenarios required additional model parameterization.

202   For initial inputs to the model under all six scenarios, and to encompass a range of initial

203   conditions typical of forests of this region, we used data from a total of six study plots (Fig. 1).

204   The first three plots were from the aforementioned HF Hemlock Removal Experiment, including

205   the two HF-HeRE hemlock control plots used for model evaluation (HeRE3-hemlock and

206   HeRE6-hemlock) and one hardwood control plot (hereafter, "HeRE7-hardwood"). These plots

207   are 0.76-ha, 0.81-ha, and 0.81-ha in size, respectively. The other three study plots were

208   associated with the 35-ha Harvard Forest ForestGEO forest dynamics plot located in the Prospect

209   Hill tract (Orwig et al. 2015), also at the Harvard Forest LTER. The ForestGEO plot is one of a

210   network of large forest plots established as part of the Smithsonian Tropical Research Institute's

211   Center for Tropical Forest Science – Forest Global Earth Observatory (CTFS- ForestGEO)

212   network of plots. For our modeling, we used data from the full ForestGEO plot (hereafter, "FG-

213   full") and two, 2-ha sub-regions of the plot that currently are dominated either by eastern

214   hemlock ("FG-hemlock") or red oak ("FG-hardwood").

215   In all simulations, we initialized the models using data for the ten tree species that

216   comprised > 95% of the total basal area of the plots (Table 3). Initial model input data for all

217   plots comprised species identities, sizes (DBH) and *x-y* locations (tree maps) of field-measured

218   trees. For the HF-HeRE plots, all trees were measured and located for individuals > 5 cm DBH

219   and 1.3 m in height; saplings (DBH < 5 cm and height < 1.3 m) were counted but not located; at

220   the HF-ForestGEO plots, all trees and saplings with DBH > 1-cm and height > 1.3-m were

221   measured and located. For the HF-HeRE plots, we used means of ten years of seedling plot data

222   as initial inputs (Table 4), while for the ForestGEO plots, we used a common seedling density of

223   250 seedlings per hectare for all species because seedling data were unavailable. Raw data for all

224   plots are available online from the Harvard Forest Data Archive

225   (http://harvardforest.fas.harvard.edu/ harvard-forest-data-archive): datasets HF126 (HF-HeRE

226   overstory vegetation), HF106 (HF-HeRE understory vegetation), and HF253 (HF ForestGEO

227   data).

228   To simulate adelgid-induced mortality in SORTIE-ND, we used a logistic equation

229   (Table 1) that estimates the proportion of trees colonized by the adelgid. This equation includes

230   parameters for initial and maximum rates of establishment, the steepness of establishment rate,

231   and the time at which half the maximum rate of establishment has occurred. For hemlock trees,

232   the NCI mortality function was adjusted with an additional parameter that changed the

233   probability of mortality as a function of time that the adelgid had been present. In our

234   simulations, we used two alternative parameter sets: one based on the scenario in which there

235   was partial resistance of eastern hemlock to the adelgid (Scenario 2) and one in which there was

236   no resistance of eastern hemlock, the adelgid spread rapidly, and all trees were killed by

237   simulated year 25 (Scenario 3). We also included functions to allow the formation of standing

238   dead trees ("snags") and their subsequent fall (Venderwel et al. 2006). To mimic salvage logging

239   (Scenario 4), we simply eliminated hemlock snag formation from the model, which forced the

240   model to delete all hemlock individuals as they died. An episodic mortality behavior was used to

241   simulate preemptive logging (Scenarios 5 and 6). Trees were killed and removed as a function of

242   parameters that controlled the timing and spatial extent of each logging event, the range of

243   diameters within which mortality occurred, and the proportion of total basal area within the

244   specified diameter range that was removed. We affected complete logging of eastern hemlock

245   (Scenario 5) or eastern hemlock and merchantable white pine (Scenario 6) at simulation year 15.

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246   Stochastic behavior in SORTIE-ND results from differences in initial conditions and

247   from using random draws from specified distributions for dispersal, growth, and mortality

248   parameters. We used field data from six plots as our initial conditions and did not vary these

249   among runs. However, comparisons of simulations initialized by different plots did allow us to

250   examine how variation in initial community structure could result in different outcomes. We did

251   use random draws from probability distributions for dispersal, growth, and mortality parameters.

252   For each plot × scenario combination, we ran 10 stochastic simulations.

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254

255   **RESULTS**

256   *Model evaluation*

257   Observed adult tree stem densities and basal areas changed from the starting conditions

258   (2003-2004) to the first (2009) and second (2014) re-measurements in the two HF-HeRE

259   hemlock control plots (plots 3 and 6) and two logged plots (plots 2 and 4) used for model

260   evaluation (Figs. 2 and 3). Over the 10-year measurement period, stem densities decreased by

261   17.5% and 5.8% in plots 3 and 6, respectively, and increased by 2.9% and 17.1% post-logging in

262   plots 2 and 4, respectively. On average, total plot basal area increased by 6.1% in plots 3 and 6

263   and by 24.6% post-logging in plots 2 and 4 over the same 10-year period. These observed

264   changes in the distributions of stem densities (Fig. 2) and basal areas (Fig. 3) by diameter classes

265   were well-simulated by SORTIE for both re-measurement times for plots 3, 6 and 2, but were

266   under-predicted for most diameter classes of trees in plot 4.

267   After logging, observed black birch (*Betula lenta* L.) sapling densities increased

268   dramatically in plots 2 and 4 after year four, from zero stems per hectare to near 10,000 stems

269   per hectare in year 10 (Fig. 4). Saplings of other species were far less prominent in the plots,

270   although there was a slight trend of increasing red maple saplings from year six and white pine

271   from year eight. Similar to observed patterns, SORTIE also simulated a large influx of black

272   birch saplings to over 10,000 stems per hectare, although this did not occur until after year nine

273   (Fig. 4), indicating a lag in the movement of seedlings to the sapling tier in the model. The model

274   similarly predicted an increase in red maple after year 14 in both plots and an increase in white

275   pine in plot 4, while other species comprised relatively minor components. Model simulations

276   indicated that over the next 20 years, although decreasing after its initial burst, black birch

277   saplings will continue to dominate the gaps created by logging, with considerable numbers of red

278   maple and, in plot 4, white pine persisting.

279

280   *Forecasts – forest dynamics and structure*

281   Under a no-adelgid-irruption scenario (Scenario 1), simulations suggested that in the four

282   hemlock-dominant plots, hemlock would continue to self-recruit and maintain its dominance

283   over time (Fig. 5); by the end of the simulation horizon, these dynamics resulted in an overall

284   loss of total basal area due to higher numbers of hemlock individuals in smaller age classes

285   (Figure 6). In the two hardwood-dominant plots, hemlock would also increase in prevalence as a

286   canopy species, mainly replacing oak as it matures and dies over time (Fig. 5), increasing the

287   overall basal area of these plots by year 200 (Fig. 6).

288   Under a scenario of partial hemlock resistance to adelgid impacts (Scenario 2), SORTIE

289   simulated a variety of impacts on species composition and structure that depended largely on the

290   initial composition of the plot. In the hemlock-dominant plots, American beech and black birch

291   recruited as saplings to high densities into the gaps created by dying hemlock trees (Fig. 7),

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292   while hemlock concomitantly retained its overall dominance and eventually began to recover

293   over time. The effect of this is that by year 200, there was an overall dampening of the size

294   structure of these plots and a reduction of up to one-half the original total basal area (Fig. 6). By

295   contrast, in the two hardwood-dominated plots, existing adult white pine and yellow birch also

296   took advantage of these gaps, increasing their dominance in the canopy over time, resulting in

297   only minor changes in the size structure of these plots relative to starting profiles (Figs. 7 and 6).

298   SORTIE projected relatively similar 200-year trajectories under the three scenarios (Figs.

299   8 to 10) in which there was complete hemlock mortality by adelgids and natural snag dynamics

300   (Scenario 3), "salvage logging" of hemlock just prior to death (Scenario 4), or preemptive

301   logging of hemlock trees (Scenario 5). These scenario simulations suggested that, with exception

302   of the HF-Hardwood plot, white pine is expected to increase significantly in abundance and basal

303   area and will dominate these plots by year 200. In the FG-Hardwood plot, the loss of adult

304   hemlock trees enabled American beech to recruit into the sapling tier canopy and yellow birch to

305   become more prevalent in the adult tier. In both the HeRE6 and HeRE6 hemlock plots in these

306   three scenarios, black birch also increased considerably in abundance over the 200-year period

307   because of hemlock mortality. In year 200, total basal areas for these two scenarios (Fig. 6) were

308   generally comparable to initial conditions, although in almost all plots there was a shift in

309   structure to increased prevalence of larger trees, presumably due to the increase in large white

310   pine canopy trees. The year-200 size structure in the HF-Hardwood plot, by contrast, contained

311   fewer large trees, likely due to the large numbers of American beech recruits into this plot, which

312   formed a dense canopy of sapling-sized trees.

313   Under a scenario of both hemlock and merchantable pine logging by year 25 (Scenario

314   6), differences in simulated community trajectories among the six plots depended on which

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315   species took most advantage of the increased light created by tree removal, and whether or not

316   white pine was able to recover and gain dominance over time (Fig. 11). Across the full FG plot

317   and within the FG-Hardwood subplot, American beech and yellow birch increased considerably

318   in abundance in the sapling and adult tiers, respectively, preventing white pine from recovering

319   in these plots. In the two HeRE hemlock plots (3 and 6), black birch became the most abundant

320   species, although the white pine individuals remaining after logging were able to grow and

321   become dominant in terms of basal area by the end of the simulation.

322

323   *Forecasts – changes in diameter growth rates upon canopy removal*

324   We examined projected species' growth rates before (year 10) and shortly after (year 17)

325   preemptive hemlock logging in Scenario 5 simulations to determine how the different species

326   would respond to major increases in light and space after disturbance. These results indicated

327   that all species would experience an increase in diameter growth upon the creation of canopy

328   openings, at all growth stages (Fig. 12). However, growth rates, and the relative increases in

329   growth after hemlock removal, differed significantly by species and study plot. White pine and

330   red oak had the highest adult and sapling growth rates at the two times and across all plots; black

331   birch also showed noticeable increases in year-17 growth rates in the two HRE-hemlock plots.

332

333   **DISCUSSION**

334   There are gaps in our understanding about how forests will respond to the decline of

335   particular tree species. Addressing such knowledge gaps in advance of the loss of foundation

336   species, such as eastern hemlock, is particularly important because of the disproportionate effects

337   foundation species have on the overall structure, composition, successional trajectory, and

338   dynamics of the forest ecosystems they define. Given the long life spans of tree species and

339   associated challenges with field experimentation, simulation modeling affords an essential tool

340   for predicting how current forest conditions and core community dynamics processes may

341   generate a range of new spatiotemporal realities for forests undergoing species decline and loss.

342   Such modeling exercises also can inform the exploration and development of management

343   strategies for at-risk forests. In this study, simulations with the SORTIE-ND individual-based

344   model highlighted possible trajectories of secondary succession in these forests following

345   adelgid-related hemlock mortality. Specifically, our modeling provides useful insights into how

346   fine-scale, community dynamics may play out across a range of disturbance and initial condition

347   scenarios.

348   Eastern white pine emerged in our simulations as the species able to take the greatest

349   advantage of the increases of space and light created by the death of hemlock trees. Although

350   generally not considered a highly versatile species, white pine is relatively shade tolerant, is a

351   prolific and widespread disperser, has a broad ecological niche, and can be competitive in in a

352   range of post-disturbance conditions (Abrams 2001). Indeed, white pine growth rates in our

353   study plots in the years after hemlock death were high relative to the other species, making it

354   highly competitive in our scenarios of hemlock decline, particularly in plots where there was a

355   strong initial white pine adult component. In our study area within central Massachusetts, white

356   pine and hemlock have had a long association in post-settlement forests, with hemlock

357   dominating during more stable periods, and white pine taking advantage of gaps formed by

358   periodic disturbances such as storms (Ireland et al. 2008). With increasing adelgid prevalence in

359   this area, simulations suggest that white pine may replace hemlock as the dominant species, at

360   least in the near term, in this novel disturbance scenario. Although some forest stands throughout

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361   New England have shown a general shift to a dominance of oaks and mixed hardwoods after

362   significant hemlock dieback (Small et al 2005), our results indicate that even in our more

363   hardwood-dominated plots, white pine will increase as the oak and red maple components of

364   these stands mature and decline naturally over time.

365   Simulations also suggest that black birch would be competitive with white pine in

366   hemlock gaps, but that its eventual relative abundance depends on some threshold of initial

367   abundance and adequate seed production, as well as enough hemlock removed to provide ample

368   light conditions for this relatively light-demanding species. This was particularly evident in the

369   HeRE3 and HeRE6 hemlock plots, where black birch seedlings had relatively higher growth

370   rates after hemlock harvesting than white pine (e.g., Fig. 12), but where slight differences in

371   initial relative abundances and canopy gap sizes in these plots likely mediated the ability for

372   black birch to take advantage of these better growth rates. In other locations in northeastern

373   forests, where hemlock trees have died naturally due to adelgid impacts (Orwig and Foster 1998,

374   Orwig et al. 2002), were killed experimentally (Orwig et al. 2013), or as a result of logging

375   (Zukswert et al. 2014), abundances of black birch seedlings and saplings have also been

376   observed to increase dramatically. Our results also suggest that, barring any other major

377   disturbances, black birch could remain relatively dominant over the 200-year timespan in plots

378   where it can establish and overtop other species. Black birch also survives several years in the

379   seedbank in much greater numbers than other species (e.g. Farnsworth et al., Sullivan and

380   Ellison). Our parameterization of SORTIE did not account for this effect, but it could favor

381   establishment and subsequent dominance of black birch in the future.

382   SORTIE also projected a considerable influx and domination of the sapling tier by

383   American beech upon the loss of hemlock in plots where there is sufficient initial occurrence of

384   beech. Even in our hardwood-dominated plots, where there was relatively little hemlock present,

385   the loss of hemlock individuals enabled beech to replace hemlock as the new shade tolerant

386   species in the understory. Our adult growth parameterization for this species in SORTIE, based

387   on previous FIA plot analyses by Canham et al. (2006, 2014), reflects a strong reduction in

388   growth in beech beyond 15-cm DBH due to the effects of beech-bark disease over the past

389   century. Indeed, beech-bark disease has been shown to cause a significant dieback of older trees

390   and an increase in the suckering and abundance of sapling-sized beech, inhibiting the

391   establishment of other, more common tree species; this scenario is playing out in many areas in

392   the northeast USA (Garnas et al. 2011, Giencke et al. 2014) and is consistent with our simulation

393   results. Such "beech brush thicket" conditions (Giencke et al. 2014) could persist indefinitely

394   and define a new future reality for some stands in our study areas over the longer term.

395   On the whole, our results indicate that community trajectories and future forest structure

396   will be qualitatively similar whether hemlock dies slowly from the adelgid, or is removed rapidly

397   through logging. These results parallel findings of the Hemlock Removal Experiment, especially

398   in comparisons between girdled and logging treatments (Lustenhouwer et al. 2012, Orwig et al.

399   2013, Ellison et al. 2014). Further, our "partial adelgid resistance" simulations (Scenario 2)

400   indicate that despite significant initial (50-year) hemlock loss, its ability to cast such deep shade

401   means that it can still retain relative dominance for a long period of time, preventing other

402   species from taking quick advantage of new canopy openings while losing basal area itself. The

403   result of this is effectively the creation of a "basal area suppression" situation, where hemlock

404   persists but prevents other species from increasing in basal area compared to starting conditions.

405   A number of management options for hemlock forests undergoing decline, and the

406   potential future implications of these options, have been explored previously (Brooks 2004,

18

407   Orwig and Kittredge 2005, Foster and Orwig 2006, Fajvan 2008). These management options

408   range from "doing nothing," to carrying out silvicultural treatments or extensive hemlock

409   logging. The first consideration arising from how to manage adelgid-affected hemlock forests

410   relates to whether the main objective of such activities is the maximization of short-term profit or

411   the long-term sustainability of the system. A focus on profit has led to the harvesting of hemlock

412   and associated merchantable timber in advance of adelgid-induced mortality. Arguments against

413   pre-emptive salvage logging include: (1) hemlock stands, even declining ones, form a unique and

414   important ecosystem; (2) it is still as yet unclear whether there are, or will be, genetically-

415   resistant hemlock individuals that could provide a refuge for future recovery or whether useful

416   biocontrol measures may be developed in future years; (3) the responses of forest stands to levels

417   of hemlock removal are site-specific, highly-variable, and therefore not always predictable. Our

418   modeling highlights the last: the observed range of successional trajectories are contingent on

419   local forest structure and dynamics. Thus, careful thought and additional research and modeling

420   are needed to further explore future realities and whether human interventions of different types

421   or intensities would produce a forest with compositional and structural conditions associated

422   with sustainable ecosystem functions.

423

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432

433

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631

632   TABLES

633   Table 1. Overview of the main SORTIE-ND behaviors and parameters used for simulations.

Behavior	SORTIE-ND behavior*	Basis for behavior algorithms	Source of model parameters
Light availability	Quadrat-based GLI light	Canham et al. 1994	C. Canham *personal communication*
Seed dispersal	Non-gap spatial disperse	Ribbens et al. 1995; Greene et al. 2004	Seed weights from literature; coefficients from Green et al. 2004
Substrate and seed survival	Substrate and no gap substrate seed survival	Kobe et al. 1995	Greene and Johnson 1998
Growth	Seedlings: Non-limited relative growth	Pacala et al. 1996	C. Canham *personal communication*
	Saplings and adults: NCI growth	Canham et al. 2006; Canham and Murphy 2016	Canham and Murphy 2016
Mortality	Seedlings: growth based mortality	Kobe and Coates 1997	C. Canham *personal communication*
	Adults and saplings: NCI mortality	Canham et al. 2006	From Canham et al. 2006 and C. Canham *unpublished data*
Insect irruption and hemlock mortality	Logistic insect infestation function NCI mortality scalar	SORTIE model documentation*	Specific to this study
Snag decay and fall	Weibull snag mortality	SORTIE model documentation*	Modified from Vanderwel et al. 2006
Hemlock removal	Episodic disturbance	SORTIE model documentation*	Specific to this study

634   * See model documentation at http://www.sortie-nd.org/help/index.html

635   ** Research carried out at Great Mountain Forest, Connecticut

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636   Table 2. A description of the SORTIE-ND forecast simulations carried out at the Harvard Forest

637   ForestGEO and Hemlock Removal Experiment plots. The proposed scenarios investigate

638   possible forest structure and composition changes associated with hemlock woolly adelgid

639   (hemlock woolly adelgid)-related impacts.

Scenario description	Research question	SORTIE parameterization
1. No irruption	What is the *status quo* forecast, assuming no hemlock woolly adelgid irruption occurs?	Standard model behaviors; no model behaviors for hemlock woolly adelgid effects or logging
2. Hemlock resistance	What is the community dynamics response to an initial decline, but not complete die-off, of hemlock over time?	50% maximum infestation of hemlock adults and saplings by year 20; very gradual mortality effect once infected; 50% annual stochastic seedling mortality; dead trees and saplings become snags and follow snag-fall behaviors
3. Irruption-decline	What is the community dynamics response to a gradual and complete mortality of hemlock within the first 20 years?	100% infestation of hemlock saplings and adults by year 15; 70% mortality of hemlock saplings and adults by year 5 and 100% by year 20; 85% annual stochastic seedling mortality; dead trees and saplings become snags and follow snag-fall behaviors
4. Irruption-salvage logging	What is the community dynamics response to the complete mortality of hemlock within the first 20 years, but with stems removed just prior to death?	100% infestation of hemlock saplings and adults by year 15; 70% mortality of hemlock saplings and adults by year 5 and 100% by year 20; 85% annual stochastic seedling mortality; trees are removed from simulation just prior to death
5. Preemptive hemlock logging	What is the community dynamics response to preemptive harvesting of all hemlock adults and saplings in year 15?	Harvesting of all hemlock basal area in year 15; 85% annual stochastic seedling mortality

6. Preemptive hemlock/pine logging	What is the community dynamics response to preemptive harvesting of all hemlock and merchantable pine adults and saplings in year 15?	Harvesting of all hemlock and merchantable pine basal area in year 15; 85% annual stochastic seedling mortality

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641

642   Table 3. Observed adult and sapling stem densities (stem ha^{-1}) and basal areas (m^2 ha^{-1}) for

643   species (acronyms in parentheses) within the Harvard Forest ForestGeo (FG) and the Hemlock

644   Removal Experiment (HeRE) study plots that comprise at least 90% of the total basal area (BA),

645   and that were used as initial conditions for scenario simulations.

646

Species	FG - Full		FG - Hemlock		FG - Hardwood		HeRE3 - Hemlock		HeRE6 - Hemlock		HeRE7- Hardwood	
	Stems	BA	Stems	BA	Stems	BA	Stems	BA	Stems	BA	Stems	BA
Red maple (ACRU)	284.9	6.0	55	1.9	325.5	6.9	74.5	2.8	90.1	6.3	284.0	6.1
Yellow birch (BEAL)	125.3	1.0	16.8	0.1	220.7	0.7	5.2	0.2	33.3	1.3	1.2	0.0
White birch (BEPA)	15.3	0.4	10.1	0.3	4.3	0.1	1.3	0.0	28.4	1.8	37.0	1.5
Black birch (BELE)	50.7	0.6	61.5	1.2	56.7	0.2	88.9	3.6	54.3	1.8	191.4	5.2
American beech (FAGR)	117.9	0.5	23.1	0.1	361.5	0.9	0.0	0.0	0.0	0.0	4.9	0.2
Eastern hemlock (TSCA)	661.7	13.6	1470.2	42.8	95.7	0.6	729.4	29.9	474.1	27.6	101.2	3.1
Eastern white pine (PIST)	70.4	4.4	38.5	6.4	144.7	2.8	26.1	3.1	50.6	9.5	258.0	12.5
Red pine (PIRE)	22.6	1.9	0.0	0.0	12.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Black cherry (PIRE)	6.6	0.1	0.0	0.0	12.5	0.2	0.0	0.0	4.9	0.2	3.7	0.1
Red oak (QURU)	120.4	8.7	18.8	0.5	177.4	18.3	78.4	5.1	18.5	2.2	104.9	6.4
Total	1506.5	38.2	1694.2	53.2	1413.9	32.0	1022.2	45.5	769.1	52.0	991.4	35.5

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648

649   Table 4. Initial seedling densities (seedlings ha^{-1}) for model evaluation and scenario simulations

650   for the Harvard Forest ForestGEO (FG) and Hemlock Removal Experiment (HeRE) study plots.

651   A constant seedling density was used for the FG plots due to a lack of seedling data. Seedling

652   values for the HeRE plots are means of seedling counts within 10, 1-m^2 sample quadrats within

653   each of the plots sampled over 10 years, scaled to a per-hectare basis.

Species	FG (Full, Hemlock, Hardwood)	HeRE2-Logged	HeRE4-Logged	HeRE3-Hemlock	HeRE6-Hemlock	HeRE7-Hardwood
Red maple	250	6700	12000	23000	57750	30500
Yellow birch	250	2000	4400	85	20	0
White birch	250	0	0	0	0	0
Black birch	250	16500	15300	0	250	0
American beech	250	0	0	0	0	0
Eastern hemlock	250	600	1500	8000	14330	1000
Eastern white pine	250	7100	500	5000	10000	28000
Red pine	250	0	0	0	0	0
Black cherry	250	100	0	2900	2000	2700
Red oak	250	1500	1200	0	1080	4500

654

655

656   Figure legends

657   Figure 1. Study location in eastern North America, and stem maps of the plots used to initialize

658   the forecasting simulation models. For the stem maps, black points are eastern hemlock and gray

659   points are all other species. Clockwise from top left: A) range of eastern hemlock and counties

660   with established hemlock woolly adelgid populations as of 2015 (data source: USFS,

661   Northeastern Area; Disclaimer: This map depicts counties with established HWA populations

662   that are confirmed and reported by respective state forest health officials. The coarse nature of

663   the map does not provide information below the county level and readers should not assume that

664   highlighted infested counties are entirely infested.); B) location of study plots at the Harvard

665   Forest Long Term Experimental Research site in central Massachusetts, USA; C) HF-HeRE plot

666   3 (hemlock); D) HF-HeRE plot 6 (hemlock); E) HF-HeRE plot 7 (hardwood); F) ForestGEO plot

667   with the two, 2 hectare sub-plots used indicated by the white outlines.

668

669   Figure 2. Comparison of observed and simulated live stem density distributions (A and B) and

670   basal area distributions (C and D) by tree diameter categories after five years (first re-

671   measurement, 2009) and ten years (second re-measurement, 2014) in the Harvard Forest

672   Hemlock Removal Experiment hemlock control plots 3 and 6 and logged plots 2 and 4. For

673   comparison purposes, we provide observed stem densities for the initial measurement (2004

674   Baseline).

675

676   Figure 3. Comparison of observed and simulated basal area distributions by tree diameter

677   categories after five years (first re-measurement, 2009) and ten years (second re-measurement,

678   2014) in the Harvard Forest Hemlock Removal Experiment for the hemlock control plots (3 and

35

679   6) and logged plots (2 and 4). For comparison purposes, we provide observed basal areas for the

680   initial measurement (2004 Baseline).

681

682   Figure 4. Comparison of observed and simulated live sapling density distributions in the Harvard

683   Forest Hemlock Removal Experiment, Hemlock Logged Plots 2 and 4, by species.

684

685   Figure 5. Simulated forest community dynamics over 200 years for Scenario 1 within the six

686   study plots, characterized in terms of changes in sapling and adult stem density (stems ha^{-1}) and

687   adult basal area (m^2 ha^{-1}) for each of ten dominant tree species. Lines represent median values

688   for each species of ten model simulations.

689

690   Figure 6. Basal area (m^2 ha^{-1}) distribution by dbh class for the six study plots for current

691   (observed) forest conditions and for simulated, year 200 conditions under the six simulation

692   scenarios (see Table 2). For observed data, values are total basal areas per dbh class; for

693   simulated data, values are means of total basal area per dbh class across 10 model runs, with

694   variation around the means indicated by two standard error bars. Above each group of bar graphs

695   are total plot basal areas.

696

697   Figure 7. Simulated forest community dynamics over 200 years for Scenario 2 within the six

698   study plots, characterized in terms of changes in sapling and adult stem density (stems ha^{-1}) and

699   adult basal area (m^2 ha^{-1}) for each of ten dominant tree species. Lines represent median values

700   for each species of ten model simulations.

701

702   Figure 8. Simulated forest community dynamics over 200 years for Scenario 3 within the six

703   study plots, characterized in terms of changes in sapling and adult stem density (stems ha^{-1}) and

704   adult basal area (m^2 ha^{-1}) for each of ten dominant tree species. Lines represent median values

705   for each species of 10 model simulations.

706

707   Figure 9. Simulated forest community dynamics over 200 years for Scenario 4 within the six

708   study plots, characterized in terms of changes in sapling and adult stem density (stems ha^{-1}) and

709   adult basal area (m^2 ha^{-1}) for each of ten dominant tree species. Lines represent median values

710   for each species of 10 model simulations.

711

712   Figure 10. Simulated forest community dynamics over 200 years for Scenario 5 within the six

713   study plots, characterized in terms of changes in sapling and adult stem density (stems ha^{-1}) and

714   adult basal area (m^2 ha^{-1}) for each of ten dominant tree species. Lines represent median values

715   for each species of 10 model simulations.

716

717   Figure 11. Simulated forest community dynamics over 200 years for Scenario 6 within the six

718   study plots, characterized in terms of changes in sapling and adult stem density (stems ha^{-1}) and

719   adult basal area (m^2 ha^{-1}) for each of ten dominant tree species. Lines represent median values

720   for each species of 10 model simulations.

721

722   Figure 12. Mean annual diameter growth rates (mm year^{-1} $\pm$ 2 S.E.) for adults, saplings and

723   seedlings in the six study plots, by species, based on Scenario 5 simulations. The left panel

724   presents growth rates for simulation year 10, before preemptive harvesting of hemlock, and the

725   right panel growth rates for year 17, two years after harvesting.
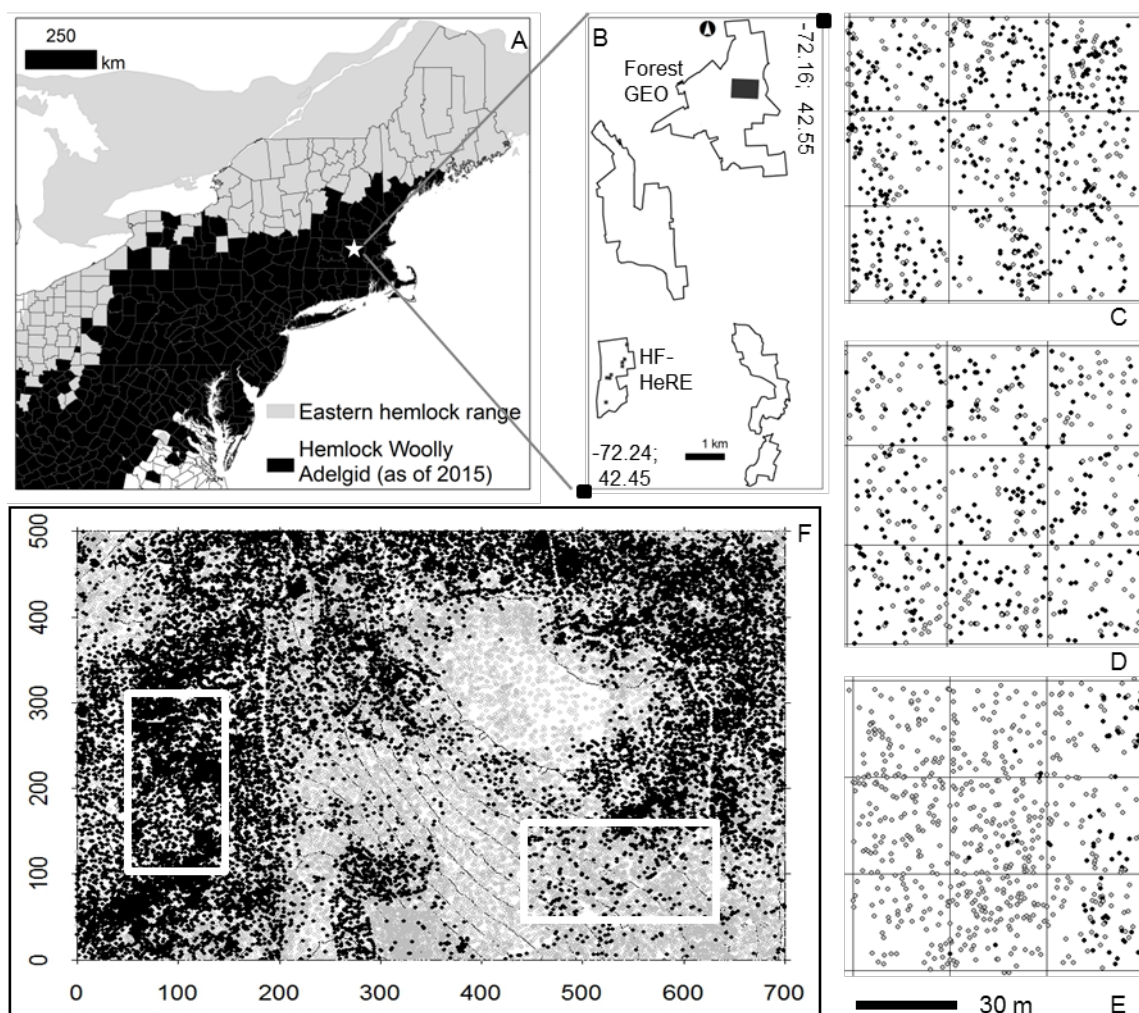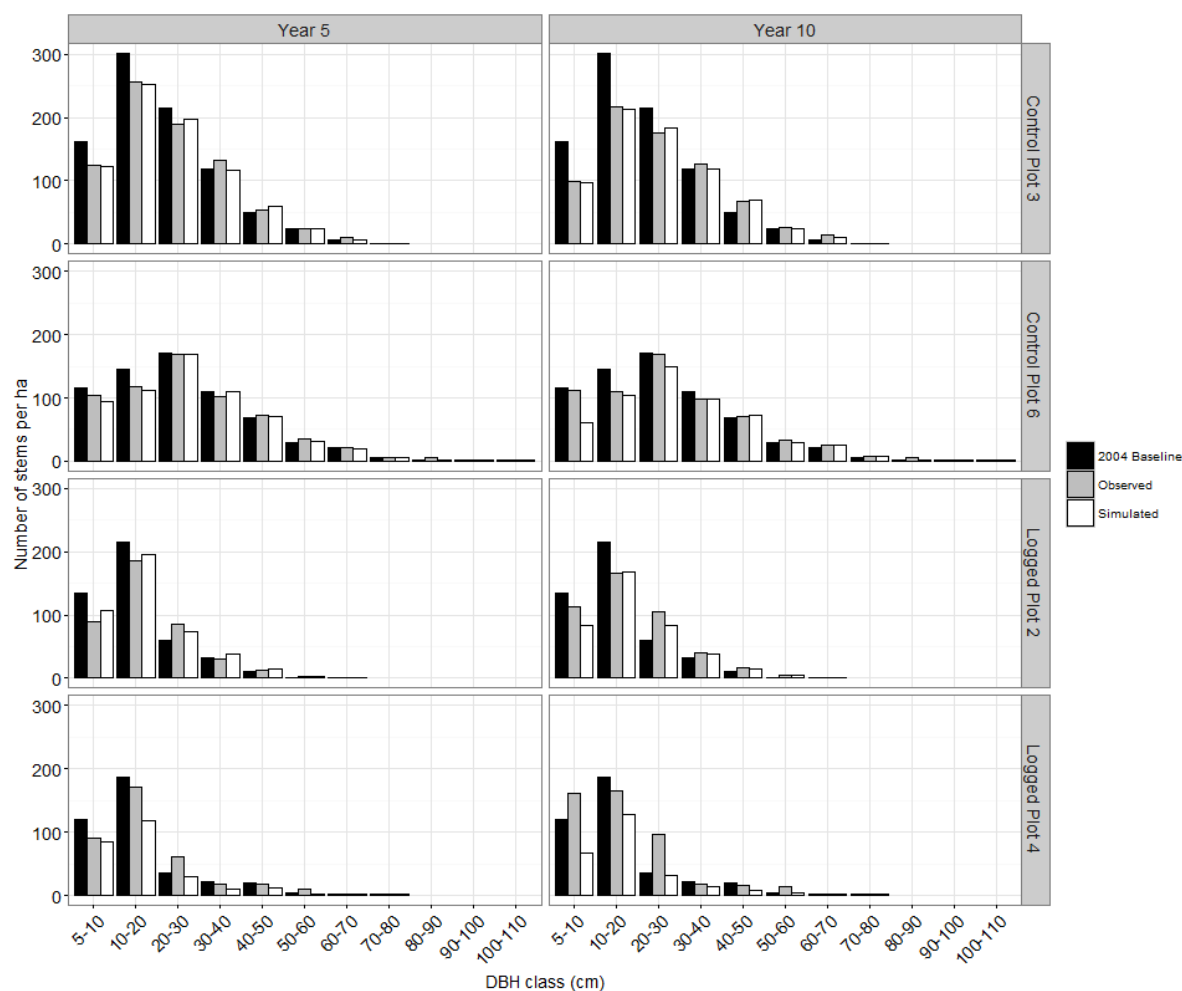
726

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728   Figure 1.
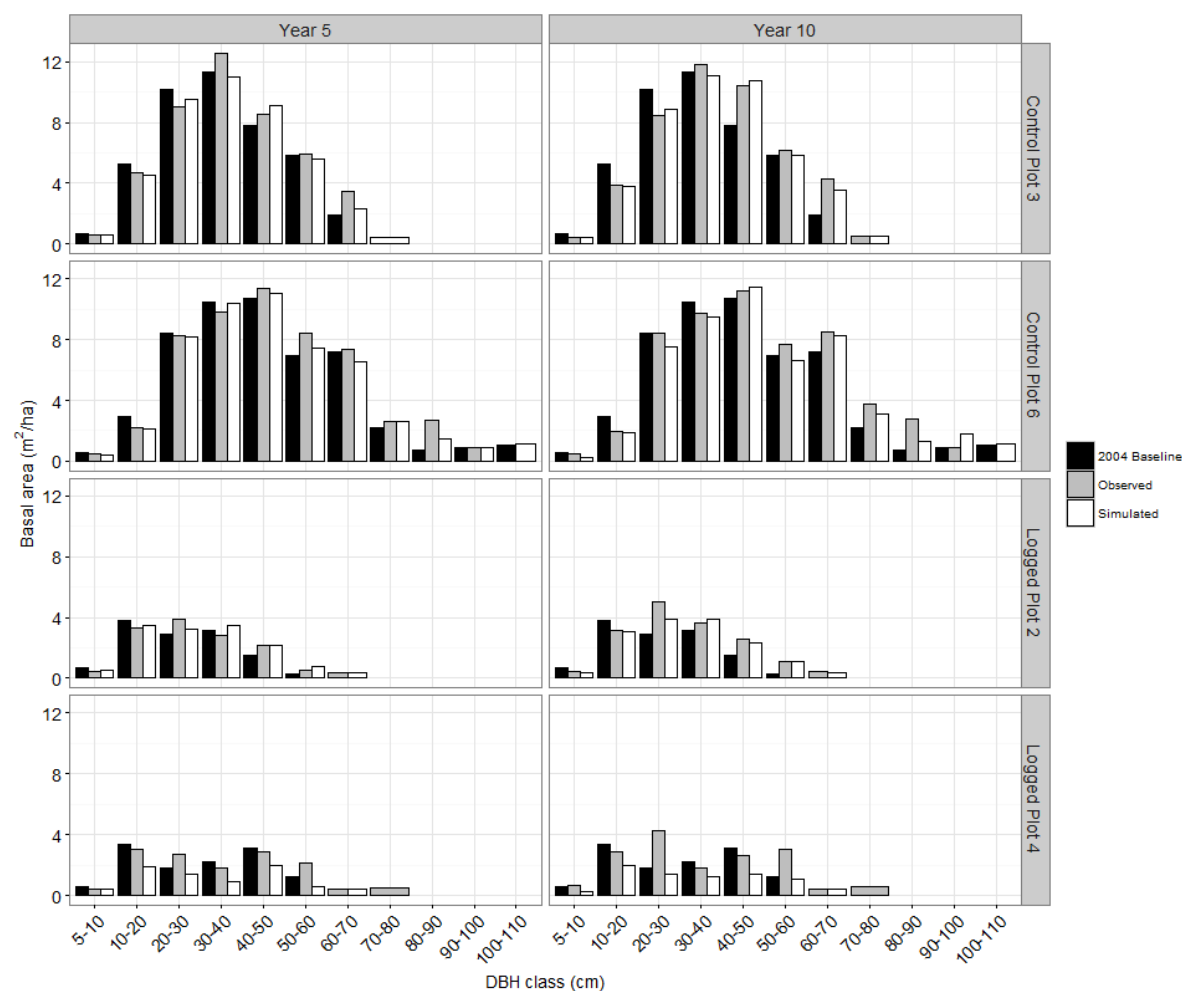
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731   Figure 2.

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733   Figure 3.

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737   Figure 4.

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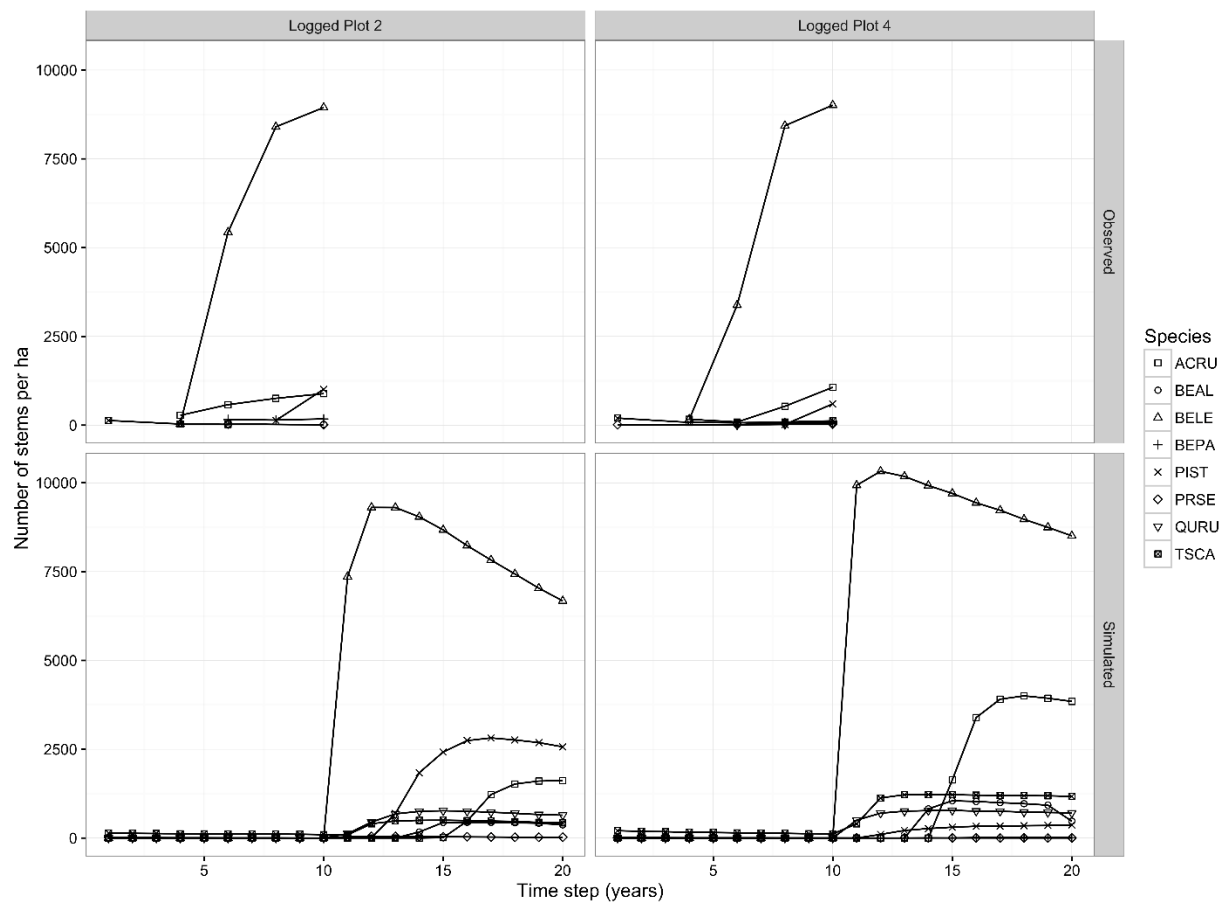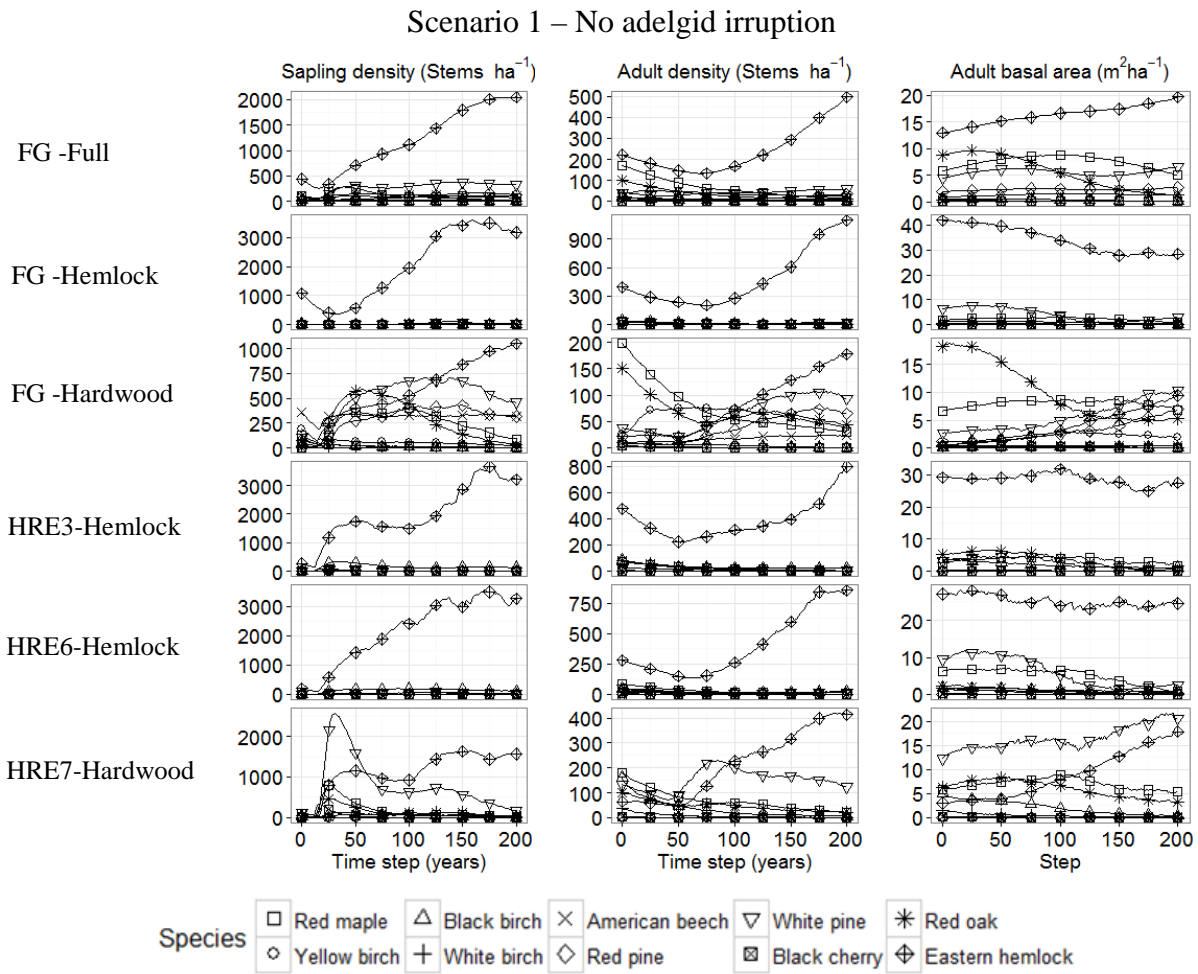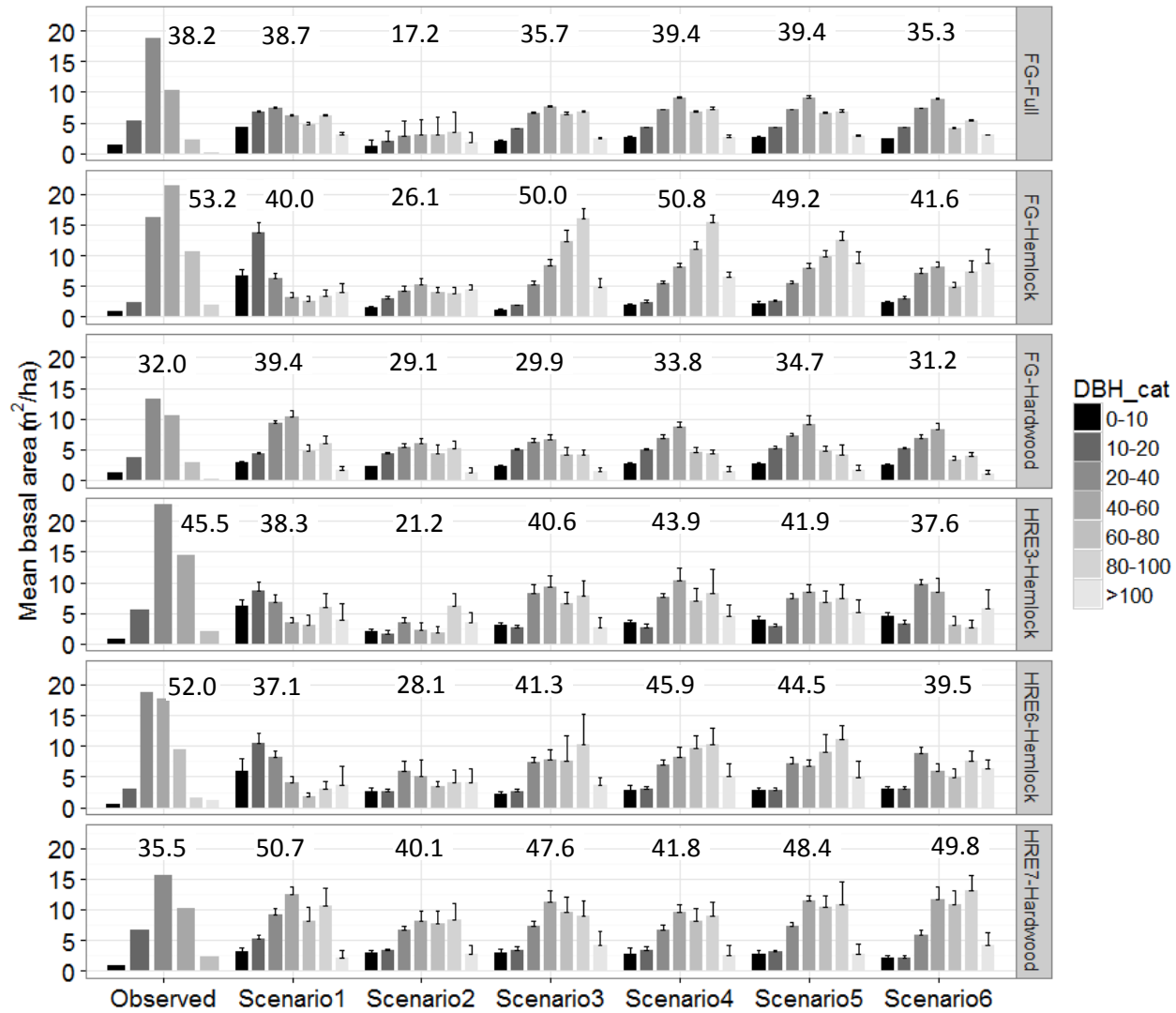Scenario 1 – No adelgid irruption

740

741   Figure 5.

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743

744   Figure 6.

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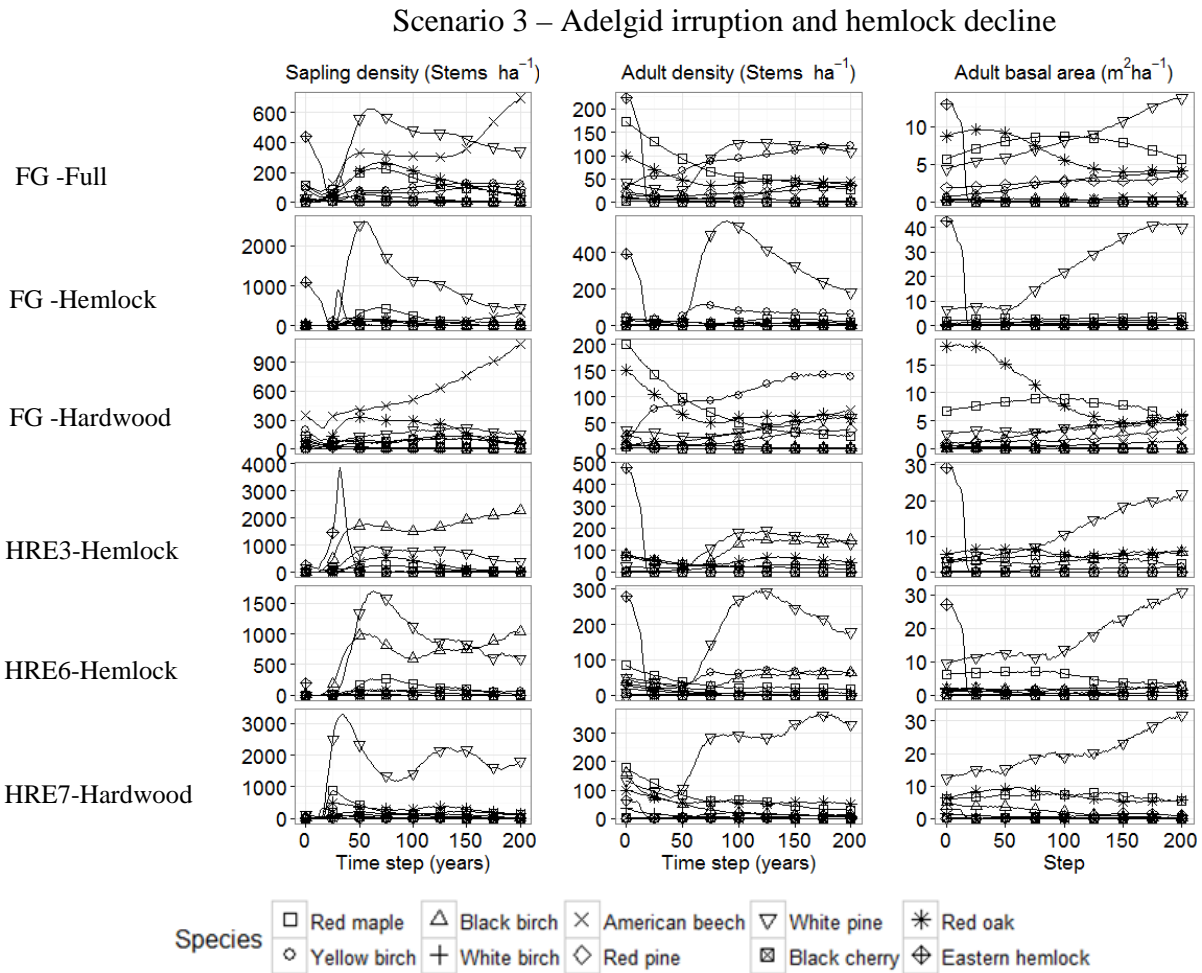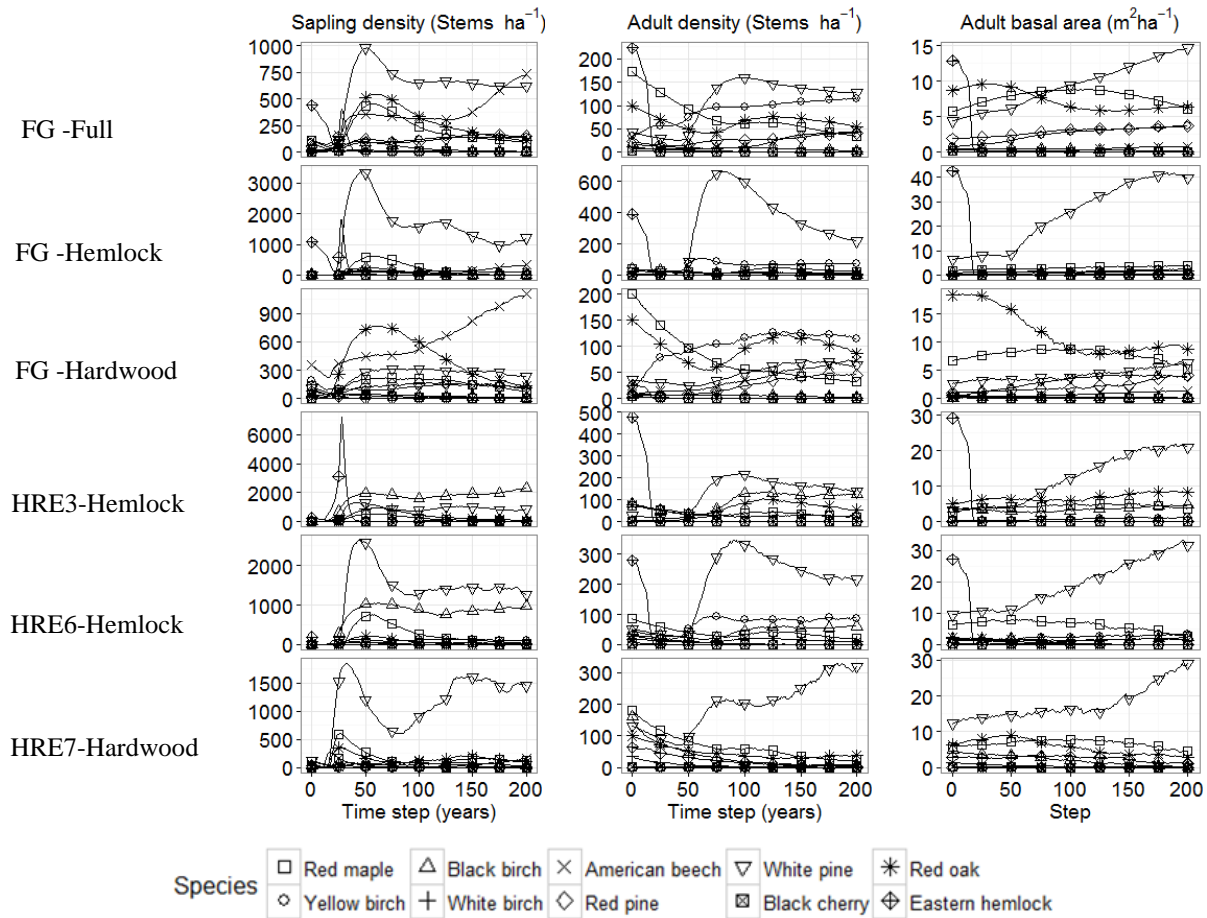## Scenario 2 – Hemlock resistance

747

748   Figure 7.
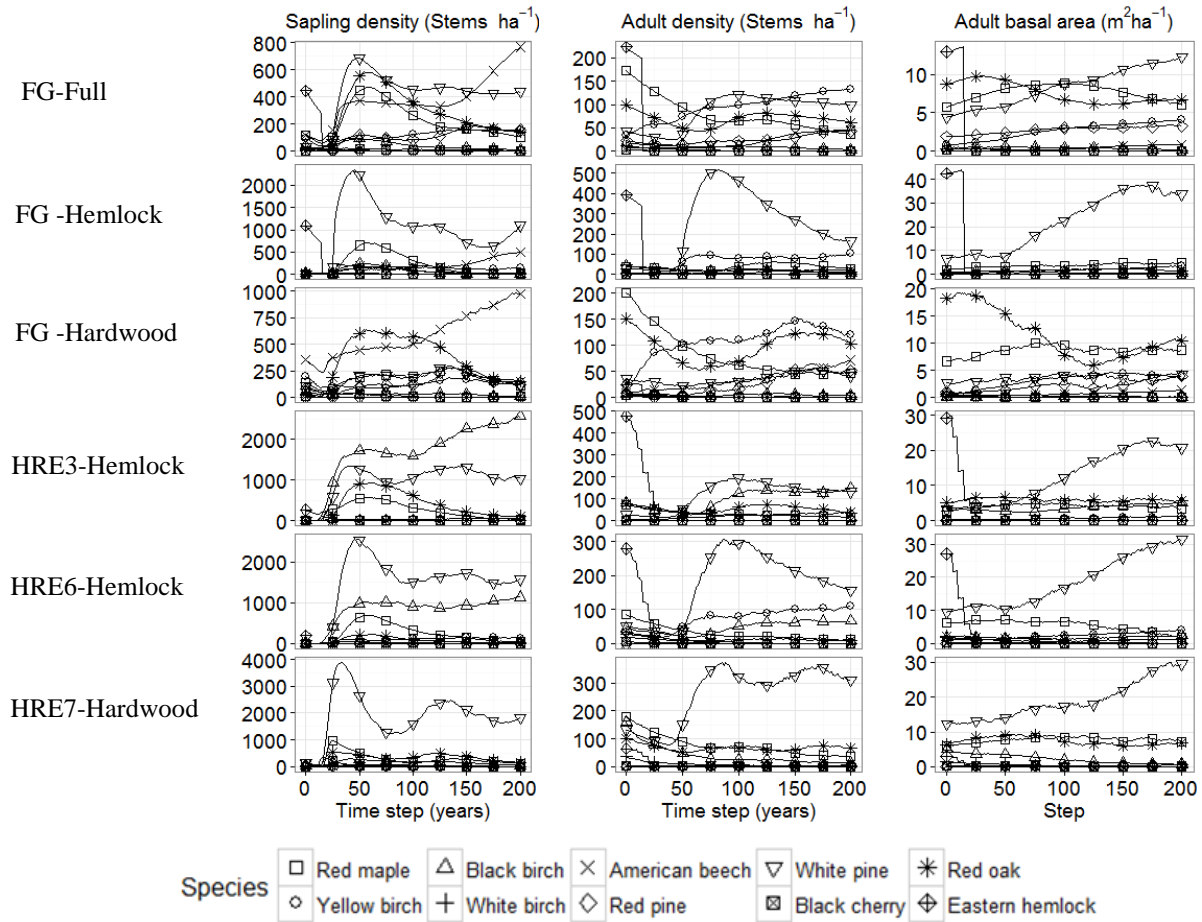
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Scenario 3 – Adelgid irruption and hemlock decline

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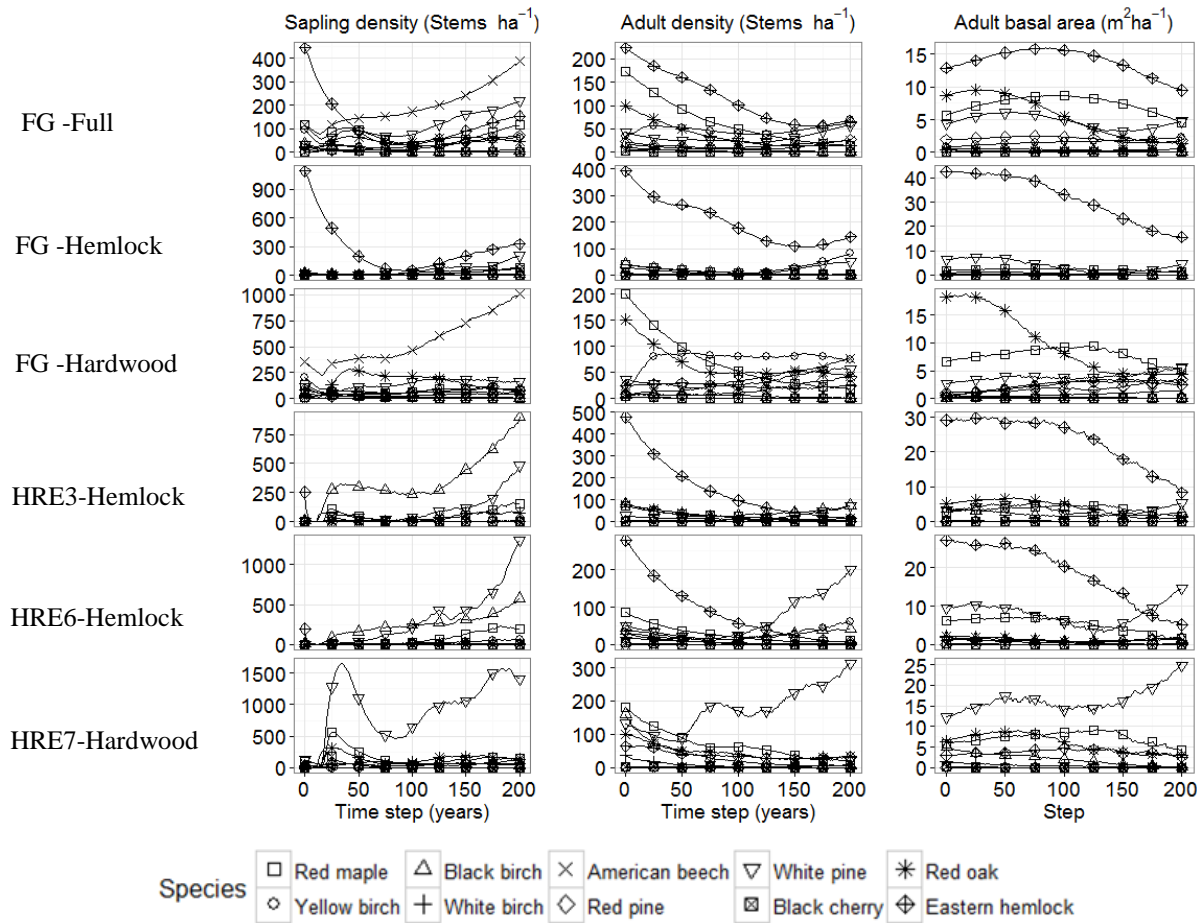
753   Figure 8.

754

Scenario 4 – Adelgid irruption and salvage logging

755

756   Figure 9.

757

Scenario 5 – Adelgid irruption and preemptive hemlock logging

758

759 Figure 10.

760

761

762

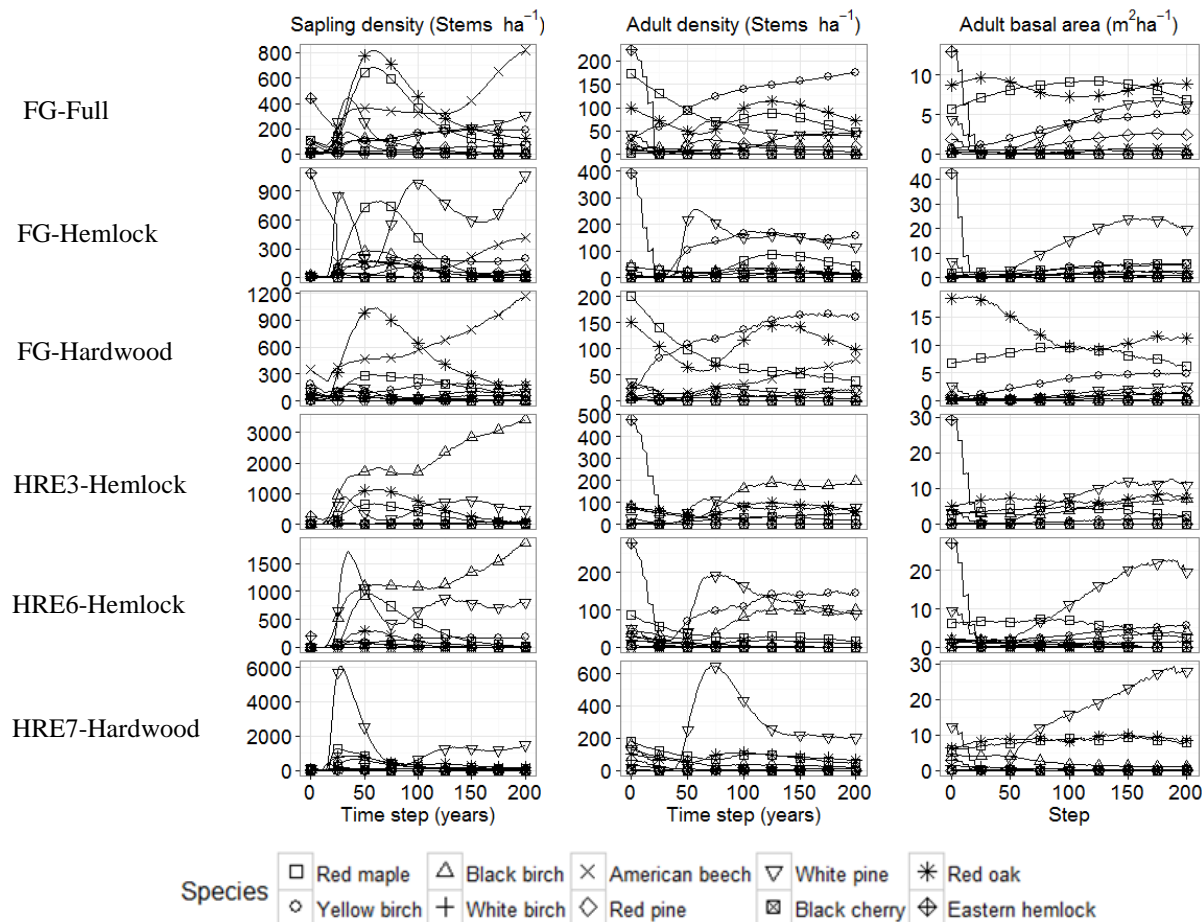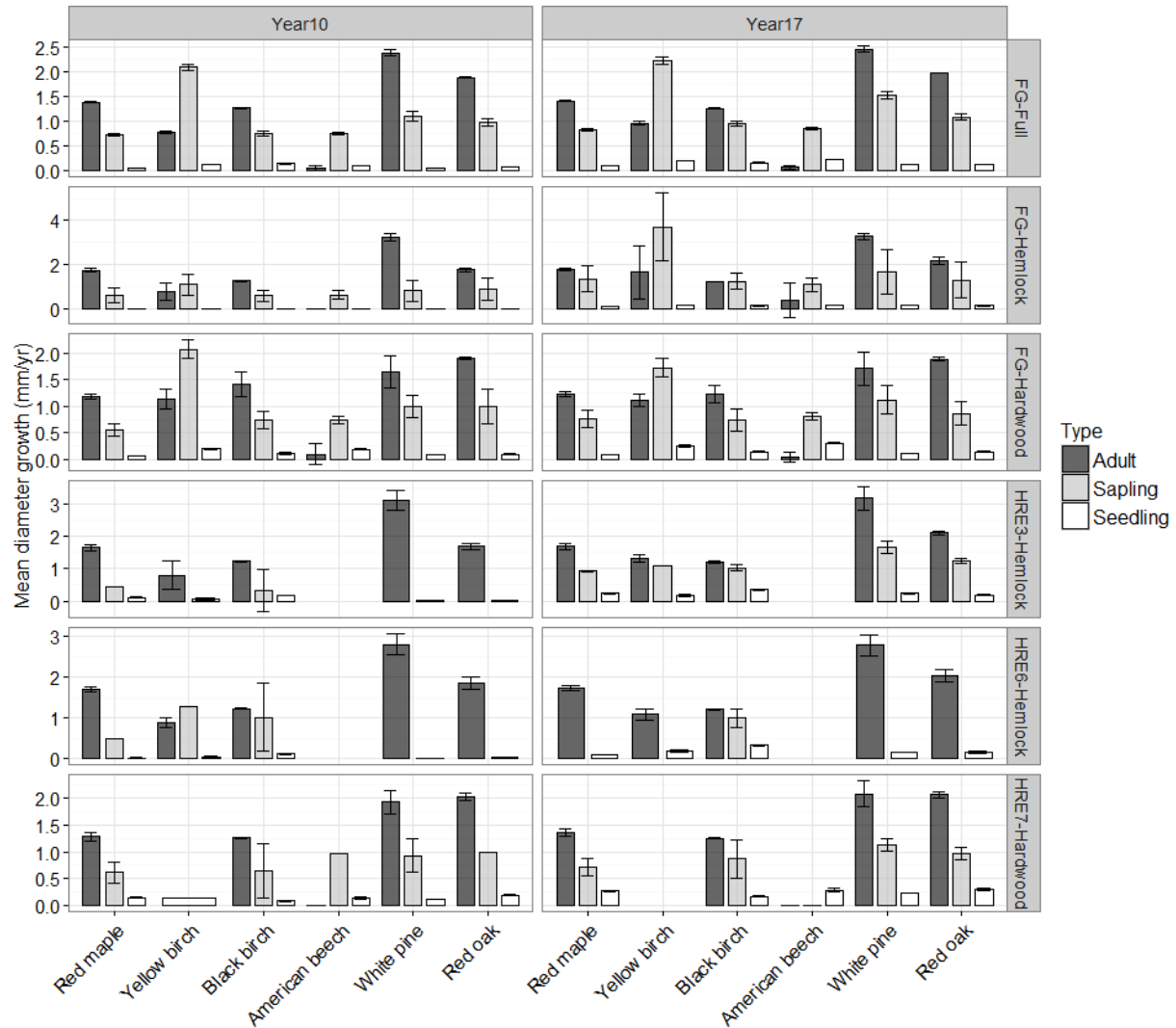Scenario 6 – Adelgid irruption and preemptive hemlock and pine logging

763

764   Figure 11.

765

766

767

768

769   Figure 12.