The Relative Contributions of Seed Bank, Seed Rain, and Understory Vegetation Dynamics to the Reorganization of Tsuga Canadensis Forests After Loss due to Logging or Simulated Attack by Adelges tsugae

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1   **The relative contributions of seed bank, seed rain, and understory vegetation dynamics to**

2   **the reorganization of *Tsuga canadensis* forests after loss due to logging or simulated attack**

3   **by *Adelges tsugae***

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22

23   **Abstract**: Profound changes are occurring in forests as native insects, nonnative insects, or

24   pathogens irrupt on foundation tree species; comprehensive models of vegetation responses are

25   needed to predict future forest composition. We experimentally simulated hemlock woolly

26   adelgid (*Adelges tsugae* Annand) infestation (by girdling trees) and preemptive logging of

27   eastern hemlock (*Tsuga canadensis* [L.] Carrière), and compared vegetation dynamics in

28   replicate 90×90-m treatment plots and intact hemlock stands from 2004-2010. Using Chao-

29   Sørensen abundance-based similarity indices, we assessed compositional similarities of trees,

30   shrubs, forbs, and graminoids among the seed bank, seed rain, and standing vegetation over time

31   and among treatments. Post-treatment seed rain, similar among treatments, closely reflected

32   canopy tree composition. Species richness of the seed bank was similar in 2004 and 2010.

33   Standing vegetation in the hemlock controls remained dissimilar from the seed bank, reflecting

34   suppressed germination. Recruits from the seed rain and seed bank dominated standing

35   vegetation in the logged treatment, whereas regeneration of vegetation from the seed bank and

36   seed rain was slowed due to shading by dying hemlocks in the girdled treatment. Our approach

37   uniquely integrates multiple regeneration components through time and provides a method for

38   predicting forest dynamics following loss of foundation tree species.

39

Introduction

40

41   A key aim of forest ecology is to elucidate factors that influence transitions of plants

42 from the seed to the canopy under a range of management conditions. Changes in forest species

43 composition through time are driven by several factors, including recruitment from the seed

44 bank, inputs from seed rain, interactions with standing vegetation, variable edaphic and climatic

45 conditions, and a range of mortality agents including insects and pathogens (Lovett et al. 2006;

46 Burton et al. 2011). Long-term, integrative studies of these ecological factors are needed to

47 predict the species composition of future forests, especially as herbivores irrupt and pathogens

48 become more prevalent. Pathogens and insects can damage or eliminate dominant and

49 foundation tree species (*sensu* Ellison et al. 2005), rapidly and radically altering the composition

50 of forest stands. Silvicultural practices and preemptive measures such as logging, undertaken to

51 remove vulnerable and/or economically valuable tree species before an infestation or infection

52 occurs, also affect seed-banking, regeneration, and forest dynamics (Graae and Sunde 2000;

53 Decocq et al. 2004).

54   Eastern hemlock (*Tsuga canadensis* [L.] Carrière) forests provide a model system in

55 which to examine these dynamics, specifically comparing responses to preemptive hemlock

56 logging or infestation by the hemlock woolly adelgid (*Adelges tsugae* [Annand]). Intact, mature

57 hemlock forests tend to be stable and long-lived, with depauperate understories suppressed by a

58 very shady microenvironment and acidic needle litter (Catovsky and Bazzaz 2000; D'Amato et

59 al. 2008). Palynological data illustrate that hemlock forests underwent a region-wide decline

60 ~5400 years ago caused by a combination of insect-driven defoliation and climatic change, but

61 they recovered to their current extent after 300-1200 years (Foster et al. 2006).

62   A similar process has been unfolding in the last 30 years. The hemlock woolly adelgid

63   has been spreading rapidly since the 1980s, defoliating trees and causing more than 95%

64   mortality in parts of its range (Orwig et al. 2008). Preemptive salvage logging has occurred in

65   many hemlock stands to extract economic value before the adelgid infests and kills the trees

66   (Foster and Orwig 2006). Slow loss of living hemlock due to the adelgid acts as a gradually

67   changing filter on vegetation recruitment, progressively suffusing the understory with light,

68   stimulating seed germination, and creating opportunities for plant colonization. For example,

69   Yorks et al. (2003) documented gradually increasing abundance of *Betula*, *Acer*, and four

70   monilophyte species in the five years following a hemlock girdling treatment.

71   In contrast, logging removes the canopy suddenly, greatly increasing light availability at

72   the forest floor in a single pulse (Krasny and Whitmore 1992). Logging also often leaves a large

73   amount of slowly-decomposing slash that initially suppresses regeneration, and effects of rutting,

74   scarification, and other disturbances can persist in second-growth hemlock stands (Smith 1986).

75   In either case, the composition of the forest eventually increases in species richness, with new

76   broad-leaved tree species coming to predominate in even-aged stands (Orwig and Foster 1998).

77   However, the near-term composition of the recovering forest is difficult to predict; stochastic

78   dynamics, coupled with a warming climate that favors increased herbivory or recruitment of

79   plant species adapted to warmer climate conditions (Paradis et al. 2008), may cause novel

80   assemblages to form (e.g., Spaulding and Rieske 2010).

81   In this paper, we present results of a seven-year study that documents species present in

82   the seed bank, seed rain, and tree, sapling, seedling, and herbaceous vegetation before and after

83   hemlock-dominated stands were subjected to three experimental treatments: (1) simulated attack

84   by *A. tsugae*; (2) preemptive logging; and (3) intact control. We ask four specific questions:

85   1. To what extent are the initial compositions of the seed bank, seed rain, canopy, and

86   existing forest-floor species similar? Comparative studies frequently report disparities

87   among the plant species compositions of the seed bank, seed rain, and standing

88   vegetation (Hopfensperger 2007). Such disparities pose challenges for predicting future

89   forest composition, but can also indicate the most important ecological filters operating

90   on particular species, life forms, and life stages (Myers and Harms 2011). Based on

91   previous studies, we expected to find little concordance in species composition among

92   these regeneration components.

93   2. Do the compositions of the seed bank, seed rain, canopy, sapling, seedling, and

94   herbaceous vegetation diverge or converge in similarity over time or among treatments?

95   We hypothesized that the composition of the developing forest-floor vegetation would

96   more closely reflect the inputs of seed rain and the seed bank as the girdled canopy

97   gradually ceased acting as a strong filter on germination and establishment of seedlings.

98   We also expected the 2010 seed bank to diverge in composition from the 2004 seed bank

99   in the logged treatment as new seed sources became available and the existing bank

100   became depleted as seeds germinated and recruited to the seedling layer.

101   3. Does the vegetation composition differ between stands undergoing mortality due to

102   simulated adelgid attack versus logging, and how does post-disturbance composition

103   compare with intact stands? We predicted that seed rain would continue to supply new

104   recruits as the canopy slowly died in the girdled treatment, while the upper layer (0-10

105   cm depth) of the forest seed bank would contribute most of the new recruits in newly

106   logged stands, as it would be most responsive to scarification during skidder activity. We

107   also expected the composition of the vegetation on the forest floor to remain stable and

108   dominated by shade-tolerant *T. canadensis* in the heavily shaded hemlock control

109   treatment (Catovsky and Bazzaz 2002).

110   4. Can we use these data to predict stand composition as post-hemlock succession proceeds?

111   The advance regeneration afforded by sapling, shrub, and herbaceous layers, plus

112   ongoing seed rain, should dominate the vegetation that develops in post-treatment years.

113   Figure 1 depicts a simple, conceptual null model in which these inputs contribute equally

114   to outcomes in stand composition. Observed departures from this model, reflected in

115   different treatment responses, would reflect contrasting ecological filters imposed by

116   processes such as insect or pathogen damage and logging. Although we anticipated that

117   the composition of the standing vegetation would differ between adelgid-impacted and

118   logged stands during early phases of stand regeneration, over much longer terms,

119   standing vegetation may converge in similarity.

120   Prior studies of regeneration in logged or adelgid-infested hemlock stands separately

121   have documented changes in plant species composition (Orwig et al. 2008), provided baseline

122   data on seed bank and understory vegetation (Catovsky and Bazzaz 2000; Yorks et al. 2000;

123   Sullivan and Ellison 2006), or used successional data to inform predictive models of tree species

124   abundance (Spaulding and Rieske 2010); ours is the first to integrate all these types of data with

125   information on temporal dynamics of seed bank and seed rain compositions in an experimental

126   context. Most previous plot-based studies have tended to focus on single guilds, such as forest-

127   floor herbs (Burton et al. 2011), or examined ecosystems other than temperate forests (e.g.,

128   Drake 1998); we document the emergence of both herbaceous and woody vegetation to present a

129   comprehensive profile of changing assemblages of forest plants.

130

Methods

Harvard Forest Hemlock Removal Experiment

This study took place in the Harvard Forest Hemlock Removal Experiment (HF-HeRE) plots, located within the 121-ha Simes Tract at the Harvard Forest Long-Term Ecological Research Site in Petersham, Massachusetts, USA (42.47^{o}–42.48^{o} N, 72.22^{o}–72.21^{o} W; elevation 215–300 m a.s.l.). The Harvard Forest lies within the hemlock/hardwood/white pine transition forest region of eastern North America, and the Simes Tract itself is classified as "hemlock-hardwoods" (Kernan 1980). The soils are predominantly coarse-loamy, mixed, active, mesic Typic Dystrudepts in the Charlton Series that are derived from glacial till (USDA n.d.). Prior to the experimental treatments described below, eastern hemlock comprised 50-69% of the (on average) 50 m^2 ha^{-1} (mean) basal area, and 55-70% of the mean 875 stems ha^{-1} (Sullivan and Ellison 2006). Other species that comprised >10% of the initial basal area in any of the plots included white pine (*Pinus strobus* L.), black birch (*Betula lenta* L.), red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.).

Full methods and diagrams of the HF-HeRE are given in Ellison et al. (2010); salient details are presented here. Canopy-level manipulations were performed in two 90 ✕ 90 m (0.81 ha) plots in each of two blocks; an additional 0.81 ha plot in each block served as a control. Blocks were chosen based on their size and capacity to accommodate 3 large treatment plots without edge effects. The "valley" block is in undulating terrain bordered on its northern edge by a *Sphagnum*-dominated wetland, whereas the "ridge" block is on a forested ridge (see site map in Ellison et al. 2010). Blocks and plots were sited and established in 2003. Within each block, the two treatment plots and the intact control plot were located within 300 m of each other, with similar topography and aspect. In 2003, *A. tsugae* was not present in any of the

154 blocks; as of 2010, the insect was gradually colonizing hemlock stands at the Harvard Forest and

155 was present throughout the Simes Tract, but not yet causing hemlock mortality.

156   The first canopy manipulation, girdling, was designed to induce the gradual physical

157 decline (i.e., defoliation, biomass loss) caused by *A. tsugae* infestation. In this treatment, *all*

158 hemlock seedlings, saplings, and mature trees were girdled using knives or chainsaws over a

159 two-day period in early May 2005. The girdled hemlocks died over the course of the next two

160 years, and since have been slowly disintegrating in a pattern quite analogous to that observed

161 following heavy *A. tsugae* infestations (see also Yorks et al. 2003).

162   The second treatment, logging, was designed to mimic the effects of a commercial

163 hemlock-salvage operation involving removal of merchantable timber, pulp, and cordwood of

164 hemlock and other species (e.g., *Pinus strobus* L. and *Quercus rubra* L.). We applied a fixed-

165 diameter-limit cut. Between 65 and 70% of the stand basal area, including all *T. canadensis*

166 trees > 20 cm diameter (at breast height, 1.3 m) and at least half of the merchantable white pine

167 and hardwoods (maple, birch, oaks), was harvested by chainsaw and removed from the two plots

168 using a rubber-tired skidder between February and April 2005 when the ground was frozen. The

169 third plot in each block was left intact, to serve as a *T. canadensis* control.

170   In this paper, we focus on species composition and abundance before treatments were

171 applied in 2005 and vegetation regeneration and reorganization for five years following the

172 hemlock removal treatments. Data on microclimate, stand structure, litterfall, coarse woody

173 debris, distribution and abundance of ants, beetles, and spiders, and fluxes of carbon and nitrogen

174 also were collected for two years prior to the 2005 treatment and are reported elsewhere (Sackett

175 et al. 2011; Lustenhouwer et al. 2012; Orwig et al. in review). Overall, changes in these variables

176 in the girdled treatment have been similar in pace and magnitude to those resulting from adelgid

177   invasion throughout New England. For example, light availability increased gradually over time

178   in the girdled treatment (as in Yorks et al. 2003) but abruptly in the logged treatment

179   (Lustenhouwer et al. 2012). Average daily soil and air temperatures in the logged and girdled

180   treatments are 2 – 4 °C warmer in summer and cooler in winter relative to the hemlock control

181   plots, and both diurnal and seasonal variances in temperatures are highest in the logged treatment

182   (Lustenhouwer et al. 2012). Decline and loss of eastern hemlock in the logged and girdled

183   treatments at HF-HeRE also have led to reductions in overstory densities and basal area

184   comparable to those seen in sites long infested by the adelgid (Orwig and Foster 1998; Orwig et

185   al. 2002) or that have been salvage-logged (Kizlinski et al. 2002).

186

187   **Composition of the seed rain**

188   To characterize the composition of the seed rain, seeds were manually removed from

189   litter collected in five litterfall baskets that were placed at random coordinates throughout each

190   90✕ 90 m plot. Baskets (40.6 cm long ✕ 33 cm wide ✕ 25.4 cm deep) were constructed of

191   Sterilite® plastic with vent and drainage holes, and lined with no-see-um cloth (0.25 mm mesh)

192   that was fastened to the edges with clips and suspended slightly above the bottom of the basket

193   to keep the litter dry. Replicate baskets were placed in the field at the beginning of September

194   2005, and material was collected quarterly in early April, mid-June, mid-October, and early

195   December of each year. Samples were air-dried and seeds separated. Seeds were identified to

196   species (when possible; to genus when not) using dichotomous keys in Montgomery (1977);

197   vouchers are stored in the Harvard Forest Herbarium. Representative individual seeds of each

198   species were weighed, and numbers of seeds in each sample were determined from the mass of

199   total samples (Greene and Johnson 1994).

200

Composition of the seed bank

202   In June 2004, we marked five randomly-chosen points in the center 30 ✕ 30 m subplot of

203   each of the experimental treatment plots (to avoid edge effects), and collected a single 60 cm ✕

204   60 cm ✕ 20 cm-deep soil monolith at each point (Sullivan and Ellison 2006). In May 2010, we

205   returned to the same points, chose a new sample location within 2 m of the original location, and

206   collected a single 15 cm ✕ 15 cm ✕ 20 cm-deep soil core at each point. In both years, we

207   returned the soil cores within five hours to the lab for planting. In both 2004 and 2010, all cores

208   were trimmed to 10 cm ✕ 10 cm ✕ 20 cm-deep blocks, and then sliced into 2-cm depth

209   increments. These samples were placed into separate 7.5 ✕ 7.5 cm cells in a divided potting tray,

210   each cell first lined with a 1 cm deep layer of milled sphagnum to facilitate drainage. One

211   replicate reference cell for each of the cores was filled entirely with milled sphagnum and

212   monitored for recruitment of "weedy" species present in the greenhouse seed rain. All trays

213   were placed in the Harvard Forest greenhouse at full light, watered twice daily, and fertilized

214   once during each growing season with 1.7 g/L of 20:20:20 fertilizer (J. R. Peters, Inc.,

215   Allentown, Pennsylvania, USA). Trays were randomly repositioned twice during each growing

216   season.

217   Seed bank composition was assessed using the direct germination method, without prior

218   sieving. Opinions differ in the literature about the relative merits of direct germination versus

219   seed extraction by suspension and filtering of seeds in water for characterizing the seed bank.

220   Studies comparing these methods have indicated that seed extraction can be ineffective for

221   detecting small-seeded species and overestimates the viable seed bank because it does not

222   distinguish non-viable seeds (Price et al. 2010). With the caveat that the direct germination

223   approach also can discriminate against seeds not adapted for greenhouse conditions, we selected

224   this method as a more reliable estimator of seeds available for regeneration in the field treatment

225   plots. Trays were monitored on a weekly to biweekly basis from June to September in both 2004

226   and 2010; after September, no new germination occurred and existing seedlings were senescing.

227   Most newly-emerging seedlings were removed to prevent competition with later-emerging

228   plants, except where removal would disturb existing, as-yet-unidentified seedlings. Unidentified

229   specimens were out-planted to larger pots in September of year 1 (2004 or 2010) to ensure that

230   root-binding would not cause death or affect their growth in year 2 (2005 or 2011). Specimens

231   still unidentified at the end of the first growing season were hardened off and watered bi-weekly

232   from November to April, during which time greenhouse temperatures were kept at 4 $^{\circ}$C.

233   Surviving seedlings were monitored throughout the second growing season (i.e., summers 2005

234   and 2011) until reproduction occurred or until plants were mature enough to identify

235   unambiguously. Haines (2011) was used for identifications and nomenclature, and Jenkins et al.

236   (2008) provided confirmation on species presence at Harvard Forest. Vouchers are stored in the

237   Harvard Forest Herbarium.

238

239   **Composition of the standing vegetation**

240   In 2003, two 30 m transects were established, running through the center 30 m $\times$ 30 m of

241   each plot, for the purposes of sampling the forest-floor vegetation. Five 1 m^2 subplots were

242   spaced evenly along each transect. Transects were permanently marked with stakes, and

243   subplots were marked at the northwest corner with flags. Percent covers of herbaceous species,

244   shrubs, and tree seedlings (< 1.3 m tall) were estimated, and numbers of tree seedlings were

245   counted in each subplot in July of each year. Saplings, defined as trees > 1.3 m tall but with

246   DBH < 5 cm, were identified to species, and all saplings in the 30 m ✖ 30 m central plot were

247   counted in 2004, 2007 and 2009. Canopy trees (minimum size: 5 cm DBH) in the entire 90 ✖ 90

248   m plot were identified, mapped, and labeled with numbered aluminum tags. Size (DBH) and

249   status (living/dead) was recorded in 2004 and 2009. Additional observations of plants within 3

250   m of the seed-bank core locations were made in May and August 2010. These species

251   occurrences were added to our list of taxa present in each treatment (Table 1), but were not used

252   for calculating relative abundances.

253

254   **Statistical analyses**

255   Data from all subsamples taken within an individual 90×90 m treatment plot – i.e.,

256   individual depth strata within seed bank cores, individual vegetation subplots, or individual litter

257   baskets – were pooled (normally averaged; summed in the case of seed rain) to yield a single

258   value for each variable for each plot. This pooling avoids pseudoreplication and inflation of

259   degrees of freedom and probability of Type I statistical errors (Gotelli and Ellison 2012). Except

260   in the multivariate analysis described at the end of this section, seed rain data were pooled for the

261   five years (2005-2009).

262   To standardize data across regeneration inputs (Fig. 1), we calculated the relative

263   abundances of each species in the seed bank, seed rain, and herbaceous and sapling layers as the

264   sum of all occurrences within each input – percent covers, numbers of seeds, or numbers of

265   germinating recruits – divided by the total number of all occurrences. Because the majority of

266   species were very rare (< 1% relative abundance), relative abundances were computed only for

267   the 14 most frequent genera observed in the combination of seed bank, seed rain, and field plots

268   (*Acer, Betula, Pinus, Prunus, Quercus, Tsuga, Mitchella, Rubus, Viburnum, Aralia, Lysimachia,*

269   *Maianthemum, Carex*, and *Juncus*; see Results). Although monilophytes and lycophytes

270   comprised a significant portion of the regenerating flora, they were largely undetected in the seed

271   bank (except for one species, *Dennstaedtia puncilobula*, that could not be ruled out as a weedy

272   greenhouse recruit), and thus were excluded from the analysis. When multiple species were

273   recorded in a given genus (i.e., *Betula*, *Rubus*, *Carex*, *Juncus*, *Aralia*, and *Viburnum*), species

274   were summed within that genus because they were very similar in physiognomy, successional

275   status, and shade-tolerance (with a possible exception of *Aralia hispida* and *A. nudicaulis*).

276   Initial analyses of block and treatment effects on germination were done using linear

277   mixed models, in which block was considered a random effect and treatment a fixed effect; F-

278   ratios for treatment effects were adjusted for the block term (Gotelli and Ellison 2012: 304).

279   Comparisons of total numbers of seeds germinating in the three treatments were done using a

280   Chi-square test. Kolmogorov-Smirnov tests were used to compare shapes of relative abundance

281   distributions among the three canopy-manipulation treatments. Kendall's coefficient of

282   concordance was used to determine whether the rank-abundance distributions of species in the

283   seed rain differed among the three canopy-manipulation treatments. Pair-wise Chao-Sørensen

284   abundance-based similarities (Chao et al. 2006) were computed among all possible pairings of

285   species compositions of the seed bank, seed rain, herbs, and saplings. The two abundances of

286   any pairwise comparison were considered significantly dissimilar if the bootstrapped 95%

287   confidence interval on the similarity index did not include 1.0.

288   In addition to exploring and analyzing the responses of individual species, we assessed

289   community-level responses using ordination and permutational multivariate analysis of variance

290   (PERMANOVA; Anderson 2001). We first computed a Bray-Curtis dissimilarity matrix from

291   the data consisting of the relative abundance of the 14 most abundant genera in the seed bank,

292   seed rain, herbaceous layer, and saplings from each treatment plot. We then modeled changes in

293   the dissimilarity as a function of regeneration component and canopy treatment (both of which

294   entered as fixed factors) and the continuous covariate was the time since treatment. The block

295   effect entered the PERMANOVA model as a "stratum" that constrained the permutations.

296   Significance tests were based on F-tests from sequential sums-of-squares from 1,000

297   permutations of the raw data.

298   Linear modeling was done with the lme function in the nlme library of the R statistical

299   software, version 2.12.2 (R Development Core Team 2007). Chi-square tests were done with the

300   chisq.test function in R's stats library, Kolmogorov-Smirnov tests that adjust for ties were done

301   using the ks.boot function in R's Matching library, and concordance of ranked abundances of

302   seed rain data among treatments was computed with the kendall function in R's irr library.

303   Computations of Chao-Sørensen similarities and bootstrapped confidence intervals were done

304   using EstimateS version 8.20 (Colwell 2006). Ordinations and PERMANOVA were done,

305   respectively, using the cca and adonis functions in R's vegan library. For clarity of presentation,

306   only means of the two replicate plots of each treatment are plotted for 2004 and 2010 seed-bank

307   and forest vegetation data and for the seed-rain data; within-treatment standard deviations are

308   included only for time series of herbaceous layer relative abundances. All raw data are available

309   from the Harvard Forest Data Archive (http://harvardforest.fas.harvard.edu/data/archive.html),

310   datasets HF-105 (seed-bank and seed-rain data), HF-106 (vegetation including herbs, shrubs, and

311   trees), and HF-126 (canopy tree data).

312

313   **Results**

314   **Composition of the seed rain**

315   Seed rain composition from 2005-2009 was similar among all three treatments (compare

316   graphs at the top of Figs. 2–4; inset of Fig. 5). Although rank abundances shifted among a few of

317   the rarer species among the treatments (Kendall's $W = 0.848$, d.f. = 5, $p = 0.026$), there were no

318   significant pair-wise differences in the shapes of the relative abundance distributions between

319   treatments (2-sample Kolmogorov-Smirnov test: hemlock control vs. girdled, $D = 0.17$, $p = 1$;

320   hemlock control versus logged, $D = 0.33$, $p = 0.93$; girdled vs. logged, $D = 0.33$, $p = 0.93$), and

321   Chao-Sørenson indices ranged from 0.99 – 1.00. The seed rain consisted primarily of *Betula*

322   species (particularly *B. lenta*, relative abundance range 0.71 – 0.91), with much smaller

323   proportions (0.04 – 0.09) of *T. canadensis* (top graphs in Figs. 2 – 4; inset of Fig. 5). *Pinus*

324   *strobus, Q. rubra*, and *A. rubrum* also appeared in multiple seed rain samples, but at very low

325   relative abundances: 0.02 – 0.06, 0.002 – 0.01, and 0.01 – 0.03 respectively. Spikes in seed

326   production by *B. lenta*, reflected in absolute increases in seeds per quarter, occurred in 2006 and

327   2009, coinciding with more modest spikes in the same years by *T. canadensis* (data not shown).

328   The other, much rarer taxa found in the seed rain were: *Swida alternifolia* (L.f.) Small*, Fraxinus*

329   *americana* L., *Nyssa sylvatica* Marsh., *Ostrya virginiana* (P.Mill.) K. Koch, *Polygonatum*

330   *biflorum* (Walter) Elliott, *Rhus hirta* (L.) Sudworth, *Carex* sp., and *Vaccinium* sp.

331   Considering the common canopy tree species in our top 14 taxa, the similarity of the

332   relative abundances of canopy species (2006-2009) to the relative abundances of species in the

333   seed rain over the same period ranged from 0.998 – 1, so the relative abundance of seeds in the

334   seed rain could be considered to be a reasonable proxy for the composition of species in the

335   canopy (see also Table 1). *Quercus alba* and *Q. bicolor* were rare members of the canopy that

336   were not found in the seed rain, seed bank, or forest-floor vegetation. *Fraxinus americana*,

337   *Nyssa sylvatica*, and *Ostrya virginiana* were present in the seed rain (Table 1), but *N. sylvatica*

338   was never found in any of the treatment plots.

339

340   **Composition of the seed bank**

341   Thirty-seven taxa germinated in the seed trays during 2010, of which two immature

342   plants (*Gaultheria* cf. *hispidula* (L.) Muhl. *ex* Bigelow and *Carex* cf. *ovales*) could only be

343   identified definitively to genus (Fig. 6). Although the total species richness of the seed bank in

344   2010 (37 taxa) was greater than the 30 taxa recorded in 2004, the average per-treatment species

345   richness (24 in the hemlock controls, 21 in the girdled treatment; and 23 in the logged treatment)

346   was nearly identical to those estimated by rarefaction for the pre-treatment control plots (24

347   species) in 2004. Species richness of germinants did not differ significantly among the three

348   treatments in 2010 ($\chi^2 = 0.2$, d.f. $= 2$, $p = 0.9$).

349   A total of 529 seedlings emerged in the seed-bank trays in 2010; a linear mixed-effects

350   model on log-transformed total germinants (+1) yielded a significant effect of block (F $= 5.01$,

351   d.f. $= 1, 56$, $p = 0.03$) but no effect of treatment (F $= 2.01$, d.f. $= 2, 56$, $p = 0.14$). Germination

352   totals were similar between 2010 and 2004 ($\chi^2 = 6.0$, d.f. $= 2$, $p = 0.19$), with 195 seedlings in the

353   girdled treatment (vs. 162 in 2004), 143 in logged treatment (vs. 147), and 191 in the hemlock

354   control treatment (vs. 138). For the most common 14 genera identified among all of the

355   regeneration input groups, the rank-abundance distributions did not differ significantly between

356   2004 and 2010 in any of the treatments (hemlock controls, $D = 0.21$, $p = 0.69$; girdled treatment,

357    $D = 0.21$, $p = 0.58$; logged treatment, $D = 0.21$, $p = 0.68$). When we compared the composition

358   of the seed bank in 2004 to the composition of the seed bank in 2010 in the control and each of

359   the two canopy manipulation treatments, the seed banks of 2004 and 2010 were most similar in

360   the hemlock control and least similar in the logged treatment (Table 2).

361   Seventeen species were observed in the seed bank in both 2004 and 2010. Of these, 13

362   were comparatively common and abundant throughout all the samples (Fig. 6). Nine "new"

363   species appeared in the 2010 control samples, 8 in the samples from girdled treatment, and 14 in

364   samples from the logged treatment (Table 1). These recent arrivals in the seed bank were

365   infrequent germinants that were also rarely documented from the standing vegetation, with the

366   exceptions of *Phytolacca americana* (detected in one of the two girdled plots), *Rubus*

367   *occidentialis* (in all treatments), and *Viburnum nudum* var. *cassinoides* (in the logged and control

368   treatments).

369   To test our hypothesis that shallow seed bank layers would contribute more substantially

370   to standing vegetation than the deeper layers, we next compared the numbers and types of

371   germinants emerging from the upper 0-10 cm strata (roughly corresponding to the O+A

372   horizons) of each core with those emerging in the lower, 10-20 cm deep stratum (roughly

373   corresponding to the B horizon; Fig. 6). The majority (57%) of the dominant taxa were present

374   in both strata, including *B. lenta*, *Rubus* spp., *Lysimachia quadrifolia* L., *Carex pensylvanica*

375   Lam., and *Juncus tenuis* Willd. However, several other forb and graminoid taxa emerged only

376   from the 10-20 cm layer (Fig. 6), likely reflecting the agricultural past of these ± 70-year-old

377   hemlock stands (Kernan 1980; Bettmann-Kerson 2007). Similar species had germinated from

378   the seed bank in 2004 (Sullivan and Ellison 2006); however, none of these taxa was observed in

379   the standing vegetation of the treatment plots between 2004 and 2010 (Table 1). We also

380   detected no significant differences in the rank-abundance distributions of the most common 14

381   genera between the upper and lower strata (hemlock control, $D = 0.21$, $p = 0.69$; girdled

382   treatment, $D = 0.14$, $p = 0.94$; logged treatment, $D = 0.14$, $p = 0.91$), and Chao-Sørenson

383   similarities ranged from 0.652 ($\pm$ 0.300, S.D.) to 0.965 ($\pm$ 0.057), so we concluded that the upper

384   horizons captured the most important species also found in the lower layer. We thus used data

385   on species composition from the upper stratum in subsequent analyses of relative abundance.

386   Examining the rank abundances of the top 14 genera germinating from the upper horizons, we

387   found no significant differences in the rank-abundance distribution between 2004 and 2010

388   (hemlock controls, $D = 0.43$; $p = 0.42$; girdled treatment, $D = 0.50$, $p = 0.36$; logged treatment, D

389     $= 0.38$, $p = 0.48$). As with the full taxon pool, a linear mixed-effects model yielded a significant

390   effect of block (F $= 7.6$, d.f. $= 1, 56$, $p = 0.008$) but no effect of treatment (F $= 2.8$, d.f $= 2, 56$, p

391     $= 0.064$) on total germinants in the upper layer.

392

393   **Composition of the standing vegetation**

394   The hemlock control treatment contained the fewest overall numbers of forest-floor

395   species (21 recorded over the six-year period), approximately half the species found in the

396   girdled treatment (50) and the logged treatment (42) (Table 1). The three treatments did,

397   however, share some species, including *Acer rubrum* seedlings, *Mitchella repens, Betula*

398   *papyrifera, Quercus rubra*, *Lysimachia borealis, Monotropa uniflora*, and several monilophyte

399   species (Table 1). The girdled treatment was most similar in species composition to the logged

400   treatment (Chao-Sørenson Index of similarity on species presence-absence S $= 0.696$), and least

401   similar to the hemlock control treatment (S $= 0.413$); the logged and control treatments shared

402   just under half of the species present (S $= 0.438$).

403

404   **Changes in vegetation composition from 2004 to 2010**

405   Star plots and time-series graphs of the relative abundances of the 14 common taxa in the

406   seed bank, seed rain, herbaceous layer, and sapling cohort illustrate the shifts in forest

407   composition occurring in the control and two canopy manipulation treatments (Figs. 2 – 4).

408   In the intact hemlock stands (Fig. 3), the forest-floor vegetation remained stable through

409   time, and was very similar in 2004 and 2010 (Table 2). *Acer rubrum* predominated, along with

410   slightly increasing proportions of *P. strobus* and occasional seedlings of *T. canadensis* and *Q.*

411   *rubra*. A few *T. canadensis* saplings were observed in 2004 and 2010; no other species were

412   present as saplings (Fig. 3). The vegetation in the control hemlock treatment in 2010 reflected a

413   moderate influence of the seed rain (similarity = 0.43; Table 2), which contained *T. canadensis*

414   seeds (produced by the canopy), as well as *P. strobus*, *A. rubrum*, and *Q. rubra.* Although a

415   large proportion of wind-dispersed *Betula* seeds were present in the seed rain (Fig. 2), the

416   majority joined the seed bank but did not emerge as seedlings in the heavily shaded understory.

417   The seed bank showed little similarity with the understory vegetation (similarity = 0.07; Fig. 2,

418   Table 2); light-demanding genera such as *Carex* and *Rubus*, though present in the seed bank,

419   never appeared under the dense *T. canadensis* canopy in the control treatment.

420   In the girdling treatment, the pre-treatment 2004 understory was composed of *T.*

421   *canadensis* seedlings, *P. strobus*, a lesser proportion of *A. rubrum*, and a small amount of *Q.*

422   *rubra* and *Mitchella repens* L. (Fig. 3). A few *Betula* saplings were also present in 2004 (Fig. 3);

423   the 49 *T. canadensis* saplings initially present in the two treatment plots were killed by girdling.

424   Although the composition of the seed rain recorded in the girdling treatment was very similar to

425   that of the hemlock control (compare Figs. 2 and 3), the proportion of *T. canadensis* seed

426   declined as the canopy trees gradually died. As in the hemlock control, the seed bank in the

427   girdled treatment bore little resemblance to the forest-floor vegetation in 2004 (Fig. 3), and also

428   reflected minimal influence of the seed rain, except for the preponderance of *Betula*. By 2010,

429   however, the seed bank may have contributed to the emergence of a small proportion of *Rubus*

430   species, and was much more similar to the forest-floor composition overall (similarity = 0.75;

431   Table 2, Fig. 3). As the canopy gradually opened, *B. lenta* seedlings became more prominent in

432   the regenerating vegetation as they germinated from the seed bank, joining *P. strobus*, *A.*

433   *rubrum*, and *T. canadensis* seedlings produced by the dying canopy trees. *Betula lenta*

434   comprised the majority of the sapling layer, with a small proportion of *Prunus* spp. recruiting

435   (Fig. 3).

436   The logged treatment showed a dramatic increase in vegetation between 2004 and 2010,

437   reflecting the sudden and nearly complete opening of the canopy (Fig. 4). Recruitment of new

438   species commenced in 2006, one year after the two plots in this treatment had been logged, and

439   accelerated in 2007. Before logging, the understory had comprised the same species as the other

440   two treatment types, dominated by *T. canadensis*, with lesser proportions of *P. strobus*, *A.*

441   *rubrum*, and *Q. rubra*. Seed rain over time, disproportionately dominated by *Betula*, was similar

442   to that observed in the hemlock and girdled treatments, with the exception of a small amount of

443   *Carex* spp. seed arriving in 2007, possibly transported by birds or wind. By 2010, the forest-

444   floor vegetation bore little resemblance to its former 2004 composition (similarity = 0.20; Table

445   2, Fig. 4). The relative abundance distribution of the seed bank became increasingly even from

446   2004 to 2010, and more similar to the regenerating vegetation, as *Rubus*, *Carex*, *Aralia*, and

447   *Lysimachia* became more prevalent over time (Fig. 4). Although *Prunus serotina* Ehrh. var.

448   *serotina* and *T. canadensis* were the only sapling species found in the logged treatment in 2004

449   (Fig. 4), and these persisted after logging, they were quickly joined by an influx of *B. lenta*

450   saplings and some *A. rubrum*. Thus, the 2010 sapling layer was highly dissimilar to the 2004

451   sapling profile (similarity = 0.03; Table 2, Fig. 4). Overall, recruitment of new species,

452   especially forbs and graminoids, took place much more rapidly in the logged treatment than in

453   the girdled treatment.

454

455   **Multivariate analyses**

456   Canonical correspondence analysis (Fig. 5) revealed similar patterns to those observed in

457   Figs. 2 – 4. After 6 years, the seed bank of the girdled and logged treatments showed increased

458   dominance of graminoids and forbs, but was essentially unchanged in the hemlock control

459   treatment. Similarly, vegetation trajectories in girdled and logged treatments moved towards

460   assemblages dominated by forbs, herbs, and early-successional trees. The understory vegetation

461   in the control treatment was similar in 2004 and 2010, but in the intervening years had moved

462   around ordination space because of year-to-year variability in seedling recruitment and mortality.

463   The first two axes of the ordination accounted for 43% of the variance in the data. Permutational

464   multivariate analysis of variance (with permutations constrained by blocks) of these data

465   identified significant differences through time ($p = 0.001$) among regeneration inputs ($p =$

466   0.001), canopy manipulation treatment ($p = 0.001$), and the regeneration input $\times$ canopy

467   treatment interaction ($p = 0.001$) (Table 3).

468

469   # Discussion

470   We have demonstrated here an approach that can be used to create a conceptual model

471   (Fig. 1) of the responses of a widespread temperate forest type to disturbances such as defoliation

472   irrupting insects, pathogens, or salvage logging. We have shown that reorganization of the herb,

473   shrub, and sapling layers has taken place more slowly in the girdled treatment, exhibiting the

474   gradual die-back typical of adelgid-infested stands, than in the logged treatment, where

475   conditions changed abruptly. Our findings parallel those of other long-term studies of declining

476   hemlock stands (Small et al. 2005; Eschtruth et al. 2006; Spaulding and Rieske 2010), and

477   accord with Kizlinski et al. (2002) and Orwig et al. (2008), who found that logging resulted in

478   faster and denser colonization by *B. lenta* than gradual mortality of the overstory due to the

479   adelgid. Observations from the girdled treatment will continue to provide predictions of the

480   responses of intact hemlock stands as the adelgid begins to infest them in coming years (Yorks et

481   al. 2003; Ellison et al. 2010).

482   Before the onset of treatments in 2005, all hemlock plots, regardless of block, were very

483   similar in species composition (Fig. 5). The canopy and understory both were dominated by *T.*

484   *canadensis* and most other understory species were absent or suppressed. Following treatments,

485   we asked if and how the current vegetation differed between logged and girdled stands. By

486   2010, plots in the girdled and logged treatments were broadly similar in species composition, but

487   differed in two important respects. First, because all seedlings, saplings, and mature hemlocks

488   were girdled, they slowly declined and by 2010, they comprised a negligible part of the

489   vegetation in the girdled treatment. Plots in the logged treatment gained a small number of *T.*

490   *canadensis* recruits, possibly contributed by seed rain from unharvested (< 20 cm diameter) but

491   reproductive trees or from trees just outside the treatment plots. Second, the abundance and

492   species richness of forbs and graminoids increased in the logged treatment quite rapidly,

493   beginning in earnest in 2007 (Figs. 4, 5). In contrast, the slowly declining canopy of hemlocks

494   in the girdled treatment suppressed recruitment of forbs and graminoids; even shrub recruitment

495   was comparatively low, but was accelerating as of 2010 (Figs. 3, 5).

496   Next, we explored whether the initial compositions of the seed bank, seed rain, canopy,

497   and forest-floor vegetation were similar within and among treatments, and observed whether the

498   composition of these regeneration components diverged through time or among treatments. The

499   seed bank composition in 2004 was dominated strongly by *Betula* spp., and bore little similarity

500   to the standing vegetation composition. The composition and richness of the 2010 seed bank

501   remained similar to the 2004 bank (Table 2), with some turnover in rare species and singletons

502   (species represented by only a single seedling). The 2010 seed bank continued to differ in

503   composition from the understory in the hemlock control treatment (Figs. 2, 5). Studies

504   comparing the composition of the seed bank and standing vegetation in intact forests usually find

505   little correspondence, with Sørenson similarities typically < 0.6 (reviewed by Hopfensperger

506   2007), and our data from our hemlock control treatment are no exception (Table 2, Figs. 2, 5).

507   Such disparities have been noted in previous studies of dense-canopy conifer forests dominated

508   by *T. canadensis* (Catovsky and Bazzaz 2000) or other species (e.g., Berger et al. 2004; Eycott et

509   al. 2006).

510   In the logged and girdled treatments, however, the composition of the standing vegetation

511   became more similar over time to the seed banks of 2004 (Table 2) and 2010 (Figs. 3, 4) as

512   more species were able to establish under the open canopy. As disturbances create new

513   opportunities for recruitment from the persistent seed bank, and the changing vegetation

514   contributes increasingly to the seed bank in turn, similarities between the seed bank and the

515   forest-floor vegetation increase, as we observed in the girdled and logged treatments (Figs. 3 ,4).

516   The preponderance of *B. lenta* seeds, plus the relative rarity of other taxa, led to higher similarity

517   in the seed banks of all treatments between 2004 and 2010 (Table 2) than inspection of the

518   relative abundance plots might suggest (Figs. 3, 4). Nevertheless, the dissimilarity between 2004

519   and 2010 in the seed banks of the logged treatment was greater than in either the control or

520   girdled treatments (Table 2). This finding was consonant with our predictions, and leads to the

521   further prediction that the future seed bank will continue to diverge in composition from the pre-

522   treatment seed bank. In the long term, the seed bank composition of the girdled treatment should

523   eventually come to resemble that of the logged treatment. Likewise, the more speciose standing

524   vegetation in these two treatments will comprise a greater diversity of life forms than in intact

525   hemlock stands as forbs, shrubs, and graminoids become more important. We also predicted,

526   and observed, that the upper layers of the seed bank (0-10 cm depth) contributed more

527   germinants and showed higher similarity to the regenerating vegetation than the lower depths.

528   A closed hemlock canopy suppresses regeneration from seed rain, whereas newly opened

529   forests are conducive to regeneration from seed rain, especially if a few canopy trees or maturing

530   saplings remain. We predicted, and observed, that similarity between the seed rain and the

531   standing vegetation would increase as the canopy became a less important ecological filter, with

532   the seed rain more strongly influencing the vegetation when a partial canopy remains and woody

533   debris accumulates slowly (as in the girdled treatment). Overall, seed rain remained the

534   predominant factor contributing to regeneration in the girdled treatment, whereas both the seed

535   rain and seed bank contributed recruits in the logged treatment. As the last girdled or adelgid-

536   attacked hemlocks die, it will become more important to understand the composition of both

537   seed rain and seed banks to make predictions about future forest composition. Likewise, we

538   need to better understand the sources of recruiting monilophytes that can become very common

539   in newly opened stands (Yorks et al. 2003); propagules of these species were generally

540   undetected in the seed rain or seed bank.

541   Because we used consistent methods to measure the compositions of the seed bank, seed

542   rain, and standing vegetation among years, our data on these different inputs could be tracked

543   and compared through time to inform a general model of forest regeneration (Fig. 1). We

544   caution that integrated studies such as this one are challenging to undertake and to interpret. The

545   timing and frequency of monitoring of different vegetation pools in the Harvard Forest Hemlock

546   Removal Experiment differed somewhat; for example, seed-rain monitoring did not commence

547   until after treatments were imposed, whereas before-and-after data were available for both the

548   seed bank and the standing vegetation. Standing vegetation was censused annually, but seed

549   bank composition was assessed at a six-year interval – insufficiently frequent to permit

550   development of a path analysis linking inputs and outputs (cf. Caballero et al. 2008). Finally,

551   sampling took place at different spatial scales within treatment plots, from randomly-located

552   small soil cores for seed banks and litter baskets for seed rain, to transects of 1 × 1 m subplots for

553   seedlings and herbaceous vegetation and larger 30 × 30-m subplots for sapling counts. However,

554   these sampling methods were appropriate for yielding accurate estimates of relative abundances

555   and species composition of each vegetation component. Ideally, integrated long-term studies

556   should be tightly coordinated in time and space to permit more rigorous quantitative comparisons

557   and development of path models. Such coordination also will allow for species responses to be

558   more mechanistically related to broader ecosystem responses (Yorks et al. 2003).

559

564   sorting seeds from litterfall samples. David Foster, David Orwig, two anonymous reviewers, and

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566

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687   water chemistry and understory vegetation: possible consequences of an invasive insect

688   herbivore. Can. J. For. Res. **33**(8): 1525–1537.

689

690

691 **Table 1**. Species found in the seed rain (R), seed bank (B), understory vegetation (V), and

692 canopy (C) samples (excluding intermediate and suppressed trees in the canopy) within each of

693 the three canopy manipulation treatments from 2005-2010. Asterisks indicate species that were

694 detected in the 2004 seed bank samples (Sullivan and Ellison 2006), but not in the 2010 seed

695 bank samples.

Species	Canopy treatment		
	Hemlock control	Hemlocks girdled	Hemlocks logged
Trees (including seedlings, saplings, and canopy)			
Acer rubrum L.	R,V,C	R,V,C	R, V,C
Betula alleghaniensis Britt.*	C	V	
Betula lenta L.	R,B,C	R,B,V,C	R,B,V,C
Betula papyrifera Marsh.	B,V	B,V,C	V
Carya sp. Nutt.	V,C	V	V
Fraxinus americana L.	R,C		
Fraxinus nigra Marsh.		C	
Nyssa sylvatica Marsh.	R		
Ostrya virginiana (P. Mill.) K. Koch			R
Pinus strobus L.	R,V,C	R,V,C	R,B,V,C
Populus grandidentata Michx.			B
Prunus pensylvanica L. f. var. *pensylvanica*		V	V
Prunus serotina Ehrh. var. *serotina*	V,C	V	V
Quercus alba L.	C	V,C	V,C
Quercus bicolor Willd.		C	
Quercus rubra L.	V,C	V,C	R,V,C
Quercus velutina Lam.			V
Tsuga canadensis (L.) Carr.	R,B,V,C	R,V,C	R,V,C
Shrubs			
Amelanchier sp. Medik.		V	
Berberis thunbergii DC.		V	
Celastrus orbiculatus Thunb.		V	
Comptonia peregrina (L.) Coult.		B	V
Corylus cornuta Marsh. ssp. *cornuta*		V	
Crataegus sp. L.		V	V
Diervilla lonicera P. Mill.			V
Gaultheria cf. *hispidula* (L.) Muhl. *ex* Bigelow		B	B
Gaultheria procumbens L.*		V	V

Species	Canopy treatment		
	Hemlock control	Hemlocks girdled	Hemlocks logged
Ilex mucronata (L.) M. Powell, Savol. & S. Andrews			V
Ilex verticillata (L.) Gray		V	V
Mitchella repens L.	V	V	B,V
Myrica gale L.			V
Rhododendron periclymenoides (Michx.) Shinners		V	
Rhus copallinum L. var. *latifolia* Engl.		V	V
Rhus hirta (L.) Sudworth	R		
Rubus allegheniensis Porter	B	V	B,V
Rubus flagellaris Willd.	B	B,V	B,V
Rubus hispidus L.	B	B,V	B,V
Rubus idaeus L. ssp. *ideaus*		V	V
Rubus occidentalis L.	B	B,V	B,V
Sambucus racemosa L.		V	V
Sassafras albidum (Nutt.) Nees			V
Sorbus americana Marsh.		V	
Swida alternifolia (L. f.) Small	R	R	
Vaccinium angustifolium Ait.*		V	R,V
Vaccinium corymbosum L.			V
Viburnum nudum L. var. *cassinoides* (Torr.) A. Gray	B	V	B
Vitis sp. L.		V	V
Forbs			
Aralia hispida Vent.		V	B,V
Aralia nudicaulis L.	V		
Chimaphila maculata (L.) Pursh		V	
Coptis trifolia (L.) Salisb.		V	
Epigaea repens L.		V	
Erichtites hieraciifolius (L.) Raf. *ex* DC. (*s.l.*)		V	V
Eurybia cf. *divaricata*	B	B	B
Euthamia graminifolia (L.) Nutt.			B
Goodyera tesselata Lodd.		V	
Hypopitys monotropa Crantz	V	V	
Lobelia inflata L.	B		
Lysimachia borealis (Raf.) U Manns & A. Anderb.	V	V	V
Lysimachia quadrifolia L.		B,V	B,V
Maianthemum canadense Desf.	B,V		
Medeola virginiana L.	V	V	
Mollugo verticillata L.		B	B
Monotropa uniflora L.	V	V	V

	Canopy treatment		
Species	**Hemlock control**	**Hemlocks girdled**	**Hemlocks logged**
Phytolacca americana L. var. *americana*		B,V	
Polygonatum biflorum (Walter) Elliott	R		
Pyrola sp. L.		V	
Solidago sp. L.		V	
Taraxacum officinale G. H. Weber *ex* Wiggers			B
Trifolium repens L.			B
Trillium erectum L.	V		
Viola labradorica Schrank	B		
Viola sororia Willd. var. *novae angliae* Duchesne	B	B	B
Graminoids			
Agrostis hyemalis (Walt.) B. S. P.	B		
Brachyeletrum erectum (Schreb.) Beauv.			V
Carex cf. *ovales* group	B	B	R,B,V
Carex debilis Michx. var. *rudgei* Bailey	B	B	
Carex deweyana Schweinitz		B	
Carex laxiflora L.	B		B
Carex pensylvanica Lam.	B	B,V	B,V
Dichanthelium acuminatum (Sw. Gould) C. A. Clark var. *fasciculatum* (Torr.) Freckmann	B		B
Dichanthelium clandestinum (L.) Gould	B		
Digitaria ischaemum (Schreb) Schreb ex Muhl.	B	B	B
Juncus brevicaudatus (Engelm). Fern	B		
Juncus tenuis Willd	B	B	B
Scirpus cyperinus (L.) Kunth		B	
Monilophytes and Lycophytes			
Dendroycopodium obscurum (L.) A. Haines	V	V	V
Dennstaedtia punctilobula (Michx.) T. Moore	V	V	V
Dryopteris carthusiana (Vill.) H.P. Fuchs	V	V	V
Dryopteris intermedia (Muhl. *ex* Willd.) Gray		V	V
Huperzia lucidula (Michx.) Trevisan	V		
Osmundastrum cinnamomeum (L.) C. Presl	V	V	
Polypodium virginianum L.	V		
Polystichum acrostichoides (Michx.) Schott	V		

696
697

698 **Table 2.** Pair-wise similarities of seed bank composition (upper 10 cm stratum) in 2004 and

699 2010, forest-floor vegetation and saplings in 2004 and 2010, seed rain from 2005 to 2009. Seed

700 bank and understory vegetation data were averaged across samples within treatment plots, and

701 seed rain was summed across years within treatment plots so as to avoid pseudoreplication and

702 achieve an appropriate Type I statistical error rate (Gotelli and Ellison 2012). Values are Chao-

703 Sørensen abundance-based similarities (Chao et al. 2006) for the given pair. Values in bold are

704 significantly different from 1.00; pairs were significantly dissimilar at the $\alpha = 0.05$ level based

705 on computation of bootstrapped 95% confidence intervals.

706

Hemlock control treatment			
	Seed bank 2010	**Understory 2010**	**Saplings 2010**
Seed rain 2005-2009	0.76	0.43	**0.32**
Seed bank 2004	0.94	**0.07**	**0.00**
Understory 2004	**0.42**	1.00	**0.14**
Saplings 2004	**0.13**	**0.24**	0.97
Girdled treatment			
	Seed bank 2010	**Understory 2010**	**Saplings 2010**
Seed rain 2005-2009	0.46	0.93	0.91
Seed bank 2004	0.93	0.75	0.59
Understory 2004	**0.08**	0.78	**0.00**
Saplings 2004	**0.07**	0.88	**0.07**
Logged treatment			
	Seed bank 2010	**Understory 2010**	**Saplings 2010**
Seed rain 2005-2009	0.77	0.63	0.98
Seed bank 2004	0.86	0.67	0.87
Understory 2004	**0.05**	**0.20**	**0.25**
Saplings 2004	**0.00**	**0.06**	**0.03**

707
708

709   **Table 3.** Summary table of the results of the permutational multivariate analysis of variance

710   (PERMANOVA) with permutations constrained by block. This analysis models community-

711   level responses (as a Bray-Curtis dissimilarity matrix) of the 14 most abundant genera in the seed

712   bank, seed rain, herbaceous layer, and saplings in each treatment. Regeneration component is

713   one of seed bank, seed rain, understory, or saplings; canopy manipulation is one of girdled,

714   logged, or hemlock control; year is one of {2004, 2005, 2006, 2007, 2008, 2009, 2010}; the

715   block effect constrains the permutations in the PERMANOVA by entering the model as a

716   "stratum."

717

Parameter	df	SS	MS	F (model)	r^2	P (> F)
Regeneration component	3	8.1	2.70	20.66	0.32	0.001
Canopy manipulation treatment	2	1.9	0.96	7.36	0.08	0.001
Year	1	1.6	1.60	12.22	0.06	0.001
Regeneration component × treatment	6	2.7	0.46	3.49	0.11	0.001
Residuals	83	10.9	0.13		0.43	
Total	95	25.2				

718

719

720 **Figure legends**

721 Fig. 1. Conceptual model illustrating how seed banks (including spores and other propagules),

722 seed rain (also including spores and other propagules), and advance regeneration contribute to

723 plant species abundance in a recovering forest stand over time. Middle panel shows temporal

724 trends in relative abundance of species colonizing the forest floor following canopy

725 manipulations in 2005; the different line types illustrate relative abundances of different taxa.

726 Diagonal white parallelograms on the left show inputs; shaded parallelograms on the right show

727 outcomes.

728

729 Fig. 2. Composition and relative abundances of the seed rain, seed banks in 2004 and 2010,

730 understory layers and sapling layers in 2004 and 2010, and dynamics of forest understory species

731 between 2005 and 2009 in the hemlock control treatment. Star plots depict relative abundances

732 of the 14 most common genera in 2004 and 2010; seed rain relative abundances are summed

733 over 2005 to 2009. Taxa are color-coded by genus and life form (trees in greens, shrubs in

734 oranges, forbs in blues, and graminoids in reds); see color wheel legend at upper left. For the

735 purposes of visualizing rare taxa clearly, all relative abundances were square-root-transformed

736 prior to plotting; note that this transformation disproportionately magnifies the relative

737 abundance of rare species. The scale bar at upper left indicates the length of a radius

738 corresponding to 100% composition of a given species (relative abundance = 1). Note that no

739 graminoids appeared in the understory between 2005 and 2009. Graphs in the center illustrate

740 mean relative abundances ($\pm$ 1 S.D.) of the 14 most common genera in the two replicate plots

741 within each treatment. Although all treatment plots were censused yearly at approximately the

742 same time, the mean points are shown here slightly offset to allow the points and error bars to be

743 distinguished. Taxa are grouped by life form (trees, shrubs, forbs, and graminoids), and color

744 coding is as shown in the color-wheel legend.

745

746 Fig. 3. Composition and relative abundances of the seed rain, seed banks in 2004 and 2010,

747 understory layers and sapling layers in 2004 and 2010, and dynamics of forest understory species

748 between 2005 and 2009 in the girdled treatment. Species codes, scales, and legends are as in

749 Fig. 1.

750

751 Fig. 4. Composition and relative abundances of the seed rain, seed banks in 2004 and 2010,

752 understory layers and sapling layers in 2004 and 2010, and dynamics of forest understory species

753 between 2005 and 2009 in the logged treatment. Species codes, scales, and legends are as in Fig.

754 1.

755

756 Fig. 5. Ordination bi-plot of the changes in the seed bank (▼:2004 versus 2010) and trajectories

757 of the seed rain (□), understory vegetation (▲), and saplings (●) (2004-2010; replicates pooled

758 across blocks). The different colors represent the different treatments: blue – hemlock control;

759 dark yellow – girdled treatment; red – logged treatment, and the start and end of each trajectory

760 are identified. Dotted lines indicate seed dynamics (seed rain, seed bank) and solid lines indicate

761 standing vegetation The inset plot expands the lower right corner of the main bi-plot to more

762 clearly show the trajectories of the saplings and seed rain, which otherwise overlap extensively

763 in the main bi-plot. Species whose loadings are > 0.1 are shown along the *x*- and *y*-axes.

764

765   Fig. 6. Mean numbers of germinating seedlings (± 1 S.D.) in the upper (0-10 cm depth) and

766   lower (10-20 cm depth) soil strata in the 2010 seed bank trial, pooled across all treatment types

767   and replicates. Means on left show the plants emerging from the upper 10 cm of the core; those

768   on the right show those emerging from the 10-20 cm depth. Taxa are grouped by trees (greens),

769   shrubs (oranges), forbs (blues), and graminoids (reds) and ordered within groups from most to

770   least abundant in the upper stratum. Asterisks indicate taxa that were identified in both the 2004

771   and 2010 seed banks.

772

773

774   Fig. 1
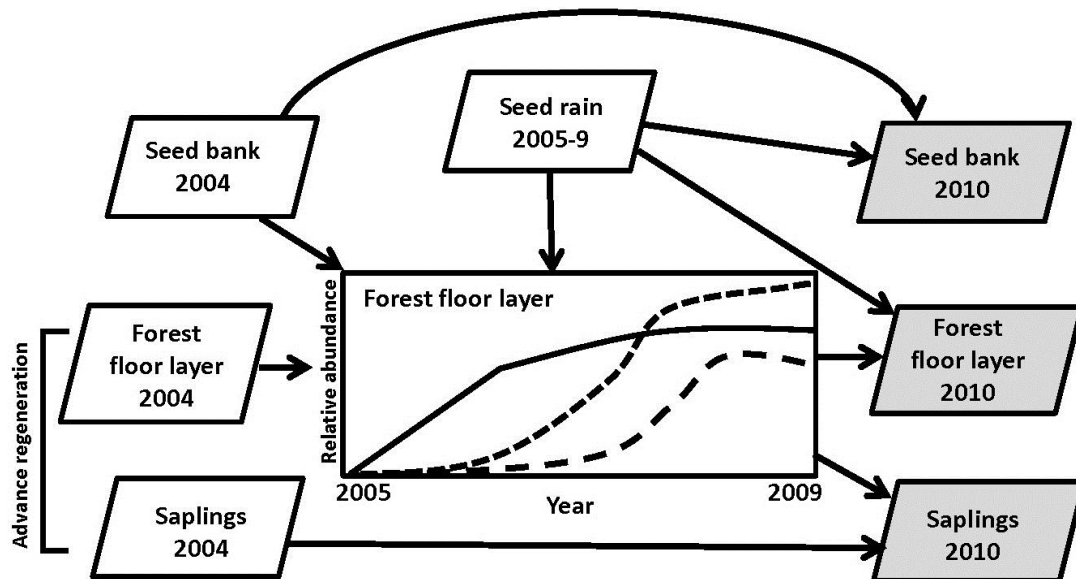
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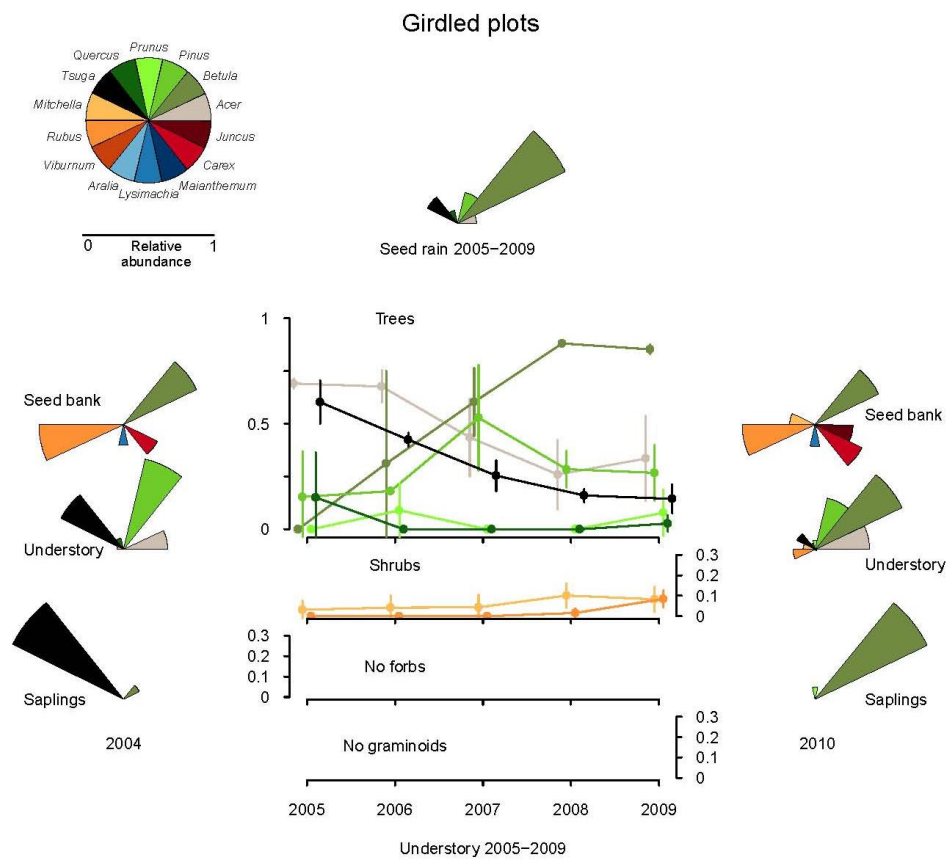779

780   Fig. 2

Hemlock control plots
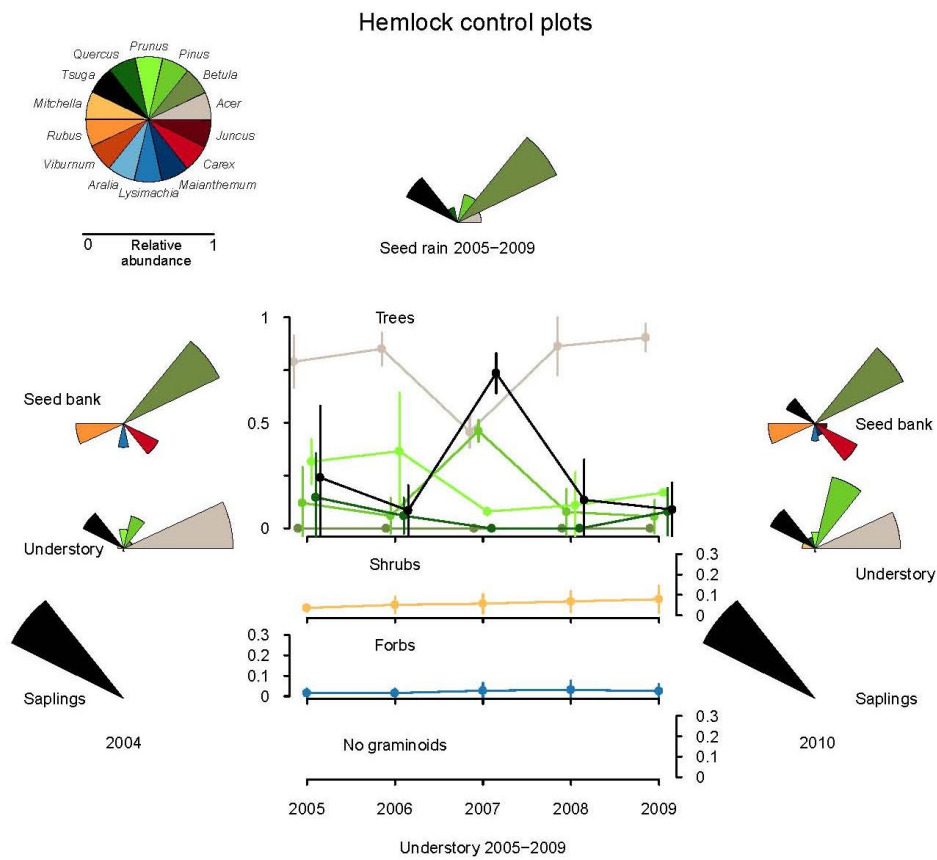
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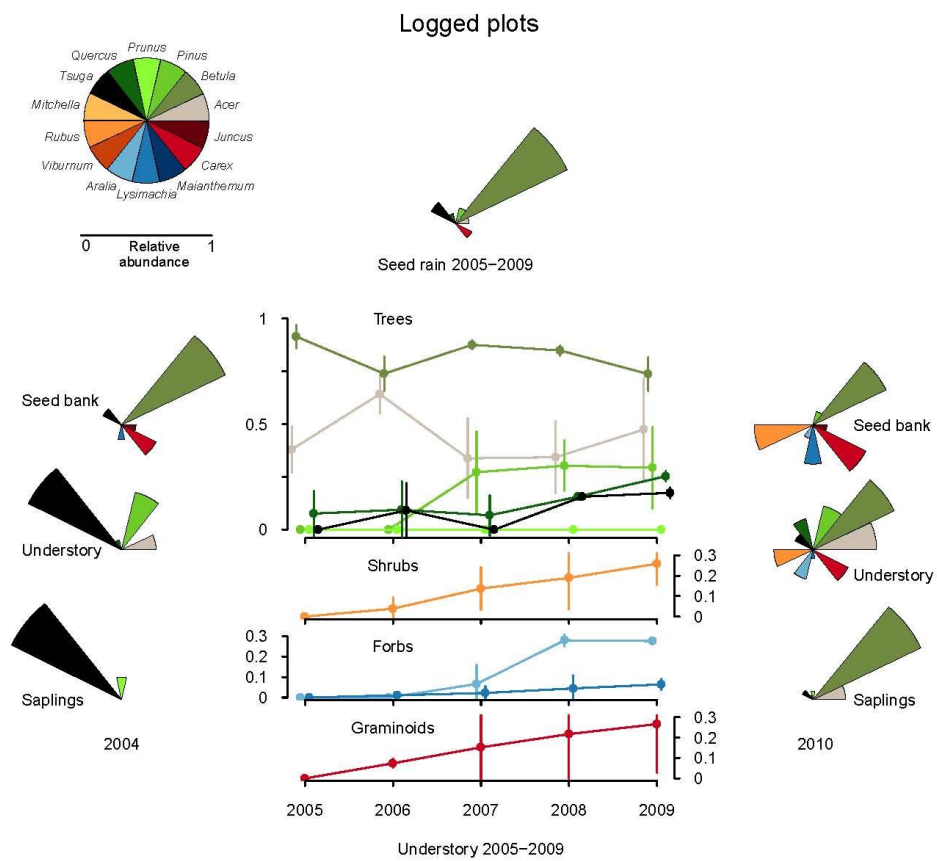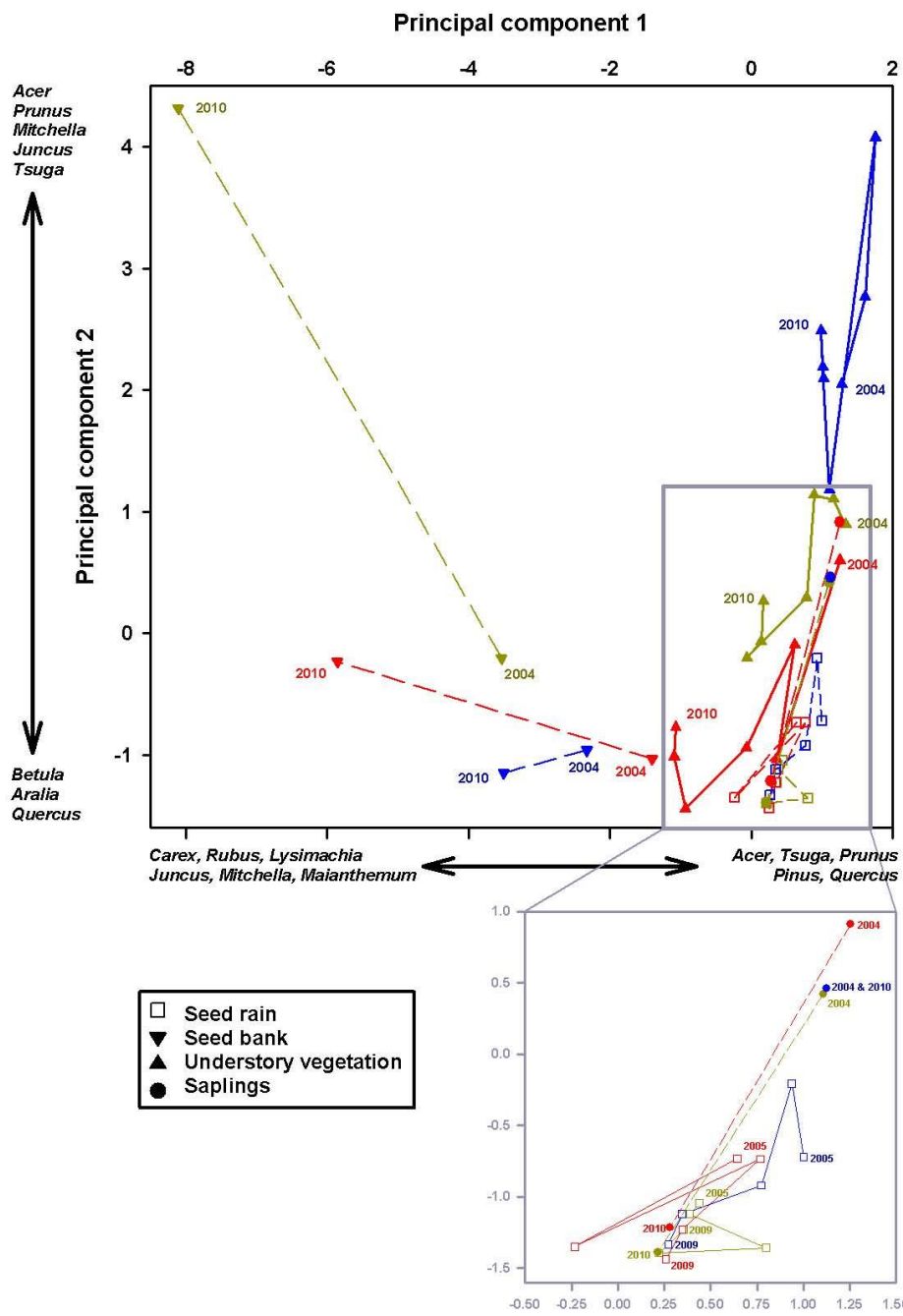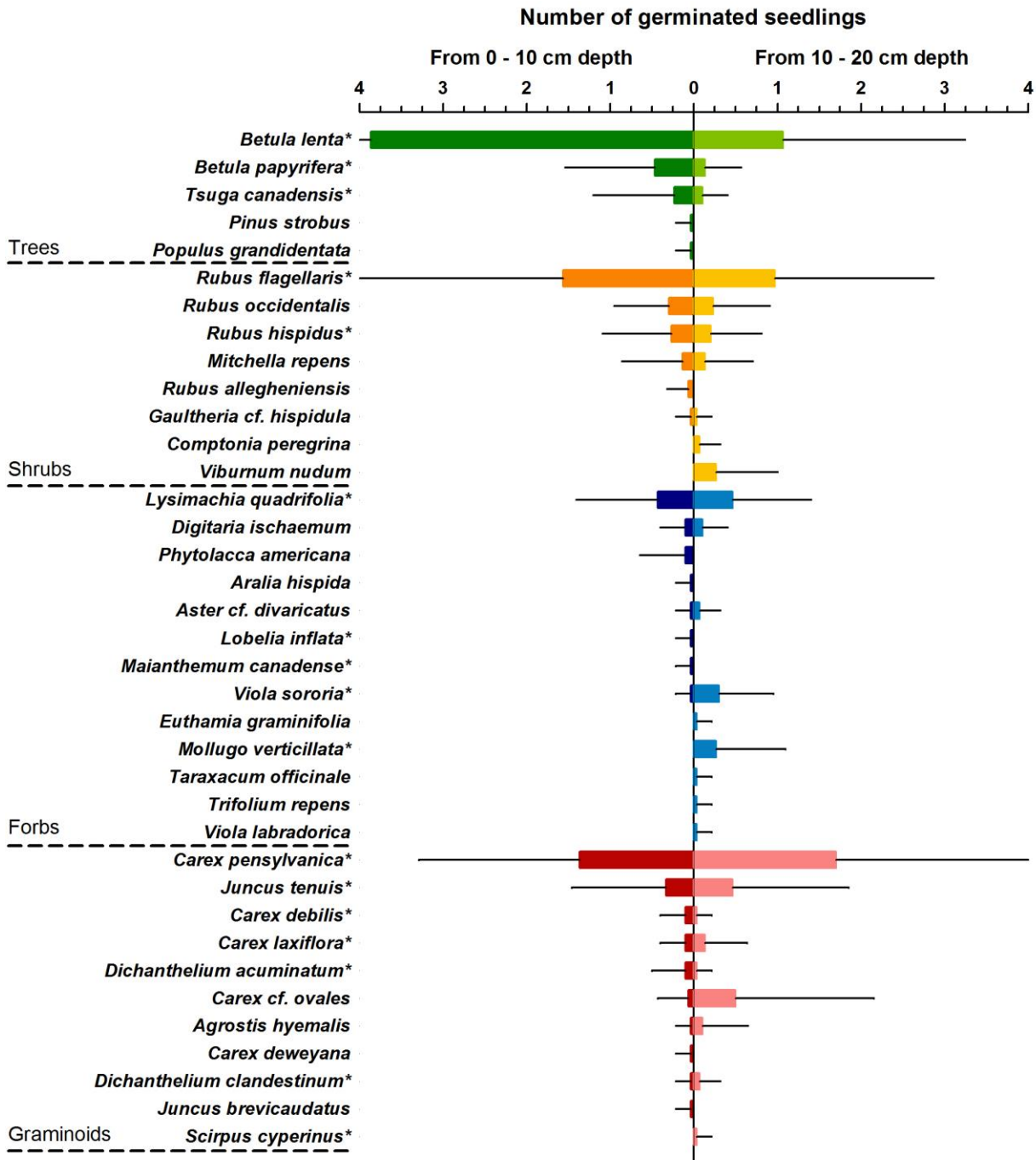785   Fig. 3

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Girdled plots

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791   Fig. 4

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795   Fig. 5

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798   Fig. 6

799

Number of germinated seedlings

800