

¹ Accounting for seed rain and other confounders
² reveals which ecosystems are most susceptible to
³ alien conifer establishment

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¹⁸ **Abstract**

- ¹⁹ 1. Plantations of alien conifer species are common worldwide, and set to
²⁰ become even more prevalent in coming decades. To minimize the rate at
²¹ which their offspring — so-called “wildlings” — colonize surroundings, and
²² reduce the burden of conifer plantations on native ecosystems, managers
²³ need to know which ecosystems are most and least susceptible.
- ²⁴ 2. We compared how likely wildlings are to establish across a wide range
²⁵ of ecosystems, focusing on four groups of alien conifer species planted in
²⁶ Norway. We used data from detailed surveys around 82 plantation stands
²⁷ to model the relationship between ecosystem type and wildling abundance,
²⁸ accounting for seed rain (estimated), climate, and other sources of variation
²⁹ between sites. We also tested whether differences in susceptibility between
³⁰ individual ecosystem types could be generalized based on broad, shared
³¹ characteristics.
- ³² 3. We found that ecosystem susceptibility to wildling establishment (modeled
³³ as relative establishment likelihood) was poorly correlated with surveyed
³⁴ wildling density (abundance/area). Susceptibility generally varied as much
³⁵ or more than wildling density, with relative establishment likelihoods
³⁶ spanning several orders of magnitude between the most and least susceptible
³⁷ ecosystems for every species group.
- ³⁸ 4. The four groups of conifer species showed somewhat similar patterns of
³⁹ establishment likelihood across ecosystem types, with intensively farmed
⁴⁰ ecosystems repeatedly among the least susceptible. We found that ecosys-
⁴¹ tems characterized by destabilizing disturbance tended to be more sus-
⁴² ceptible than others, but broad ecosystem characteristics did not clarify
⁴³ patterns of susceptibility much, neither within nor across species groups.
- ⁴⁴ 5. *Synthesis and applications* Differences in wildling establishment between

45 ecosystems can be exploited to keep alien conifers within plantation bound-
46 aries. Stands hemmed in by agriculture or other unsusceptible ecosystems
47 will result in relatively few wildlings, while stands near susceptible ecosys-
48 tems like landslides will need monitoring and control. Managers should
49 be aware that the density of wildlings in a given ecosystem may not re-
50 flect its relative susceptibility, because variation in seed rain, climate, and
51 site characteristics obscures the relationship between ecosystem type and
52 wildling establishment.

53 **Keywords**

54 alien species, conifer, establishment likelihood, disturbance, invasibility, planta-
55 tion, seed dispersal, Wald Analytical Long-distance Dispersal (WALD)

56 **1 Introduction**

57 Plantations of alien conifers are widespread globally, and offspring from these
58 plantations frequently establish in surrounding areas (Richardson & Rejmánek,
59 2004). In many instances these naturalized offspring, or wildlings, harm biodi-
60 versity and other values, so controlling their spread is prudent. In particular,
61 plantations that contribute to the presence of alien conifers in protected areas
62 may generate substantial control costs (McConnachie et al., 2015). Controlling
63 wildlings protects plantation surroundings and prevents secondary, potentially in-
64vasive spread. Accordingly, guidelines for sustainable use of alien trees emphasize
65 that restricting trees to the areas set aside for their cultivation is fundamental
66 to good forestry practice (Brundu et al., 2020).

67 The number of wildlings and their distance from the nearest plantation stand
68 varies a lot from site to site, even among conspecific stands of similar age
69 (Fernandes et al., 2018; Nygaard & Øyen, 2017), which makes it hard to predict
70 and manage their spread. To better understand this variation, we need to
71 consider both dispersal and establishment, which jointly generate patterns of
72 wildling abundance in space. Dispersal at a given site is affected by conditions
73 related to the species' dispersal syndrome — for instance wind exposure and
74 topography, in the case of a wind-dispersed species. Establishment is affected by
75 biotic and abiotic conditions where seeds arrive.

76 Wildling spread may be reduced by inhibiting either dispersal or establishment,
77 but inhibiting establishment is of particular interest because it directly suppresses
78 wildling abundance. The conditions affecting establishment are also generally
79 easier to manipulate than those affecting dispersal, either directly through
80 intervention or indirectly through site selection. The question, then, is: how
81 can we identify establishment-inhibiting conditions in a manner applicable to

82 plantation management?

83 In Norway, the national land mapping classification system sorts variation in
84 local ecological conditions (Halvorsen et al., 2020). It aims for reproducible and
85 value-neutral classification of ecosystems by rule-based discretization of species
86 turnover along important environmental gradients (Halvorsen et al., 2020). As a
87 result, its ecosystem types (hereafter: “ecosystems”) encapsulate much of the
88 variation likely to regulate wildling establishment — in competition, nutrient
89 availability, disturbance, etc. (Richardson & Pyšek, 2012). It also identifies
90 broad similarities between ecosystems, which might be used to tease out generic
91 trends in establishment likelihood.

92 Naively, the density of wildlings in a given ecosystem would seem to indicate
93 how likely they are to establish there. But to estimate ecosystem establishment
94 likelihoods based on wildling abundance around plantation stands, we must
95 account for (1) seed dispersal, and (2) sources of variation in establishment beside
96 ecosystem type. For example, low establishment likelihood in an ecosystem
97 frequently located close to plantations may be masked by copious seed rain
98 (Rouget & Richardson, 2003). Likewise, an ecosystem may appear to promote
99 establishment if it tends to co-occur with climatic conditions that support
100 germination. Once estimated, unconfounded establishment likelihoods may be
101 used to predict how susceptible the surroundings of an unobserved plantation
102 are, based on ecosystem composition.

103 Determining which ecosystems are most susceptible so that interventions can be
104 prioritized objectively is among the most urgent objectives for invasion science
105 (Pyšek et al., 2020). Stands of wind-dispersed, alien conifers present a unique
106 opportunity to assess ecosystem invasibility (to these species), because we can
107 estimate ecosystem exposure (seed rain) directly, rather than by proxy (Catford
108 et al., 2012). We examine plantations of alien conifers in Norway to investigate

¹⁰⁹ the following questions:

- ¹¹⁰ 1. How much does wildling establishment likelihood differ from surveyed
- ¹¹¹ wildling density across ecosystems?
- ¹¹² 2. In which ecosystems are wildlings of alien conifers most and least likely to
- ¹¹³ establish?
- ¹¹⁴ 3. Can overarching characteristics of ecosystems be used to generalize patterns
- ¹¹⁵ of wildling establishment?

¹¹⁶ 2 Methods

¹¹⁷ 2.1 Field data

¹¹⁸ We registered wildlings and ecosystems around 82 reproductive plantation stands
¹¹⁹ across Norway, comprising four groups of alien conifers (hereafter: “species”;
¹²⁰ fig. 1). The sample contained (1) forty-two sites with Sitka spruce (*Picea*
¹²¹ *sitchensis*) or its fertile hybrid, Lutz spruce (*Picea x lutzii*), (2) nineteen with
¹²² Norway spruce (*Picea abies*), (3) fifteen with larch species (*Larix* spp.), and (4)
¹²³ six with lodgepole pine (*Pinus contorta*). Note that Norway spruce is native to
¹²⁴ Norway, but the plantations included in this study were located in parts of the
¹²⁵ country where its natural distribution is highly restricted. We selected stands
¹²⁶ using aerial imagery, aiming for those isolated from conspecific stands. We
¹²⁷ collected field data for each stand in one of six field campaigns during the period
¹²⁸ 2016-2019 (reported in Olsen et al., 2016, 2019; Appelgren, 2018; Appelgren &
¹²⁹ Torvik, 2017; Kyrkjeeide et al., 2017; Sandven et al., 2019).

¹³⁰ Within a 2x2 km plot centered on the stand of interest, we mapped all conspecific
¹³¹ stands (except in the 2016 field campaign). Within the central 500x500 m of
¹³² that plot, we mapped wildlings and ecosystems. We used GPS to register the
¹³³ point-positions of all wildlings over 30 cm in height, recording a single position

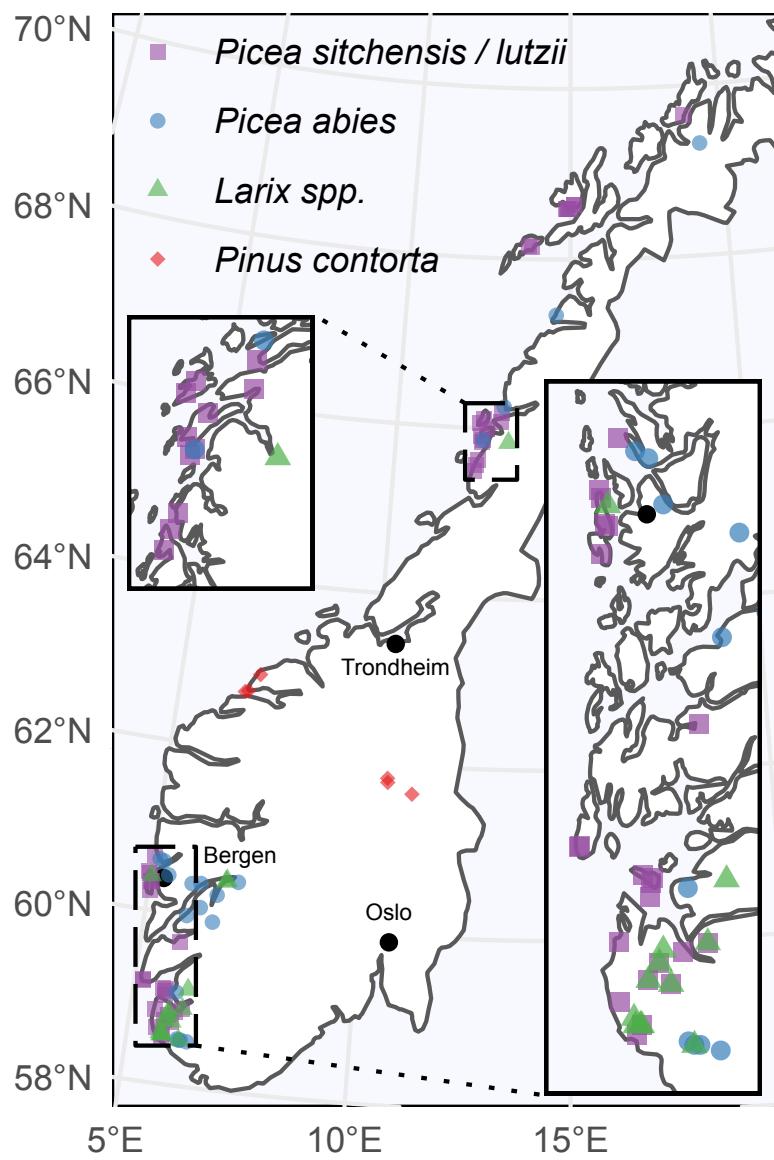


Figure 1: Locations of the 82 plantation stands in the sample.

for groups of wildlings occurring with less than 5 m between them. A few exceptionally dense groups of wildlings were mapped by registering polygons instead of points and estimating the number of individuals by transect counts. Concurrently, we registered polygons for all terrestrial and wetland ecosystems, following the Nature in Norway classification system (version 2.0 or 2.1, Halvorsen et al., 2015, based on the principles summarized in Halvorsen et al., 2020). This system is the national standard for land cover mapping and provides full spatial coverage (i.e. any location is assignable to an ecosystem). We mapped ecosystems at a scale of 1:5000, which means that any polygon over 250 m² was registered (Bryn & Halvorsen, 2015). Regularly patterned occurrence of more than one ecosystem in polygons smaller than the minimum size were registered as so-called mosaic polygons.

We estimated or measured (by clinometer) the heights of the 82 central stands. We also estimated their ages at the time of the field campaign, either by contacting land owners and municipal officials, or by counting growth rings. Details of all 82 stands are provided in the Appendix (table 4).

2.2 Seed dispersal

To account for the influence of seed dispersal on wildling abundance, we needed estimates of the spatial distribution of seed rain within the 500x500 m plots. We considered all conspecific stands within a 1 km radius of the plot center to be potential seed sources, and used two models of seed dispersal to derive different estimates of relative seed rain in space. Acknowledging the uncertainty involved in estimating seed dispersal, we explored one empirically-parameterized, isotropic model and one mechanistically-derived, anisotropic model.

The first model was a static seed dispersal kernel with parameter estimates generalized from multiple data sets. Specifically, we selected from Bullock et

160 al. (2017) the kernel that performed best for wind-adapted seeds from 5-15 m
161 tall trees (an Exponential Power function). Seventy-two of the 82 stands in our
162 data set matched this height range better than a taller range with a different
163 empirical kernel.

164 The second model was an anisotropic implementation of the Wald Analytical
165 Long-distance Dispersal model (WALD, Katul et al., 2005), following Skarpaas
166 & Shea (2007). We parameterized the model with: site- and season-specific
167 wind vectors retrieved from meteorological data sets (MET Norway; Reistad
168 et al., 2011; Haakenstad & Haugen, 2017), wind turbulence estimated from
169 local ecosystem composition, seed release height based on stand height, and
170 species-specific seed terminal velocities from literature.

171 We transformed field-mapped polygons of potential seed sources into hexagonally
172 gridded point sources, with a density of 0.1 m^{-2} for the first model and 0.01 m^{-2}
173 for the second model (to reduce computation time). Then we applied our two
174 dispersal models to estimate the distribution of relative seed rain from all point
175 sources in a grid of 10 m cells. We chose this cell size to be similar to the smallest
176 allowed ecosystem polygon.

177 A full description of our implementation of the WALD model and additional
178 details about seed source polygons are given in the Appendix.

179 2.3 Establishment likelihood

180 For our analysis of establishment likelihood, wildling occurrences and ecosystems
181 were rasterized to the same 10 m grid as the seed dispersal models (fig. 2). Rather
182 than assigning a single ecosystem to each grid cell, we assigned ecosystems in
183 proportion to their areal coverage of the cell (i.e. each ecosystem was rendered as a
184 separate raster variable with a [0,1] range). This allowed us to capture ecotones in

185 the model and avoid overreliance on the spatial precision of ecosystem boundaries.
186 Area covered by mosaic polygons was divided evenly among the constituent
187 ecosystem types. Cells with > 0.5 “tree plantation” were excluded from our
188 analyses because some of the field campaigns did not register wildlings when they
189 occurred in this ecosystem. The resulting data set was used to calculate wildling
190 densities (abundance/area) and to model relative establishment likelihoods. For
191 the density calculation, wildling abundance was tallied in proportion to the
192 ecosystem composition of its grid cell. For example, a cell occupied by three
193 wildlings and half-covered by a given ecosystem would tally 1.5 wildlings for that
194 ecosystem.

195 We used a directed acyclic graph (DAG) to diagram causal relationships among
196 the factors we expected to influence wildling abundance per cell (fig. 3). In the
197 DAG, the unmeasured, proximate causes of wildling abundance — total seed rain
198 over the lifetime of the stand and establishment likelihood — are descendants
199 of variables that we could observe or model. We included an effect of elevation
200 relative to the stand on seed rain because neither of our models of seed dispersal
201 account for uneven terrain.

202 For all species, wildling abundance showed a high frequency of zeros that was
203 underestimated by the best fitting negative binomial distribution. Accordingly,
204 we applied zero-inflated generalized linear models, fitted with the glmmTMB
205 package (version 1.0, Brooks et al., 2017) in R (version 3.6, R Core Team, 2020).
206 These zero-inflated models regard zeros as the mixed product of a binomial
207 process as well as a (conditional) count process that can take different error
208 distributions (Zuur et al., 2009). Preliminary models fitted with a negative
209 binomial error distribution in the count process (ZINB) sometimes showed resid-
210 ual underdispersion, so we switched to a generalized Poisson error distribution
211 (ZIGP), which can accommodate both over- and underdispersion (Brooks et al.,

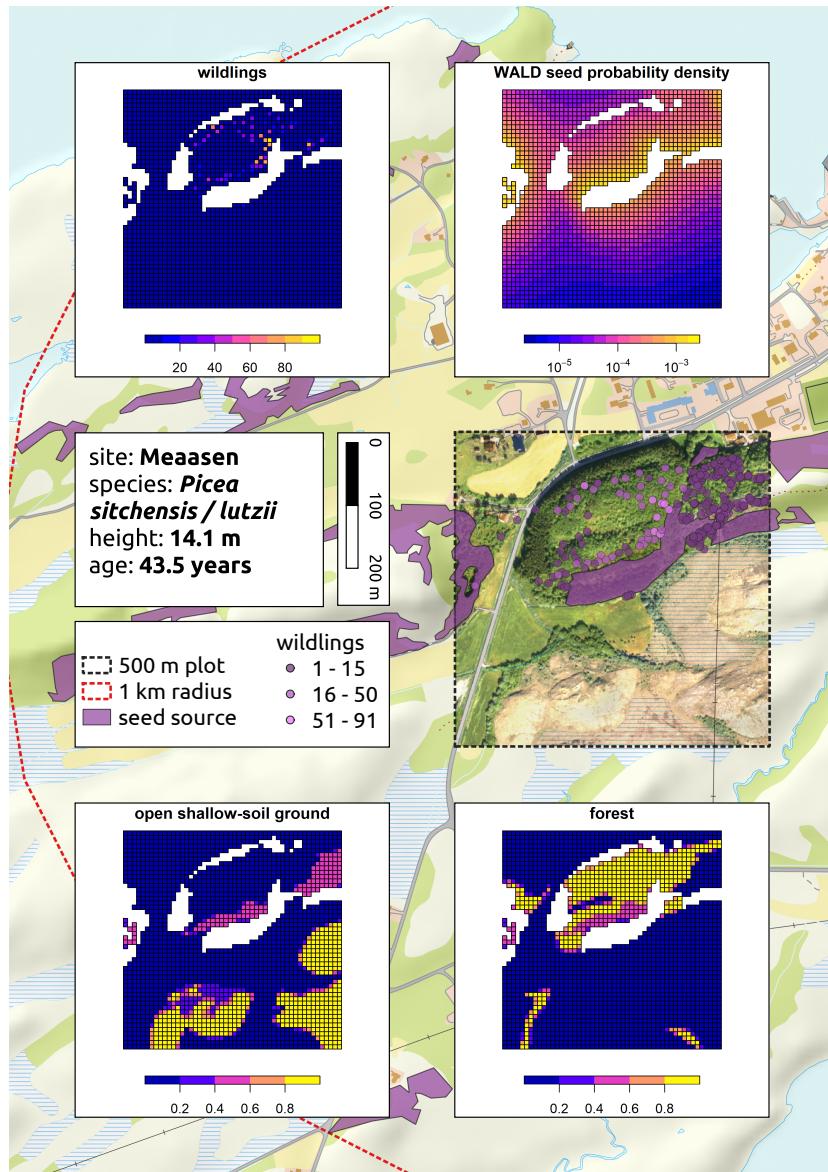


Figure 2: An illustration of one of the 82 plantations: Meaasen. The background map shows the surroundings of the plantation, and the 500x500 m plot is overlaid with an aerial photograph. The middle row of panels shows data as registered in the field. The top and bottom rows of panels show selected variables for the 500x500 m plot, as used in the regression model (with a spatial grain of 10 m). Grid cells without data are either seed sources or "tree plantations" of other species.

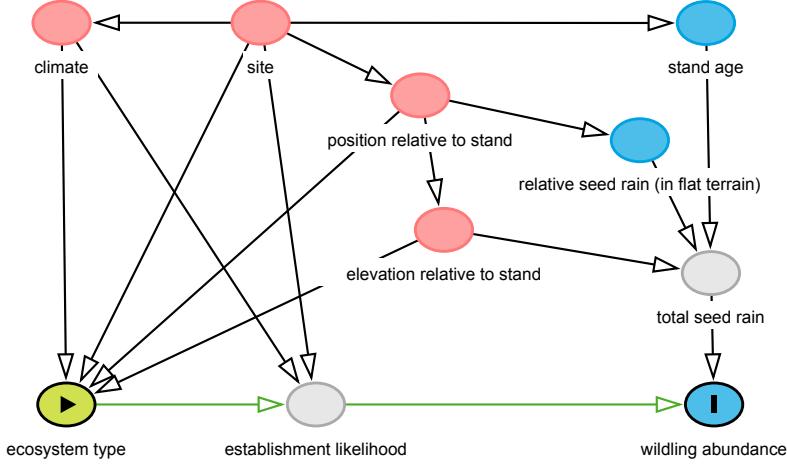


Figure 3: A directed acyclic graph showing the assumed causal relationships motivating our statistical model of ecosystems' effects on wildling abundance. Red variables causally affect both the ecosystem type and wildling abundance, blue variables causally affect only wildling abundance, and grey variables are unobserved. Green arrows show the causal pathway of interest.

²¹² 2019).

²¹³ We modeled the binomial process as dependent on stand age and site, with site
²¹⁴ as a random variable. We expected that younger stands would exhibit more
²¹⁵ wildling-free cells than predicted under a constant establishment rate from age
²¹⁶ zero, because of their infertile juvenile period. We also expected the frequency
²¹⁷ of zeros to vary with site, because our field work documented that some land
²¹⁸ owners had occasionally made efforts to remove wildlings. Excess zeros that
²¹⁹ arose in these ways would therefore not bias our estimates of establishment
²²⁰ likelihood (Blasco-Moreno et al., 2019).

²²¹ To estimate the causal influence of ecosystems on wildling abundance in accord-
²²² ance with the DAG (McElreath, 2020; Textor et al., 2016), we modeled the
²²³ count process as dependent on ecosystem, site, climate, elevation relative to the
²²⁴ stand, and relative seed rain. We also included stand age in the count process
²²⁵ model because it reduced the unexplained variance associated with the random

226 effect of site, and because we could interpret its coefficient as an unconfounded
 227 total effect on wildling abundance (Westreich & Greenland, 2013). Climate was
 228 represented as mean annual temperature (Bio1) and precipitation of the coldest
 229 quarter (Bio19), at 30 arcsecond resolution, from CHELSA data (Karger et al.,
 230 2017). We chose these variables because they showed the strongest correlations
 231 with Norwegian vegetation zones and sections, respectively (Bakkestuen et al.,
 232 2008). For lodgepole pine we excluded Bio1 because the two climatic variables
 233 were highly correlated ($\rho = 0.98$). Elevation relative to the stand was taken with
 234 respect to the highest point of the central stand, from digital elevation models at
 235 1 or 10 m resolution (Norwegian Mapping Authority). Relative seed rain directly
 236 represents relative exposure in the count process, so we entered the natural log
 237 of this variable as an offset term (coefficient fixed at 1; Zuur et al., 2009). We
 238 expect, for example, that a doubling in seed rain would result in a doubling in
 239 wildling abundance, all else being equal.

240 To summarize, for each species we modeled:

$$\begin{aligned}
 \text{wildlings}_{ij} &\sim ZIGP(\pi_i, \mu_{ij}, \phi) \\
 \text{logit}(\pi_i) &= \text{StandAge}_i + \text{Site}_i \\
 \log(\mu_{ij}) &= \sum_{k=1}^K \text{EcosystemType}_{ijk} + \text{Site}_i + \text{Bio1}_i + \text{Bio19}_i + \\
 &\quad \text{RelativeElevation}_{ij} + \text{StandAge}_i + \\
 &\quad \text{offset}(\log(\text{RelativeSeedRain}_{ij})) \\
 \text{Site}_i &\sim \text{Normal}(0, \sigma^2)
 \end{aligned} \tag{1}$$

241 where π is the probability of a zero from the binomial process, while μ and ϕ
 242 are the mean and dispersion of the generalized Poisson distribution, respectively
 243 (Brooks et al., 2019). Subscripts i , j , and k index sites, cells, and ecosystems.

244 For each species, wildling-free ecosystems were dropped as predictors (to avoid
245 model convergence issues stemming from complete separation), along with the
246 cells that were comprised mostly (> 0.5) of one of these ecosystems. The values
247 of Bio1, Bio19, elevation relative to the stand, and stand age were standardized,
248 and the natural log of relative seed rain was centered. We fitted three parallel
249 models for each species: (1) with relative seed rain derived from the static
250 dispersal kernel, (2) with relative seed rain derived from the WALD dispersal
251 model, and (3) without relative seed rain. From these three we selected that
252 with the best AIC. Three models (Sitka/Lutz spruce and lodgepole pine with
253 static dispersal kernel; larches without seed rain) did not converge and were
254 excluded from selection. To catch problems with our model specification, we
255 looked for deviation from uniformity in quantile-scaled, simulated residuals, using
256 the DHARMA package (version 0.3.3, Hartig, 2020). We also ran DHARMA's
257 tests for residual over/underdispersion and zero-inflation. Relative establishment
258 likelihoods among ecosystems were calculated as predictions from the conditional
259 count part of the model (holding covariates at their mean values).

260 To test whether higher-level characteristics of ecosystems can be used to generalize
261 patterns of susceptibility, we aggregated ecosystems by their category (terrestrial
262 or wetland) and structuring process (none, environmental stress, regulating
263 disturbance, destabilizing disturbance, moderate anthropogenic disturbance, or
264 strong anthropogenic disturbance), as defined in the Nature in Norway system
265 (Appendix, table 5). We then refitted our selected models with these eight strata
266 replacing ecosystems, and obtained estimates of relative establishment likelihood
267 for each category and structuring process.

Table 1: Correlations between wildling densities and relative establishment likelihoods across ecosystem types, for each species group.

species group	Pearson	Spearman
<i>Picea sitchensis / lutzii</i>	0.23	0.55
<i>Picea abies</i>	0.22	0.73
<i>Larix spp.</i>	1.00	0.89
<i>Pinus contorta</i>	0.07	0.38

268 3 Results

269 Wildling densities across ecosystems ranged 0-211/ha for Sitka/Lutz spruce
 270 (unstratified mean: 28), 0-49/ha for Norway spruce (unstratified mean: 6),
 271 0-1045/ha for larches (unstratified mean: 13), and 0-219/ha for lodgepole pine
 272 (unstratified mean: 34). Relative establishment likelihoods differed considerably
 273 from relative wildling densities, except in larches (table 1). For instance, our
 274 model estimated that Sitka/Lutz spruce is three times more likely to establish in
 275 “boreal heath” than in “artificial substrate”, despite wildling density being three
 276 times lower in “boreal heath” (fig. 4). The variation in relative establishment
 277 likelihoods generally matched or exceeded that in corresponding wildling densities
 278 (Appendix table 6).

279 For all species, models using relative seed rain estimates from the WALD dispersal
 280 model predicted wildling abundance best (Appendix, table 7). Site had a strong
 281 influence on wildling abundance for Sitka/Lutz spruce and lodgepole pine, such
 282 that site variation swamped much of the variation between ecosystems for these
 283 species. The direct effects of climate on establishment likelihood varied by
 284 species and was strongest for larches (Appendix, tables 8-11). The direct effects
 285 of elevation relative to the stand on wildling abundance were comparatively
 286 modest and acted in different directions for different species. Stand age did not
 287 significantly affect wildling abundance in any species, except that older stands of

²⁸⁸ Sitka/Lutz spruce had fewer wildling-free cells (structural zeros) than younger
²⁸⁹ stands.

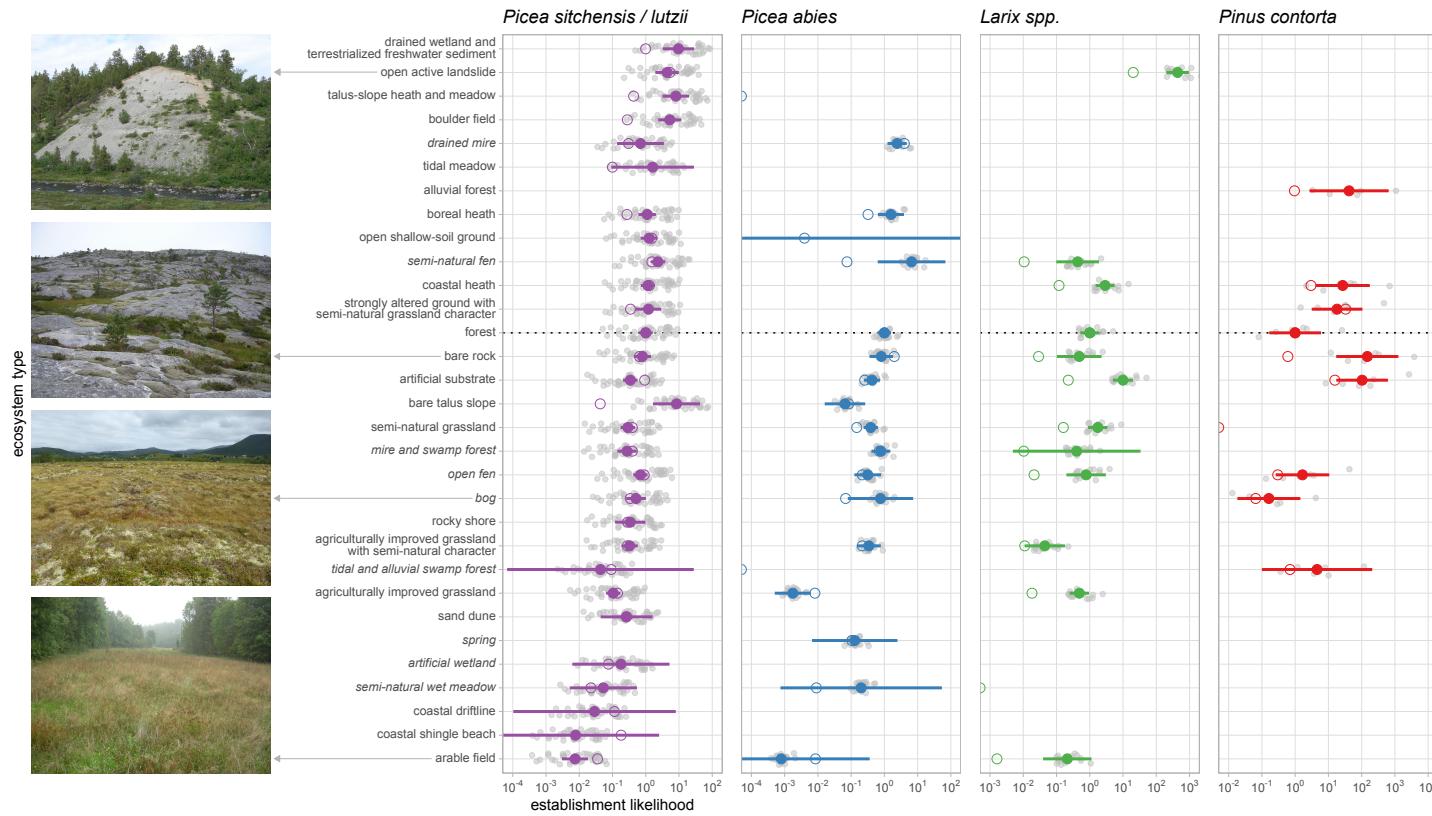


Figure 4: Relative densities (unfilled points) and relative establishment likelihoods (filled points) of four alien conifer species groups across ecosystem types, using 'forest' as the reference ecosystem. Zero density is plotted at the lower limit of the x-axis. Relative establishment likelihoods are shown with 95 % confidence intervals. Grey points depict relative establishment likelihoods for individual sites in our data set. The order of ecosystem types along the y-axis is determined by a confidence-weighted mean of their percentile-ranked establishment likelihoods within species, such that types with consistently high establishment likelihood across species are at the top. Photos licensed CC BY 4.0 Rune Halvorsen.

Table 2: Spearman correlations of relative establishment likelihoods in ecosystem types, between pairs of species groups.

	<i>Picea abies</i>	<i>Larix spp.</i>	<i>Pinus contorta</i>
<i>Picea sitchensis / lutzii</i>	0.37	0.5	0.12
<i>Picea abies</i>		0.18	-0.1
<i>Larix spp.</i>			-0.1

290 Among ecosystems with at least one wildling, estimated establishment likelihoods
 291 varied by 3–5 orders of magnitude for the different species. Patterns of relative
 292 establishment likelihood were modestly similar between species, with positive
 293 rank correlations in four of six species pairs (table 2). “Arable fields” showed
 294 some of the lowest establishment likelihoods of any ecosystem for all species
 295 where it appeared. Meanwhile, ecosystems with high establishment likelihoods
 296 tended to be rarer types (e.g. “open active landslides”) but also included “boreal
 297 heath” and “coastal heath”.
 298 Variation in establishment likelihoods shrank when ecosystems were aggregated by
 299 category or structuring process, to 0–3 orders of magnitude (fig. 5). The model for
 300 lodgepole pine did not converge and was disregarded, but none of the remaining
 301 species showed large differences in establishment likelihood between terrestrial
 302 and wetland ecosystems. At most, larches were three times less likely to establish
 303 in wetlands. Ecosystems structured by destabilizing disturbance tended to show
 304 high establishment likelihoods. However, the association between structuring
 305 process and establishment likelihood was heterogeneous across species.

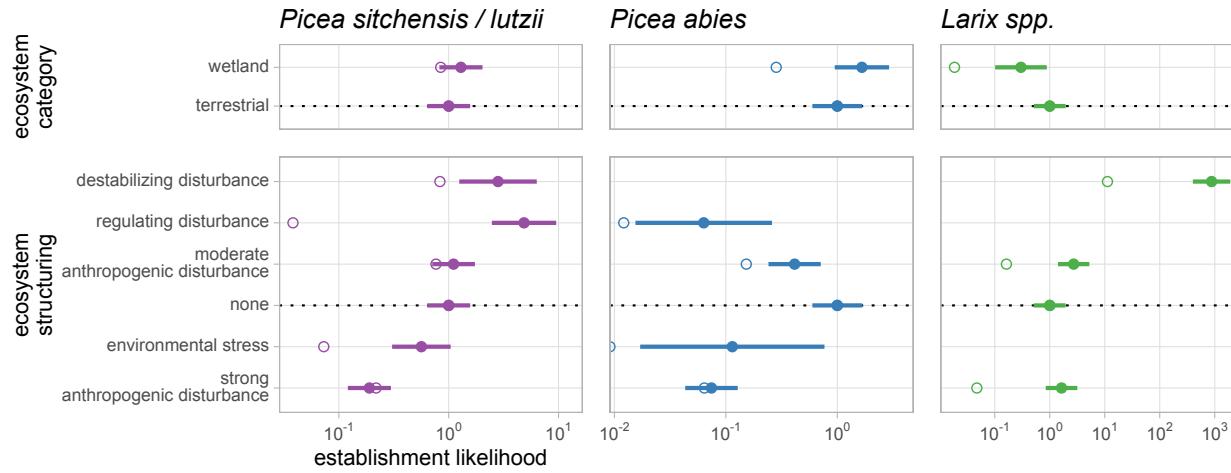


Figure 5: Relative densities (unfilled points) and relative establishment likelihoods (filled points) of three alien conifer species groups among categories of ecosystem types (top) or structuring processes in ecosystem types (bottom). Relative establishment likelihoods are shown with 95 % confidence intervals. The horizontal dotted lines indicate the reference strata.

306 **4 Discussion**

307 **4.1 How does wildling density relate to ecosystem suscep-**
308 **tibility?**

309 Confounders of the relationship between ecosystem type and wildling density
310 caused density to mischaracterize differences in establishment likelihood between
311 ecosystems. For example, the density of Sitka/Lutz spruce wildlings was about
312 equal in “bare talus slopes” and “arable fields”, but we estimate that establish-
313 ment likelihood is actually about 1000 times higher in the former. The nonzero
314 effects of hypothesized confounders (like seed rain, climate, and site) imply that
315 our modeled estimates of establishment likelihood are less biased measures of
316 ecosystem susceptibility. Furthermore, variation in establishment likelihood was
317 no smaller than variation in wildling densities, as might have been the case if
318 confounding variables had amplified differences in ecosystem establishment.

319 Because wildling abundance is the product of seed rain and establishment
320 likelihood, we needed to estimate seed rain independently of our wildling data
321 to model establishment likelihood properly. By including relative seed rain as
322 an offset in the model, we ensured that seed rain and establishment likelihood
323 were not conflated, at the cost of assuming that our relative seed rain estimates
324 were accurate. Exploring the alternative, we found that if we included relative
325 seed rain as a covariate rather than an offset that its coefficient was estimated
326 near one, and that estimated relative establishment likelihoods remained mostly
327 unchanged (Appendix, fig. 6). Although wildlings cannot rigorously validate
328 seed dispersal models (due to survivorship bias), the superior fits of models with
329 WALD-derived seed rain offsets compared to models with statically-derived seed
330 rain offsets supports the WALD model estimates. The mechanistic nature of the
331 WALD model also makes us more confident in its estimates across species and

³³² sites than we would be in a purely phenomenological model (Bullock et al., 2018).
³³³ Nevertheless, that seed rain was modeled and not measured is a limitation of
³³⁴ our method, and it makes the establishment likelihoods we estimate less certain.
³³⁵ For example, changes in the distribution of seed rain as a stand matures were
³³⁶ not accounted for, nor was secondary seed dispersal from the few reproductive
³³⁷ wildlings we observed.

³³⁸ The inconsistent effects of relative elevation on wildling abundance indicate that
³³⁹ there is no rule of thumb for management about wildlings moving up or down
³⁴⁰ slopes. However, since we defined elevation relative to the central stand, it
³⁴¹ is possible that seed sources above or below the central stand partly masked
³⁴² slope effects. On the other hand, our results were consistent with the idea
³⁴³ that prevailing winds during the dispersal season affect the direction of wildling
³⁴⁴ spread, since the WALD model provided the best fit. Meanwhile, the weak and
³⁴⁵ uncertain effects of stand age on wildling abundance suggests that other site
³⁴⁶ characteristics tend to outweigh the magnitude of wildling accumulation over
³⁴⁷ time.

³⁴⁸ Our models do not estimate climate's total causal effect on wildling abundance,
³⁴⁹ because they set aside its influence on ecosystems (Westreich & Greenland, 2013).
³⁵⁰ Therefore, we interpret the estimated climatic effects with respect to physiological
³⁵¹ constraints within a given ecosystem. The negligible effect of precipitation and
³⁵² weakly positive effect of mean annual temperature on Sitka/Lutz spruce wildling
³⁵³ abundance is consistent with Sitka spruce's wide climatic tolerance relative to
³⁵⁴ climatic variation in Norway and its oceanic affinity (Peterson et al., 1997). For
³⁵⁵ Norway spruce, our results support a previous finding that seedling recruitment
³⁵⁶ increases towards the wetter end of Norwegian climate (Tingstad et al., 2015),
³⁵⁷ although most of our sites circumscribed a narrow part of that range. Warm
³⁵⁸ and wet conditions seem to suppress larch establishment in Norway, which may

³⁵⁹ be taken into consideration when managing these plantations.

³⁶⁰ A curious feature of our results that needs more research is the large amount of
³⁶¹ unexplained variation in Sitka/Lutz spruce and lodgepole pine wildling abun-
³⁶² dance between sites. This means that our ability to predict the spread of these
³⁶³ species at a specific site, relative to others, is limited. Nevertheless, ecosystem
³⁶⁴ comparisons can and should still guide management. Bianchi et al. (2019) strug-
³⁶⁵ gled to predict regeneration density within Sitka spruce plantations from stand
³⁶⁶ density (among other predictors), which suggests that the unexplained site-level
³⁶⁷ variation in our models was not caused by our assumption of constant seed
³⁶⁸ source density. Alternative sources of heterogeneity may include: (1) disturbance
³⁶⁹ legacies not captured in the delineation of ecosystem types (especially in grazing
³⁷⁰ pressure; Miller et al., 2021), (2) demographic characteristics of plantations,
³⁷¹ potentially related to provenance (especially in cone production; Taylor et al.,
³⁷² 2016), (3) wildling control by property owners, or (4) ecological differences
³⁷³ between Sitka and Lutz spruce or subspecies of lodgepole pine.

³⁷⁴ 4.2 Which ecosystems are susceptible?

³⁷⁵ In a large database of vegetation plots across Europe, Chytrý et al.(2008) found
³⁷⁶ that alien plants as a group are consistently found at low rates in mires and
³⁷⁷ heaths, and high rates in arable, man-made, and coastal ecosystems. The conifer
³⁷⁸ species we examined do not conform closely to these broader trends in ecosystem
³⁷⁹ invasibility, showing relatively high rates of establishment in heaths and very
³⁸⁰ low rates of establishment in arable ecosystems. To the extent that there are
³⁸¹ similarities across these four species, they appear to establish more easily in
³⁸² ecosystems infrequently hit by intense disturbances (e.g. rock fall in “bare talus
³⁸³ slope”) than in ecosystems frequently experiencing less intense disturbances
³⁸⁴ (e.g. flooding in “semi-natural wet meadow”).

385 Of the species in this study, lodgepole pine's establishment is best studied, and
386 our results are consistent with this literature. "Bare rock" harbors very few
387 competitors and showed highest lodgepole pine establishment of all ecosystems
388 (Despain, 2001), and ecosystems with canopy cover generally showed low estab-
389 lishment (Langdon et al., 2010; Taylor et al., 2016). It is difficult to evaluate
390 our results against the recruitment patterns that have been described for the
391 three other species. For instance, Sitka spruce grows poorly under moisture
392 stress and tolerates flooding well (Peterson et al., 1997), which might account for
393 why it was equally likely to establish in wetland and terrestrial ecosystems. Yet
394 it also established well in "open shallow-soil ground", despite this ecosystem's
395 characteristically dry soil. This illustrates the trouble with deriving predictions
396 from generalized statements about species autecology. Furthermore, ecosystems
397 that would seem inhospitable based on their overall characteristics may actu-
398 ally contain many localized opportunities for establishment, because seedling
399 mortality is strongly regulated by microsites (Macek et al., 2017). From this
400 perspective, our estimates of establishment likelihood measure the density of
401 suitable microsites in a given ecosystem.

402 The breadth in establishment likelihood suggests that differences between ecosys-
403 tems deserve careful consideration when managing wildling spread. This knowl-
404 edge may be applied in at least two ways. First, as a preventative measure, we
405 recommend siting new stands where surrounded by high proportions of ecosys-
406 tems with low establishment likelihood. In particular, "arable fields" repress
407 wildling establishment for all species and are common near existing stands, so
408 picking sites hemmed in by this kind of agricultural land should be both effective
409 and feasible. This would probably reduce the rate of wildling establishment by
410 orders of magnitude, even if long distance dispersal might preclude complete
411 containment (Albert et al., 2008). In some cases it may also be desirable to

412 transform ecosystems adjacent to existing stands to prevent (further) spread,
413 for example by intensifying mowing regimes. Second, as a reactive measure, we
414 advise using relative ecosystem susceptibility as a starting point for allocating
415 monitoring and control resources in proportion to risk. Prioritizing ecosystems
416 that are highly susceptible and also rare (e.g. “open active landslide”) is especially
417 likely to be cost-efficient.

418 The establishment patterns we quantify probably hold, more or less, outside
419 Norway (Chytrý, Maskell, et al., 2008). From a manager’s perspective, we
420 expect that the ecosystems we report may translate well to equivalent types
421 in similar classification systems, because the Nature in Norway classification is
422 rule-based and aims for observer neutrality. At the same time, we urge caution
423 in extending our establishment estimates to ecosystems that are only broadly
424 similar, because similar types frequently showed markedly different susceptibility
425 (e.g. Norway spruce in “agriculturally improved grassland with semi-natural
426 character” vs. “agriculturally improved grassland”).

427 An observational study like ours informs management of long-lived, naturalized
428 species more directly than experimental studies, because longer time frames
429 are examined. It measures long-term survival under a wide range of natural
430 conditions experienced by the wildlings. In contrast, seeding experiments gener-
431 ally observe only the youngest life stages, and the factors controlling individual
432 success differ at later life stages (Dovčiak et al., 2008). On the other hand, exper-
433 iments might be more useful when the observed wildling spread is not broadly
434 representative (e.g. for species expanding from a single, recent introduction).

435 4.3 What do susceptible ecosystems have in common?

436 The overarching characteristics that we used to aggregate ecosystems did not
437 generalize differences in susceptibility well, especially not across species, so these

438 classifications have limited utility for management. Note that different sets of
439 ecosystems comprised the strata for each species, depending on their presence
440 in the data, and these differences in ecosystem composition help explain why
441 the patterns of aggregated establishment likelihood varied between species. This
442 constraint hinders species comparisons but underlines our main takeaway from
443 these results — that the susceptibility of an individual ecosystem frequently
444 diverges from those of related ecosystems.

445 Within species, we urge careful interpretation of the comparisons among ecosys-
446 tem categories and structuring processes. Many areas where conifer establishment
447 is nearly impossible, like paved surfaces and annually plowed fields, count as
448 terrestrial and strongly anthropogenically disturbed, which lowers the relative
449 establishment likelihood of these two strata. Our results do not imply, for exam-
450 ple, that a strong anthropogenic disturbance event will decrease establishment
451 likelihood of Sitka/Lutz spruce relative to an ecosystem’s prior state. Rather,
452 we find that ecosystems structured by strong anthropogenic disturbance, on the
453 whole, are less susceptible to Sitka/Lutz spruce wildlings than other ecosystems.

454 5 Conclusions

455 One of the main novelties of this study is that we inferred susceptibility-
456 invasibility using mechanistically reconstructed, spatial estimates of seed
457 rain. Scientists studying invasibility at national and continental scales have
458 already recognized the importance of normalizing observed levels of invasion
459 by a spatially explicit estimate of exposure (i.e. propagule pressure; Colautti
460 et al., 2006; Chytrý, Jarošík, et al., 2008). However, many studies quantifying
461 ecosystem invasibility have not been able to adjust for propagule pressure,
462 typically because it is impossible to reconstruct the underlying dispersal history

⁴⁶³ (Catford et al., 2012). We found that accounting for seed rain and other
⁴⁶⁴ confounders of the relationship between ecosystems and wildling abundance
⁴⁶⁵ reshuffles estimates of ecosystem invasibility considerably.

⁴⁶⁶ Wildling spread from plantations is a growing problem (Richardson & Rejmánek,
⁴⁶⁷ 2004) and will probably worsen with recent pushes to increase tree planting
⁴⁶⁸ worldwide (Brundu et al., 2020). Meanwhile, remotely sensed and surveyed
⁴⁶⁹ data are increasing the availability of detailed and accurate maps of ecosystems
⁴⁷⁰ across large areas, which presents opportunities to manage wildling spread more
⁴⁷¹ efficiently. Specifically, differences in ecosystem susceptibility may be leveraged
⁴⁷² to reduce the rate of wildling establishment through deliberate site selection for
⁴⁷³ new stands or targeted interventions around existing stands. However, managers
⁴⁷⁴ should not judge ecosystem susceptibility based on wildling density alone, nor
⁴⁷⁵ on generalizations across ecosystems.

⁴⁷⁶ **6 Authors' contributions**

⁴⁷⁷ JV, SLO, and OSk conceived the ideas and designed methodology; SLO, LA,
⁴⁷⁸ MOK, AO, JS, OSt, and ØS collected the data; JV analyzed the data and led
⁴⁷⁹ the writing. All authors contributed to drafts and gave approval for publication.

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⁴⁸⁸ **8 Data availability statement**

⁴⁸⁹ Data will be made available via the Dryad Digital Repository.

490 **9 Appendix**

491 The WALD model (Katul et al., 2005) takes the form of an inverse Gaussian
492 distribution whose mean (μ) and shape (λ) parameters are calculated from
493 physical characteristics of the dispersal system:

$$\mu = \frac{HU}{F} \quad (2)$$

$$\lambda = \left(\frac{H}{\sigma} \right)^2 \quad (3)$$

495 where H is the seed release height, U is the mean horizontal wind velocity
496 between H and the ground, F is the terminal velocity of the seed, and σ is
497 a wind turbulence parameter. We set H to the height of the central stand,
498 estimated U from a computed vertical wind profile, obtained F from literature,
499 and calculated σ from an equation for turbulent flow as a function of vegetation
500 height (eq. A4 in Skarpaas & Shea, 2007). We parameterized separate WALD
501 models for 20° sectors around each seed source, to make seed dispersal anisotropic
502 (directional). In each sector we estimated mean vegetation height based on the
503 composition of mapped ecosystem types (Appendix, table 5). Simultaneously,
504 we randomly sampled 100 wind velocities in the direction of the sector during
505 the species' dispersal season. The 100 resulting WALD kernels produced the
506 seed probability density in the sector, and individual sectors were weighed by the
507 frequency of corresponding wind directions (again, during the species' dispersal
508 season). The wind data were obtained either from the nearest weather station
509 (MET Norway), a 2.5 km resolution interpolated hindcast covering southern
510 Norway (Haakenstad & Haugen, 2017), or a 10 km resolution hindcast covering
511 all of Norway (Haakenstad et al., 2020; Reistad et al., 2011). We used weather
512 station data if the station was less than 2.5 or 10 km away (depending on hindcast

⁵¹³ coverage), or else the highest resolution hindcast.

Table 3: Dispersal traits

species group	seed terminal velocity	dispersal season	references
<i>Larix spp.</i>	1.0 m/s	Dec - May	2, 3
<i>Picea abies</i>	0.58 m/s	Nov - May	2, 4
<i>Pinus contorta</i>	0.82 m/s	Sep - Dec	2
<i>Picea sitchensis / lutzii</i>	0.94 m/s	Oct - Feb	1, 2

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514 Some of the seed source polygons we registered in the field had distinctive
 515 features that we accounted for as follows. Seed source polygons for which the
 516 species of interest only made up a fraction of the stand composition (e.g. in
 517 Olsen et al., 2019) were used with their point source density adjusted accordingly.
 518 For example, a stand identified as composed of Sitka spruce and Norway spruce
 519 was assigned a seed source point density half that of a Sitka spruce monoculture.

⁵²⁰ Likewise, ‘mixed forest’ stands (e.g. in Appelgren, 2018) were assigned 0.1 times
⁵²¹ the seed source point density of a monoculture. Seed source polygons identified
⁵²² as logged (e.g. in Appelgren, 2018) were included as seed sources only if we could
⁵²³ confirm that they were logged no earlier the decade prior to mapping, using time
⁵²⁴ series of aerial photos.

Table 4: Plantation stands

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b	
Olsen et al. 2016	<i>Pinus contorta</i>	Fiskvikrokkdalen	292498	6843676	11	58	2.36	12.8	
Olsen et al. 2016	<i>Pinus contorta</i>	Gulemyrane	94625	7000110	9*	42	7.22	48.0	
Olsen et al. 2016	<i>Pinus contorta</i>	Selvik	74593	6978018	8	45	7.25	40.0	
Olsen et al. 2016	<i>Pinus contorta</i>	Skarsheia	78833	6979095	6	45	6.60	36.7	
Olsen et al. 2016	<i>Pinus contorta</i>	Sollitangen	260896	6859024	12	37	2.60	6.7	
23	Olsen et al. 2016	<i>Pinus contorta</i>	Tomasmyra	260694	6864426	12	29	2.44	6.2
Olsen et al. 2016	<i>Picea sitchensis / lutzii</i>	Gryttingdalen-vest	503887	7613803	8	52	4.56	49.0	
Olsen et al. 2016	<i>Picea sitchensis / lutzii</i>	Gryttingdalen-oest	504335	7613736	8	52	4.50	50.5	
Olsen et al. 2016	<i>Picea sitchensis / lutzii</i>	Holmsnes-nordvest	493935	7609464	11	49	5.36	45.3	
Olsen et al. 2016	<i>Picea sitchensis / lutzii</i>	Holmsnes-soeroest	494675	7608420	11	45	5.46	44.0	
Olsen et al. 2016	<i>Picea sitchensis / lutzii</i>	Hov	496920	7608739	11	56	5.22	50.9	
Olsen et al. 2016	<i>Picea sitchensis / lutzii</i>	Raavollmarka	499105	7608885	18	59	4.80	51.1	
Appelgren and Torvik 2017	<i>Larix spp.</i>	Anisdal	-36439	6529890	22	56	7.37	38.8	

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
Appelgren and Torvik 2017	<i>Larix spp.</i>	Haalandsbotten	-37108	6532830	20	57.5	7.00	38.9
Appelgren and Torvik 2017	<i>Larix spp.</i>	Roeynaasen	-31279	6547997	25	77.5	6.88	36.5
Appelgren and Torvik 2017	<i>Larix spp.</i>	Storemo	-107	6588189	23	60	7.15	33.0
Appelgren and Torvik 2017	<i>Larix spp.</i>	Toegjefjellet	-22293	6546411	20	60	6.69	39.6
Appelgren and Torvik 2017	<i>Larix spp.</i>	Voren	-26899	6554824	20	62	6.42	39.6
Appelgren and Torvik 2017	<i>Picea abies</i>	Mysingveien	-10547	6522150	21	52	6.34	53.9
Appelgren and Torvik 2017	<i>Picea abies</i>	Ollestad	-2440	6519912	20*	58	6.76	42.5
Appelgren and Torvik 2017	<i>Picea abies</i>	Varland	-15600	6584801	22	60	6.94	36.2
Appelgren and Torvik 2017	<i>Picea sitchensis / lutzii</i>	Dale	-30398	6586913	25	77	7.10	40.6
Appelgren and Torvik 2017	<i>Picea sitchensis / lutzii</i>	Fjoesne	-11052	6650525	22	50	6.11	60.1
Appelgren and Torvik 2017	<i>Picea sitchensis / lutzii</i>	Kvia	-42603	6539369	20	57.5	8.02	30.6
Appelgren and Torvik 2017	<i>Picea sitchensis / lutzii</i>	Roeynaasen	-31321	6548005	23	77.5	6.88	36.5
Appelgren and Torvik 2017	<i>Picea sitchensis / lutzii</i>	Toegjefjellet	-22347	6546467	20	60	6.69	39.6

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
Appelgren and Torvik 2017	<i>Picea sitchensis / lutzii</i>	Voren	-26991	6554850	18	52.5	6.42	39.6
Appelgren and Torvik 2017	<i>Picea sitchensis / lutzii</i>	Aarheia	-33443	6589861	28	60	7.31	38.2
Kyrkjeeide et al. 2017	<i>Picea abies</i>	Myklebostad	481205	7469940	20*	97	4.99	24.9
Kyrkjeeide et al. 2017	<i>Picea abies</i>	Tennes	668660	7695332	20*	87	1.87	18.6
Kyrkjeeide et al. 2017	<i>Picea sitchensis / lutzii</i>	Hagheia	445925	7560670	18*	55	4.89	49.4
Kyrkjeeide et al. 2017	<i>Picea sitchensis / lutzii</i>	Harteigen	449285	7559665	15*	51.5	5.38	48.4
Kyrkjeeide et al. 2017	<i>Picea sitchensis / lutzii</i>	Haakoeya	647074	7731726	17*	42†	3.16	30.0
Appelgren 2018	<i>Larix spp.</i>	Engjane	-34540	6529860	15	45	7.19	40.3
Appelgren 2018	<i>Larix spp.</i>	Hyljafjellet	-34030	6529963	15	45	7.30	39.6
Appelgren 2018	<i>Larix spp.</i>	Hoegaas	-25415	6560056	20	57.5	6.77	38.8
Appelgren 2018	<i>Larix spp.</i>	Myrvoll	-12944	6522033	12	17.5	7.06	43.4
Appelgren 2018	<i>Larix spp.</i>	Oaland	-7652	6563045	17	52.5	5.48	49.7
Appelgren 2018	<i>Picea abies</i>	Efteland	-15304	6523548	20	45	6.69	53.8

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
Appelgren 2018	<i>Picea abies</i>	Myrvoll	-13000	6522143	18	71.5	7.06	43.4
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Foersvoll	-29434	6588711	24	54	7.22	37.7
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Hommeland	-17515	6559100	17	47	6.01	40.1
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Hyljafjellet	-34044	6529954	13.5	45	7.30	39.6
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Oaland	-7648	6563033	15	52.5	5.48	49.7
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Sandve	-58701	6601600	11	30	7.83	38.8
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Skorphella	-30767	6581293	13	35	7.87	31.3
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Starebakkane	-43287	6563381	18	52.5	8.08	27.9
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Veggjaberget	-35788	6526000	12	27.5	8.04	35.0
Appelgren 2018	<i>Picea sitchensis / lutzii</i>	Vikra	-59126	6601266	22*	78	7.97	37.5
Olsen et al. 2019	<i>Larix spp.</i>	Stordalslia	418827	7303180	11.9	16.5	4.62	52.2
Olsen et al. 2019	<i>Picea abies</i>	Storbergan	413255	7349964	13.1	49	5.02	55.6
Olsen et al. 2019	<i>Picea abies</i>	Svinnes	385625	7306386	15.3	36.5	5.57	41.0

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Alstahaugmyran	382564	7311547	15.7	31.5	5.49	45.7
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Hamran	373448	7266074	17.2	26	5.69	42.3
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Langvassfjellet	409484	7330371	17.6	36.5	4.87	54.0
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Meaasen	386111	7333724	14.1	43.5	5.70	34.5
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Myrmo	391075	7321058	18.8	37	5.22	37.4
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Olabergan	410600	7341996	18.8	29	5.31	45.0
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Plogskjaeret	378814	7280849	16.1	26	5.57	43.5
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Sandmoan	382107	7329122	10.8	33	5.73	33.7
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Steinaasen	375834	7274496	17.9	35	5.50	37.6
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Svinnes	385652	7306426	16.4	37.5	5.65	40.1
Olsen et al. 2019	<i>Picea sitchensis / lutzii</i>	Valan	383545	7304119	15.5	35	5.61	41.5
Sandven et al. 2019	<i>Larix spp.</i>	Ytre-bjotveit	49799	6729344	19.4	72	5.52	34.5
Sandven et al. 2019	<i>Larix spp.</i>	Knappeidet	-47542	6737678	17.2	32	7.99	39.4

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
Sandven et al. 2019	<i>Larix spp.</i>	Indre-bjotveit	51174	6730928	24.5	84	5.82	35.9
Sandven et al. 2019	<i>Picea abies</i>	Boerve	37746	6711673	31.9	64	5.49	46.6
Sandven et al. 2019	<i>Picea abies</i>	Skare	31612	6676392	22	66	4.41	50.6
Sandven et al. 2019	<i>Picea abies</i>	Oeystese	16634	6726920	15.6	57	6.42	67.4
Sandven et al. 2019	<i>Picea abies</i>	Vasshjallane	65573	6728437	22.8	56	5.53	29.8
Sandven et al. 2019	<i>Picea abies</i>	Hjelmtveit	-31407	6756542	21.4	57	7.15	57.3
Sandven et al. 2019	<i>Picea abies</i>	Bondhusdalen	15726	6695404	16.2	55	5.67	44.0
Sandven et al. 2019	<i>Picea abies</i>	Saeboe	-36690	6759365	21.2	51	7.07	59.8
Sandven et al. 2019	<i>Picea abies</i>	Indre-arna	-25457	6738087	14.4	52	6.94	45.2
Sandven et al. 2019	<i>Picea abies</i>	Kvamskogen	4982	6726838	20.4	101	4.98	57.1
Sandven et al. 2019	<i>Picea abies</i>	Rosendal	-1965	6685031	16.8	49	6.94	55.3
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Midtre-fjell	-47585	6729572	23.5	50	7.74	44.8
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Oevre-manger	-43485	6764574	17.5	46	7.78	53.3

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Fuglavassstoppen	-50243	6740596	19.5	48	7.86	46.0
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Kvitefjella	-48847	6730154	21.1	50	7.57	47.6
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Kausland	-50236	6718477	22.2	44	7.84	46.2
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Misje	-51009	6743828	20.8	54	7.99	45.1

Note:

Easting and Northing are given for UTM zone 33N. Height is given in meters and age in years.

^a mean annual temperature (°C)

^b precipitation in coldest quarter (cm)

* interpolated as the mean height of conspecific stands, inversely weighted by difference in age

† interpolated as the mean age of conspecific stands in the same region

Table 5: Ecosystem types

type	code	category	structuring	vegetation height ^a
bare rock	T1	terrestrial		0.0
open shallow-soil ground	T2	terrestrial		0.5
arctic-alpine heath and lee side	T3	terrestrial		0.5
forest	T4	terrestrial		10.0
rocky shore	T6	terrestrial	environmental stress	0.0
tidal meadow	T12	terrestrial	environmental stress	0.5
bare talus slope	T13	terrestrial	regulating disturbance	0.0
talus-slope heath and meadow	T16	terrestrial	regulating disturbance	0.5
open active landslide	T17	terrestrial	destabilizing disturbance	0.0
open alluvial sediment	T18	terrestrial	destabilizing disturbance	0.0
sand dune	T21	terrestrial	destabilizing disturbance	0.0
coastal driftline	T24	terrestrial	destabilizing disturbance	0.5
boulder field	T27	terrestrial	regulating disturbance	0.0

Table 5: Ecosystem types (*continued*)

type	code	category	structuring	vegetation height ^a
coastal shingle beach	T29	terrestrial	regulating disturbance	0.0
alluvial forest	T30	terrestrial	destabilizing disturbance	10.0
boreal heath	T31	terrestrial	moderate anthropogenic disturbance	0.5
semi-natural grassland	T32	terrestrial	moderate anthropogenic disturbance	0.5
semi-natural tidal and salt meadow	T33	terrestrial	moderate anthropogenic disturbance	0.5
coastal heath	T34	terrestrial	moderate anthropogenic disturbance	0.5
artificial substrate	T35	terrestrial	strong anthropogenic disturbance	0.0
artificial substrate	T37	terrestrial	strong anthropogenic disturbance	0.0
artificial substrate	T39	terrestrial	strong anthropogenic disturbance	0.0
artificial substrate	T43	terrestrial	strong anthropogenic disturbance	0.0
drained wetland and terrestrialized freshwater sediment	T36	terrestrial	strong anthropogenic disturbance	0.5
tree plantation	T38	terrestrial	strong anthropogenic disturbance	10.0
strongly altered ground with semi-natural grassland character	T40	terrestrial	strong anthropogenic disturbance	0.0

Table 5: Ecosystem types (*continued*)

type	code	category	structuring	vegetation height ^a
agriculturally improved grassland with semi-natural character	T41	terrestrial	strong anthropogenic disturbance	0.5
landscaped patch or field	T42	terrestrial	strong anthropogenic disturbance	0.0
arable field	T44	terrestrial	strong anthropogenic disturbance	0.5
agriculturally improved grassland	T45	terrestrial	strong anthropogenic disturbance	0.5
open fen	V1	wetland		0.0
mire and swamp forest	V2	wetland		10.0
bog	V3	wetland	environmental stress	0.0
spring	V4	wetland	environmental stress	0.0
tidal and alluvial swamp forest	V8	wetland	environmental stress	10.0
semi-natural fen	V9	wetland	moderate anthropogenic disturbance	0.0
semi-natural wet meadow	V10	wetland	moderate anthropogenic disturbance	0.0
peat quarry	V11	wetland	strong anthropogenic disturbance	0.0
drained mire	V12	wetland	strong anthropogenic disturbance	0.0

Table 5: Ecosystem types (*continued*)

type	code	category	structuring	vegetation height ^a
artificial wetland	V13	wetland	strong anthropogenic disturbance	0.0

^a approximate vegetation heights (meters) are used only to estimate wind turbulence

Table 7: Comparison of models with different seed dispersal estimates

species group	seed dispersal estimate	AIC	dAIC	df
<i>Picea sitchensis / lutzii</i>	WALD	51967	0	38
	Exponential Power	NA	NA	NA
	none	54478	2510	38
<i>Picea abies</i>	WALD	9681	0	26
	Exponential Power	25316	15636	26
	none	9781	101	26
<i>Larix spp.</i>	WALD	10058	0	21
	Exponential Power	27310	17252	21
	none	NA	NA	21
<i>Pinus contorta</i>	WALD	3319	0	17
	Exponential Power	NA	NA	17
	none	3372	53	17

Table 6: Proportional variability in wildling densities among ecosystems compared to proportional variability in establishment likelihoods among ecosystems.

	density	establishment likelihood
<i>Picea sitchensis / lutzii</i>	0.635	0.735
<i>Picea abies</i>	0.755	0.755
<i>Larix spp.</i>	0.776	0.721
<i>Pinus contorta</i>	0.753	0.824

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Table 8: Model summary for *Picea sitchensis* / *lutzii*. The conditional submodel is glmmTMB's genpois (Generalized Poisson) family with dispersion parameter $\phi^2 = 7.745472$

Term	Fixed effects		Random effects	
	Estimate	95% CI	SD (Intercept)	N
Conditional model				
Intercept	-1.80	-2.28, -1.31		
age	-0.08	-0.54, 0.38		
bio01	0.54	0.01, 1.08		
bio19	-0.03	-0.55, 0.5		
relelev	-0.12	-0.19, -0.05		
T45	-2.25	-2.42, -2.08		
artificial	-1.07	-1.27, -0.87		
T44	-4.90	-5.68, -4.12		
T32	-1.24	-1.42, -1.06		
V9	0.84	0.63, 1.05		
T34	0.15	0.01, 0.29		
V12	-0.37	-1.92, 1.19		
V1	-0.37	-0.53, -0.22		
T13	2.13	0.57, 3.7		
T41	-1.12	-1.44, -0.79		
T1	-0.23	-0.63, 0.16		
V2	-1.29	-1.77, -0.82		
T2	0.24	-0.12, 0.59		
T40	0.19	-0.56, 0.94		
V10	-2.94	-5.22, -0.65		

T27	1.66	1, 2.32
T17	1.48	0.81, 2.14
T29	-4.86	-10.63, 0.9
T16	2.08	1.31, 2.86
V8	-3.14	-9.58, 3.31
T31	0.10	-0.3, 0.5
V3	-0.67	-1.17, -0.18
T6	-1.07	-2.02, -0.12
V13	-1.72	-5.06, 1.62
T12	0.48	-2.34, 3.29
T24	-3.55	-9.16, 2.06
T21	-1.33	-3.06, 0.4
T36	2.26	1.28, 3.25
site		1.42 42

Zero-inflation model

Intercept	0.39	-0.06, 0.84
age	-0.78	-1.19, -0.36
site		1.19 42

Table 9: Model summary for *Picea abies*. The conditional model is glmmTMB's genpois (Generalized Poisson) family with dispersion parameter $\text{phi}^2 = 2.495544$

Term	Fixed effects		Random effects	
	Estimate	95% CI	SD (Intercept)	N
Conditional model				
Intercept	-2.03	-2.49, -1.57		

age	0.02	-0.45, 0.49
bio01	-0.13	-0.71, 0.44
bio19	0.55	0.03, 1.06
relelev	0.39	0.28, 0.5
T45	-6.34	-7.5, -5.18
artificial	-0.86	-1.26, -0.46
T44	-7.14	-13.24, -1.03
T32	-0.95	-1.23, -0.66
V9	1.88	-0.47, 4.24
V12	0.88	0.33, 1.43
V1	-1.15	-1.97, -0.34
T13	-2.73	-4.07, -1.39
T41	-1.07	-1.78, -0.37
T1	-0.22	-0.89, 0.46
V2	-0.24	-0.72, 0.24
T2	-11.23	-39.45, 16.98
V10	-1.61	-7.23, 4.01
T31	0.46	-0.38, 1.29
V4	-2.05	-4.98, 0.87
V3	-0.27	-2.54, 2
site		0.58 19

Zero-inflation model

Intercept	1.72	0.92, 2.52
age	0.34	-0.41, 1.09
site		1.53 19

Table 10: Model summary for Larix spp. The conditional model is glmmTMB's genpois (Generalized Poisson) family with dispersion parameter $\text{phi}^2 = 6.713045$

Term	Fixed effects		Random effects	
	Estimate	95% CI	SD (Intercept)	N
Conditional model				
Intercept	-4.78	-5.44, -4.12		
age	-0.53	-1.56, 0.5		
bio01	-1.90	-2.67, -1.13		
bio19	-1.93	-3.02, -0.83		
relelev	0.48	0.39, 0.57		
T45	-0.72	-1.22, -0.23		
artificial	2.30	2, 2.6		
T44	-1.56	-3.16, 0.05		
T32	0.56	0.22, 0.89		
V9	-0.84	-2.25, 0.57		
T34	1.06	0.62, 1.5		
V1	-0.25	-1.54, 1.04		
T41	-3.11	-4.35, -1.88		
T1	-0.73	-2.23, 0.77		
V2	-0.91	-5.31, 3.5		
T17	6.09	5.47, 6.71		
site			0.86	15
Zero-inflation model				
Intercept	-0.36	-1.62, 0.9		
age	0.29	-0.83, 1.41		

site	1.24	15
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Table 11: Model summary for *Pinus contorta*. The conditional model is glmmTMB's genpois (Generalized Poisson) family with dispersion parameter $\phi^2 = 68.49936$

Term	Fixed effects		Random effects	
	Estimate	95% CI	SD (Intercept)	N
Conditional model				
Intercept	-7.11	-8.9, -5.31		
age	0.46	-1.24, 2.15		
bio19	-1.73	-3.46, 0.01		
relelev	0.92	0.49, 1.34		
artificial	4.64	3.81, 5.47		
T34	3.30	2.28, 4.31		
V1	0.51	-0.4, 1.41		
T1	5.00	3.36, 6.64		
T40	2.90	2.36, 3.44		
T30	3.74	1.56, 5.91		
V8	1.52	-2.08, 5.12		
V3	-1.82	-3.17, -0.47		
site			1.96	6
Zero-inflation model				
Intercept	-0.16	-0.49, 0.18		
age	-0.08	-0.41, 0.26		
site			0.00	6

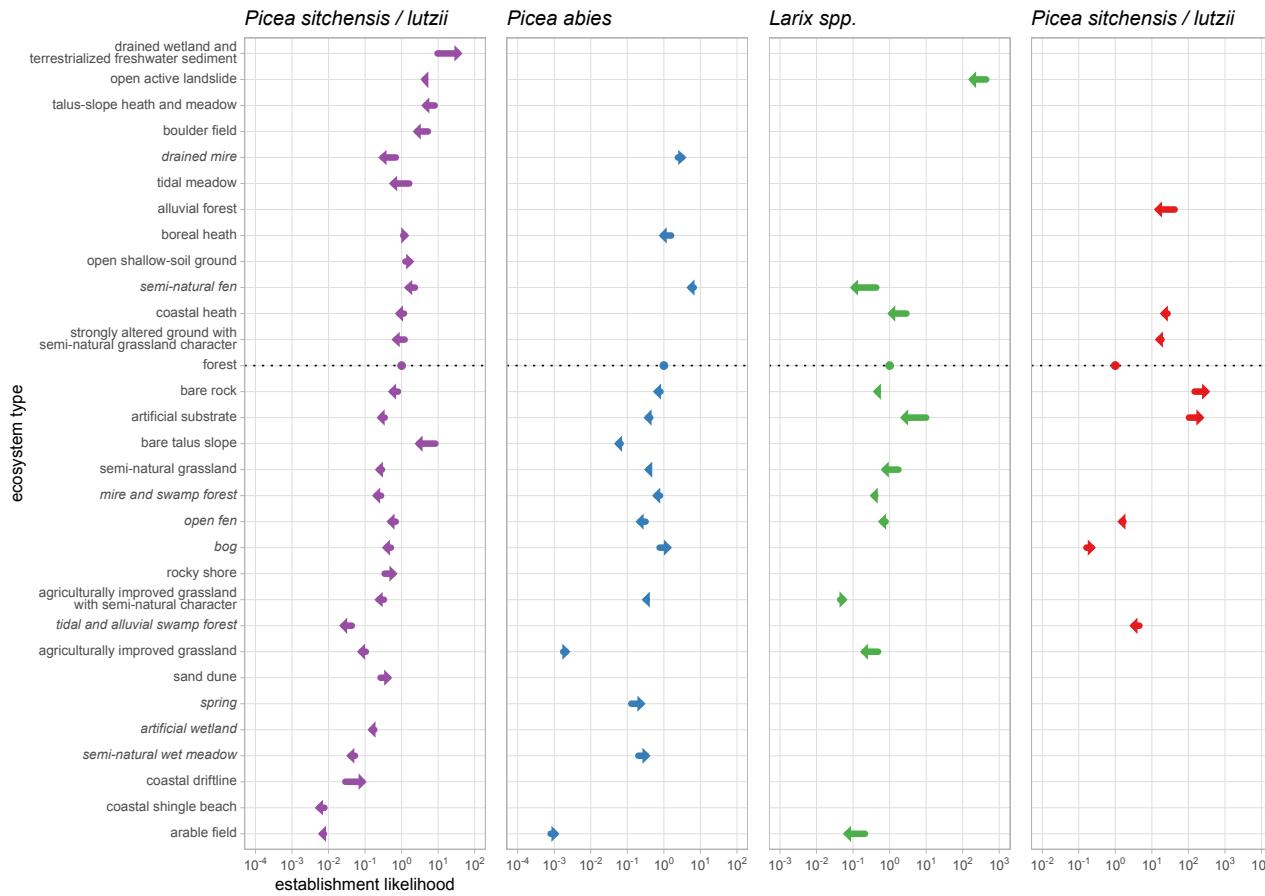


Figure 6: Shifts in estimated relative establishment likelihoods when relative seed rain (from the WALD dispersal model) is included in the model as a covariate rather than an offset. Arrows point from the models with offsets to the models with covariates.

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