



Plant establishment in a new habitat can be mediated by soil-related abiotic and biotic factors. Our study shows that unfavorable soil chemistry and lack of beneficial mycorrhizal fungi in boreal forests greatly diminished the potential survival and growth of sugar maple seedlings. Predicting future changes in forest composition under climate warming will require consideration of soil properties as well as the mycorrhizal status of tree species.

1 **Title**

2 Soil abiotic and biotic properties constrain the establishment of a dominant temperate tree into
3 boreal forests

4

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23 **Abstract**

24 1. Climate warming is expected to cause the poleward and upward elevational expansion of
25 temperate plant species, but non-climatic factors such as soils could constrain this range
26 expansion. However, the extent to which edaphic constraints on range expansion have an
27 abiotic (e.g., soil chemistry) or biotic (e.g., micro-organisms) origin remains undetermined.

28 2. We conducted greenhouse experiments to test if the survival and growth of a major North
29 American temperate tree species, *Acer saccharum* (sugar maple), is independently or jointly
30 constrained by abiotic and biotic properties of field-collected soils from within and beyond
31 the species' elevational range.

32 3. Abiotic factors, particularly low base cation concentrations were major constraints to
33 seedling establishment in boreal forest soils (beyond the range edge), but insufficient
34 arbuscular mycorrhizal fungal inoculum (biotic factor) also strongly reduced seedling
35 performance in these soils.

36 4. *Synthesis.* Our results suggest that forecasting future changes in forest composition under
37 climate warming requires consideration of soil properties as well as the mycorrhizal status of
38 tree species.

39

40 Second abstract (French)

41 Le réchauffement climatique devrait entraîner l'expansion des espèces tempérées vers les
42 pôles et en altitude, mais des facteurs non-climatiques pourraient limiter cette expansion. Les
43 sols en particulier pourraient potentiellement contraindre l'expansion des essences tempérées
44 dans les forêts boréales à cause de propriétés édaphiques biotiques (micro-organismes p. ex.)
45 et/ou abiotiques (propriétés chimiques p. ex.). Dans cette étude, nous avons mené des
46 expériences en serre utilisant des manipulations et traitements de sols frais récoltés sur le
47 terrain. Nous avons ainsi testé si l'établissement, dans la forêt boréale, d'une espèce d'arbre
48 dominante en forêt tempérée d'Amérique du Nord (*Acer saccharum*) est limitée par les
49 propriétés édaphiques. Nous avons évalué le rôle joué par les micro-organismes et la chimie
50 du sol sur la survie, la biomasse et la performance globale des semis. Les facteurs abiotiques

51 tels que de faibles concentrations en cations pourraient constituer des contraintes édaphiques
52 importantes à l'établissement d'*Acer saccharum* au-delà de son aire de répartition, mais aussi
53 les facteurs biotiques tel que le faible potentiel d'inoculum de champignons mycorhiziens
54 arbusculaires dans les sols boréaux. Nos résultats suggèrent que la prévision des changements
55 futurs dans la composition de la forêt sous l'effet du réchauffement climatique nécessite de
56 prendre en compte les propriétés édaphiques, ainsi que les traits souterrains des arbres tels que
57 leur stratégie mycorhizienne.

58

59 **Keywords**

60 Plant-soil interactions, sugar maple, temperate-boreal ecotone, range expansion, mycorrhizas
61

62 **Introduction**

63 Climate warming has caused many terrestrial and aquatic organisms to expand their ranges
64 poleward and upward in elevation (Parmesan, 2006; Pecl et al., 2017). If plant distributions
65 were primarily determined by climatic conditions, plant distributions should shift
66 geographically in concert with climate, but many studies show that suitable climatic
67 conditions for a given species shift much faster than species range limits (Corlett & Westcott,
68 2013; Savage & Vellend, 2015; Zhu, Woodall, & Clark, 2012). Although such lags in species
69 range expansion can be due to demographic factors such as propagule availability (Engler et
70 al., 2009), they may also indicate negative impacts of non-climatic factors (Putnam & Reich,
71 2017; Van der Veken, Rogister, Verheyen, Hermy, & Nathan, 2007). Reduction in survival,
72 growth and fecundity are often observed in plants that are transplanted beyond their range
73 limits (Hargreaves, Samis, & Eckert, 2014; Stanton-Geddes & Anderson, 2011), but the
74 underlying causes are rarely known. Further investigation – experimental studies in particular
75 – are needed to understand the underlying processes and external drivers of species range
76 limits and potential range shifts (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Sexton,
77 McIntyre, Angert, & Rice, 2009).

78

79 Plant establishment beyond current geographic range limits could be constrained due to biotic
80 and/or abiotic factors, with many such factors involving belowground soil characteristics
81 (Chapin, Walker, Fastie, & Sharman, 1994; Lafleur, Paré, Munson, & Bergeron, 2010;
82 Tomiolo & Ward, 2018). For example, beyond range edges the positive effects of soil biota
83 such as mutualists can be reduced or absent and the negative effects of generalist soil-borne
84 pathogens can be increased. Similarly, unfavourable soil chemical properties (e.g., low pH) or
85 physical structure (e.g., thicker litter layer) beyond a species' range could impede plant
86 establishment. By contrast, there are many reported cases of plant species that actually show
87 higher establishment success outside their current range. For instance, species can escape
88 their native soil-borne pathogens when establishing outside their range, as described for
89 invasive plants under the “enemy release hypothesis” (Keane & Crawley, 2002; Liu & Stiling,
90 2006). However, interactions among abiotic and biotic factors could lead to more complex
91 outcomes such as the “happy edge”, where success is highest at the edge of a species' range
92 (Urli, Brown, Perez, Chagnon, & Vellend, 2016). Abiotic and biotic factors have often been
93 treated separately in studies of range limits, but they might interact in important ways – a
94 topic largely unexplored to date (Gaston, 2009; Lau, McCall, Davies, McKay, & Wright,
95 2008; Sexton et al., 2009; but see Johnson, Miller, & Wilson, 2017).

96

97 Elevational gradients are valuable model systems to understand how abiotic and biotic factors
98 independently or jointly influence range shifts in response to climate change
99 (HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013), and they are comparable in
100 many (but not all) respects to latitudinal gradients over longer distances (Diaz, Grosjean, &
101 Graumlich, 2003; Sundqvist, Sanders, & Wardle, 2013). Strong gradients in vegetation
102 composition can occur over short spatial scales at ecotones, with the temperate-boreal ecotone
103 as a striking example (Evans & Brown, 2017). Temperate forests are usually dominated by
104 broadleaf, deciduous trees. By contrast, boreal forests are dominated by coniferous trees on
105 soils that tend to be more acidic and nutrient-poor than those of temperate forests, with
106 important impacts on plant growth (Collin, Messier, & Bélanger, 2017; Evans & Brown,

107 2017). Soil microbial communities – also important for plant performance – can also be
108 highly variable along elevational gradients and among forest types (Geml, 2017; Yang et al.,
109 2014). For example, ectomycorrhizal associations are dominant in boreal forests, but coexist
110 with arbuscular mycorrhizas in temperate forests (Phillips, Brzostek, & Midgley, 2013; Read
111 & Perez-Moreno, 2003). Therefore, even if climatic conditions in the boreal forest becomes
112 suitable for temperate plants, their establishment could nonetheless be strongly constrained
113 not only by physical substrate conditions but also the absence of mutualistic organisms such
114 as arbuscular mycorrhiza fungi (Evans & Brown, 2017). Therefore, understanding the abiotic
115 and biotic belowground processes constraining the establishment of temperate tree species
116 into boreal forests is essential to predicting the future distribution of the temperate forest with
117 increasing temperature.

118

119 Our study sought to determine the establishment success of a dominant temperate tree (*Acer*
120 *saccharum*; hereafter sugar maple) in soils sampled along an elevational gradient from the
121 temperate (core range) to the boreal (beyond) forest, and to understand the relative
122 importance of abiotic and biotic belowground factors. To do so, we conducted two
123 greenhouse experiments: one using unmanipulated soil originating from the three forest types
124 and a second involving manipulations of soil biota. Based on the hypothesis that abiotic and
125 biotic soil properties constrain upward elevational range expansion, we predicted that: (i)
126 sugar maple seedlings would show higher survival and performance in soils from within the
127 species range, (ii) these soil effects would be due both to abiotic conditions and also biotic
128 factors, both of which should be more favourable within the species range. Alternatively,
129 release from specialised soil pathogens could result in higher seedling performance at or
130 beyond the species' range edge. If seedling survival or performance varies according to
131 inoculum source on replicate samples of the same soil origin, we can infer an important role
132 of biotic factors. On the other hand, differences among sterilised samples of different soil
133 origins would be indicative of effects of abiotic factors. Soil pH, carbon, nitrogen,

134 phosphorus, cations, base saturation and root colonization by arbuscular mycorrhizal fungi
135 were measured as potential drivers of seedling survival and performance.

136

137 **Methods**

138 *Study system*

139 The study system is located in Parc national du Mont-Mégantic, a protected area of 55 km² in
140 south-eastern Québec, Canada. The study area has been described in detail elsewhere (Brown
141 & Vellend, 2014; Savage & Vellend, 2015). Mont Mégantic is part of the Monteregian Hills,
142 mainly composed of leucogranite and syenite at the surface (Feininger & Goodacre, 2003).
143 Soils are ferro-humic and humo-ferric shallow podzols with a sandy loam texture derived
144 from rocky glacial tills with talus slope at higher elevation (Marcotte & Grantner, 1974). The
145 climate in this region is characterised by warm, wet summers and cold winters with abundant
146 snowfall (SEPAQ, 2010). Elevation in the park ranges from 430 m to 1105 m above sea level
147 (asl). Average temperatures range from -10.2 °C in January to 17.3 °C in July with possible
148 daily maxima above 30°C and an annual mean of 3.9 °C at low elevations (599 m asl). At
149 high elevation (1089 m asl), average temperatures range from -12.4 °C in January to 14.9 °C
150 in July for an annual mean of 1.2 °C (data available from 2013 to 2017 for weather stations
151 IQUBECNO2 and IQUBECNO3 at www.wunderground.com/weatherstation/overview.asp).
152 With decreasing temperature, the length of the growing season is reduced from ~100 days at
153 low elevations to ~80 days at high elevations (SEPAQ, 2010).

154

155 Since 1950, the mean annual temperature in our study region of southern Québec has
156 increased by up to 2 °C and by 2050 it is predicted to further increase between by 1.7–4.6 °C
157 (Ouranos, 2015). If temperature limits the distribution of sugar maple, the species is expected
158 to migrate upward in elevation and northward in latitude (Frumhoff, McCarthy, Melillo,
159 Moser, & Wuebbles, 2007). Studies have shown that sugar maple can successfully establish
160 in boreal forests, probably favoured by the relatively broad tolerance of seedlings and seed
161 germination to variable soil conditions (Kellman, 2004; Solarik, Gravel, Ameztegui,

162 Bergeron, & Messier, 2016), yet the species is known to be sensitive to acidic soils (St Clair,
163 Sharpe, & Lynch, 2008). At least one study has reported upward elevational migration of
164 sugar maple (Beckage et al., 2008). However, sugar maple establishment in boreal forests is
165 known to be limited by both aboveground and belowground factors, such as unsuitable soil
166 and seed predation (Brown & Vellend, 2014; Collin et al., 2017). The studied gradient
167 exhibits a striking elevational transition from a sugar maple dominated temperate forest at low
168 elevation to the boreal forest at high elevation, where sugar maple is absent except near the
169 ecotone. This elevational gradient constitutes an ideal study system for our research exploring
170 the relative importance of abiotic and biotic factors on sugar maple establishment into boreal
171 forests because it allows us to minimise variation in important factors such as parent material,
172 aspect and regional climate (local temperature declines with increasing elevation – the
173 gradient of primary interest).

174

175 *Study sites and soil sampling*

176 Our soil sampling sites were on the eastern slope of Mont Saint-Joseph (45°27' N 71°06' W),
177 which is underlain by uniform parent material (i.e. syenite), from 723 m to 914 m asl.
178 Categorisation of the plots was based on elevation as well as on the canopy dominance of
179 sugar maple. Temperate forest plots were dominated by sugar maple, mixed plots had
180 approximately 50% canopy cover of sugar maple, whereas sugar maple was absent from
181 boreal forest plots. To obtain 10 plots of 20 m × 20 m distributed evenly within each forest
182 type, sampling was performed along 10 elevational transects with one plot of each of the three
183 forest types per transect (see Fig. S1): temperate forest (723–821 m asl), mixed forest (748–
184 882 m asl) and boreal forest (875–914 m asl), according to previous studies (Urli et al., 2016).
185 The ecotone between these two forest types, the elevation of which fluctuates somewhat north
186 to south, is a mixture of maple (*Acer* spp.), fir (*Abies balsamea*), and spruce (*Picea* spp.), with
187 abundant yellow birch (*Betula alleghaniensis*).

188

189 Soil samples were collected on the eastern slope of Mont Saint-Joseph in June 2016. In each
190 plot, four soil pits were dug in order to obtain representative soil samples at the plot level. For
191 each pit, soil from the top 20 cm was collected separately for different horizons. Organic
192 horizons were separated as L (litter; original structures easily distinguishable), F (fragmented;
193 partial decomposition, structures difficult to recognise), and H (humus; decomposed organic
194 matter, original structures indistinguishable), while the mineral horizons were Ae
195 (characterised by leaching/eluviation of clay, Fe, Al or organic matter) and B (characterised
196 by illuviation/enrichment in organic matter and accumulation of Fe or Al oxides) (Soil
197 Classification Working Group, 1998). Because soil profiles differed along the elevation
198 gradient (Fig. S2), the thickness of each horizon was recorded in each pit, so that it could be
199 recreated in experimental pots. Samples were bulked for each horizon in each plot, and
200 different horizons were kept separate.

201

202 *Experimental design*

203 To test if boreal soils (biotic and abiotic properties combined) constrained sugar maple
204 establishment, we used fresh untreated soil sampled from the three forests in a first
205 experiment. Starting sample size was 10 for each forest type, so 30 pots in total. In the second
206 (concurrent) experiment, to disentangle the effects of biotic (i.e. soil inoculum) and abiotic
207 (i.e. soil origin) factors on tree establishment, we applied four soil treatments to the soil from
208 each sampling site: (i) sterilisation without inoculum (referred to as sterile soil), (ii)
209 sterilisation followed by inoculation with boreal forest soil (boreal inoculum), (iii)
210 sterilisation followed by inoculation with mixed forest soil (mixed inoculum), (iv)
211 sterilisation followed by inoculation with temperate forest soil (temperate inoculum).
212 Inoculation was done by adding 7 % (mass basis) of fresh soil.

213

214 We used gamma ray irradiation to sterilise soils because it has fewer effects on soil chemistry
215 compared to other soil sterilisation methods (McNamara, Black, Beresford, & Parekh, 2003).
216 The soils were irradiated to a minimum of 50 kG γ (Nordion Inc., Laval, Canada). An

217 experimental unit consisted of a subsample of the soil from a given field plot, subjected to one
218 of the four treatments. For the second experiment, starting sample size was 10 for each
219 treatment combination, and so there were 120 pots: four treatments \times three soil origins \times 10
220 replicates (transects).

221

222 Prior to the experiment, sugar maple seeds were cold stratified to break dormancy. This was
223 performed at the Berthier Seed Center (Sainte-Geneviève-de-Berthier, Québec). After
224 emergence, seeds were planted in the experimental pots. Seedlings were grown for two
225 growing seasons at $\sim 20\text{--}30\text{ }^{\circ}\text{C}$ (July 2016–June 2017) with a dormant winter pause of three
226 months at $\sim 3\text{--}5\text{ }^{\circ}\text{C}$ (December 2016–February 2017). In all pots, horizons were kept separate
227 (including inoculum) to maintain realistic podzolic soil profiles. The experiment was
228 conducted under controlled conditions within research greenhouses of the Montréal Botanical
229 Garden (Québec, Canada). Soil was placed into 1-L pots (20 cm high \times 5 cm wide). The
230 amount (i.e. thickness) of soil by horizon in the pots depended on actual site measurements
231 (averaged by plot). One seedling was planted per pot after the radicle had emerged. During
232 the first month after transplantation, dead seedlings were immediately replaced with live ones,
233 but after one month we considered mortality to be a treatment effect and not transplant shock.
234 A shade cloth (allowing passage of 36 % of natural light) was positioned over the pots to
235 reduce light in the greenhouse and simulate a partially shaded environment during the first
236 year of growth. Pots were arranged in 10 blocks, with all the samples from the three plots in a
237 given transect (1–10 in Fig. S1) in the same block. Soil inoculation after sterilisation was
238 done using inoculum from the same block (e.g. sterilised temperate soil inoculated with a
239 boreal soil from the same transect).

240

241 *Soil chemical analyses*

242 For each soil horizon in each field plot, we measured several chemical properties. Soil was
243 first air-dried and sieved (2 mm mesh size for organic horizons and 6 mm mesh size for
244 mineral horizons) prior to analysis for organic carbon (C), total nitrogen (N), total phosphorus

245 (P), labile inorganic P and pH. Total C and N contents were determined by automated
246 combustion and gas chromatography with thermal conductivity detection using a Vario
247 MICRO cube analyser (Elementar, Langensfeld, Germany). Total P was determined by
248 ignition at 550 °C followed by extraction in 1 M sulfuric acid. Soil pH was determined in
249 both deionised water and 10 mM CaCl₂ using a glass electrode, and a soil-to-solution ratio of
250 1:8 for L and F horizons, 1:4 for H horizon and 1:2 for A, B horizons. After Bray-1
251 extraction, Bray P (labile P) in the extraction material was determined using automated
252 molybdate colorimetry on a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO). Exchangeable
253 cations were determined for all H, Ae and B horizons by extraction in 0.1 M BaCl₂ (2 hours,
254 1:30 soil to solution ratio) and detection by inductively-coupled plasma optical-emission
255 spectrometry (ICP–OES) with an Optima 7300 DV (Perkin-Elmer Ltd, Shelton, CT, USA).
256 Total exchangeable bases (TEB) was calculated as the sum of the charge equivalents of Ca,
257 K, Mg and Na. Effective cation exchange capacity (ECEC) was calculated as the sum of the
258 charge equivalents of Al, Ca, Fe, K, Mg, Mn and Na. Base saturation was calculated as (TEB
259 / ECEC) × 100.

260

261 *Seedling measurements*

262 Surviving seedlings from the two experiments were harvested in June 2017 and processed
263 individually within 24 h. For each seedling, leaves, petioles, stems and roots were separated,
264 measured, and weighed before and after oven-drying at 60 °C for 72 h. Total biomass was
265 estimated as the dry weight of all structures combined. Other size traits were measured but
266 not used in the analysis due to strong correlations and thus redundancy (Table S1). A
267 representative sample of the roots of each seedling were cleared in 10% w/v KOH, then
268 stained in an ink and vinegar solution at 90°C (Vierheilig, Coughlan, Wyss, & Piché, 1998).
269 Colonization of the root system by fungal structures was determined using a semi-quantitative
270 scale following a protocol (available at dx.doi.org/10.17504/protocols.io.36grd6) modified
271 from Zemunik et al. (2018). Using standard light microscopy, we recorded structures of
272 arbuscular mycorrhizal fungi such as hyphae, arbuscules, vesicles, coils as well as fungal

273 endophytes (presence of chytrids, hyphae diameter less than 2 μm with presence of
274 microsclerotia).

275

276 *Statistical analysis*

277 To quantify the effect of soil origin (forest type) on seedling survival and biomass
278 (*experiment 1*), we used a linear mixed-effect models to compare the impacts of the three
279 types of forest soil (fixed factor) along 10 elevational transects (random factor). To test the
280 relative importance of abiotic and biotic factors and their potential interaction (*experiment 2*)
281 in a crossed experimental design, we used a hierarchical model; this model compared the
282 impacts of the abiotic components of different soil origins (i.e. initially sterilised temperate,
283 mixed or boreal soil) and the four biotic (inoculum source) treatments (i.e. sterile soil,
284 inoculum of temperate, mixed or boreal soil) on seedling survival and biomass. Soil of
285 experiment 2 were sampled along the 10 elevational transects (random factor), therefore soil
286 origin and inoculum source (fixed factors) are nested within transects in the model. We
287 calculated coefficients of variation among treatment means to compare the impact of biotic
288 vs. abiotic factors.

289

290 For both experiments, survival and final biomass were first modelled individually, and then
291 jointly using a Hurdle analysis providing a measure of performance that integrates survival
292 and biomass (hereafter, performance, which is survival multiplied by biomass). We used the
293 Bernoulli distribution for survival, and the gamma distribution for biomass (see model
294 specification in the supplementary material). For the biomass estimation, only surviving
295 seedlings were used (see Tables S2 and S3 for corresponding sample sizes). We implemented
296 a Bayesian approach using JAGS (Plummer, 2003), since initial data analyses with general
297 linear mixed effect models in R revealed significant issues regarding model convergence due
298 to the large number of zeros in the data (>50%) and the hierarchical design. The model ran an
299 update on three parallel chains of length 500,000 and a thinning rate of 10 following a run
300 with three parallel chains of length 5,000 and a burn-in of 4,000 iterations with a thinning rate

301 of 10, for a total of 150,000 iterations conserved. We used uninformative priors for the shape
302 parameter and semi-informative priors for all betas (model coefficients) for both parts of the
303 model (see model specification in the supplementary material for further details).
304 Convergence was assessed for each parameter estimate by visually inspecting the three
305 Markov chains and by examining the \hat{R} values which quantify consistency (Zuur & Ieno,
306 2016). Model validation was then assessed visually by plotting the residuals against the fitted
307 values and with each covariate in the model. No significant heterogeneity issues, and no clear
308 outliers in residual patterns, were found. Model fit was assessed using Pearson's residuals
309 χ^2 by comparing the observed residuals over residuals from data simulated under the model.
310 The lack-of-fit statistic $\chi_{obs}^2/\chi_{sim}^2$, which is expected to be equal to 1 if the model fits the data
311 perfectly (Kery & Schaub, 2011), was equal to 0.82, indicating a good model fit. Adjusted-
312 R^2 values were used as approximate assessments of the percentage of variance that is
313 explained by the models. This was done by linearly fitting observed values to their predicted
314 values. Soil characteristics were modelled using linear mixed-effect models and root
315 colonization by bootstrapping. Analyses with root hyphal colonization as an explanatory
316 variable of dry mass, and with soil characteristics as explanatory variables of performance,
317 were done using generalised linear mixed-effect models. For the statistical analysis, we used
318 R (R Core Team, 2018) with the following packages: *brms* (Bürkner, 2017), *dplyr* (Wickham,
319 Francois, Henry, & Müller, 2017), *emmeans* (Lenth, 2019), *ggplot2* (Wickham, 2016), *ggpubr*
320 (Kassambara, 2018), *lattice* (Sarkar, 2008), *nlme* (Pinheiro, Bates, DebRoy, Sarkar, & Team,
321 2012), *R2jags* (Su & Yajima, 2015), *reshape2* (Wickham, 2007), *rjags* (Plummer, 2018).

322

323 **Results**

324 *Seedling survival, biomass and performance along the elevational gradient (Experiment 1)*

325 Seedling survival and biomass of survivors were more than twice as high in untreated soils
326 from temperate and mixed forests compared to soils from boreal forests (Fig. 1a–b).

327 However, we note that the 90 % credible intervals for predicted seedling survival and biomass

328 overlap among forest types. Overall seedling performance was much lower in boreal soils,
329 and the most favourable soil tended to be from the mixed forest (Fig 1c); indeed, there was a
330 77 % decrease in mean performance in boreal soils compared to mixed-forest soils, which
331 differ from one another with >90 % confidence (see Table S5 for a summary of the results).

332

333 *Overall performance impacted by abiotic and biotic factors (Experiment 2)*

334 The integrated measure of performance (i.e., survival multiplied by biomass) showed
335 differences of moderate magnitude among soil origins and inoculum sources (Fig. 2; see also
336 Table S6 for a summary of the results). Performance was lower in the treatments with boreal
337 soil origin (on average 37 % lower compared to temperate soil origin) and with boreal soil
338 inoculum (44 % lower). Performance was greatest in soils of temperate origin and with the
339 temperate inoculum source. Considering soil origin and inoculum source simultaneously (Fig.
340 2c), the performance of seedlings grown in temperate or mixed-forest soil was relatively low
341 if the inoculum did not come from the temperate forest. For temperate and boreal inocula, the
342 boreal soil origin had a detrimental effect on seedling performance. In the absence of
343 inoculum (i.e., in sterile soils), seedling performance was always low.

344

345 The model that included the interaction term (soil origin \times inoculum source) fit the data better
346 (higher adjusted- R^2), suggesting that the effects of inoculum source on overall performance
347 depended on soil origin and vice-versa (Fig. 2c). For soils of temperate origin, mean values
348 for each inoculum source (i.e., from temperate, mixed and boreal forests, not including sterile
349 soils) had a coefficient of variation (CV) of 45 %; the CV was 30 % in the mixed-forest soil
350 and 29 % in the boreal soil. The magnitude of the soil origin effect on seedling performance
351 (calculated as the CV among medians on sterilised soils) was 47 %.

352

353 *Seedling survival and biomass impacted by abiotic and biotic factors (Experiment 2)*

354 Survival was strongly impacted by the inoculum source (i.e. soil biota), but the magnitude of
355 effect varied across soil origins. Survival was especially low in sterile soil (Fig. 2a). Overall,
356 seedlings grown in sterile soil had, on average, 57 % lower survival probability compared to
357 the treatment with boreal inoculum and 89 % lower compared to the treatment with temperate
358 inoculum (see Table S6 for a summary of the results). Although the 90 % credible intervals
359 overlapped for survival among different inoculum sources, average survival was lower in
360 boreal and sterile inoculum (Fig. S3). When soil origin and inoculum source were considered
361 simultaneously, the probability of survival was clearly lower within sterile soils regardless of
362 soil origin.

363

364 The final biomass of surviving seedlings tended to be greater in soils originating in the
365 temperate forest, being 36 % and 44 % greater than in mixed-forest and boreal soils,
366 respectively (Fig S3). When the impact of soil origin and inoculum source were considered
367 simultaneously, biomass showed a large difference between the temperate inoculum and the
368 other inocula if the seedlings were grown in soils of temperate and mixed-forest origin (Fig
369 2b). The effect of the boreal soil origin on seedling biomass was negative regardless of the
370 inoculum (mean biomass lower than 1 g). The effect of the temperate inoculum was
371 approximately twice as high in temperate soil than in boreal soil.

372

373 *Change in soil properties along the elevational gradient*

374 Averaged across horizons, soil pH, effective cation exchange capacity (ECEC), and base
375 saturation tended to decrease from temperate to boreal soils (Fig. 3). In contrast, the soil C:N
376 ratio and labile P tended to increase along the elevational gradient (Fig. 3). As expected, soil
377 in mixed forests tended to have intermediate values of soil characteristics except for total P,
378 which was highest in mixed forests. All the soil physico-chemical parameters measured were
379 strongly influenced by depth (see Fig. S4). The first two organic horizons (L, F) had high pH,
380 C:N ratio and labile P. The Ae horizons tended to have lowest values of pH, ECEC, C:N ratio
381 and total P in all forest type. Soil properties in the Ae horizon in temperate forest were

382 variable, but this horizon was encountered in only two plots. Seedling performance was
383 positively correlated with ECEC (Fig. S5), with an estimated effect size different from zero
384 with 90 % confidence.

385

386 *Abiotic and biotic factors impact root colonization by fungi*

387 Seedlings grown in fresh (unsterilised) temperate soil tended to have higher colonization by
388 hyphae, arbuscules and endophytes compared to seedlings grown in the mixed-forest and
389 boreal soils (experiment 1; Fig. S6). Mycorrhizal root colonization in fresh soils was higher
390 than in soils initially sterilised with or without subsequent inoculum (experiment 2, Fig. S7).
391 Inoculum source and soil origin had important impacts on root colonization by fungi (Fig. 4).
392 Seedlings that were grown with the temperate inoculum had higher root colonization by
393 arbuscular mycorrhizal fungal hyphae compared to seedlings with mixed-forest or boreal
394 inoculum (Fig. 4). Seedlings grown in soils of temperate origin were generally more strongly
395 colonized (Fig. 4). In sterile soil, hyphae were very rare and arbuscules never recorded (Fig.
396 4, Fig. S8). Similar trends were observed for coils (Fig. S8). As expected, colonization by
397 endophytes was lower in sterilised soil and more evenly distributed among soil types and
398 inoculum treatments (Fig. S8). The presence of vesicles did not show a clear pattern. Seedling
399 dry mass was positively correlated with colonization by coils, arbuscules and hyphae, and
400 negatively correlated with endophytes (Table S4). Furthermore, hyphal root colonization was
401 positively correlated with higher biomass of seedlings that survived (Fig. S9).

402

403 **Discussion**

404 Our study provides novel insights into the importance of non-climatic factors in constraining
405 plant establishment and range expansion by disentangling the relative importance of soil
406 abiotic factors (physico-chemical characteristics) and biotic properties (soil biota). The
407 combined effects of abiotic and biotic soil factors greatly diminished the potential survival
408 and growth of sugar maple seedlings in the boreal forest. In sterilised soils (i.e., with soil
409 biota eliminated), seedling survival and growth were always very low, suggesting a crucial

410 role of beneficial soil biota, most likely arbuscular mycorrhizal fungi. In addition, given
411 strong differences in seedling performance among soils of different origin – even when
412 sterilised – our study also points to an important role of soil abiotic properties, most likely
413 base cations, in constraining the establishment of sugar maple in the boreal forest. Together,
414 our results show how soil abiotic and biotic factors can jointly constrain the establishment of
415 a dominant temperate tree species into boreal forests. Such belowground factors should be
416 considered when projecting future tree species distributions with climate change.

417

418 Under projected changes in climate, many temperate tree species have been predicted to
419 expand their distributions beyond the current temperate-boreal ecotone (McKenney, Pedlar,
420 Lawrence, Campbell, & Hutchinson, 2007). If not limited by dispersal and demographic
421 factors, this shift is predicted to be of dozens of kilometres northward by the end of the
422 current century. However, based on geographic distributions of seedlings vs. adult trees, few
423 North American tree species show signs of ongoing northward shifts (i.e., seedlings occurring
424 further north than adult trees), despite recent increases in mean annual temperature (Zhu et al.,
425 2012). Plant-soil interactions are known to influence plant performance and might be a major
426 factor limiting temperate tree migration (Pither, Pickles, Simard, Ordonez, & Williams, 2018;
427 Vissault, 2016). Sugar maple specifically is expected to migrate beyond its current range,
428 toward the boreal forest (Frumhoff et al., 2007; Talluto, Boulangeat, Vissault, Thuiller, &
429 Gravel, 2017), but edaphic conditions have been hypothesised to constrain such range
430 expansion (Cleavitt, Battles, Fahey, & Blum, 2014). Our study shows that sugar maple
431 expansion is likely to be constrained by lower seedling survival and growth on boreal soils
432 (Fig. 1) and, importantly, that such edaphic constraints have joint abiotic (e.g., low base
433 cations) and a biotic (e.g., low arbuscular mycorrhizal fungal inoculum potential) causes.
434 Declines in seedling performance are often observed in plants that are transplanted beyond
435 their range limits, and our study contributes further evidence in the literature that non-climatic
436 factors can play a central role (Tomioło & Ward, 2018).

437

438 Mycorrhizal associations may be an important predictor of plant species distributions
439 (Klironomos et al., 2011; Pringle et al., 2009). This symbiosis can even allow plants to
440 expand their niche (Gerz, Bueno, Ozinga, Zobel, & Moora, 2018). The lack of mycorrhizal
441 symbionts has been a major factor determining the spread of some introduced plants, as for
442 ectomycorrhizal *Pinus* spp. (Dickie, Bolstridge, Cooper, & Peltzer, 2010; Nuñez, Horton, &
443 Simberloff, 2009). However, arbuscular mycorrhizal fungi (AMF) are very ancient plant
444 symbionts (Field & Pressel, 2018) and many species have a cosmopolitan distribution (but see
445 Bruns & Taylor, 2016; Davison et al., 2015; Morton & Bentivenga, 1994), dispersing over
446 short and long distances (Correia, Heleno, Silva, Costa, & Rodríguez-Echeverría, 2019; Egan,
447 Li, & Klironomos, 2014), and showing low host specificity (van der Heijden, Martin, Selosse,
448 & Sanders, 2015). Therefore, it has been suggested that the distributions of plants that form
449 arbuscular mycorrhizal associations might not be constrained by the presence of the fungal
450 symbionts (Richardson, Allsopp, D'Antonio, Milton, & Rejmánek, 2000). For example, an
451 observational study that compared adult and seedling distributions suggested that differences
452 in northward range expansion of North American temperate tree species is not predictable
453 based on the type of mycorrhizal association (Lankau, Zhu, & Ordonez, 2015). However,
454 northward of temperate forests, there are boreal forests that are mainly dominated by trees
455 that form ectomycorrhizal associations (e.g., *Picea* spp.) (Read & Perez-Moreno, 2003),
456 which may act as a barrier for arbuscular mycorrhizal plant species since arbuscular
457 mycorrhizal fungi are obligate symbionts. Our results suggest that boreal soils are not
458 favourable to the symbiosis between arbuscular mycorrhizal fungi and the seedlings of sugar
459 maple. As such, our study highlights the importance of considering the mycorrhizal status of
460 plants in both “donor” and “recipient” communities when trying to forecast range expansions.
461
462 The poorer performance of seedlings under sterilised and boreal conditions further suggests
463 that arbuscular mycorrhizal fungi are most likely to be the reason for the observed biotic
464 effect. In fact, we found considerably lower root colonization intensity by arbuscular
465 mycorrhizal fungi in seedlings inoculated with boreal forest soils (Fig. 4), and a positive

466 correlation between seedling biomass and the amount of mycorrhizal root colonization (Fig.
467 S9). The few arbuscular mycorrhizal fungi that might be present in boreal soils because of
468 understory plants or fungal spore dispersal (Öpik et al., 2008) appear to be insufficient for
469 roots of sugar maple seedlings to be well colonized. This is supported by the fact that
470 unsterilised fresh soils (used in experiment 1) tended to favour seedling performance and root
471 colonization compared to the corresponding inoculum treatments on sterilised soil (see Fig.
472 S6 and S10). This is possibly due to the presence of a lower number of viable mycorrhizal
473 propagules (e.g. fewer fragments of colonized roots) in the inoculated sterilised soil. Soil
474 biotic factors strongly influenced the performance of sugar maple seedlings, and particularly
475 their survival, as suggested by previous studies (Brown & Vellend, 2014; Cleavitt et al., 2014;
476 Cleavitt, Fahey, & Battles, 2011; Putnam & Reich, 2017). It has also been shown that fungal
477 and bacterial belowground communities on sugar maple roots are different between areas of
478 high abundance and the elevational range limit (Wallace, Laforest-Lapointe, & Kembel,
479 2018). In agreement with other studies, soil biota acted as important drivers of success of
480 plant establishment (Ma et al., 2019; Pringle et al., 2009).

481

482 Performance of sugar maple seedlings was negatively impacted in terms of survival and
483 subsequent growth by the abiotic component of boreal soil. Compared to soils from temperate
484 forests, boreal soils tend to be more acidic and nutrient poor (e.g. lower availability of cations
485 and nitrogen, Fig. 3), characteristics that are known to affect the nutrition of sugar maple at
486 early stages of development (Collin et al., 2017). This supports the hypothesis that upward
487 and northward migration of sugar maple could be constrained by unsuitable soil physico-
488 chemical properties. It is worth noting that soil chemistry was strongly influenced by depth.
489 The Ae horizons characteristic of podzols tended to show the lowest concentrations of
490 nutrients and pH, which could affect seedling growth, thus highlighting the importance of
491 maintaining ecological realism by reconstructing soil profiles within the experimental units
492 (Heinonsalo, Hurme, & Sen, 2004). Litter layer depth also can play an important role, acting
493 as a barrier to seedling establishment (Cleavitt et al., 2011). Although sugar maple seedlings

494 express broad tolerance for diverse abiotic soil factors (Arii & Lechowicz, 2002; Kellman,
495 2004), the presence of soil mutualists seems important as suggested by low performance in
496 the sterile soil. Arbuscular mycorrhizal fungi are also sensitive to abiotic factors but their
497 presence is crucial for the plant partner for nutrient acquisition, particularly phosphorus
498 (Hodge & Storer, 2014; Smith & Smith, 2011), as well as for defense against pathogens
499 (Jung, Martinez-Medina, Lopez-Raez, & Pozo, 2012; Smith & Read, 2010). Soil chemistry
500 can influence seedlings both directly via nutrient availability and indirectly via effects on the
501 soil biota. For example, sugar maple root colonization by arbuscular mycorrhizal fungi is
502 known to diminish when soil pH is decreased (Coughlan, Dalpé, Lapointe, & Piché, 2000;
503 Juice et al., 2006), which might explain the lower colonization and performance of seedlings
504 grown in boreal soils (where pH was lower), thus negatively impacting their overall seedling
505 performance, even when inoculated with temperate forest soil.

506

507 One must be cautious in using results from a greenhouse experiment to draw inferences about
508 dynamics in the field, given additional, untested factors that can also influence plant
509 performance. For example, intraspecific variation via local adaptation or maternal effects
510 (e.g., on seed size) – not assessed in this study – may be important for sugar maple
511 establishment (Solarik, Messier, Ouimet, Bergeron, & Gravel, 2018; Walters & Reich, 2000).

512 In addition, environmental parameters such as temperature can affect sugar maple
513 germination, seedling survival and growth (Fisichelli, Stefanski, Frelich, & Reich, 2015; e.g.
514 Solarik et al., 2016; Wright et al., 2018). Responses of soil microorganisms to climate change
515 are difficult to predict but will inevitably influence many abiotic and biotic factors (Jansson &
516 Hofmockel, 2019), some of which that could feedback positively to plant performance,
517 potentially facilitating range expansion. For example, it has been experimentally shown that
518 higher soil temperature can stimulate microbial activity that increases mineralisation of
519 organically bound nutrients (Wan, Hui, Wallace, & Luo, 2005; Zak, Holmes, MacDonald, &
520 Pregitzer, 1999), which can facilitate nutrient acquisition by sugar maple, although this also
521 limits the benefits provided by AM fungi (St Clair et al., 2008). Availability of light and water

522 can strongly influence sugar maple performance (discussed in detail by St Clair et al., 2008).
523 These environmental features could interact in complex ways with mutualistic or harmful
524 organisms (e.g. Hawkes, Hartley, Ineson, & Fitter, 2008; Sanders-DeMott, McNellis, Jabouri,
525 & Templer, 2018). In our study, temperature, light and water availability were experimentally
526 controlled to avoid any potential confounding effects with the factors of primary interest in this
527 study – soil chemistry and microbiota. While it is possible that different levels of these
528 environmental factors would have altered our experimental results, we have no a priori reason
529 to suspect that the effects of soil factors specifically were qualitatively different than what one
530 would expect in the field. Indeed, the relatively high temperatures experienced in the
531 greenhouse might reflect expected future conditions with climate warming. A better
532 understanding of the impacts of the interactions among temperature, light and water
533 availability with biotic factors at the different stages of development of sugar maple would be
534 needed to better forecast its future distribution.

535

536 Our study builds on several others at the same field site (Mont Mégantic) or in the same
537 region (southern Québec) focused specifically on non-climatic belowground factors that
538 might limit or favor sugar maple's establishment into the boreal forest (Brown & Vellend,
539 2014; Collin, Messier, Kembel, & Bélanger, 2018; Urli et al., 2016). Our study highlights the
540 importance of one group of beneficial soil biota, namely arbuscular mycorrhizal fungi.
541 However, the possible effect of soil-borne pathogens merits further investigation. In previous
542 studies, sugar maple showed negative conspecific density dependence (Johnson, Beaulieu,
543 Bever, & Clay, 2012) and increased seedling survival in the boreal forest at Mont Mégantic
544 (in a field experiment) with or without protection from insect herbivores, leading Urli et al.
545 (2016) to hypothesise potential release from soil pathogens in the boreal forest. In contrast,
546 our experiment points to an overall net positive effect of soil biota in this system, and other
547 studies have not found strong negative plant-soil feedbacks for sugar maple (Bennett et al.,
548 2017; McCarthy-Neumann & Ibáñez, 2012). The low performance of sugar maple seedlings
549 on sterile soils from all sources suggests that the beneficial role of soil mutualists such as

550 arbuscular mycorrhizal fungi outweighs potential negative impacts of soil-borne generalist
551 pathogens, at least at our field site. Furthermore, compared to sterile soils, seedlings showed
552 marked positive responses to soil biota (inocula) when growing on soils from within their
553 current range (temperate and mixed forests), and weaker responses when grown in boreal soil
554 (Fig. 2). That said, we must be cautious in extrapolating results from the greenhouse to the
555 field. Our study focused mainly on soil micro-organisms as biotic factors, but sugar maple
556 might also be susceptible to other enemies such as seed-consuming rodents for seed predation
557 (Brown & Vellend, 2014) or insect herbivores (Urli et al., 2016). Beyond its elevational
558 range, sugar maple seedlings appear to be favored by release from insect herbivory (Urli et
559 al., 2016); however, our results suggest that the presence of mutualist organisms might remain
560 a key factor for its establishment, as other studies have suggested for annual plants and shrubs
561 (Morriën & Putten, 2013; Sedlacek, Bossdorf, Cortés, Wheeler, & van Kleunen, 2014;
562 Stanton-Geddes & Anderson, 2011).

563

564 Belowground mutualists can be important determinants of plant distributions, especially in a
565 context of range expansion and invasion (Richardson et al., 2000). Therefore, the
566 incorporation of microbial ecology and especially mycorrhizal ecology into predictive
567 ecosystem models might have great potential (Johnson et al., 2006; Treseder et al., 2012).
568 Specifically, our results suggest that integrating belowground traits such mycorrhizal status
569 may improve modelling future changes in forest composition and functioning (Brzostek,
570 Rebel, Smith, & Phillips, 2017). Some classic ideas in biogeography suggest that species
571 distributions are limited by biotic factors (e.g., competition) at their warm edges (e.g., at low
572 latitude or elevation) and by abiotic factors (e.g., harsh climate) at their cold edges (e.g.
573 Dobzhansky, 1950; Pianka, 1966 and references therein). Evidence in support of this idea
574 includes studies having shown that climatic and soil physico-chemical factors are important
575 determinants of plant distributions (Beauregard & Blois, 2014; Bertrand, Perez, & Gégout,
576 2012; Coudun, Gégout, Piedallu, & Rameau, 2006). On the other hand, our results indicate
577 that even at cold range limits biotic factors such as soil microbial mutualists can be important

578 determinants of potential range shifts, and thus need to be incorporated into forecasts of future
579 changes in terrestrial ecosystems.

580

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592

593 **Data and Code Availability Statement**

594 Data is available at <https://doi.org/10.5281/zenodo.3524285>

595 Code for statistical analysis is available at <https://doi.org/10.5281/zenodo.3533170>

596

597 **Authors' contributions**

598 EL, MV and AC conceived the ideas and designed methodology; AC, VP, FB and BT
599 collected the data; XGM and AC analysed the data; AC, EL and MV interpreted the results;
600 AC led the writing of the manuscript. All authors contributed critically to the drafts and gave
601 final approval for publication.

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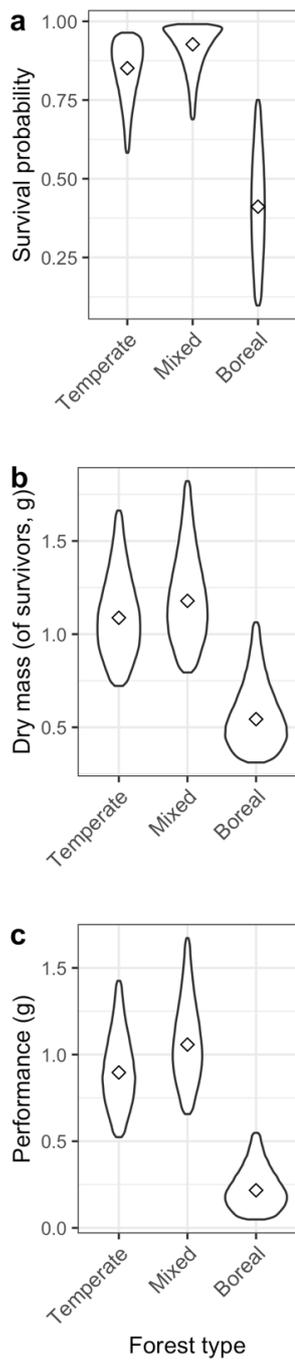
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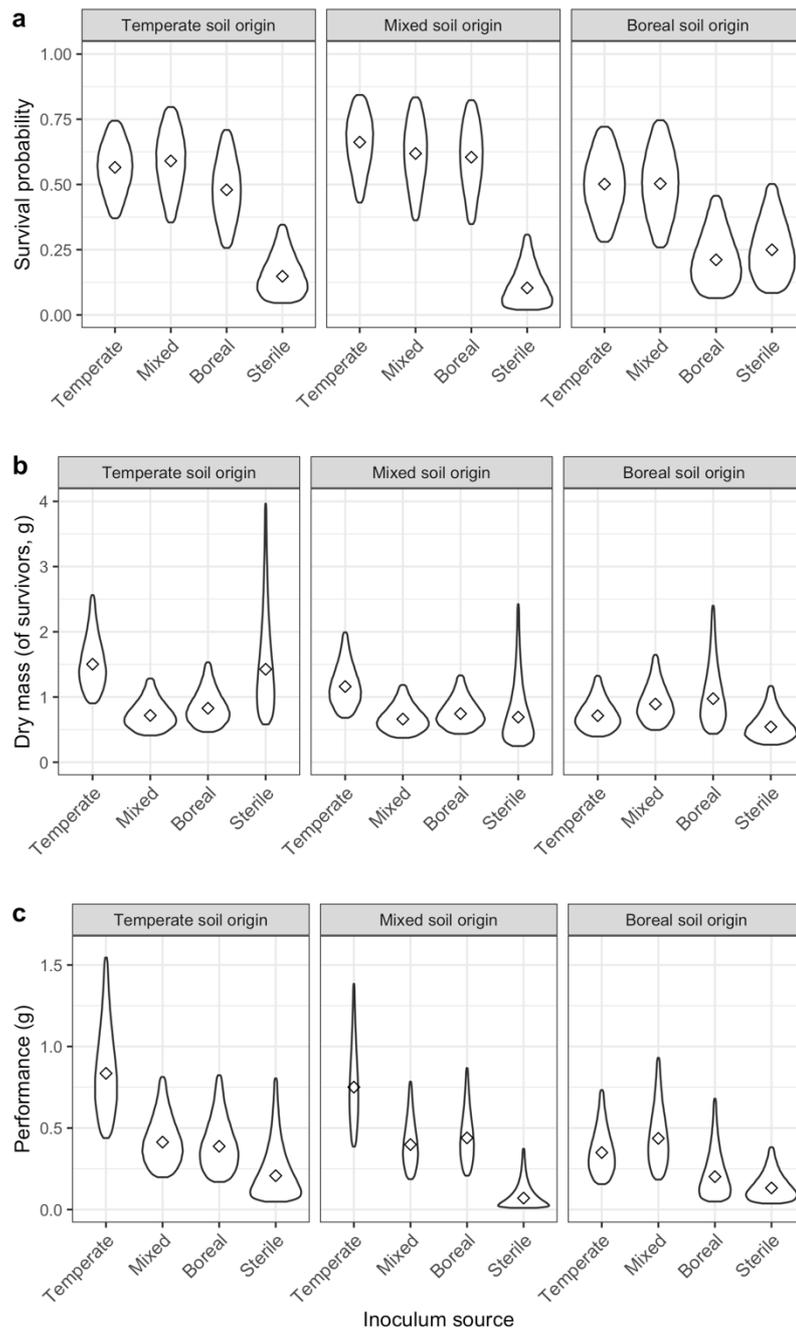
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925 **Figures**



926

927 **Figure 1.** Effects of soils originating from the different forest types (along the elevational
928 gradient) on the (a) survival probability, (b) dry mass and (c) performance (i.e. dry mass
929 including survival probability) of sugar maple seedlings. In these violin plots, the width of the
930 polygon represents the density of the expected values. Upper and lower limits of the violin
931 plots represent 90% credible intervals (the vertical length of each polygon). Diamonds show
932 medians.



933

934 **Figure 2.** Effects of soil origin (abiotic and biotic factors) and inoculum source (only biotic

935 factors) on sugar maple seedling (a) survival probability, (b) dry mass and (c) performance

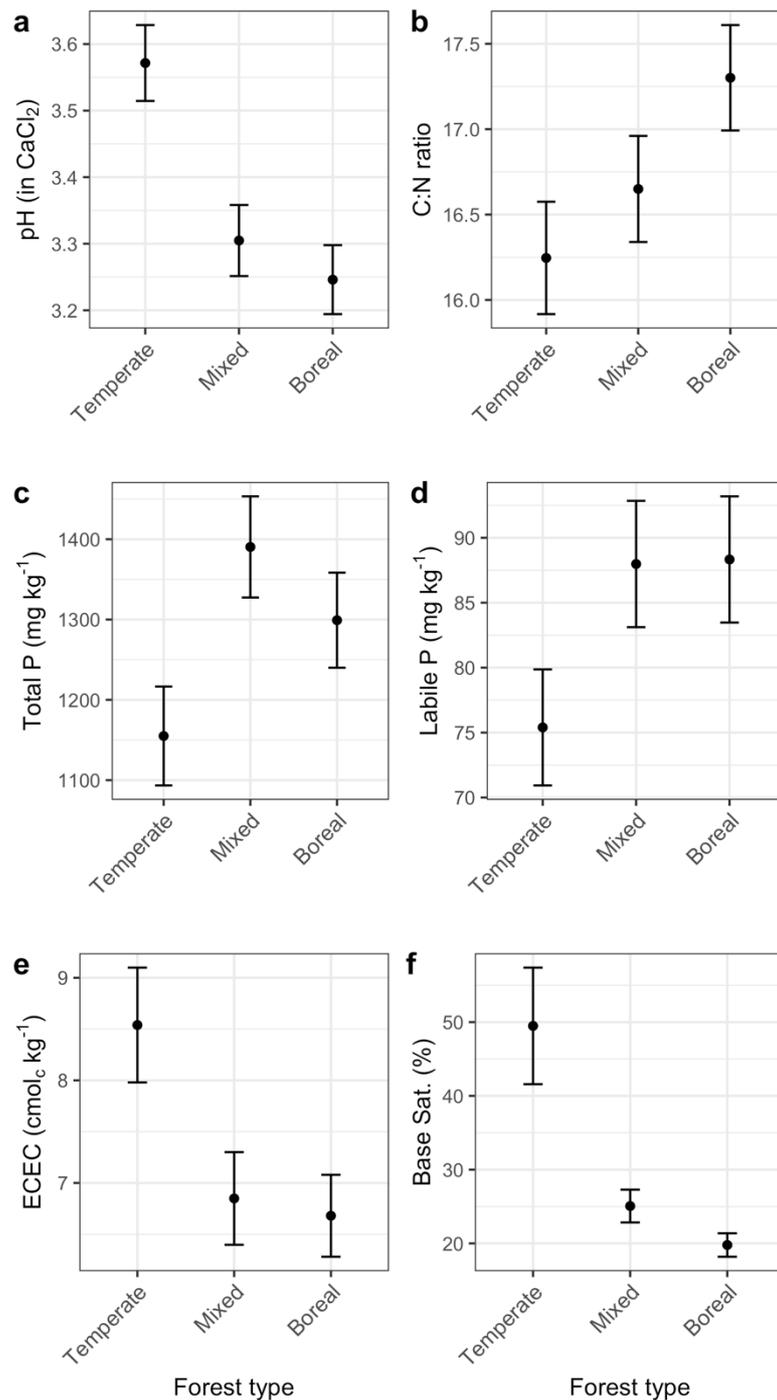
936 (i.e. dry mass including survival probability). Only one individual survived in sterilized

937 temperate soil, so the expected dry mass showed large uncertainties which limits our

938 predictions (i.e. the fit of the model). In these violin plots, the width of the polygon represents

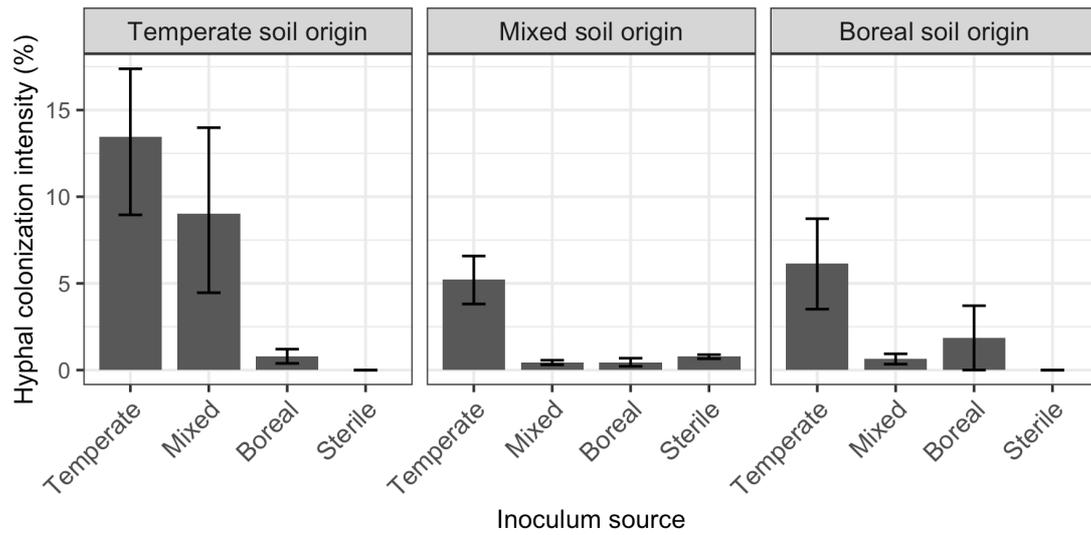
939 the density of the expected values. Upper and lower limits of the violin plots represent 90%

940 credible interval. Diamonds show medians.



941

942 **Figure 3.** Soil characteristics for each forest type (temperate, mixed, and boreal): (a) pH (in
 943 CaCl₂), (b) C:N ratio, (c) total P, (d) labile P (e) effective cation exchange capacity (ECEC)
 944 and (f) base saturation. Values were averaged across horizons, and error bars represent the
 945 standard error of the mean of the estimated parameters.



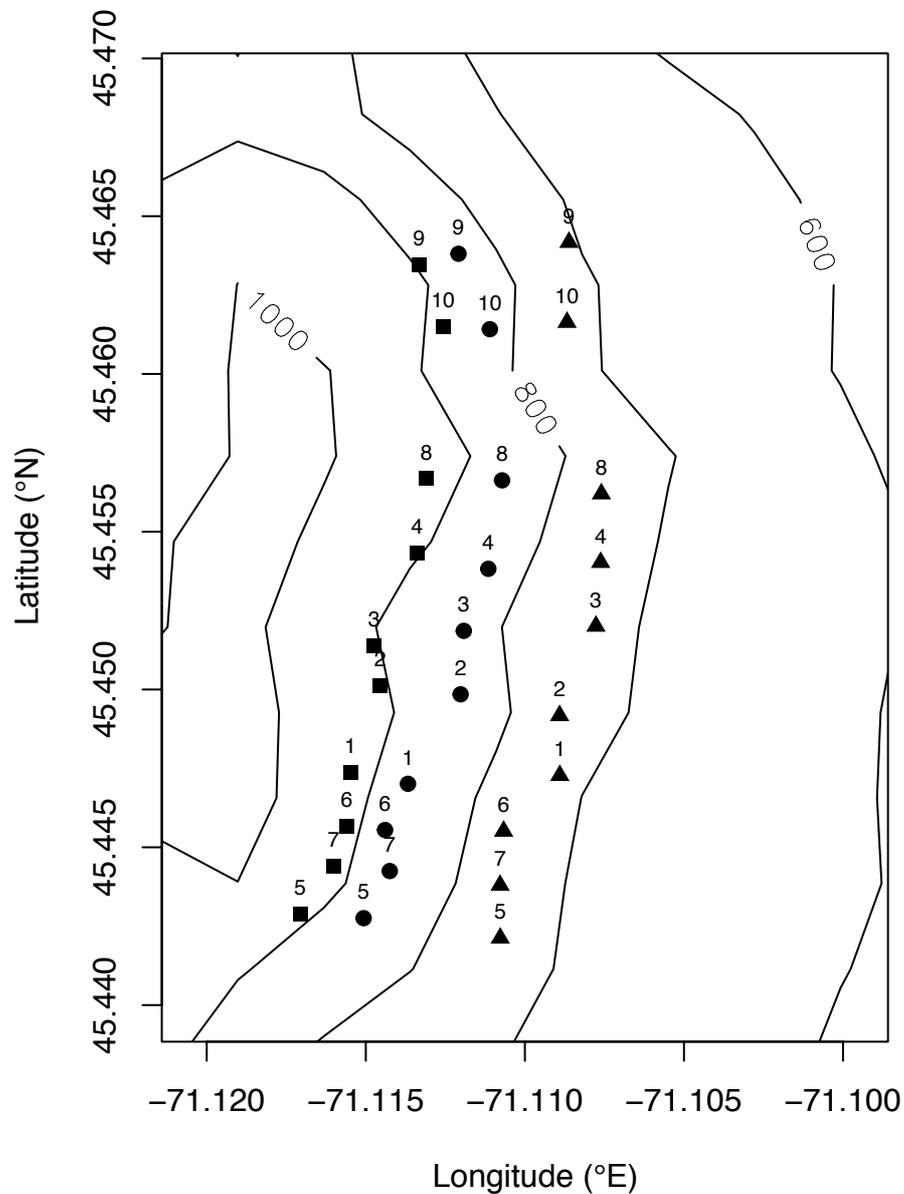
946

947 **Figure 4.** Effects of soil origin (abiotic and biotic factors) and inoculum source (only biotic

948 factors) on observed root colonization intensity by hyphae in sugar maple seedlings. Error

949 bars represent the standard error of the mean of the observed parameters.

1 **Supplementary materials**



2

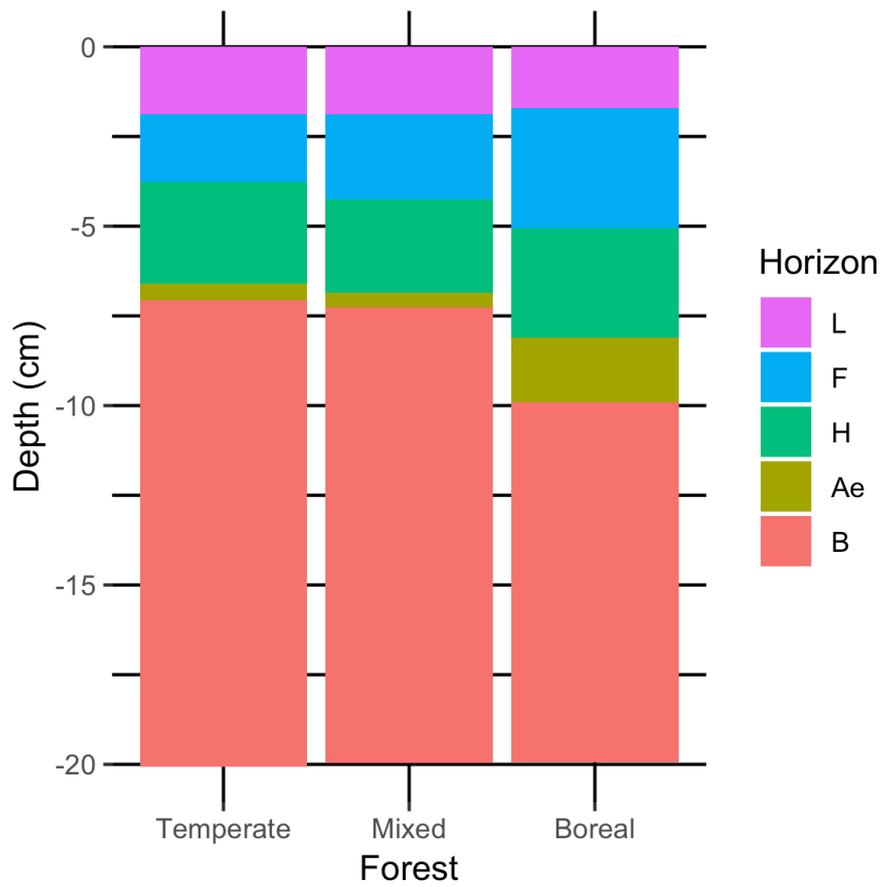
3 **Figure S1.** Distribution of the soil sampling plots along the elevational gradient (east to west)

4 of the eastern slope of Mont Saint-Joseph (Qc, Canada) and the three forest types: temperate

5 (square), mixed (circle), boreal (triangle). Transects 1 to 10 are in order of sampling time and

6 correspond to blocks within the greenhouse. Elevations of the contour lines are in meters

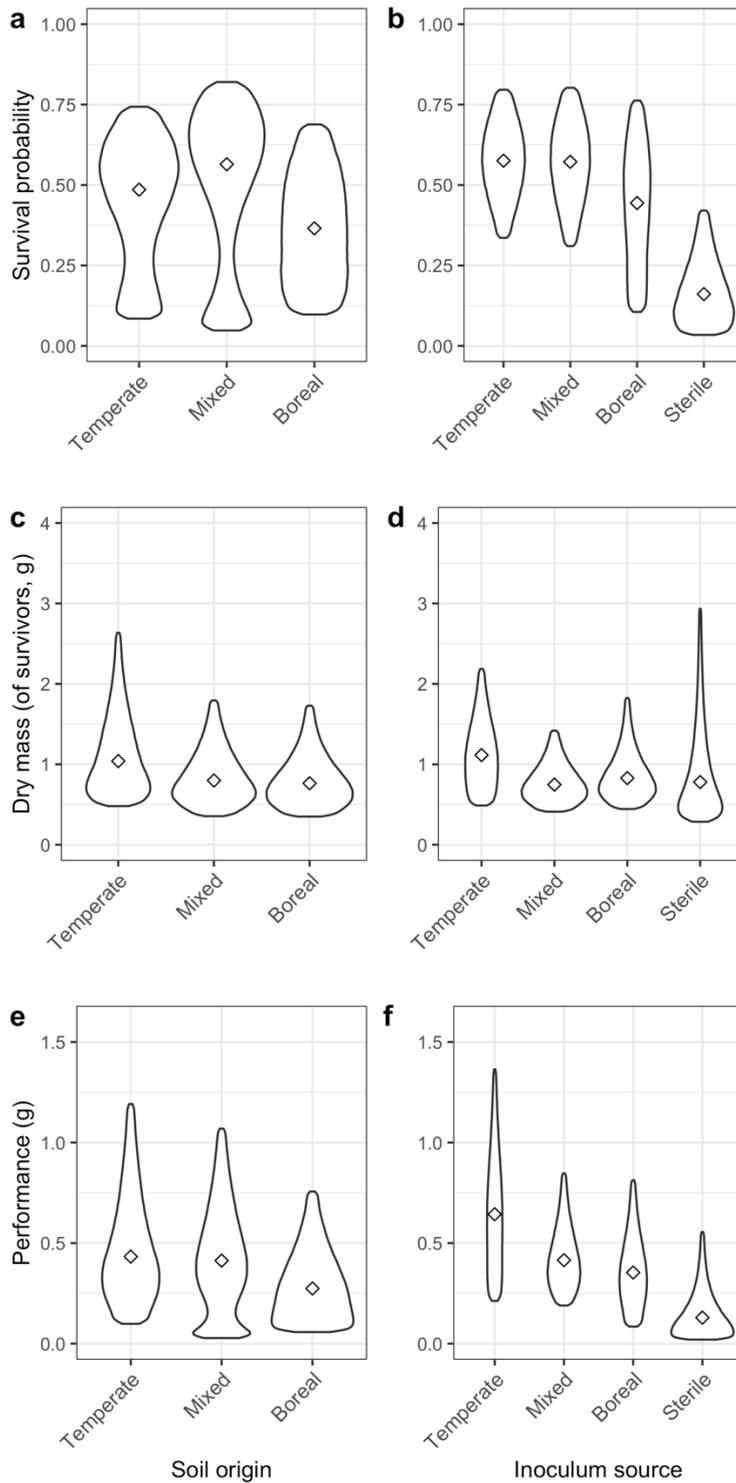
7 above sea level.



8

9 **Figure S2.** Soil profile by horizons of the three type of forests averaged across the 10

10 transects based on four pits of 20 cm depth.



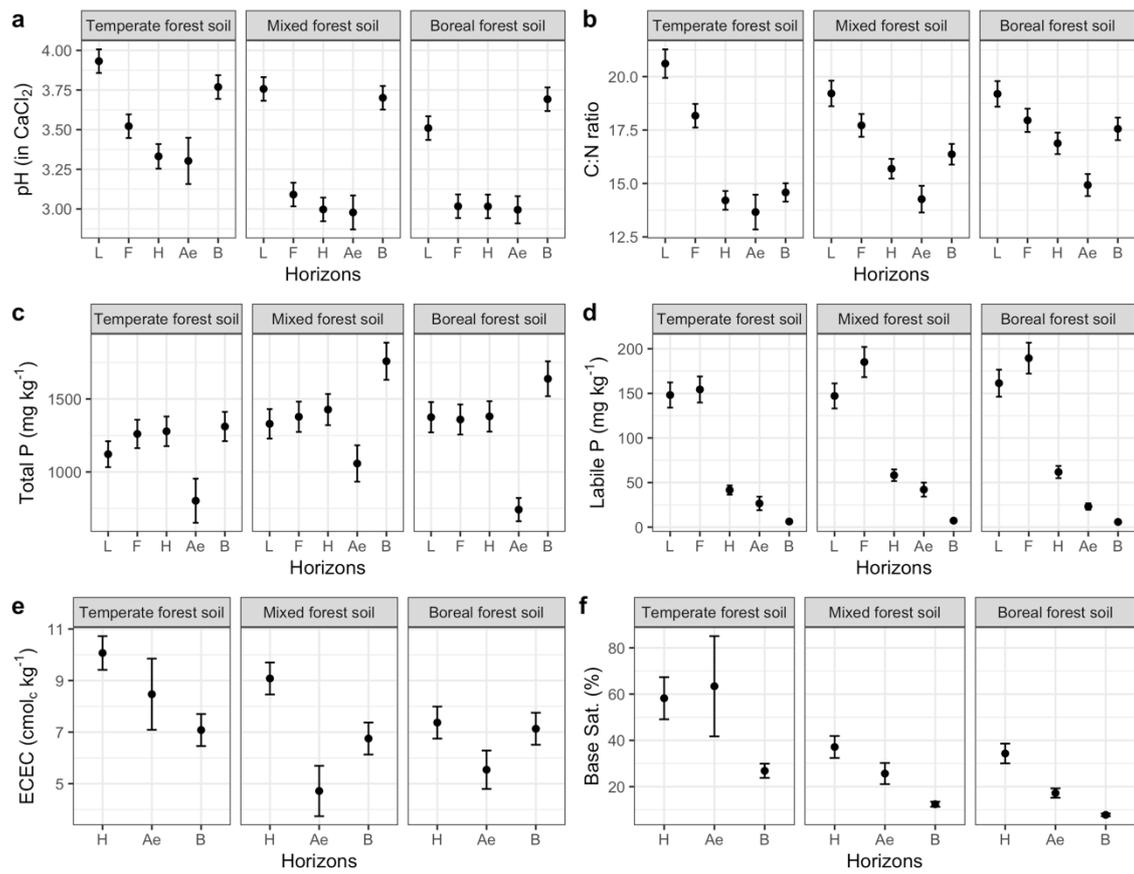
11

12 **Figure S3.** Average effects soil origin (abiotic and biotic factors) and inoculum source (only
 13 biotic factors) on sugar maple seedling survival (a, b), biomass (c, d) and performance (e, f).

14 In these violin plots, the width of the polygon represents the density of the expected values.

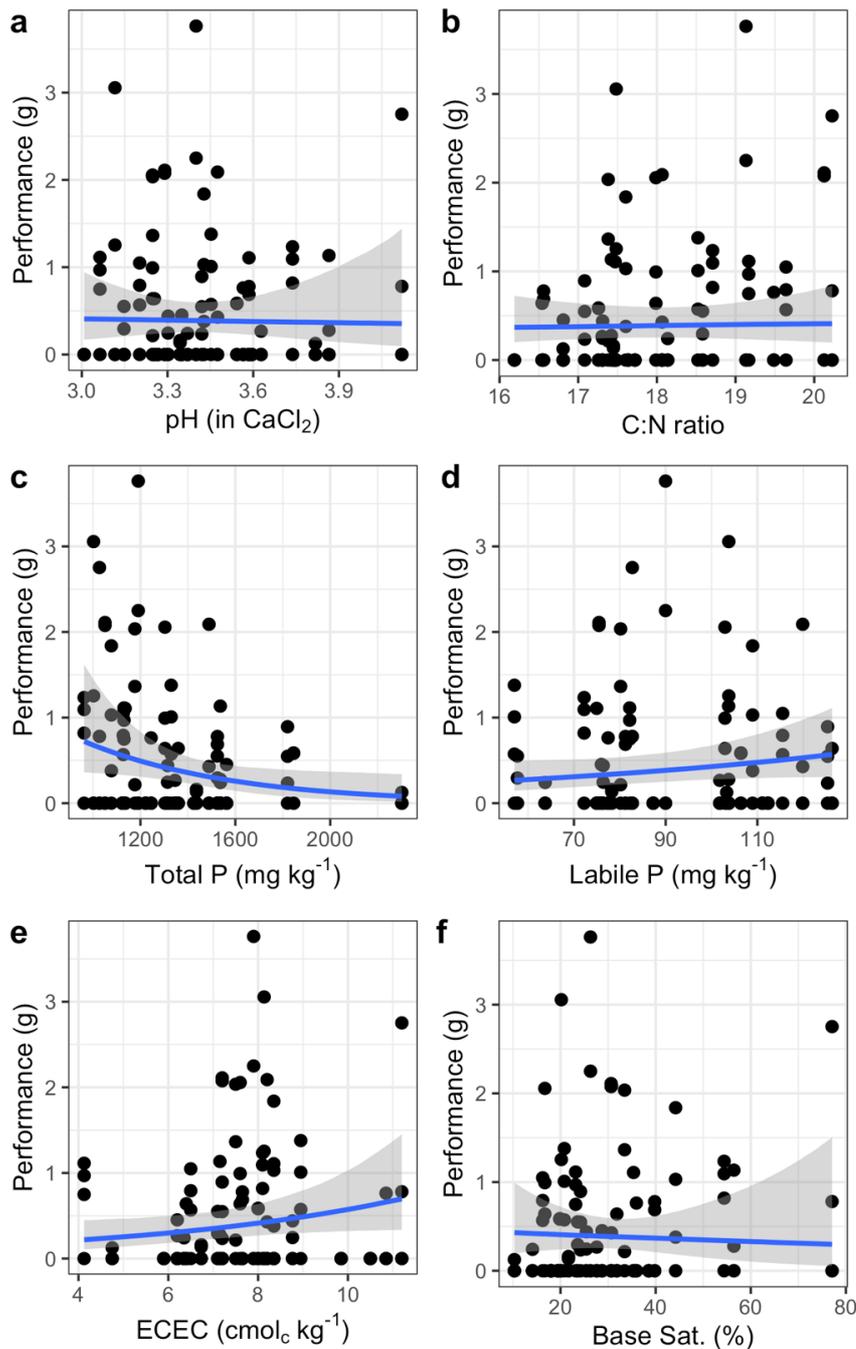
15 Upper and lower limits of the violin plots represent 90% credible interval. Diamonds show

16 medians.



17

18 **Figure S4.** Soil characteristics for each forest type by horizons (a) pH (in CaCl₂), (b) C:N
 19 ratio, (c) total P, (d) labile P (e) effective cation exchange capacity (ECEC) and (f) base
 20 saturation. ECEC and base saturation were not calculated on highly organic sample (L and F
 21 horizons). Error bars represent the standard error of the mean of the estimated parameters.



22

23 **Figure S5.** Plots of marginal effects of (a) pH (in CaCl₂), (b) carbon:nitrogen ratio, (c) total

24 phosphorus, (d) labile (Bray) P (e) effective cation exchange capacity (ECEC) and (f) base

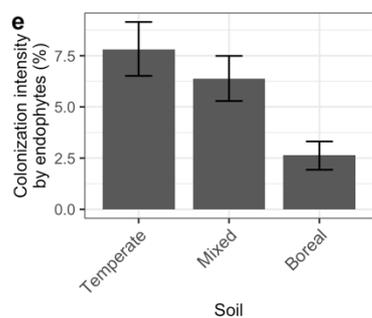
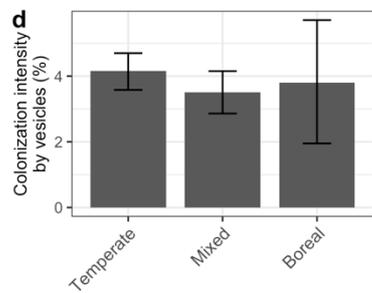
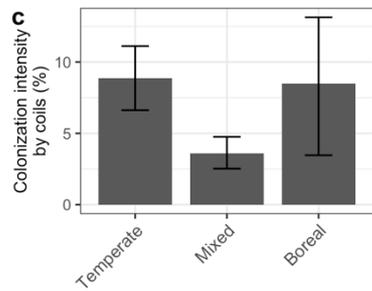
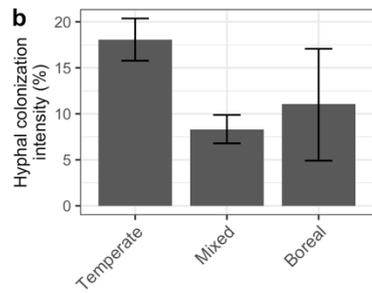
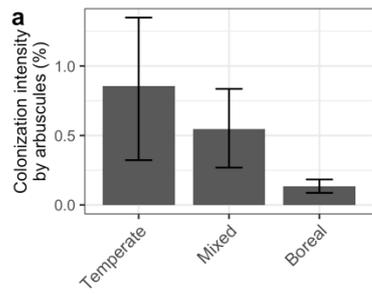
25 saturation on sugar maple seedling performance. Values of soil variables were averaged

26 across horizons. Blue lines represent the slopes with credible intervals at 90 % shown in

27 shaded grey. ECEC had an estimate of effect that differed from zero with 90% confidence.

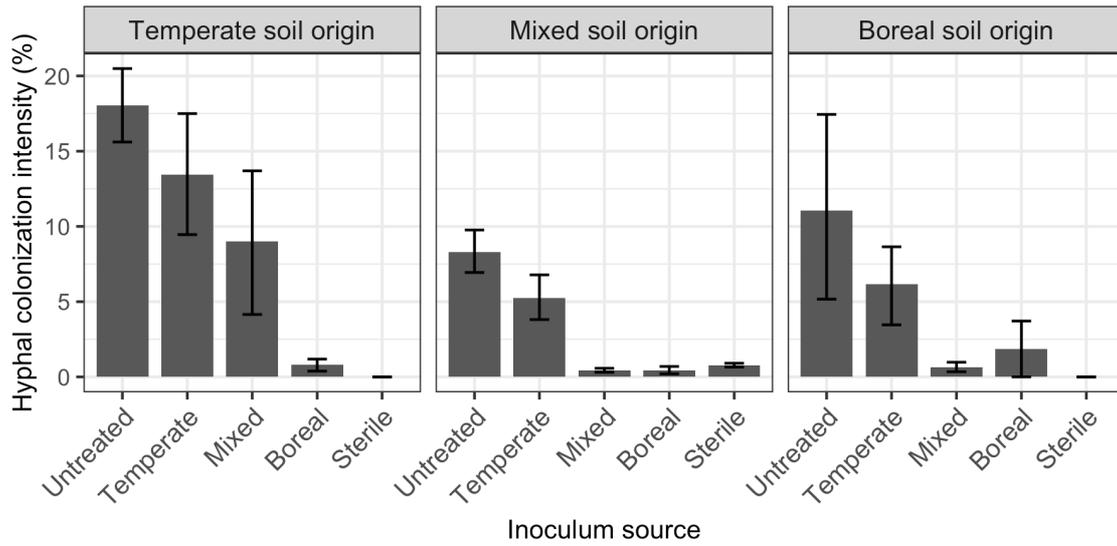
28 Modelling was done using a Hurdle analysis with the soil variables as fixed factors and block

29 as a random factor.



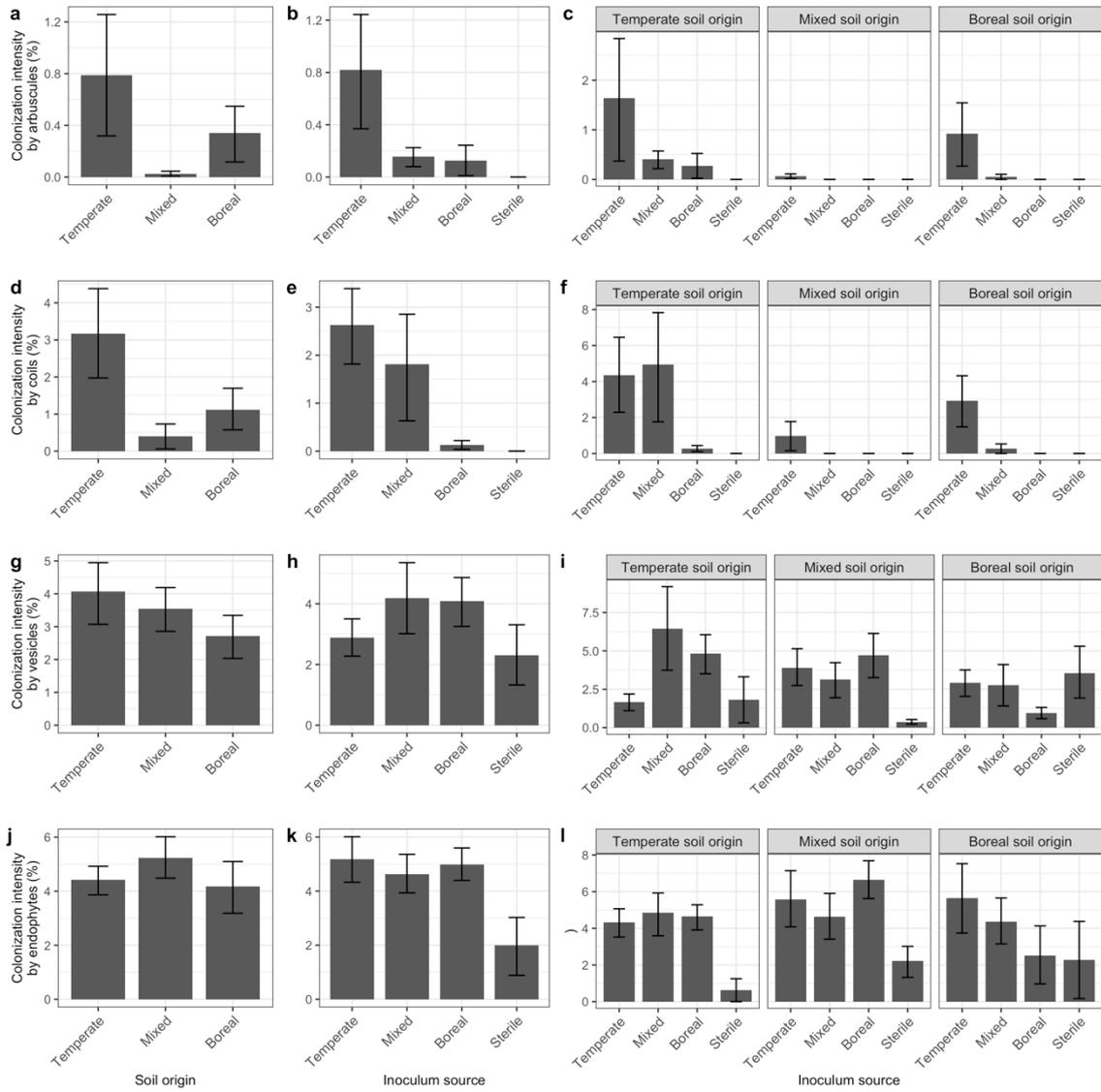
30

31 **Figure S6.** Root colonization (experiment 1) by different fungal structures: a) arbuscules, b)
 32 fungal hyphae, c) coils, d) vesicles and e) fungal endophytes. Error bars represent the standard
 33 error of the mean of the observed parameters.



34

35 **Figure S7.** Effects of soil origin combined with inoculum source from experiment 1 and
 36 untreated soil from experiment 2 on hyphal root colonization of sugar maple seedlings. Error
 37 bars represent the standard error of the mean of the observed parameters.

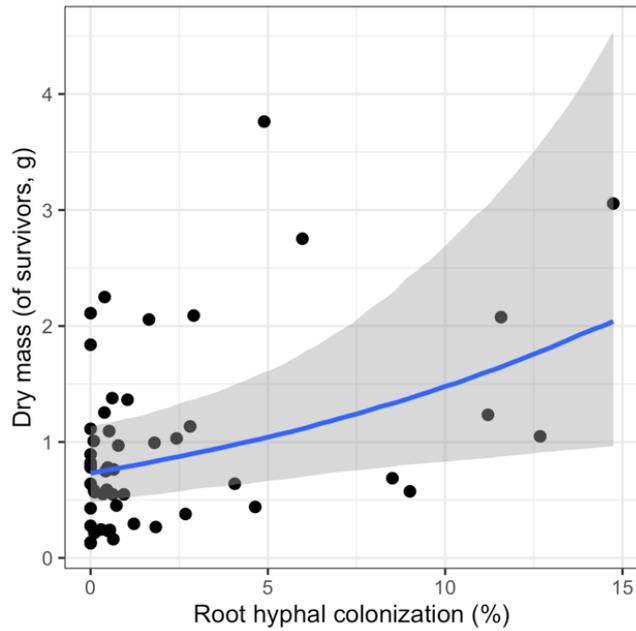


38

39 **Figure S8.** Root colonization (experiment 2) by different fungal structures: arbuscules (a, b,

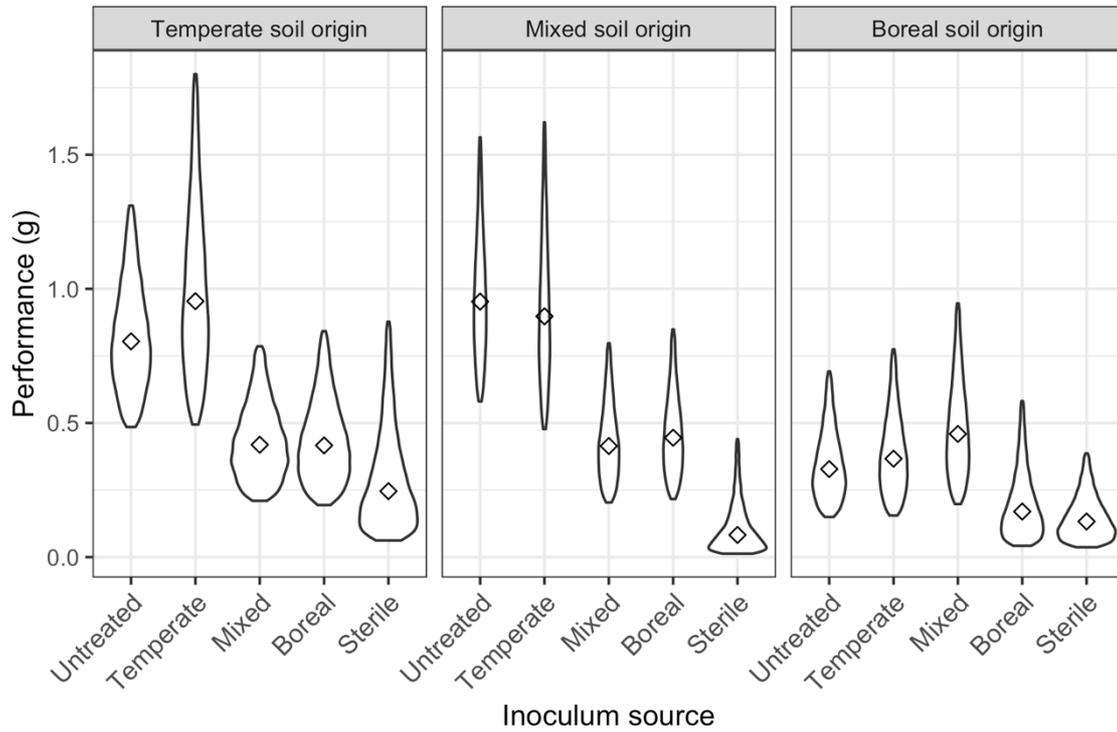
40 c) and coils (d, e, f), fungal vesicles (g, h, i) and fungal endophytes (j, k, l). Error bars

41 represent the standard error of the mean of the observed parameters.



42

43 **Figure S9.** Plot of the marginal effect of root hyphal colonization on sugar maple seedling
 44 dry mass. Analysis was done using a generalised linear mixed-effects model with root hyphal
 45 colonization as a fixed factor and block as a random factor. The blue line represents the slope
 46 with credible interval at 90 % shown in shaded grey. The estimate of the slope differs from
 47 zero with 90% confidence. Note that two seedlings with much higher root hyphal colonization
 48 (>39%) than the others (<15%) were removed from the analysis; although the positive effect
 49 of colonization on dry mass still holds when these two extreme values are included.



50

51 **Figure S10.** Comparison of the performance of sugar maple seedlings in untreated soil vs
 52 treated soil (temperate, mixed or boreal inoculum and sterile) of the same soil origin
 53 (temperate, mixed or boreal). Based on the same Hurdle analysis than experiment 1 but
 54 combining data of untreated and treated soil (experiments 1 and 2). Means are shown with
 55 90% credible intervals.

56 **Table S1.** Spearman's rank correlation between dry mass and other measured seedling traits
 57 for the experiment 1 (sample size is 21) and experiment 2 (sample size is 54).

	Leaf area	Stem length	Root length
Dry mass	0.87***	0.57***	0.94***
<i>Experiment 1</i>			
Dry mass	0.88***	0.61***	0.94***
<i>Experiment 2</i>			

58 *** P-values < 0.001.

59 **Table S2.** Observed number of seedlings that survived in experiment 1 and subsequent
60 sample size for the modelling of dry mass.

	Forest type		
	Temperate	Mixed	Boreal
Survivors	9	9	4

61

62 **Table S3.** Observed number of seedlings that survived in experiment 2 and subsequent sample
 63 size for the modelling of dry mass.

	Soil origin											
	Temperate		Mixed		Boreal							
Survivors	18		21		15							
Inoculum source	Temperate	Mixed	Boreal	Sterile	Temperate	Mixed	Boreal	Sterile	Temperate	Mixed	Boreal	Sterile
Survivors	6	6	5	1	7	6	6	1	5	5	2	3

64

65 **Table S4.** Spearman's rank correlation between dry mass and traits of fungal colonization for
 66 experiment 1 (sample size is 21) and experiment 2 (sample size is 54).

	Arbuscules	Hyphae	Vesicles	Coils	Endophytes
Dry mass	0.22	0.26	0.13	0.34	0.11
<i>Experiment 1</i>					
Dry mass	0.46***	0.32*	0.13	0.49***	-0.29*
<i>Experiment 2</i>					

67 * P-values < 0.05; ** P-values < 0.01; *** P-values < 0.001.

68 **Table S5.** Results of the Hurdle analysis for experiment 1. Effect of forest type on survival
 69 probability, dry mass and performance of sugar maple seedlings. Mean with standard error and
 70 credible interval (CI) at 90%.

	Forest type	Mean	Standard error	Lower CI	Higher CI
Survival probability	Temperate	0.82	0.12	0.58	0.96
	Mixed	0.89	0.10	0.69	0.99
	Boreal	0.42	0.20	0.10	0.75
Dry mass (g)	Temperate	1.13	0.30	0.72	1.66
	Mixed	1.23	0.34	0.79	1.82
	Boreal	0.60	0.27	0.31	1.06
Performance (g)	Temperate	0.93	0.29	0.52	1.43
	Mixed	1.10	0.33	0.66	1.67
	Boreal	0.25	0.17	0.05	0.55

71

72 **Table S6.** Results from the Hurdle analysis for experiment 2. Effect of soil origin and inoculum
73 source on survival probability, dry mass and performance of sugar maple seedlings. Mean with
74 standard error and credible interval (CI) at 90%.

	Soil origin	Inoculum	Mean	Standard	Lower CI	Higher CI
		source		error		
Survival probability	Temperate	Temperate	0.56	0.11	0.37	0.74
		Mixed	0.58	0.13	0.35	0.80
		Boreal	0.48	0.14	0.26	0.71
		Sterile	0.17	0.09	0.05	0.35
	Mixed	Temperate	0.65	0.13	0.43	0.84
		Mixed	0.61	0.14	0.36	0.83
		Boreal	0.60	0.14	0.35	0.82
		Sterile	0.13	0.09	0.02	0.31
	Boreal	Temperate	0.50	0.13	0.28	0.72
		Mixed	0.50	0.15	0.26	0.75
		Boreal	0.23	0.12	0.06	0.46
		Sterile	0.27	0.13	0.08	0.50
Dry mass (g)	Temperate	Temperate	1.59	0.54	0.90	2.56
		Mixed	0.77	0.29	0.41	1.28
		Boreal	0.89	0.35	0.46	1.53
		Sterile	1.75	1.27	0.58	3.96
	Mixed	Temperate	1.23	0.42	0.68	1.99
		Mixed	0.71	0.26	0.37	1.18
		Boreal	0.80	0.30	0.44	1.33
		Sterile	0.94	0.98	0.25	2.42
	Boreal	Temperate	0.77	0.30	0.39	1.32
		Mixed	0.96	0.38	0.49	1.65
		Boreal	1.14	0.69	0.44	2.40
		Sterile	0.61	0.31	0.27	1.17
Performance (g)	Temperate	Temperate	0.89	0.36	0.44	1.55
		Mixed	0.45	0.20	0.20	0.81
		Boreal	0.43	0.21	0.17	0.82
		Sterile	0.29	0.29	0.05	0.80
	Mixed	Temperate	0.80	0.32	0.39	1.38
		Mixed	0.43	0.19	0.19	0.78
		Boreal	0.48	0.22	0.21	0.87

	Sterile	0.12	0.17	0.01	0.37
Boreal	Temperate	0.39	0.19	0.16	0.73
	Mixed	0.48	0.24	0.18	0.93
	Boreal	0.26	0.23	0.05	0.68
	Sterile	0.16	0.12	0.04	0.38

75

76 **Modelling specification**

77 1. Gamma distribution part of the model

78 Bayesian theorem:

79 $P(\mu, r|Y) \propto P(Y|u, r) \times P(u) \times P(r)$

80 where $Y \sim \text{Gamma}(u, r)$

81

82 Gamma distribution likelihood function:

83 $f(y|\mu, r) = \frac{1}{\Gamma(r)} \times \left(\frac{r}{\mu}\right) \times y^{r-1} \times e^{-\frac{y \times r}{\mu}}$

84

85 $L(y|\mu, r) = \prod_{i=1}^n f(y|\mu, r) = \prod_{i=1}^n \frac{1}{\Gamma(r)} \times \left(\frac{r}{\mu}\right) \times y^{r-1} \times e^{-\frac{y \times r}{\mu}}$

86

87 where $\log(\mu_i) = \theta_{c_i} \times X_{c_i} + a_{c_i}$ and

88 $\theta_{c_i} \times X_{c_i} = \beta_{c1} + \beta_{c2-4} \text{Soil origin} + \beta_{c5-9} \text{Inoculum source}$

89 $+ \beta_{c10-24} (\text{Soil origin} * \text{Inoculum source})$

90 The index c refers to the continuous (gamma) distribution part of the model and a_{c_i} refers to

91 the random intercept block for the continuous part of the model. X_{c_i} refers to a matrix of

92 dummy variable for the different inoculum source, soil origin and their interaction. Theta

93 (θ_{c_i}) is a matrix containing the betas.

94

95 For experiment 1, there is only one forest as predictor which gives:

96 $\theta_{c_i} \times X_{c_i} = \beta_{c1} + \beta_{c2-4} \text{Forest type}$

97

98 Priors:

99 Random effect (intercept)

100 $a_{c_i} \sim N(0, \tau_c)$

101 $f(a_{c_i} | 0, \tau_c) = P(a_{c_i} | 0, \tau_c) = \frac{1}{\sqrt{(1/\tau_c)}\sqrt{2\pi}} \times e^{-\frac{(a_{c_i}-0)^2}{1/\tau_c}}$

102 Where $\tau_c = 1/\sigma_c \times \sigma_c$

103 and $\sigma_c \sim U(0,100)$

104

105 Fixed effect thetas

106 $\theta_{c_i} \sim N(\mu_{\theta_{c_i}}, \sigma^2)$

107 $f(\theta_{c_i} | \mu_{\theta_{c_i}}, \sigma^2) = P(\theta_{c_i} | \mu_{\theta_{c_i}}, \sigma^2) = \frac{1}{\sigma\sqrt{2\pi}} \times e^{-\frac{(\theta_{c_i}-\mu_{\theta_{c_i}})^2}{\sigma^2}}$

108 where $\mu_{\theta_{c_i}}$ was fixed to 0 and variance was fixed to 3.

109

110 Shape parameter

111 $r \sim U(a, b)$

112 where a was fixed to 0 and b was fixed to 5

113 $f(r | a, b) = P(r | a, b) = \frac{1}{b-a}$

114

115 Posterior distribution:

116 $P(\mu, r | Y) = \prod_{i=1}^n \frac{1}{\Gamma(r)} \times \left(\frac{r}{\mu}\right) \times y^{r-1} \times e^{-\frac{y_i \times r}{\mu}} \times \prod_i \frac{1}{\sigma\sqrt{2\pi}} \times e^{-\frac{(\theta_{c_i}-\mu)^2}{\sigma^2}} \times \frac{1}{b-a} \times$

117 $\prod_i \frac{1}{\sqrt{(1/\tau_c)}\sqrt{2\pi}} \times e^{-\frac{(a_i-0)^2}{1/\tau_c}}$

118

119 2. Bernoulli distribution part of the model

120 Bayesian theorem:

121 $P(\pi | Y) \propto P(Y | \pi) \times P(\pi)$

122 where $Y \sim Bern(\pi)$

123

124 Bernoulli distribution likelihood function:

125 $f(y|\pi) = \pi^y \times (1 - \pi)^{1-y}$

126 $L(y|\pi) = \prod_{i=1}^n f(y|\pi) = \prod_{i=1}^n \pi^y \times (1 - \pi)^{1-y}$

127 where $\text{logit}(\pi_i) = \theta b_i \times X b_i \times a_{b_i}$ and

128 $\theta b_i \times X b_i = \beta_{b1} + \beta_{b2-4} \text{Soil origin} + \beta_{b5-9} \text{Inoculum source}$

129 $+ \beta_{b10-24} (\text{Soil origin} * \text{Inoculum source})$

130 The index b refers to the binary part of the model and a_{b_i} refers to the random intercept block

131 for the binary part of the model. $X b_i$ refers to a matrix of dummy variable for the different

132 inoculum source, soil origin and their interaction. Theta (θb_i) is a matrix containing the betas.

133

134 For experiment 1, there is only one forest as predictor which gives:

135 $\theta c_i \times X c_i = \beta_{c1} + \beta_{c2-4} \text{Forest type}$

136

137 Priors:

138 Random effect (intercept)

139 $a_{b_i} \sim N(0, \tau_b)$

140 $f(a_{b_i} | 0, \tau_b) = P(a_{b_i} | 0, \tau_b) = \frac{1}{\sqrt{(1/\tau_b)}\sqrt{2\pi}} \times e^{-\frac{(a_{b_i}-0)^2}{1/\tau_b}}$

141 where $\tau_b = 1/\sigma_b \times \sigma_b$

142 and $\sigma_b \sim U(0,100)$

143

144 Fixed effect thetas

145 $\theta b_i \sim N(\mu_{\theta b_i}, \sigma^2)$

146

147 $f(\theta b_i | \mu_{\theta b_i}, \sigma^2) = P(\theta b_i | \mu_{\theta b_i}, \sigma^2) = \frac{1}{\sigma\sqrt{2\pi}} \times e^{-\frac{(\theta b_i - \mu_{\theta b_i})^2}{\sigma^2}}$

148 where $\mu_{\theta b_i}$ was fixed to 0 and variance was fixed to 3

149

150 Posterior distribution

$$151 \quad P(\pi|Y) = \prod_{i=1}^n \pi^{y_i} \times (1 - \pi)^{1-y_i} \times \prod_i^n \frac{1}{\sigma\sqrt{2\pi}} \times e^{-\frac{(\theta b_i - \mu_{\theta b_i})^2}{\sigma^2}} \times \prod_i^n \frac{1}{\sqrt{(1/\tau_b)}\sqrt{2\pi}} \times e^{-\frac{(a_{b_i} - 0)^2}{1/\tau_b}}$$

152

153 3. Hurdle model

$$154 \quad P(Y = y | \theta_c, \theta_b) = \begin{cases} (1 - \pi_i), & y_i = 0 \\ \pi_i \times f_{\text{gamma}}(Y|\mu, r), & y_i > 0 \end{cases}$$

155 where $\pi = 1$ is considering a success

156

157 Model validation was implemented in one step (see the model code). The advantage of doing

158 so is that the expected values and the Pearson's residuals could have been calculated within

159 the model code (specified in the model code).

160 Explanation: Let $f(Y_i | \theta)$ be any distribution and $L(Y | \theta) = \prod_i^n f(Y_i | \theta)$ is likelihood

161 function. Using the mathematical rule $e^{\log(x)} = x$, we have: $\prod_i^n f(Y_i | \theta) = \prod_i^n e^{\log(f(Y_i | \theta))}$

162 $= \prod_i^n e^{l_i}$, where $l_i = \log(f(Y_i | \theta))$. Using the fact that $0! = 1$ and something to the power

163 of zero is define as 1, we can rewrite the likelihood function as the likelihood function of a

164 Poisson distribution with observed values 0 and mean values $-l_i$. Since the mean of a

165 Poisson distribution must be non-negative a positive constant C is added to the mean, such as

166 $C - l_i > 0$, and does not affect the likelihood estimation.

$$167 \quad L(Y | \theta) = \prod_i^n e^{l_i} = \prod_i^n \frac{(-l_i)^0 \times e^{-(-l_i)}}{0!} = \prod_i^n f_{\text{poisson}}(0 | -l_i) = \prod_i^n f_{\text{poisson}}(0 | -l_i + C)$$

168

169 All parameters within l_i could fit any distribution and their posterior distribution could be

170 obtained within the JAGS function. Using the step function within the model code to figure

171 out whether the biomass value for an observation y_i is equal to 0 or not, allow to determine

172 which part of the log likelihood is to be calculated.