1   Intended for *Restoration Ecology*

2

3   Title:

Identifying effective tree planting schemes to restore forest

carbon and biodiversity in Shiretoko National Park

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22   Running head: A model-based forest restoration experiment

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Abstract

Growing interest in ecosystem restoration has recently turned the focus on tree planting, one of the most widely used restoration tools globally. Here, we study the restoration potential of tree planting in a cool-temperate forest in Shiretoko National Park, northern Japan. We used simulation modeling to investigate the long-term success of tree planting in restoring biodiversity and the climate change mitigation function relative to intact natural forests. Specifically, we investigated 31 different restoration scenarios, consisting of five planting densities (1,000 to 10,000 trees ha^{-1}) × six levels of planted tree species richness (one to six species) + one no-planting scenario. We examined these scenarios at different distances from natural forests serving as a seed source (0 to 300 m) to quantify the potential for natural regeneration.

In restoration areas in close proximity to a natural forest, species-rich high density planting scenario performed best, reaching >50% of the reference values from intact natural forests within 33 years for both restoration goals. However, variation in restoration outcomes was small when >2,500 trees ha^{-1} of >4 species were planted, regardless of distance to seed source. In contrast, biodiversity restoration was considerably delayed in scenarios that planted species richness was low as well as in restoration areas that were far from a seed source yet relied solely on natural regeneration. We here demonstrate how forest landscape simulation can be used to identify viable restoration options for managers across multiple restoration goals as an important step to bridge the research-implementation gap in forest restoration.

Implications for Practice (LL 48)

✓ Planting late-successional tree species can accelerate carbon and biodiversity restoration in a cool temperate ecosystem. Restoration success is achieved early when mixed species are planted, and planting densities are increased with distance to seed source.

✓ Biodiversity recovery lags behind carbon recovery. High density plantings of a single species and no-planting far from a seed source extends restoration times of biodiversity to a century or more.

✓ Model-based simulations with varying levels of human intervention can highlight management measures that are effective, and also identify options that are unlikely to result in successful restoration. In this way, simulation can provide the options space from which decision makers can choose, given social and economic constraints.

Keywords: forest landscape model, ecosystem services, species richness, planting density, passive/active restoration, long-term forest restoration.

Introduction

Restoring degraded land to natural vegetation has multiple benefits for society, improving ecosystem service supply and biodiversity (Benayas et al. 2009). In the context of forest restoration, tree planting has increasingly come into focus, particularly since the carbon capture and storage by trees plays a vital role in mitigating climate change (Forster et al. 2021). Under the United Nations (UN) Decade on Ecosystem Restoration, declared by the UN General Assembly in 2019, many tree planting initiatives have been launched from local to global scales, including the Bonn Challenge (www.bonnchallenge.org), New York Declaration on Forests (forestdeclaration.org), 20 × 20 (initiative20x20.org), and AFR100 (afr100.org). To make these critical efforts truly effective, scholars have provided qualitative (e.g., Brancalion & Holl 2020; Di Sacco et al. 2021) and quantitative suggestions (e.g., Brancalion et al. 2019; Strassburg et al. 2020) for restoration planting.

In degraded areas adjacent to intact forests, vegetation recovery often proceeds through natural regeneration also without human intervention (e.g., Crouzeilles et al. 2017; Crouzeilles et al. 2020; Poorter et al. 2021). Although such passive restoration approach could be cost-effective, natural regeneration and planting are not mutually exclusive and can be used complementarily (Reid et al. 2018). For instance, if old-growth natural forest conditions are the target of restoration, supplemental tree planting of late-successional species in a cohort of naturally regenerating early-seral species likely shortens the time to achieve restoration goals (Cole et al. 2011; Osorio-Salomón et al. 2021). Effective restoration approaches thus need to adjust important parameters, including planting density and species richness of planting trees, to the spatial context of a restoration site, such as the distance to an intact natural forest that can provide seed input and foster natural regeneration (Reid et al. 2015).

Although a number of restoration experiments have been initiated to identify promising

94 restoration approaches (TreeDivNet, https://treedivnet.ugent.be/), long study periods are needed

95 to gauge restoration success and accumulate local expertise (Verheyen et al. 2016). In addition,

96 important aspects such as the above-mentioned spatial context of a restoration site are difficult to

97 consider experimentally. One way to complement *in situ* experiments is by using simulation

98 models such as forest landscape models, FLMs (Shifley et al. 2017; Petter et al. 2020). FLMs

99 enable the simulation of forest recovery explicitly in time and space, considering a variety of

100 management scenarios (e.g., Temperli et al. 2012; Braziunas et al. 2018; Krofcheck et al. 2019).

101   Shiretoko National Park is a focal area of forest restoration in Japan, with the aim to swiftly

102 restore near-natural forest cover (Suzuki et al. 2021). Located in the northeast of Hokkaido,

103 Shiretoko National Park was designated in 1964 and covers 39,000 ha of land and sea (Fig. 1).

104 Some parts of the park were deforested for agricultural use in the early 20th century (Fig. S1 and

105 S2). Since 1977 numerous restoration efforts have been made on a total of 861 ha of deforested

106 area to restore mixed conifer-broadleaf natural forests (100m2.shiretoko.or.jp). These restoration

107 efforts are hampered by the prevailing harsh environmental conditions, as well as by browsing of

108 Ezo deer (*Cervus nippon yesoensis*) and the invasion of dwarf bamboo (*Sasa kurilensis* and *S.*

109 *spiculosa*). Consequently, assisted natural regeneration approaches have been applied, aiming to

110 control the population of Ezo deer, establishing deer fences, and scarifying the soil with heavy

111 machinery (Nishizawa et al. 2016; Ishinazaka 2016). Given that these measures are highly

112 resource intensive and that the area is a center for tourism, identifying time- and cost-efficient

113 restoration pathways is of critical importance for local authorities. Here, our objective was to

114 simulate vegetation recovery after agricultural abandonment under a variety of different planting

115 strategies for Shiretoko National Park. Specifically, we aimed to determine the ecological

116 potential of tree planting for the restoration of biodiversity and the climate change mitigation

117 function.

Methods

Study area

We studied the cool-temperate forests of Shiretoko National Park, located at N44°08′ to 11′ and E145°03′ to 08′ in the north-east of Hokkaido, Japan (Fig. 1). In 2005, the United Nations Educational, Scientific and Cultural Organization (UNESCO) identified this area as a World Natural Heritage based on criteria ix (significant ecological and biological processes) and x (significant natural habitat for biodiversity; whc.unesco.org/en/list/1193). Approximately 90% of the terrestrial area of the national park is intact natural vegetation, extending over three climate zones (elevation between 0 and 1,660 m asl): alpine, sub-alpine, and cool-temperate (Fig. S1). The cool-temperate zone is mostly mixed conifer-broadleaf forests dominated by Sakhalin fir (*Abies sachalinensis*), Painted maple (*Acer mono*), Castor aralia (*Kalopanax septemlobus*), and Japanese oak (*Quercus mongolica* ssp. *crispula*). A total area of 861 ha was converted to agricultural land from natural forest by domestic settlers since 1914 (Fig. S1 and Fig. S2). The settlers abandoned these areas by the late 1960s. As the first national trust movement in Japan, the local government of Shari Town purchased the deforested areas (861 ha) for restoration from 1977 to 1997. The restoration agency is the Shiretoko Nature Foundation, which is supported by citizens and companies from all over Japan (www.shiretoko.or.jp).

Simulation model

We simulated the effect of different restoration strategies using iLand, a process- and individual-based FLM (Seidl et al. 2012). iLand simulates the life history of individual trees explicitly in time and space. It considers species-specific responses to environmental drivers (e.g., light availability, temperature, water, and nutrient availability), disturbances (e.g., wind, bark beetles, and fire), and management (e.g., planting, thinning, and harvesting). Trees taller than 4 m are

142   represented as individuals, while saplings below 4 m are simulated as size × species cohorts at 2

143   × 2 m horizontal resolution. Environmental conditions (climate and soil) are considered to be

144   homogeneous within 100 × 100 m cells.

145   The iLand model explicitly simulates the three fundamental processes of forest dynamics:

146   tree growth, mortality, and regeneration. Tree growth is modeled based on a light-use efficiency

147   approach that calculates carbon fixation from photosynthesis and its allocation to stem, branch,

148   foliage, and root compartments, accounting for adaptive responses of each individual to its

149   immediate surrounding. Tree mortality is simulated as a combination of species-specific life

150   history parameters (maximum age and height) and individual tree stress. The latter is calculated

151   based on the carbon balance of a given tree, with stress occurring when a tree's maintenance

152   respiration exceeds its carbon gains (carbon starvation). Disturbance-related tree mortality was

153   not considered in this application of the model. Regeneration processes considered are 1) the

154   distribution of seeds from mature trees, 2) the suitability of a site for local establishment, and 3)

155   the growth of saplings based on environmental modifications of a species-specific height growth

156   potential. Detailed documentation of the model as well as its source code are available at

157   http://iland-model.org. iLand has been successfully applied in the Pacific Northwest (Seidl et al.

158   2012; Seidl et al. 2014b) and Northern Rocky Mountains (Braziunas et al. 2018; Hansen et al.

159   2018) of North America as well as in several countries of Central Europe (e.g., Seidl et al. 2014a;

160   Pedro et al. 2015; Thom et al. 2017). The current contribution is the first application of the model

161   in Asia, which is why we describe our parameterization and evaluation efforts in more detail in

162   the following section.

163

164   ***Model parameterization and evaluation***

165   We parameterized five coniferous and twelve broadleaved species common in Shiretoko National

166   Park (Table S1). Most species-specific parameters were collected from the peer-reviewed

167   literature and online sources. A small subset of parameters (e.g., aging and stress-related

168   mortality) were determined by iteratively comparing simulation results with 12 years of observed

169   data to fill gaps in the literature and ensure model-internal consistency of the compiled parameters

170   (see Supplement S1). For site-specific driver data, we obtained historical climate information at

171   daily time step (temperature, vapor pressure deficit, precipitation, and radiation) from 1980 to

172   2019 from the Agro-Meteorological Grid Square Data, NARO (Ohno et al. 2016;

173   amu.rd.naro.go.jp, accessed 21 July 2020). Soil-related parameters (plant-available nitrogen, soil

174   texture, and effective soil depth) were obtained from an *in-situ* field survey (Mori et al. 2015). All

175   parameter values used in the simulations are given in Table S2.

176   We subsequently evaluated the model using forest monitoring data from the Forestry Agency

177   of Japan (Fig. 1, plot A to D). The Forestry Agency of Japan has conducted tree surveys on four

178   1-ha plots (two sites) in the cool-temperate natural forests of Shiretoko National Park every six

179   years since 2005 (Fig. 1 and Fig. S1). This survey includes measurements of height (2005 only),

180   diameter at breast height, location, and survival of all trees over 2 m in height that are identified

181   by aluminum tags throughout the plots. These raw data are available at the website of the Forestry

182   Agency   of   Japan

183   (www.rinya.maff.go.jp/hokkaido/policy/business/pr/siritoko_wh/hozen_saisei.html, accessed 13

184   July 2016). We evaluated the ability of iLand to simulate growth and mortality by comparing

185   simulations at the four 1-ha tree census plots to these independent observations. We furthermore

186   simulated successional trajectories from bare ground for 300 years, testing if the model is able to

187   reproduce the current species composition in intact natural forests. A detailed account of the model

188   evaluation exercises is given in Supplement S1. Overall, results showed good correspondence

189   with field observations and ecological expectations, supporting the applicability of the model to

190   study vegetation dynamics at Shiretoko National Park (Supplement S1).

191

192   ***Restoration simulation experiment***

193   We used iLand to assess the potential of 31 different restoration scenarios for a 1-ha restoration

194   site surrounded by cool-temperate natural forests in Shiretoko National Park (Fig. 2). Site

195   conditions were those of site 2 described above, corresponding most closely to the conditions

196   prevailing in the southwestern parts of Shiretoko National Park, which are the main focal areas

197   of restoration efforts (Fig. S1). We tested the combination of five different planting densities and

198   six species richness levels (i.e., a total of 30 planting scenarios) with regard to their restoration

199   effect. Planting densities ranged from 1,000 to 10,000 trees ha^{-1} (1,000, 2,500, 5,000, 7,500,

200   10,000 trees ha^{-1}). Planting species were the top six species from the abundance rank of the four

201   1-ha natural forest plots (*A. sachalinensis*, *A. mono*, *K. septemlobus*, *Q. mongolica* ssp. *crispula*,

202   *Prunus ssiori*, and *Magnolia hypoleuca*; Table S3). The proportions of each species were

203   equalized (Table S4). The Shiretoko Nature Foundation plants trees between 0.5 and 5.0 m in

204   height that are grown in a nursery from seeds collected in natural forests. In this study, we used a

205   uniform plant size of 1.3 m height for planting trees. We also simulated a no-planting scenario in

206   which recovery proceeds only through natural regeneration (a total of 31 restoration scenarios).

207   In addition, we accounted for the widely varying spatial context of restoration site by considering

208   different distances to the nearest natural forest stands. Specifically, we studied six different spatial

209   context patterns for each restoration scenario, simulating distances of 0, 20, 50, 100, 200, and 300

210   m to the natural forest stand (Fig. 2). In total, we simulated 186 different combinations of tree

211   density, species mixture, and distance to natural forest.

212   We simulated vegetation development after agricultural abandonment (i.e., zero initial tree

213   cover) under each scenario for 300 years but focused our analysis on the first decades of

214   restoration (see details below). Climate data for the simulations was generated by randomly

215   sampling from the period 1980 to 2019 with replacement, assuming stable climate conditions. We

216   also assumed that the restoration area is fully fenced and soil scarified, i.e., other inhibiting factors

217   of vegetation development in Shiretoko National Park were excluded. These boundary conditions

218   were the same for all simulations (i.e., in planting and no-planting scenarios). To quantify

219   uncertainties related to species parameters (Supplement S1), we created ten alternative species

220   parameter sets. Specifically, we multiplied random values ranging from 0.8 to 1.2 to the original

221   parameters of intrinsic mortality, stress-related mortality, fecundity, and seed dispersal distance.

222   We then ran five replicate simulations for each species parameter sets to account for stochasticity

223   in the simulations (5 replicates × 10 additional datasets).

224

225   ***Data analysis***

226   To quantify the restoration potential of the different scenarios, we compared simulation results to

227   reference conditions from natural forests. Reference conditions were derived from the four 1-ha

228   natural forest plots described above (Table S3). We analyzed six ecological indicators based on

229   trees over 4 m in height, related to two general restoration objectives. For the restoration objective

230   climate change mitigation, we analyzed net primary productivity (NPP) as an indicator of carbon

231   uptake as well as total carbon in the above- and below-ground biomass and the growing stock of

232   trees as indicators of carbon storage in forest ecosystems. The restoration of biodiversity was

233   assessed via indicators of tree species richness, the Shannon-Wiener diversity (calculated from

234   the growing stock of trees), and community similarity to natural forest conditions. Community

235   similarity was based on the Bray-Curtis similarity index (B) defined as:

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$$B = 1 - \frac{\sum_{i=1}^{n} |X_{i,j} - X_{i,k}|}{\sum_{i=1}^{n} (X_{i,j} + X_{i,k})} \quad (1)$$

238

239   where i is species, j and k are the restoration and reference site, respectively, and X is abundance

240   (Doi & Okamura 2011). B ranges from 0 (different) to 1 (similar). We set tree density (D), growing

241   stock of trees (S), and tree height (H) as abundance X and created an integrated similarity index

242   (ISI) as:

243

$$ISI = 1 - \left(\frac{\sum_{i=1}^{n} |D_{i,j} - D_{i,k}|}{\sum_{i=1}^{n} (D_{i,j} + D_{i,k})} + \frac{\sum_{i=1}^{n} |S_{i,j} - S_{i,k}|}{\sum_{i=1}^{n} (S_{i,j} + S_{i,k})} + \frac{\sum_{i=1}^{n} |H_{i,j} - H_{i,k}|}{\sum_{i=1}^{n} (H_{i,j} + H_{i,k})} \right) / 3 \quad (2)$$

245

246   ISI ranges from 0 (different) to 1 (similar).

247   We evaluated restoration potential based on the time needed to recover to 50% of the

248   reference value (hereafter referred to as restoration time; Fig. S3). Reference values for all six

249   indicators are given in Table 1. Following the precautionary principle and presenting conservative

250   estimates for restoration practitioners, we report the maximum restoration time among the six

251   indicators for each scenario and distance to natural forest. The R statistical software (R Core Team

252   2021) with the vegan package (Oksanen et al. 2020) was used for all analyses of model outputs.

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Results

258 **Results**

259 The restoration times for a site in the immediate vicinity of a natural forest (distance-to-natural-

260 forest of 0 m) varied from 19 to >100 years among indicators and restoration scenarios (Fig. 3).

261 For climate change mitigation, the shortest restoration times were achieved by planting a single

262 species (*A. sachalinensis*) at very high density (10,000 trees ha^{-1}, Fig. 3a-c). Generally, restoration

263 times for the climate change mitigation function decreased with higher planting density and lower

264 species richness (Fig. 3a-c). This trend was similar at higher distances to natural forest (Fig. S4

265 to S6). Without planting, recovery times for NPP, total carbon, and growing stock were 17, 21,

266 and 20 years longer compared to the best restoration times achieved in planting scenarios (Fig. 3).

267 These differences increased with distance to natural forest (Fig. S4 to S6).

268 With regard to the restoration of biodiversity, restoration times decreased with increasingly

269 species rich plantations (Fig. 3d-f). Restoration time for the indicator species richness increased

270 with planting density particularly for plantations consisting of a small number of species (Fig. 3d),

271 as densely planted stands reduce the probability of migrated species from neighboring stands to

272 establish. However, restoration time for the similarity index (ISI) decreases with planting density

273 because the reference natural forest is dominated by four species (Table S3). Restoration time for

274 the Shannon-Wiener diversity thus differed markedly between planting three and four species

275 (Fig. 3e). These trends were also robust for other distances to natural forest (Fig. S7 to S9). In the

276 no-planting scenario, recovery times for species richness, Shannon-Wiener diversity, and

277 community dissimilarity (ISI) were 5, 14, and 10 years longer, respectively, compared to the

278 shortest restoration times achieved with planting (Fig. 3). These differences increased with

279 distance to natural forest, especially for ISI (Fig. S4 to S6). Some restoration scenarios failed to

280 reach 50% of the reference values for biodiversity in the first 50 years after the initiation of

281 restoration (Fig. 3). This was mostly the case in scenarios that planted trees at low species richness

282　and high density (Fig. 3). The risk for this protracted restoration success increased with distance

283　to natural forest (Fig. S7 to S9).

284　　　　The maximum restoration times among all six indicators are shown in Fig. 4. The risk for

285　protracted restoration (restoration times >50 years) increased with distance from natural forests

286　(between 39% to 68% in the considered 31 restoration scenarios, Fig. 4), mainly due to a slower

287　recovery time of biodiversity-related indices (Fig. S7 to S9). The no-planting scenario resulted in

288　protracted restoration success at all distances from natural forest (Fig. 4). At more than 100 m

289　distance from the nearest natural forest, it took more than 100 years to recover to at least 50% of

290　the reference values (Fig. 4e-f). A sensitivity analysis indicated that our findings are generally

291　robust to model parameter uncertainty, with high congruence in the emerging patterns across

292　scenarios and variation in restoration times remaining within ±5 years (Fig. S11).

293

Discussion

Ecological restoration potential

We here show that tree planting can generally accelerate restoration success at Shiretoko National Park. We, however, also highlight that outcomes vary considerably with restoration goals and indicators analyzed. Maximum restoration time across indicators was mainly driven by biodiversity-related indicators because restoring biodiversity takes longer than restoring the climate change mitigation function of forests in our study system. This is in line with other studies on forest recovery, indicating that ecosystem functioning recovers considerably faster than species composition (Martin et al. 2013; Seidl et al. 2014b). We moreover found trade-offs between the two restoration goals: While dense, single-species plantations quickly restored the climate change mitigation function, they considerably delayed the recovery of biodiversity, with restoration times of more than 100 years. This is because dense canopies of *A. sachalinensis*, a dominant species adapted to the harsh environmental conditions prevailing at Shiretoko National Park, are highly productive and limit the establishment and growth of other species for an extended period of time (Nonoda et al. 2008). Indeed, only one tree species of the local tree species pool (*Betula ermanii*) has been able to establish in the understory of mature, dense *A. sachalinensis* plantation in Shiretoko National Park (Fig. 5a).

We here selected species for restoration plantings based on their abundance in natural forests. With the exception of *A. sachalinensis*, all other species planted in our simulations were broadleaved trees, including *A. mono*, *P. ssiori*, and *M. hypoleuca*, which grow relatively slowly under the environmental conditions prevailing at Shiretoko National Park. We thus did not find positive effects of tree diversity on climate change mitigation in the first decades of forest restoration (Tilman 2014). Biomass-focused restoration projects will likely increase in the future given the urgent need to mitigate climate change (IPCC 2021) and a growing market for trading

318   carbon credits (Gren & Aklilu 2016). In our study, a sole focus on climate change mitigation in

319   restoration could lead to management decisions that are detrimental for biodiversity. Yet, fostering

320   biodiversity could also have positive effects on forest carbon storage not considered here, e.g.,

321   increasing the stability of carbon uptake in the face of disturbance (Isbell et al. 2015, Sebald et al.

322   2021) and improving soil carbon storage (Cardinale et al. 2012; Chen et al. 2018). Moreover,

323   increasing biodiversity can have positive effects on a variety of other ecosystem services

324   (Cardinale et al. 2012). We thus advocate for a broad consideration of different restoration effects

325   when making restoration decisions.

326   In restoration areas adjacent to a seed source, low-cost restoration approaches such as the

327   no-planting scenario simulated here are a viable alternative if decision makers can tolerate a delay

328   in restoration progress of approx. 15 years. The adoption of such low-cost approaches could help

329   to increase the overall area restored, given limited resources available for restoration. However,

330   our analysis highlights that the spatial arrangement of such passive restoration areas (i.e.,

331   landscape context; Haire & McGarigal 2010) is of key importance, with restoration success by

332   means of natural regeneration decreasing distinctly with distance to seed source. If biotic

333   homogenization is already high (Mori et al. 2018) and restoration patches are large, plantations

334   that decrease in stem density from the center to the edges of a patch might be effective in balancing

335   restoration costs and speed of recovery. If, on the other hand, restoration areas are embedded in a

336   matrix of natural forest, as is the case in many areas of Shiretoko National Park, natural

337   regeneration is an important process fostering restoration.

338   While we find advantages of an active restoration approach by means of tree planting over a

339   passive, no-planting approach, it needs to be interpreted in the specific context of our study area.

340   We here studied restoration in a cool-temperate forest with a small number of woody species

341   occurring naturally (<20 species), where four dominant tree species (*A. sachalinensis*, *A. mono*,

342   *K. septemlobus*, and *Q. mongolica* ssp. *crispula*) account for approximately 80% of the total

343   number of stems in natural forests. In ecosystems with a considerably higher tree species pool,

344   such as in the tropics and sub-tropics, a restoration approach that relies more on natural

345   regeneration might be advantageous, not least because of the challenging logistics of obtaining

346   plants for a large number of species (Shono et al. 2007; Chazdorn & Guariguata 2016). The

347   advantages of active restoration, therefore, should be evaluated based on specific designs as well

348   as the respective environmental context (Erskine et al. 2006; Corbin & Holl 2012). Such a more

349   nuanced perspective can help to overcome the sometimes overly simplistic discussion of planting

350   vs. natural regeneration for restoration (Reid et al. 2018).

351

352   *Contrasting science and implementation perspectives*

353   Identifying goals and examining their compatibility is a key issue to be addressed in restoration

354   (Pichancourt et al. 2014; Brancalion & Holl 2020). This is underscored by our findings that

355   optimal restoration management differs between the two restoration goals investigated here, i.e.,

356   climate change mitigation and biodiversity restoration. Identifying restoration goals often is a

357   highly complex task that requires the consideration of many factors, including financial, logistical,

358   legal, and cultural constraints (e.g., Young 2005; de Marques & Peres 2015; Brakes et al. 2021).

359   Furthermore, restoration agencies frequently need to integrate the multiple objectives of their

360   stakeholders. In the case of the Shiretoko Nature Foundation, these consist of more than 45,000

361   individual donors and 50 corporations making contributions (www.shiretoko.or.jp/). Naturally,

362   this broad and diverse group has a wide range of ideas regarding the priorities of restoration.

363   Given these inherent social-ecological uncertainties, it will hard find one-size-fits-all

364   approach, and thus a discussion focused solely on which practices are optimal from a scientific

365   perspective may not contribute to resolving the research-implementation gap, i.e., the mismatch

366   between knowledge generated by scientists and approaches implemented by practitioners (Cabin

367   et al. 2010). For instance, we here focused on climate change mitigation and biodiversity

368   restoration, yet if other ecosystem services (e.g., timber production, water purification, and

369   disaster reduction) or other facets of biodiversity (e.g., β, functional, and phylogenetic diversity)

370   were also considered important, optimal scenarios would differ from the ones identified here

371   (O'Connell et al. 2018; Doelman et al. 2020). However, our study clearly highlights the restoration

372   scenarios that can be omitted from the socio-ecological decision space because they are highly

373   likely to fail in reestablishing forest ecosystems within reasonable time frames (Masaki 2018).

374   Specifically, these scenarios at high risk of restoration failure are low density single-species

375   plantations and no planting far from seed sources. In discussing our results with a senior

376   restoration manager of the Shiretoko Nature Foundation, he deemed an extension of the

377   restoration time by 20 years over the shortest restoration time (high density and high species

378   richness scenario) acceptable, and preferred the no-planting approach in restoration sites close to

379   natural forest due to resource constraints on planting trees (Ryota Matsubayashi 2021, personal

380   communication). This indicates the importance of such interactive science communication

381   (Anderson 2014; Seavy & Howell 2010; Busbridge et al. 2021) as well as the utility of presenting

382   a comprehensive set of scenarios, including ecologically effective and also high-risk pathways,

383   to provide decision makers with an ecological option space in which to integrate social

384   considerations.

385

386   ***Limitations and conclusions***

387   When interpreting our results, some limitations need to be considered. First, our restoration

388   scenarios assumed planting trees with a height of 1.3 m, i.e., larger than the size typically used

389   for restoration (0.3 to 0.5 m). Planting larger trees may reduce restoration times as trees are faster

390   able to outgrow competing forest floor vegetation and create a forest microclimate. On the other

391   hand, planting larger trees often results in reduced growth in the first years after planting due to

392   an inadequate root system and suboptimal plant water uptake (Watson 2005). Therefore, choosing

393   larger trees does not necessarily yield shorter recovery times. Moreover, intraspecific variation in

394   fitness of the planted individuals can have distinct influences on the emerging stand development

395   trajectories (Yoda 1963; Masaki 2018). Our results do not reflect such effects of variation in size

396   and genetics on the growth and mortality of planting trees.

397   Second, uncertainty remains regarding belowground processes. We here assumed that there

398   is no difference in soil conditions between restoration sites and surrounding natural forests, based

399   on *in-situ* observations (Mori et al. 2015). Yet, in many instances, degraded restoration sites might

400   differ considerably in their soil conditions compared to natural forests mainly due to past land use.

401   Furthermore, iLand does currently not consider belowground competition for nutrients (Seidl et

402   al. 2012), yet such processes can significantly affect vegetation development in high density

403   plantations (Nambiar & Sands 1993; Brancalion et al. 2019). Moreover, we here assumed

404   stationary environmental conditions over time, yet vegetation development trajectories may

405   change if future climate change significantly alters climatic conditions and disturbance regimes

406   (e.g., Meli et al. 2017; Thom et al. 2017; Braziunas et al. 2018).

407   Although our data supports a positive effect of planting for restoration, planting is not a

408   panacea of forest restoration, and priority should be given to drivers that caused forest degradation

409   and inhibit vegetation recovery (Holl 2017; Brancalion & Holl 2020; Holl & Brancalion 2020).

410   In this regard, we here note that our simulations assumed no inhibiting influence of Ezo deer

411   (emulating stands in exclosures) and no competition from dwarf bamboo (assuming soil

412   scarification) (Fig. 5b to d; Yoshida et al. 2005; Nishizawa et al. 2016). Furthermore, we only

413   considered the planting of late-successional species, aiming to restore old-growth conditions as

414   found in natural forests. However, also other planting approaches may contribute towards

415   restoration objectives, e.g., the planting of early-successional species (*B. ermanii* and *Alnus*

416   *hirsuta* in our study) could effectively mimick post-disturbance vegetation recovery.

417   Whether practitioners choose to plant or work with natural regeneration, monitoring is

418   essential to ensure that the chosen path is congruent with the expected outcomes. Also, restoration

419   policies must be flexible enough to be adjusted based on monitoring outcomes, including options

420   such as additional planting, weeding, and thinning in response to the emerging stand trajectories

421   (Brancalion & Holl 2020; Di Sacco et al. 2021). Such an adaptive management policy is a

422   powerful approach for dealing with future uncertainty, including global climate change and

423   associated change in disturbance regime (Millar et al. 2007; Seidl 2014; Tanner-McAllister et al.

424   2017). In closing, we highlight that in addition to experimental and observational approaches,

425   simulation modeling can make an important contribution towards evidence-based and quantitative

426   restoration ecology (O'Grady 2020).

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Acknowledgements

Authors' contributions

YK conceived the ideas, analysed the data. YK, ASM designed methodology; YK, KFS, ASM collected the data; RS, WR provided technical support on the simulation model; YK, RS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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620 **Table 1:** Reference values determined from simulations of natural forests at Shiretoko National Park (reference natural forest stands, cf. Table S3). We

621 considered restoration to be successful when a restoration site reached ≥50% of the reference value. All values relate to trees >4 m in height. dim =

622 dimensionless.

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Index	Description	Unit	Reference value
Climate change mitigation			
Net primary productivity	10-year average of net primary productivity in reference natural forest stands.	Mg Biomass ha^{-1}	28.4
Total carbon in living biomass	10-year average of carbon in above- and below-ground live tree biomass in reference natural forest stands.	Mg C ha^{-1}	222
Growing stock of trees	10-year average of growing stock in reference natural forest stands.	m^3 ha^{-1}	410
Biodiversity Conservation			
Species richness	Initial number of tree species present in the reference natural forest stand.	species	18
Shannon-Wiener diversity	Initial Shannon-Wiener index in the reference natural forest stand.	dim	2.70
Integrated similarity index (ISI)	ISI (Eq. 2) ranges from 0 (different) to 1 (similar).	dim	1.0

624

625
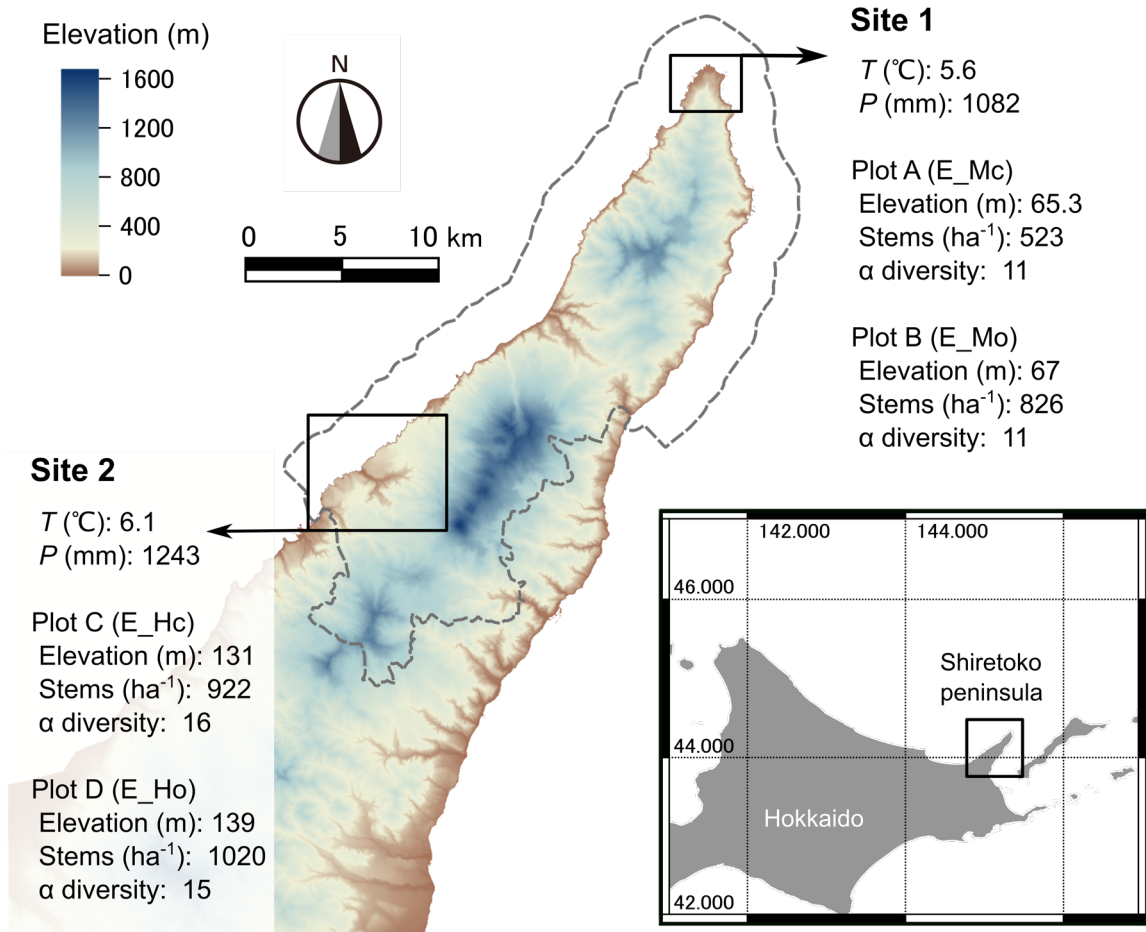
Fig. 1: Map of Shiretoko Peninsula in northeastern Hokkaido, Japan. Locations of tree census

plots in natural forest (plot A to D) are shown in the main panel. The gray dashed line denotes the

boundary of Shiretoko National Park. *T* is mean annual temperature, and *P* is mean annual

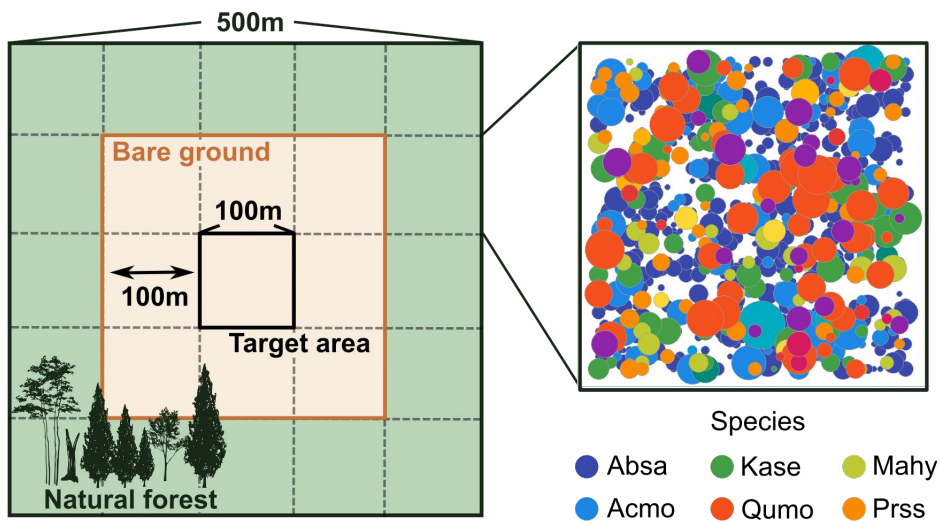precipitation (1980 to 2019). α diversity denotes the number of tree species in the natural forest

plots. The elevation map was downloaded from the Geospatial Information Authority of Japan

website (fgd.gsi.go.jp/download/menu.php, accessed 19 Nov. 2020). See also Fig. S1 for detailed

vegetation in sites 1 and 2.

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639 **Fig. 2:** Design of the restoration simulations (upper left panel). The example illustrated here is

640 for a distance of 100 m to the natural forest edge. In addition to this particular pattern, we also

641 simulated distances of 0, 20, 50, 200, and 300 m to natural forest. In each of the surrounding

642 natural forest cells (green), a typical natural forest of Shiretoko National Park was simulated

643 (upper right panel, cf. Table S3). Circle size is proportional to tree size (crown projection area),

644 and circle color indicates different tree species. Absa = *Abies sachalinensis*, Acmo = *Acer mono*,

645 Kase = *Kalopanax septemlobus*, Mahy = *Magnolia hypoleuca*, Prss = *Prunus ssiori*, Qumo =

646 Quercus *mongolica* ssp. *crispula*. Images in lower panels illustrate a natural forest (a) and a target

647 area (bare ground) for restoration (b).
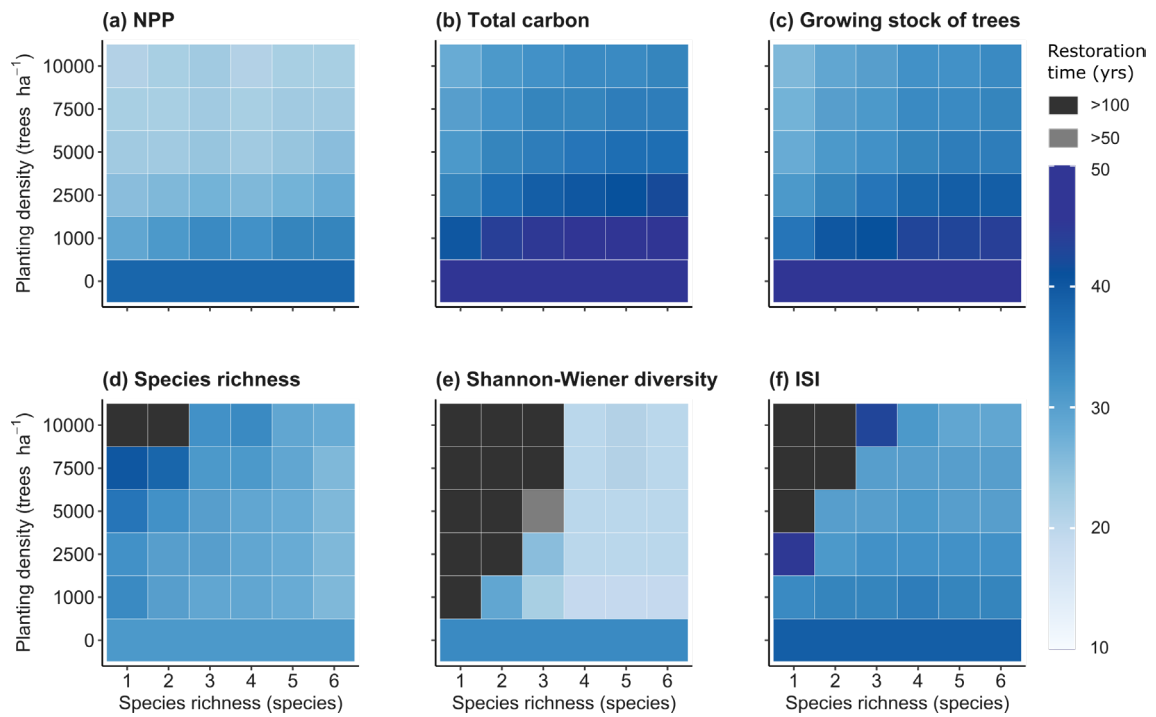
Fig. 3: Restoration time (in years) for the six indicators (panels a through f) for a distance-to-natural-forest of 0 m under different planting densities and species richness scenarios. A planting density of 0 trees ha^{-1} corresponds to the no-planting scenario (natural regeneration only). All results relate to trees >4 m in height. See also Figs. S4 to S9 for other distances to natural forest.
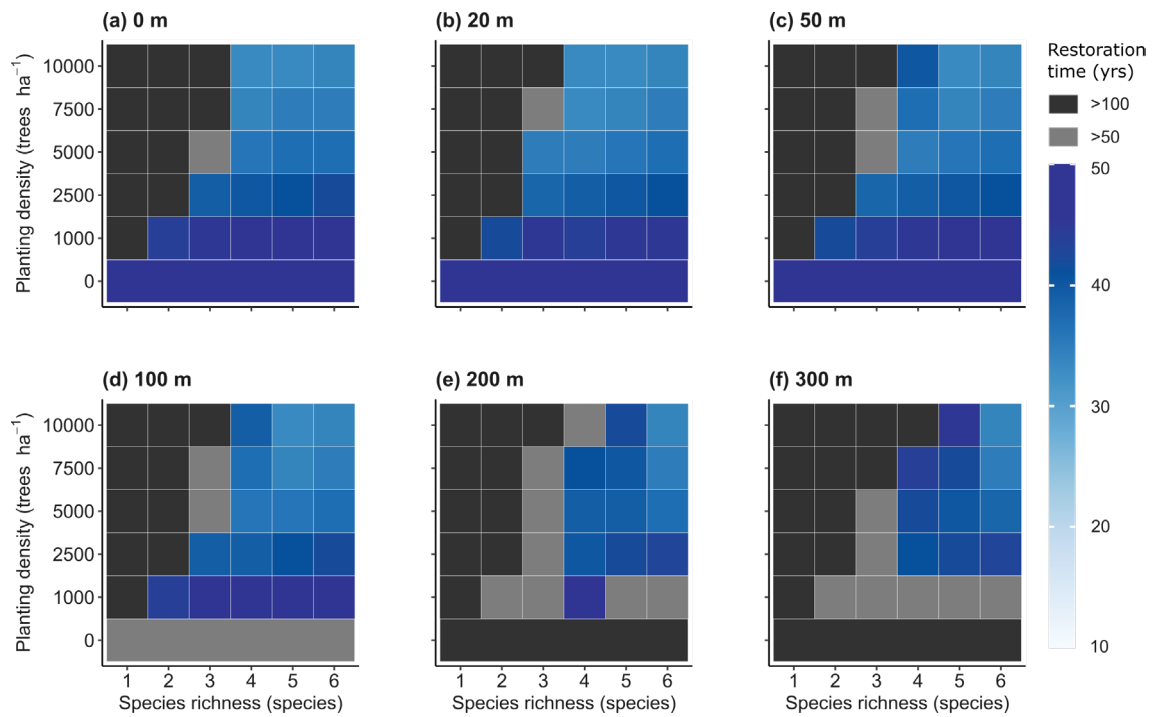
Fig. 4: The maximum restoration time (in years) among the six indicators for distance-to-natural-forest of 0 to 300 m (panels a through f) under different planting densities and species richness scenarios. Note that panel (a) integrates across all panels of Fig. 3 and shows the maximum value for each richness and density combination. A planting density of 0 trees ha^{-1} corresponds to the no-planting scenario (natural regeneration only). All results relate to trees >4 m in height. See also Fig. S10.
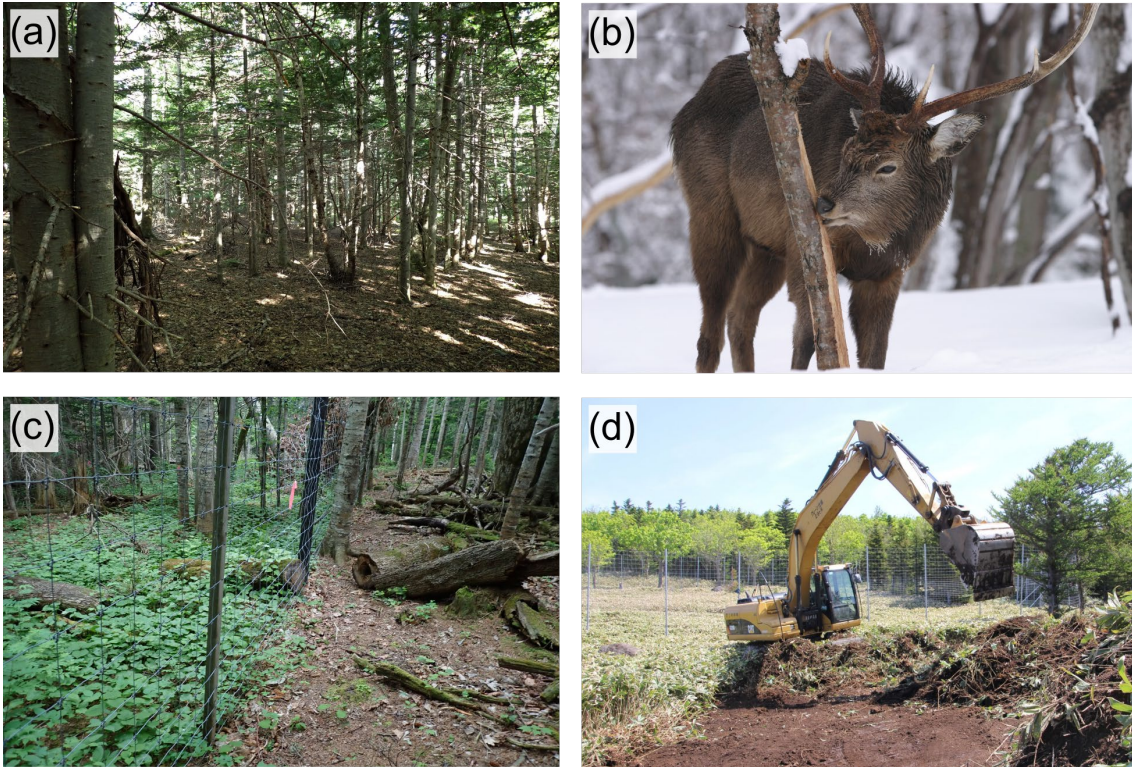
Fig. 5: (a) A high density, mature *Abies sachalinensis* plantation in Shiretoko National Park. (b) Ezo deer (*Cervus nippon yesoensis*), one of the iconic ungulate herbivores in the Park. Due to their overabundance, they inhibit the regeneration and growth of trees by browsing and bark stripping. Since the 2010s, population control is enforced by the Shiretoko Nature Foundation (Ishinazaka 2016). (c) A fence to exclude Ezo deer and foster vegetation development. There is a clear difference in understory vegetation between inside (left) and outside (right) the fence. (d) A site where soil scarification is applied as a measure to contain dwarf bamboo species that reduce the probability of tree establishment. Heavy machinery was used to dig up the roots of bamboo and return the topsoil to the site. (a), (b), and (d) were taken by the Shiretoko Nature Foundation, and (c) was taken by Keita Nishizawa.

Title:

Identifying effective tree planting schemes to restore forest carbon and biodiversity in Shiretoko National Park

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Growth and mortality

We initialized trees over 4 m in height with the same individual size and location for each of the four 1-ha plots (Figs. 1 and A1). Trees that were alive from 2005 to 2017 were included for the growth analysis and those that were alive in 2005 were included for the mortality test (Fig. A1). We estimated the height of some trees that were missing in the observations in 2005 using height-diameter allometries reported by Kobayashi et al. (2021). Sprouts that were over 10 cm in diameter at breast height were treated as individual trees, and smaller sprouts were excluded. The dimensions of plot C were 80 m in length and 120 m in width, therefore, we corrected the tree locations to fit into a square of 100 × 100 m. We simulated forest dynamics assuming no disturbance using the same climate data as the observation period. In all plots, other environmental drivers were the same as that in site 2. Tree mortality in iLand is modeled as a probabilistic event; thus, the simulations were replicated ten times.

For growth evaluation, we examined the interspecific variations in growth rates depending on climate and shading status based on basal area increment (BAI) and relative BAI, as:

$$\text{BAI}_{i,j} = \frac{\text{BA}_{i,j,2017} - \text{BA}_{i,j,2005}}{(2017 - 2005)} \quad (1)$$

$$\text{relative BAI}_{i,j} = \frac{\text{BAI}_{i,j}}{\text{BA}_{i,j,2005}} \quad (2)$$

where BA is the basal area (cm^2), i is the species, and j is the plot. The numbers 2017 and 2005 are the start and end observation years, respectively. The results of the linear regressions between iLand's estimate and observation of both BAI and relative BAI did not deviate significantly from the 1:1 line (log$_{10}$-transformed BAI: intercept = −0.14, slope = 1.06, R^2 = 0.84, relative BAI: intercept = 1.36, slope = 0.46, R^2 = 0.24). The mean absolute error (MAE) and root mean squared error (RMSE) also showed high predictability of growth simulation (BAI: MAE = 329.6 cm^2 ha^{-1} year^{-1}, RMSE = 591.5 cm^2 ha^{-1} year^{-1}, relative BAI: MAE = 1.00 %, RMSE =1.27 %).

The observed and predicted annual mortality rates for each 1-ha plot are shown in Table A1. The predicted mortality rates at site 1 (plots A and B) were similar to the observations but were relatively high at site 2 (plots C and D). We adjusted the mortality-related parameters (intrinsic and stress-related mortality) to fit the observations at site 2 but found that considerable changes in the regeneration trajectories to natural forest negatively affected the evaluation of regeneration (see below). This is possibly because our observation data did not identify the reasons for tree death. Causes for the observed mortality rates include tree death by wind (Nishimura, 2006), bark-stripping by Hokkaido sika deer (Kushiro Nature Conservation Office, 2017), and processes such

as aging or carbon starvation included in iLand. Therefore, we refrained from altering mortality parameters specifically for site 2 and alternatively created ten additional parameter sets for the mortality-related parameters by multiplying random values ranging from 0.8 to 1.2 to conduct a sensitivity analysis for the main results.

Regeneration

We evaluated iLand's ability to simulate stand trajectories leading to similar stands as the four 1-ha plots starting from bare ground with only natural regeneration. To provide seed input, we surrounded each of the 1-ha bare ground plots with stands reflecting the current species composition in natural forest (Fig. A3). We simulated succession for 300 years, assuming no disturbance and climate change. There were five replicates, and the environmental conditions of the bare ground were kept the same as those of the natural forest plots. We randomly sampled the climate data from 1980 to 2019 over 300 years.

In the bare ground surrounded by plots B to D, the typical successional pattern in Japanese cool-temperate forests was reproduced as expected as shown in Fig. A4 (Kato, 1952; Tsuda et al., 2002), i.e., early successional species, such as Erman's birch (*Betula ermanii*), Manchurian alder (*Alnus hirsuta*), and Japanese rowan (*Sorbus commixta*), were replaced by later successional species for 80 to 100 years, such as Sakhalin fir (*Abies sachalinensis*) and painted maple (*Acer mono*). We could not find studies that recorded the time of the replacement, but our results are satisfactory given that the average life of Japanese white birch (*Betula platyphylla*; closely related to Erman's birch) and Manchurian alder is approximately 100 years (Hoppou Ringyou Kai, 1988). On the other hand, plot A showed fewer early successional species and was dominated by Sakhalin fir from the beginning (Fig. A4). A long-term vegetation survey (>60 years) in a wind-disturbed secondary forest in central Hokkaido showed similar patterns (Kosugi et al., 2016). Indeed, in the natural forests of Shiretoko National Park, the majority of regenerating species are Sakhalin fir, unless there is a large-scale gap formation (Suzuki et al., 2021). Thus, these results are in line with the general ecological theories and field observations.

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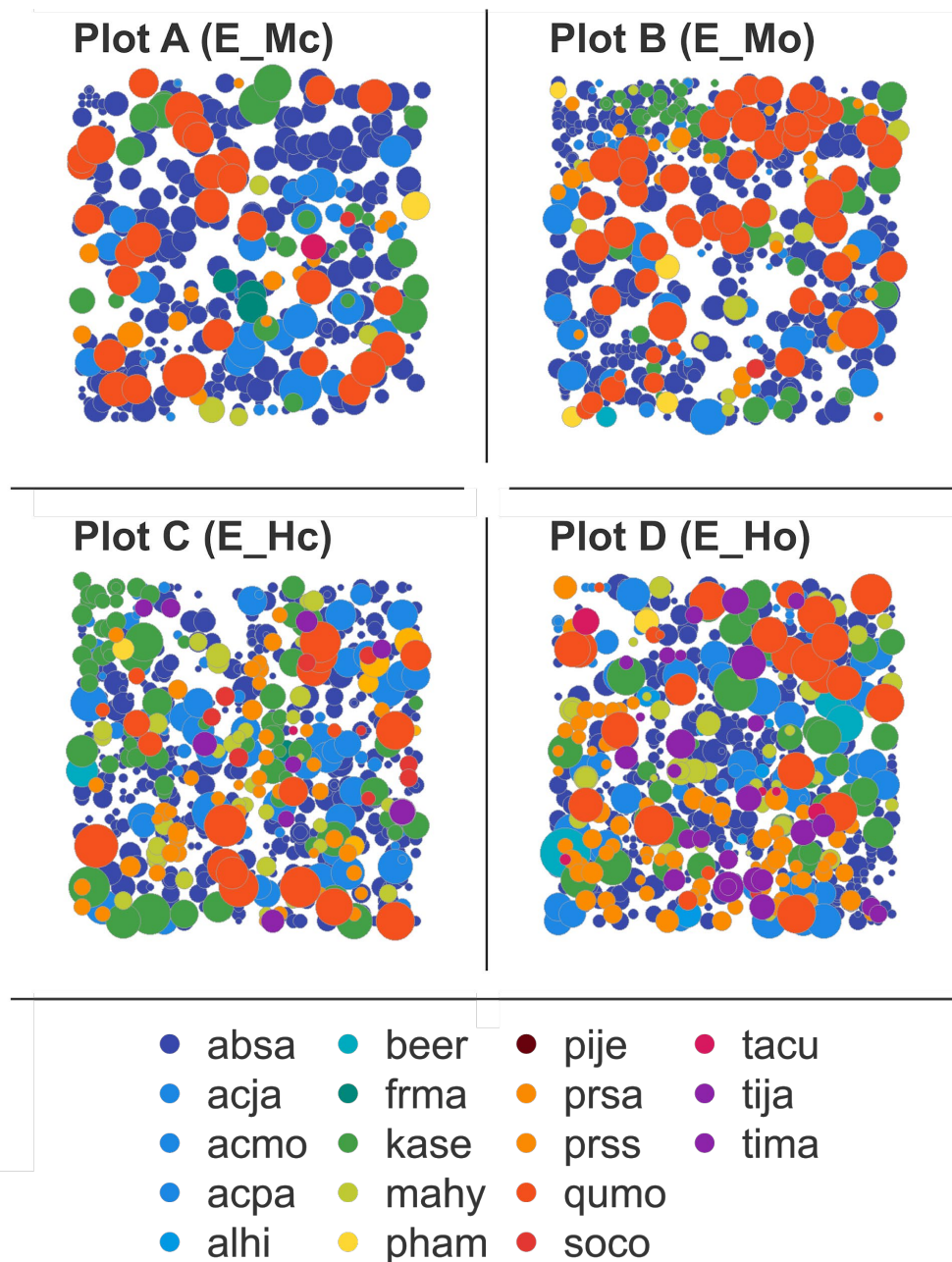
Fig. A1: Location of individual trees that were alive from 2005 to 2017 in four 1-ha plots. The size of the circle is proportional to tree size (crown projection area) and colors denote species. absa = *Abies sachalinensis,* acja = *Acer japonicum,* acmo = *Acer mono*, acpa = *Acer palmatum* var. *matumurae*, alhi = *Alnus hirsuta*, beer = *Betula ermanii*, frma = *Fraxinus mandshurica* var. *japonica,* kase = *Kalopanax septemlobus*, mahy = *Magnolia hypoleuca*, pham = *Phellodendron amurense*, pije = *Picea jezoensis,* prsa = *Prunus sargentii*, prss = *Prunus ssiori*, qumo = *Quercus mongolica* ssp. *crispula*, soco = *Sorbus commixta*, tacu = *Taxus cuspidata*, tija = *Tilia japonica,* tima = *Tilia maximowicziana.*
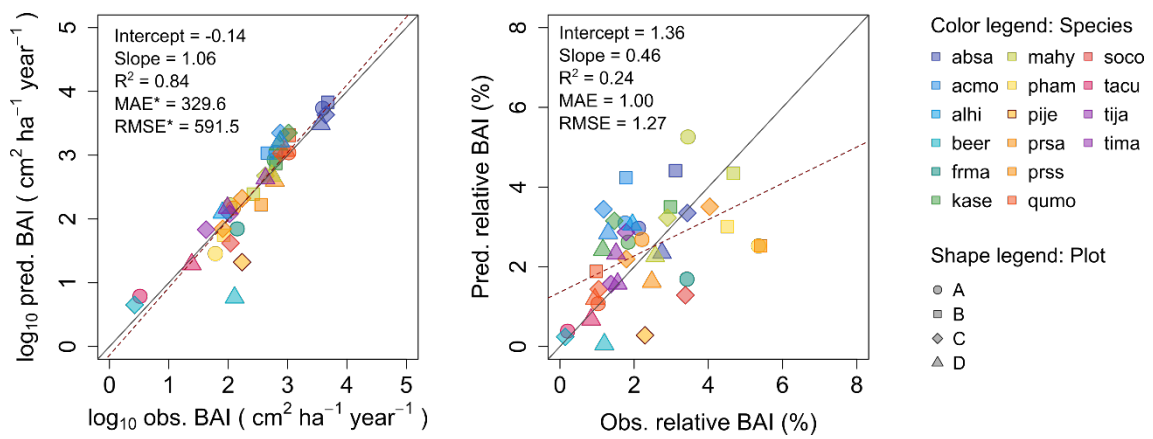
Fig. A2: Simulated and observed basal area increments (BAIs) and relative BAIs for each species and plot. Multiple R-squared (R^2), mean absolute error (MAE), and root mean squared error (RMSE) are shown in each panel. Colors and shapes denote species and plots, respectively. absa = *Abies sachalinensis,* acja = *Acer japonicum,* acmo = *Acer mono*, acpa = *Acer palmatum* var. *matumurae*, alhi = *Alnus hirsuta*, beer = *Betula ermanii*, frma = *Fraxinus mandshurica* var. *japonica,* kase = *Kalopanax septemlobus*, mahy = *Magnolia hypoleuca*, pham = *Phellodendron amurense*, pije = *Picea jezoensis,* prsa = *Prunus sargentii*, prss = *Prunus ssiori*, qumo = *Quercus mongolica* ssp. *crispula*, soco = *Sorbus commixta*, tacu = *Taxus cuspidata*, tija = *Tilia japonica*, tima = *Tilia maximowicziana*. *Values without logarithmic transformation.
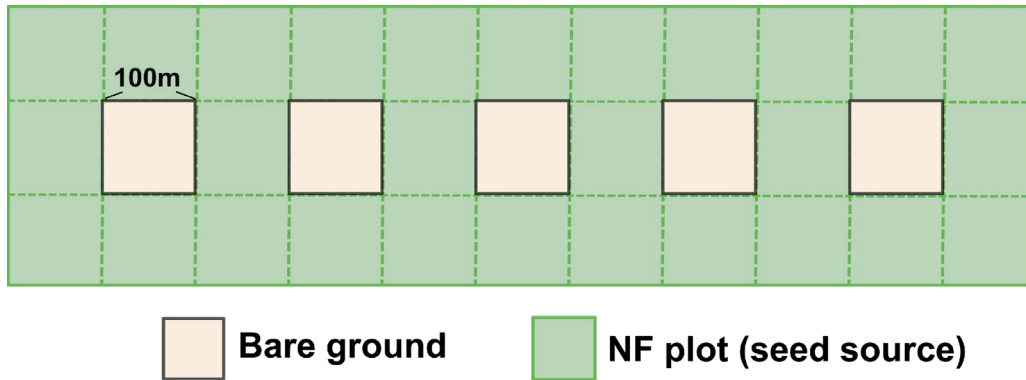
Fig. A3: Simulation layout of regeneration evaluation in the 1-ha bare ground. Seeds arrive from all directions. Simulation was conducted for each of the four 1-ha plots with five replicates. The same tree arrangements as in the mortality test were used in the plots as shown in Fig. A1.
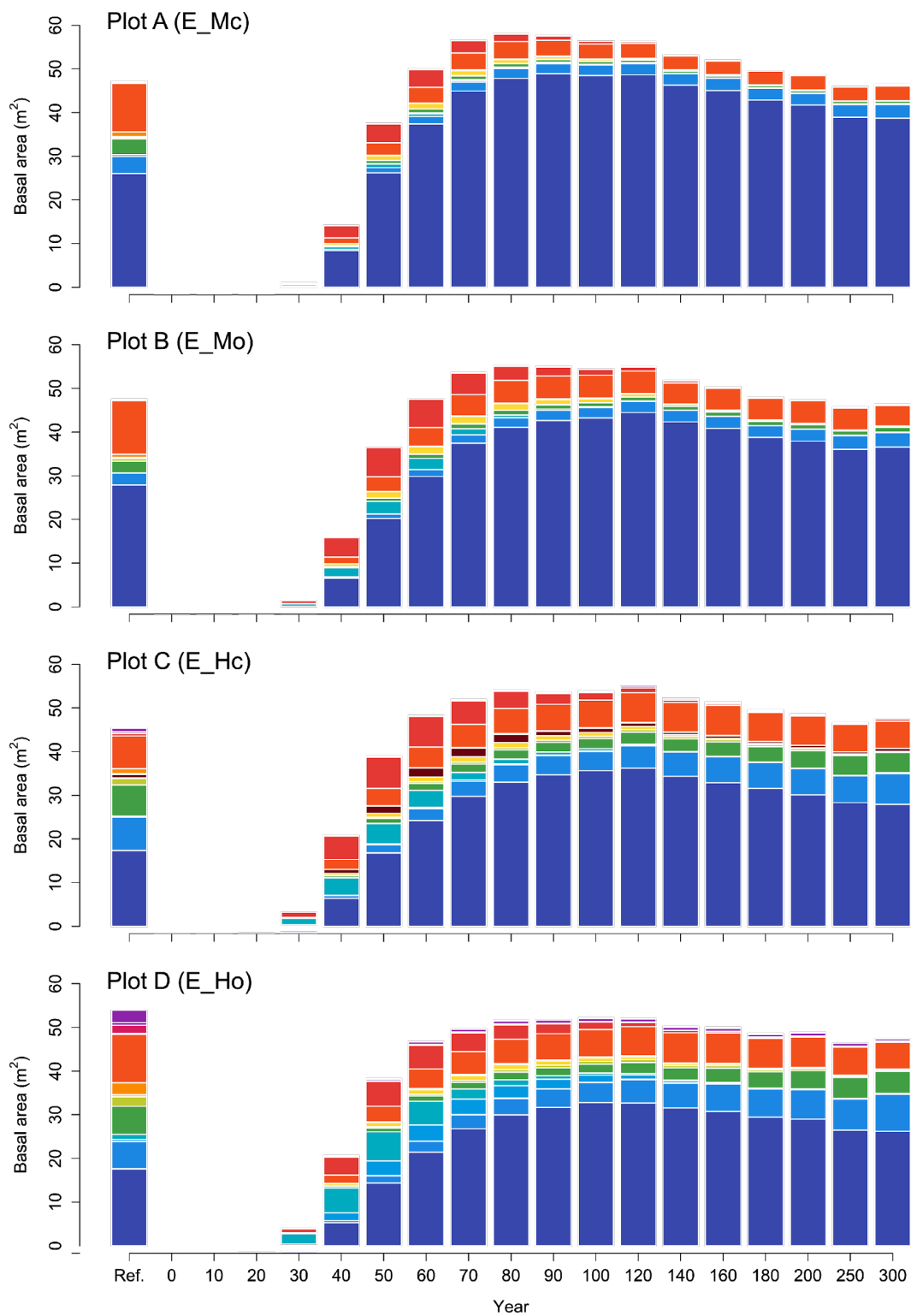
Fig. A4: Changes in species composition of trees over 4 m in height in the 1-ha bare ground over 300 years. Ref. denotes initial species composition in each of the four surrounding reference stands. Colors correspond to Fig A1.

Table A1: Observed and predicted annual mortality rate (% trees) in the four 1-ha plots.

Plot	Mortality (%)	
	Obs.	**Pred. (mean ± s.d.)**
A	1.77	1.62 ± 0.07
B	1.69	1.46 ± 0.04
C	1.09	2.08 ± 0.06
D	1.68	2.8 ± 0.06