

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

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## 2 Abstract

1. Plantations of alien conifer species are common worldwide, and set to become even more prevalent in coming decades. The rate at which their offspring colonize surroundings varies among plantations, and the reasons for this variation are often unclear. To minimize the spread of so-called “wildlings” and the burden of conifer plantations on native ecosystems, managers need to know which ecosystems are most and least susceptible.
2. We compared how likely wildlings are to establish across a wide range of ecosystems, focusing on four groups of alien conifer species planted in Norway. We used data from detailed surveys around 82 plantation stands to model the relationship between ecosystem type and wildling abundance — accounting for seed rain (estimated), climate, and other sources of variation between sites. We also tested whether differences in susceptibility between individual ecosystem types could be generalized based on broad, shared characteristics.
3. We found that the rank order of ecosystems by susceptibility (modeled as relative establishment likelihood) differed from their rank order by wildling density, and that susceptibility generally varied as much or more than wildling density. For all species groups, relative establishment likelihoods spanned several orders of magnitude between the most and least susceptible ecosystems.
4. The four groups of conifer species showed somewhat similar patterns of establishment likelihood across ecosystem types, with intensively farmed ecosystems repeatedly among the least susceptible. We found that ecosystems characterized by destabilizing disturbance tended to be most susceptible, but broad ecosystem characteristics did not clarify patterns of susceptibility much, neither within nor across species groups.
5. *Synthesis and applications* Differences in wildling establishment between ecosystems can be exploited to keep alien conifers within plantation boundaries. Stands hemmed in by agriculture or other unsusceptible ecosystems will result in relatively few wildlings, while stands near landslides and other susceptible ecosystems will need monitoring and control. Managers should be aware that the density of wildlings in a given ecosystem may not

reflect its relative susceptibility, because variation in seed rain, climate, and site characteristics obscures the relationship between ecosystem type and wildling establishment.

### 3 Keywords

alien species, conifer, establishment likelihood, disturbance, invasibility, plantation, recruitment, seed dispersal, Wald Analytical Long-distance Dispersal (WALD)

### 4 Introduction

Plantations of alien conifers are widespread globally, and offspring from these plantations frequently establish in surrounding areas (Richardson and Rejmánek 2004). In many instances these naturalized offspring, or wildlings, harm biodiversity and other values, so controlling their spread is prudent. In particular, plantations that contribute to the presence of alien conifers in protected areas may generate substantial control costs as a result (McConnachie et al. 2015). Controlling wildlings protects plantation surroundings and prevents secondary, potentially invasive spread. Accordingly, guidelines for sustainable use of alien trees stress that containing them to the areas set aside for their cultivation is fundamental to good forestry practice (Brundu et al. 2020).

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

Inhibiting establishment is of particular interest because it directly regulates wildling abundance. The conditions affecting establishment are also generally easier to manipulate than those affecting dispersal, either directly through intervention or indirectly through site selection. The question, then, is: how can we identify establishment-inhibiting conditions in a manner applicable to plantation management?

In Norway — and similarly in other countries — the national land mapping classification system sorts variation in local ecological conditions (Halvorsen et al. 2020). It builds on the continuum concept (Austin 1985), aiming for reproducible and value-neutral classification of ecosystems by rule-based discretization of species turnover along important environmental gradients (Halvorsen et al. 2020).

As a result, it encapsulates in its ecosystem types (hereafter: “ecosystems”) much of the variation likely to regulate wildling establishment — in competition, nutrient availability, disturbance, and the like (Richardson and Pyšek 2012). It also identifies broad similarities between ecosystems, which might be used to tease out generic trends in establishment likelihood.

To estimate how likely wildlings are to establish in particular ecosystems based on observations of their abundance around plantations, we must account for (1) seed dispersal, and (2) sources of variation in establishment beside ecosystem type. For example, low establishment likelihood in an ecosystem frequently located close to plantations can be masked by copious seed rain (Rouget and Richardson 2003). Likewise, an ecosystem may appear to promote establishment if it tends to co-occur with climatic conditions that support germination. Unconfounded establishment likelihoods can then be used to predict how susceptible the surroundings of an unobserved stand are, based on ecosystem composition.

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

1. How do estimates of establishment likelihood differ from observed wildling densities?
2. In which ecosystems are wildlings of alien conifers most and least likely to establish?
3. Can overarching characteristics of ecosystems be used to generalize patterns of wildling establishment?

## 5 Methods

### 5.1 Field data

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

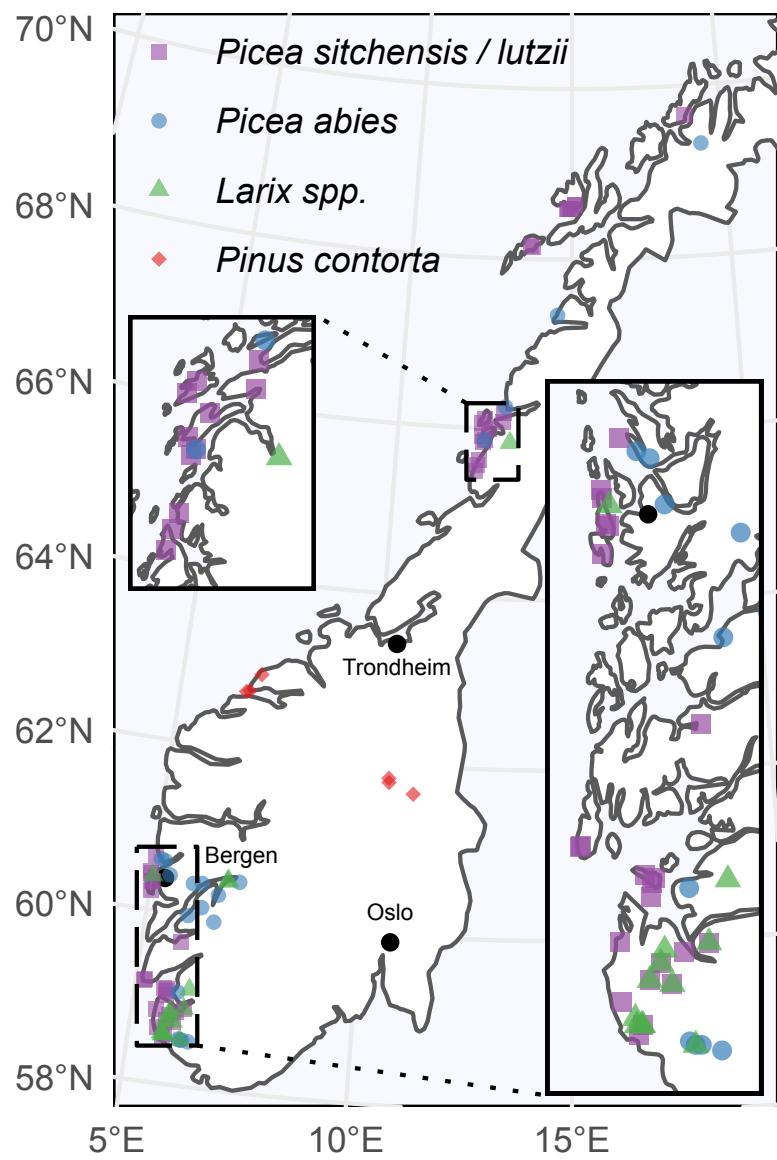


Figure 1: Locations of the 82 plantations in the data set.

Within a 2x2 km plot centered on the stand of interest, we mapped all conspecific stands (except in the 2016 field campaign). Within the central 500x500 m of that plot, we mapped wildlings and ecosystems. We used GPS to register the point-positions of all wildlings over 30 cm in height, recording a single position 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 ecosystems, following the Nature in Norway classification system (version 2.0 or 2.1, Halvorsen et al. 2015, based on the principles summarized in 2020). The Nature in Norway system is the national standard for land cover mapping and provides full spatial coverage (i.e. any location and any kind of land cover is assignable to an ecosystem). We mapped ecosystems at a scale of 1:5000, which means that any polygon over 250 m<sup>2</sup> was registered (Bryn and Halvorsen 2015). Regularly patterned occurrence of more than one ecosystem in polygons smaller than the minimum size were registered as so-called mosaic polygons.

For each of the central stands we measured the height of a representative individual by clinometer. We also estimated the age of the stand 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).

## 5.2 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 central stand to be potential seed sources. We used two models of seed dispersal to derive two different estimates of relative seed rain in space. Acknowledging the uncertainty involved in estimating seed dispersal (Nathan et al. 2012), 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 al. (2017) the kernel that performed best for wind-adapted seeds from 5-15 m tall trees (an Exponential Power function). Seventy-two of the 82 stands in our data set matched this height range better than a taller range with a different empirical kernel.

The second model was an anisotropic implementation of the Wald Analytical Long-distance Dispersal (WALD, Katul et al. 2005) model, following Skarpaas & Shea (2007). We parameterized the model with: site- and season-specific wind vectors retrieved from meteorological data sets, wind turbulence estimated from local ecosystem composition, seed release height based on stand height, and species-specific seed terminal velocities from literature.

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

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

### 5.3 Establishment likelihood

For our analysis of establishment likelihood, we rasterized wildling occurrences and ecosystems to the same 10 m grid as the seed dispersal models (fig. 2). Rather than assigning a single ecosystem to each grid cell, we applied fuzzy logic and assigned ecosystems in proportion to their areal coverage of the cell. In other words, each ecosystem was rendered as a separate raster variable with values in the range [0,1]. We allowed mixed cell composition to capture ecotones in the model and avoid overreliance on the precision of mapped ecosystem boundaries. Area covered by mosaic polygons was divided evenly among the constituent ecosystem types. We excluded the “tree plantation” ecosystem from our analyses because some of the field campaigns did not register wildlings occurring there. Grid cells comprised mostly of “tree plantation” ( $> 0.5$ ) were dropped. The resulting data set was used both to calculate densities of wildlings (abundance/area) and model relative establishment likelihoods. For the density calculation, wildling abundance was tallied in proportion to the ecosystem composition of the grid cells they occupied. For example, a cell occupied by three wildlings and half-covered by a given ecosystem would tally 1.5 wildlings for that ecosystem.

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

For all species, wildling abundance showed a high frequency of zeros that was underestimated by the best fitting negative binomial distribution. Accordingly, we applied zero-inflated generalized linear models, fitted with the glmmTMB package (version 1.0, Brooks et al. 2017) in R (version 3.6, R Core Team 2020). These zero-inflated models regard zeros as the mixed product of a binomial process as well as a (conditional) count process that can take different error distributions (Zuur et al. 2009). Preliminary models fitted with a negative binomial error distribution in the count process (ZINB) sometimes showed residual underdispersion, so we switched to a generalized Poisson error distribution

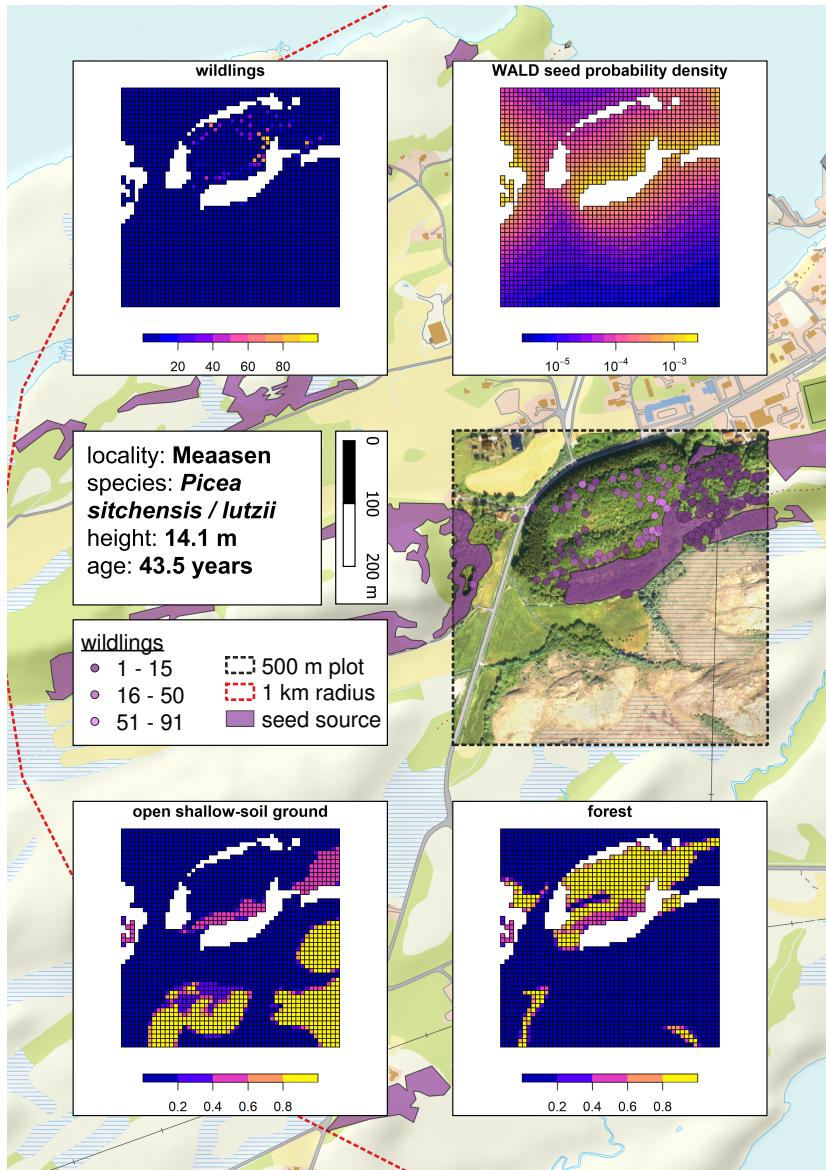


Figure 2: An illustration of one of the 82 plantations: Meaasen. The background map shows the surroundings of the plantation, and the 500x500 m plot is overlaid with an aerial photograph. The middle row of panels shows the data as registered in the field (but without ecosystem type polygons). The top 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 (corresponding to the polygons shown) or "tree plantations" of other species (such as one along the road).

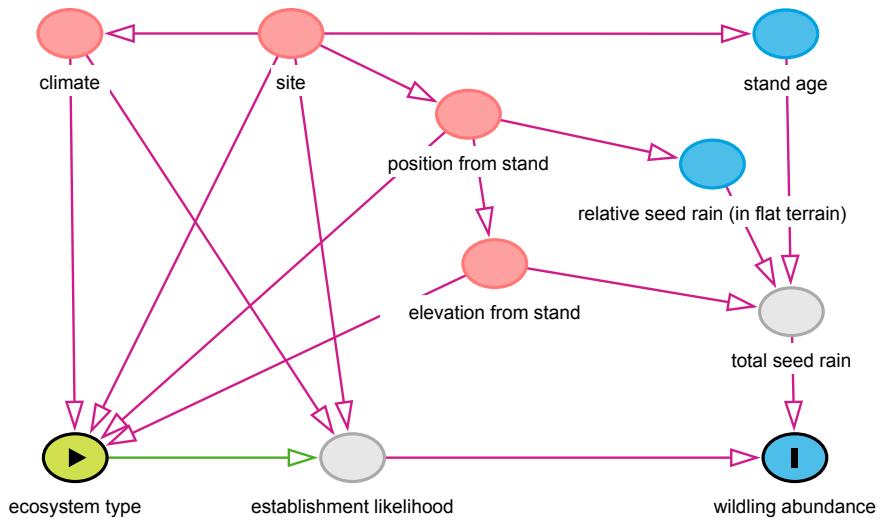


Figure 3: A directed acyclic graph showing the causal relationships motivating our statistical model of ecosystems' effects on wildling abundance. Red variables causally affect both the ecosystem type and wildling abundance, blue variables causally affect only wildling abundance, and grey variables are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

(ZIGP), which can accomodate both over- and underdispersion (Brooks et al. 2019).

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

To estimate the causal influence of ecosystems on wildling abundance in accordance with the DAG (McElreath 2020, Textor et al. 2016), we modeled the count process as dependent on ecosystem, site, climate, elevation from the stand, and relative seed rain. We also included stand age in the count process because it reduced the unexplained variance associated with the random effect of site, and because we could interpret its coefficient as an (unconfounded) total effect on wildling abundance (Westreich and Greenland 2013). Climate was represented as mean annual temperature (Bio1) and precipitation of the coldest quarter (Bio19), at 30-arcsecond resolution, from CHELSA data (Karger et al. 2017). We chose these variables because they showed the strongest correlations with Norwegian vegetation zones and sections, respectively (Bakkestuen et al. 2008). For lodgepole pine we used only Bio19 because the two variables were highly correlated ( $\rho = 0.98$ ). Elevation from the stand was taken with respect to the highest point of the central stand, from digital elevation models at 1 or 10 m resolution (Norwegian Mapping Authority). Relative seed rain directly represents relative exposure in the count process, so we took the natural log of this variable and entered it as an offset term (coefficient fixed at 1) (Zuur et al. 2009). We expect, for example, that a doubling in seed rain would result in a doubling in wildling abundance, all else being equal.

To summarize, for each species we modeled:

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

where  $\pi$  is the probability of a zero from the binomial process, while  $\mu$  and  $\phi$  are the mean and dispersion of the generalized Poisson distribution, respectively (Brooks et al. 2019). Subscripts  $i$ ,  $j$ , and  $k$  index sites, cells, and ecosystems.

For each species, ecosystems where wildlings were totally absent were dropped as predictors (to avoid model convergence issues stemming from complete separation), along with the cells that were comprised mostly ( $> 0.5$ ) of these ecosystems. We standardized the values of Bio1, Bio19, elevation from the stand, and stand age, and centered the natural log of relative seed rain. We fitted three parallel models for each species: (1) with relative seed rain derived from the empirical dispersal kernel, (2) with relative seed rain derived from the WALD dispersal model, and (3) without relative seed rain. From these three we selected that with the best AIC. Two models (larches without seed rain and lodgepole pine with empirical dispersal kernel) did not converge and were excluded from selection. To catch problems with our model specification, we looked for deviation from uniformity in quantile-scaled, simulated residuals, using the DHARMA package (version 0.2.7, Hartig 2020). We also ran DHARMA's tests for residual over/underdispersion and zero-inflation. Relative establishment likelihoods among ecosystems were calculated as predictions from the conditional count part of the model (holding covariates at their mean values), and scaled by the value for “forests” (which were common in the sample).

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

## 6 Results

Wildling densities across ecosystems ranged 0-211/ha for Sitka/Lutz spruce (unstratified mean: 28), 0-49/ha for Norway spruce (unstratified mean: 6), 0-1045/ha for larches (unstratified mean: 13), and 0-219/ha for lodgepole pine (unstratified mean: 34). Relative establishment likelihoods differed considerably from relative wildling densities, except in larches (table 1). For instance, our model estimated that Sitka/Lutz spruce is three times more likely to establish in “boreal heath” than in “artificial substrate”, despite wildling density being three times lower in “boreal heath” (fig. 4). The magnitude of variation in relative establishment likelihoods generally matched or exceeded the magnitude of variation in corresponding wildling densities (Appendix table 11).

For all species, models using relative seed rain estimates from the WALD dispersal model predicted wildling abundance best (Appendix, table 6). Omitting seed rain altogether produced better model fits than using an offset of seed rain derived from the empirical dispersal kernel. Site had a strong influence on wildling abundance, especially for Sitka/Lutz spruce and lodgepole pine, such that for these species site variation swamped much of the variation between

Table 1: Correlations between wildling densities and relative establishment likelihoods in 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

ecosystems. The direct effects of climate on establishment likelihood — not including its effect mediated by ecosystems — varied by species and was strongest for larches (Appendix, tables 7-10). For larches there were negative effects of both precipitation and temperature (50 mm increase in coldest-quarter precipitation and 0.9 °C increase in mean annual temperature both estimated to decrease establishment seven-fold). For Sitka/Lutz spruce there was a smaller positive effect of temperature, for Norway spruce a smaller positive effect of precipitation, and for lodgepole pine a smaller negative effect of precipitation. The direct effects of elevation from the stand on wildling abundance (through seed rain) were comparatively modest and acted in different directions for different species. Stand age did not significantly affect wildling abundance in any species, except that older stands of Sitka/Lutz spruce had fewer wildling-free cells (structural zeros) than younger stands.

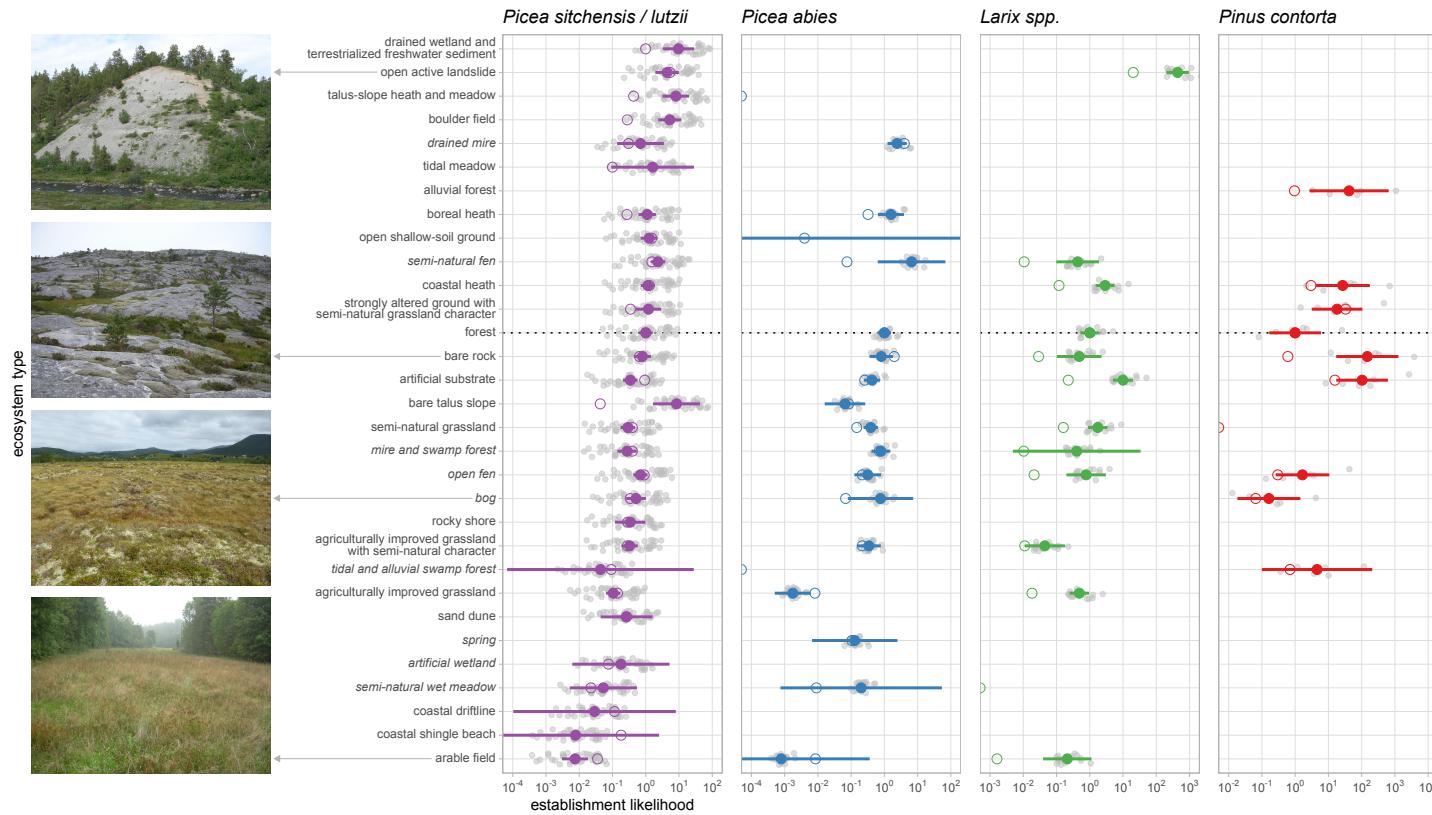


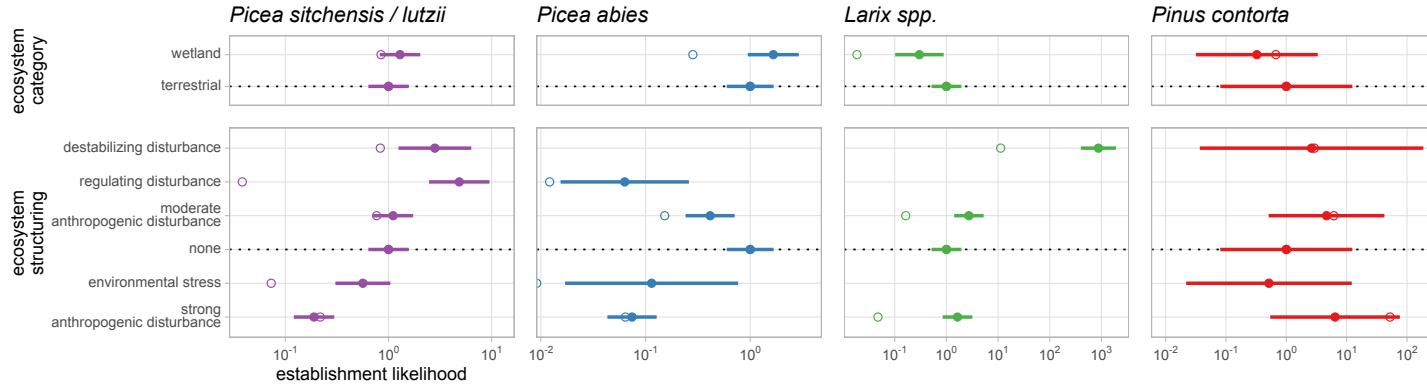
Figure 4: Relative densities (unfilled points) and relative establishment likelihoods (filled points) of four alien conifer species groups in various ecosystem types, using 'forest' as the reference level. Zero density is plotted at the lower limit of the x-axis. Estimates of relative establishment likelihood are shown with 95 % confidence intervals. Grey point clouds 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. Wetland ecosystem types are shown in italic font. Ecosystem types without wildlings and covering less than one hectare across all sites for that species are not displayed. 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

Among ecosystems with at least one wildling, estimated establishment likelihoods varied by 3–5 orders of magnitude for the different species. Patterns of relative establishment likelihood were modestly similar between species, with positive rank correlations in four of six species pairs (table 2). “Arable fields” showed some of the lowest establishment likelihoods of any ecosystem for all species where it appeared. Meanwhile, ecosystems with high establishment likelihoods tended to be rarer types (e.g. “open active landslides”) but also included “boreal heath” and “coastal heath”.

Variation in establishment likelihoods shrank when ecosystems were aggregated by category or structuring process, to 0–3 orders of magnitude (fig. 5). None of the species showed large differences in establishment likelihood between terrestrial and wetland ecosystems. At most, larches and lodgepole pine were three times less likely to establish in wetlands. Ecosystems structured by destabilizing disturbance tended to show higher establishment likelihoods than those structured by environmental stress and those without disturbance structuring. However, the association between structuring process and establishment likelihood was heterogenous across species.



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Figure 5: Relative densities (unfilled points) and relative establishment likelihoods (filled points) of four alien conifer species groups among categories of ecosystem types (top) or structuring processes in ecosystem types (bottom). Estimates of relative establishment likelihood are shown with 95 % confidence intervals. The horizontal dotted lines mark the reference level for the scaling. Strata without wildlings and covering less than one hectare across all sites for that species are not displayed.

## 7 Discussion

### 7.1 How does wildling abundance relate to ecosystem susceptibility?

Confounding of the relationship between ecosystem type and wildling abundance caused wildling density to mischaracterize differences in establishment likelihood between ecosystems. The nonzero effects of hypothesized confounders (like seed rain, climate, and site) imply that our modeled estimates of establishment likelihood are less biased. We caution, therefore, that direct inference from observations of wildling abundance misguides intuition about relative ecosystem susceptibility. For example, the density of Sitka/Lutz spruce wildlings was about equal in “bare talus slopes” and “arable fields”, but we estimate that establishment likelihood is actually about 1000 times larger in the former. Furthermore, variation in establishment likelihood was no smaller than variation in wildling densities, as might have been the case if confounding variables had amplified differences in ecosystem establishment.

Because wildling abundance is the product of seed rain and establishment likelihood, we needed to estimate seed rain independently of our wildling data to model establishment likelihood properly. Otherwise variation in wildling abundance caused by differential establishment likelihood might be attributed to differential seed rain, or vice versa. By including relative seed rain as an offset in the model, we ensure that seed rain and establishment likelihood are not conflated, at the cost of assuming that our relative seed rain estimates are accurate. Exploring the alternative, we found that if we included relative seed rain as a covariate rather than an offset — allowing the spatial distribution of seed rain to be adapted to patterns of wildling abundance — that its coefficient was estimated near one, and that estimated relative establishment likelihoods remained mostly unchanged (Appendix, fig. 6). This result is consistent with the assumption that our WALD-derived estimates of relative seed rain capture true differences in seed rain. Although survivorship bias in our data prevents rigorous comparison of seed dispersal models, the superior fits of models with WALD-derived seed rain offsets, compared to models with empirically-derived seed rain offsets, also suggests that the WALD model described seed dispersal well. Lastly, the mechanistic nature of the WALD model also makes us more confident in its estimates across species and sites than we would be in a purely phenomenological model (Bullock et al. 2018). Nevertheless, that seed rain was modeled and not measured is a limitation of our method, and it makes the establishment likelihoods we estimate less certain. For example, changes in the distribution of seed rain as a stand matures were not accounted for, nor was secondary seed dispersal from the few reproductive wildlings we observed.

The inconsistent effects of elevation from the stand on wildling abundance suggests that terrain does not affect seed dispersal much or that vertical distance alone misses its effect. In any case, there is no rule of thumb for management that wildlings tend to move up or down slopes. Similarly, the weak effects of

stand age on wildling abundance suggests that wildlings do not accumulate over the lifetime of the stand, or at least that this accumulation tends to be weak and/or non-linear. There is no indication that management should prioritize old stands ahead of young stands.

We reiterate that our models do not estimate the climate's total causal effect on wildling abundance, because they set aside its influence on ecosystems (Westreich and Greenland 2013). Therefore, we interpret the estimated climatic effects with respect to physiological constraints within a given ecosystem. The negligible effect of precipitation and weakly positive effect of mean annual temperature on Sitka/Lutz spruce wildling abundance is consistent with Sitka spruce's wide climatic tolerance relative to climatic variation in Norway, as well as its oceanic affinity (Peterson et al. 1997, Vollering et al. 2019, Appendix F). For Norway spruce, our results support a previous finding that seedling recruitment increases towards the wetter end of Norwegian climate (Tingstad et al. 2015), although most of our sites circumscribed a narrow part of that range. Warm and wet conditions seem to suppress larch establishment in Norway, which can be taken into consideration when managing these plantations. Lastly, the large confidence interval around lodgepole pine's estimated negative response to precipitation reflects that the sample contained only six sites from two climates.

A curious feature of our results that needs more research is the large amount of unexplained variation in Sitka/Lutz spruce and lodgepole pine wildling abundance between sites. This means that our ability to predict the spread of these species at a specific site, relative to other sites, is limited (even if the site's ecosystem composition is known). Nevertheless, ecosystem comparisons can and should guide management. Bianchi et al. (2019) struggled to predict regeneration density within Sitka spruce plantations from bare ground cover, moss cover, stand age, and stand density. The inadequacy of stand density as a predictor in this context suggests that the unexplained site-level variation in our models was not caused by differences in the densities of seed sources (which we assumed to be constant). Alternative explanations could include: (1) property owners removing wildlings, (2) disturbance legacies not captured in the delineation of ecosystem types (especially in grazing pressure; Miller et al. 2021), or (3) differing demographic characteristics among plantations (especially in cone production; Taylor et al. 2016), potentially as a result of provenance. Ecological differences between Lutz and Sitka spruce might also explain some of the site variation in that case.

## 7.2 Which ecosystems are susceptible?

In a large database of vegetation plots across Europe, Chytrý et al.(2008b) found that alien plants as a group are consistently found at low rates in mires and heaths, and high rates in arable, man-made, and coastal ecosystems. The conifer species we examined do not conform closely to these broader trends in ecosystem invasibility, showing relatively high rates of establishment in heaths and very low rates of establishment in arable ecosystems. To the extent that there is any discernable pattern across these species, they appear to establish more easily in

ecosystems infrequently hit by intense disturbances (e.g. debris flows in “open active landslides”, rock fall in “bare talus slope”, or fire in “coastal heath”) than in ecosystems frequently experiencing less intense disturbances (e.g. erosion in “sand dunes” or flooding in “semi-natural wet meadow”) This pattern could be a function of the balance between disturbance-induced mortality and opportunities for establishment.

Of the species in this study, lodgepole pine’s establishment is best studied, and our results are consistent with this literature. “Bare rock” harbors very few competitors and showed highest lodgepole pine establishment of all ecosystems (Despain 2001), and ecosystems with canopy cover generally showed low establishment (Taylor et al. 2016, Langdon et al. 2010). It is difficult to evaluate our ecosystem susceptibility results against the recruitment patterns that have been described for the three other species. For instance, Sitka spruce grows poorly under moisture stress and tolerates flooding well (Peterson et al. 1997), which might account for why it was equally likely to establish in wetland and terrestrial ecosystems. Yet it also established well in “open shallow-soil ground”, despite this ecosystem’s characteristically dry soil. This illustrates the trouble with deriving predictions for management units such as ecosystems from generalized statements about species autecology; should we expect few Sitka spruce wildlings in “open shallow-soil ground” because it is dry, or many because it provides ample light and reduced competition (Peterson et al. 1997)? Furthermore, ecosystems that would seem inhospitable based on their overall characteristics may actually contain many localized opportunities for establishment, because seedling mortality is strongly regulated by microsites (Macek et al. 2017). From this perspective, our estimates of establishment likelihood measure the density of suitable microsites in a given ecosystem.

The breadth in establishment likelihood suggests that differences between ecosystems deserve careful consideration when managing wildling spread. This knowledge can be applied in at least two ways. First, as a preventative measure, we recommend siting new stands where surrounded by high proportions of ecosystems with low establishment likelihood. In particular, “arable fields” repress wildling establishment for all species and are common near existing stands, so picking sites hemmed in by this kind of agricultural land should be both effective and feasible. This would probably reduce the rate of wildling establishment by orders of magnitude, even if long distance dispersal might preclude complete containment (Albert et al. 2008). In some cases it may also be desirable to alter ecosystems adjacent to existing stands to prevent (further) spread, for example by intensifying mowing regimes to promote the appearance of “agriculturally improved grassland”. Second, as a reactive measure, we recommend allocating resources for monitoring and control in proportion to relative ecosystem susceptibility. Prioritizing ecosystems that are highly susceptible and also rare (e.g. “open active landslide”) is especially likely to be cost-efficient.

The establishment patterns we quantify probably hold, more or less, beyond Norway (Chytrý et al. 2008b). From a manager’s perspective, we expect that

the ecosystems we report may translate well to equivalent types in similar classification systems, because the Nature in Norway classification is rule-based and aims for observer neutrality. At the same time, we urge caution in extending our establishment estimates to ecosystems that are only broadly similar, because we found that similar types frequently showed markedly different susceptibility (e.g. Norway spruce in “agriculturally improved grassland with semi-natural character” vs. “agriculturally improved grassland”).

An observational study like ours informs management of long-lived, naturalized species more directly than experimental studies, because longer time frames are examined. It measures long-term survival — often the quantity of interest — under a wide range of natural conditions experienced by the wildlings. In contrast, seeding experiments generally observe only the youngest life stages, and the factors controlling individual success differ at later life stages (Dovčiak et al. 2008). For example, Sitka spruce appears more likely to germinate in disturbed soil (Vikane et al. 2013), but less likely to survive there (Peterson et al. 1997). On the other hand, experiments might be more useful when observed wildling spread is not representative of patterns in the wider landscape (e.g. for species expanding from a single, recent introduction).

### 7.3 What do susceptible ecosystems have in common?

The overarching characteristics that we used to aggregate ecosystems did not generalize differences in susceptibility well, especially not across species, so these classifications have limited utility for management. Note that different sets of ecosystems comprised the strata for each species, depending on their presence in the data, and these differences in ecosystem composition help explain why the patterns of aggregated establishment likelihood varied between species. This constraint hinders species comparisons but underlines our main takeaway from these results — that the susceptibility of an individual ecosystem frequently diverges from those it is classified with.

Within species, we urge careful interpretation of the comparisons among ecosystem categories and structuring processes. Many areas where conifer establishment is nearly impossible, like paved surfaces and annually plowed fields, count as terrestrial and strongly anthropogenically disturbed, which lowers the relative establishment likelihood of these two strata. Our results do not imply, for example, that a strong anthropogenic disturbance event will decrease establishment likelihood of Sitka/Lutz spruce relative to an ecosystem’s prior state. Indeed, Vikane et al. (2013) show, for example, that burning in coastal heathland increases Sitka spruce establishment. Rather, we find that ecosystems structured by strong anthropogenic disturbance, on the whole, are less susceptible to Sitka/Lutz spruce wildlings than other ecosystems.

## 8 Conclusions

Wildling spread from plantations is a growing problem (Richardson and Rejmánek 2004) and will probably worsen with recent pushes to increase tree planting worldwide (Brundu et al. 2020). Meanwhile, remotely sensed and survey data are making detailed and accurate maps of ecosystems increasingly available over large extents (Horvath et al. 2019), which presents opportunities to manage wildling spread more efficiently (Buckley et al. 2005). Specifically, differences in ecosystem susceptibility can be leveraged to reduce the rate of wildling establishment (potentially by orders of magnitude) through deliberate site selection for new stands or targeted interventions around existing stands. However, managers should be cautious judging ecosystem susceptibility based on descriptions of the species' autecology, observed wildling densities, or generalizations about susceptibility across ecosystems.

One of the main novelties of this study is that we inferred susceptibility/invasibility using mechanistically reconstructed, spatial estimates of seed rain. Scientists studying invasibility at national and continental scales have already recognized the importance of normalizing observed levels of invasion by a spatially explicit estimate of exposure (i.e. propagule pressure; Chytrý et al. 2008a). However, many studies quantifying ecosystem invasibility have not been able to adjust for propagule pressure, typically because it is impossible to reconstruct the underlying dispersal history (Catford et al. 2012). We found that accounting for seed rain and other confounders of the relationship between ecosystems and wildling abundance reshuffles estimates of ecosystem invasibility.

## 9 Authors' contributions

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

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## 11 Appendix

The WALD model takes the form of an inverse Gaussian distribution whose mean ( $\mu$ ) and shape ( $\lambda$ ) parameters are calculated from physical characteristics

of the dispersal system:

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

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

where  $H$  is the seed release height,  $U$  is the mean horizontal wind velocity between  $H$  and the ground,  $F$  is the terminal velocity of the seed, and  $\sigma$  is a wind turbulence parameter. We set  $H$  to the height of the central stand, estimated  $U$  from a computed vertical wind profile, obtained  $F$  from literature, and calculated  $\sigma$  from an equation for turbulent flow as a function of vegetation height (eq. A4 in Skarpaas and Shea 2007). We parameterized separate WALD models for 20° sectors around each seed source, to make seed dispersal anisotropic (directional). In each sector we estimated mean vegetation height based on the composition of mapped ecosystem types (Appendix, table 5). Simultaneously, we randomly sampled 100 wind velocities in the direction of the sector during the species' dispersal season. The 100 resulting WALD kernels produced the seed probability density in the sector, and individual sectors were weighed by the frequency of corresponding wind directions (again, during the species' dispersal season). The wind data were obtained either from the nearest weather station (MET Norway), a 2.5 km resolution interpolated hindcast covering southern Norway (Haakenstad and Haugen 2017), or a 10 km resolution hindcast covering all of Norway (Reistad et al. 2011, Haakenstad et al. 2020). We used weather station data if the station was less than 2.5 or 10 km away (depending on hindcast 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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Some of the seed source polygons we registered in the field had distinctive features that we accounted for as follows. Seed source polygons for which the species of interest only made up a fraction of the stand composition (e.g. in Olsen et al. 2019) were used with their point source density adjusted accordingly. For example, a stand identified as composed of Sitka spruce and Norway spruce was assigned a seed source point density half that of a Sitka spruce monoculture. Likewise, ‘mixed forest’ stands (e.g. in Appelgren 2018) were assigned 0.1 times the seed source point density of a monoculture. Seed source polygons identified as logged (e.g. in Appelgren 2018) were included as seed sources only if we could confirm that they were logged no earlier than the decade prior to mapping, using time series of aerial photos.

Table 4: Plantation stands

reference	species group	site	easting	northing	height	age	bio01 <sup>a</sup>	bio19 <sup>b</sup>
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
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
Appelgren and Torvik 2017	<i>Larix spp.</i>	Haalandsbottn	-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

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 <sup>a</sup>	bio19 <sup>b</sup>
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
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 <sup>†</sup>	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
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

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 <sup>a</sup>	bio19 <sup>b</sup>
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
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>	Plogskaeret	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
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

Table 4: Plantation stands (*continued*)

reference	species group	site	easting	northing	height	age	bio01 <sup>a</sup>	bio19 <sup>b</sup>
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
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Fuglavasstoppen	-50243	6740596	19.5	48	7.86	46.0
Sandven et al. 2019	<i>Picea sitchensis / lutzii</i>	Kvitfjella	-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.

<sup>a</sup> mean annual temperature (°C)

<sup>b</sup> 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 <sup>a</sup>
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
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

Table 5: Ecosystem types (*continued*)

type	code	category	structuring	vegetation height <sup>a</sup>
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
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
artificial wetland	V13	wetland	strong anthropogenic disturbance	0.0

<sup>a</sup> approximate vegetation heights (meters) are used only to estimate wind turbulence

Table 6: Comparison of models with different seed dispersal estimates

species group	seed dispersal estimate	AIC	dAIC	df
Picea sitchensis / lutzii	WALD	51967.261	0.0000	38
	Exponential Power	128861.239	76893.9779	38
	none	54477.712	2510.4515	38
Picea abies	WALD	9680.586	0.0000	26
	Exponential Power	25316.450	15635.8645	26
	none	9781.127	100.5414	26
Larix	WALD	10057.588	0.0000	21
	Exponential Power	27310.048	17252.4596	21
Pinus contorta	WALD	3319.143	0.0000	17
	Exponential Power	NA	NA	17
	none	3372.102	52.9581	17

Table 7: 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
<b>Conditional model</b>				
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
<b>Zero-inflation model</b>		
Intercept	0.39	-0.06, 0.84
age	-0.78	-1.19, -0.36
site		1.19 42

Table 8: Model summary for *Picea abies*. The conditional model is glmmTMB's genpois (Generalized Poisson) family with dispersion parameter  $\phi^2 = 2.495544$

Term	Fixed effects		Random effects	
	Estimate	95% CI	SD (Intercept)	N
<b>Conditional model</b>				
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
<b>Zero-inflation model</b>				
Intercept	1.72	0.92, 2.52		
age	0.34	-0.41, 1.09		
site			1.53	19

Table 9: 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
<b>Conditional model</b>				
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
<b>Zero-inflation model</b>				
Intercept	-0.36	-1.62, 0.9		
age	0.29	-0.83, 1.41		
site			1.24	15

Table 10: 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
<b>Conditional model</b>				
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
<b>Zero-inflation model</b>				
Intercept	-0.16	-0.49, 0.18		
age	-0.08	-0.41, 0.26		
site			0.00	6

Table 11: Proportional variability in wildling densities among ecosystems compared to proportional variability in establishment likelihoods among ecosystems.

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

*References:*

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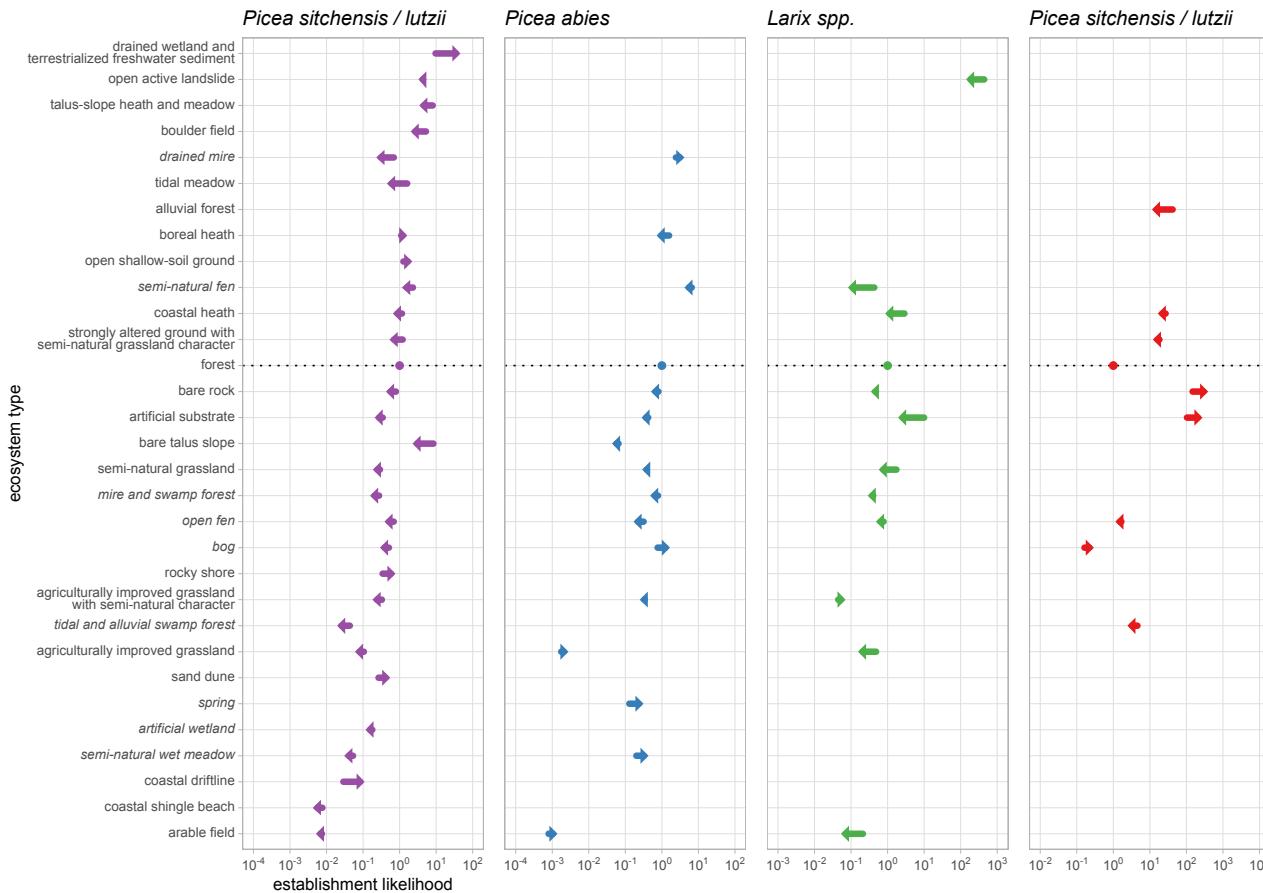


Figure 6: Shifts in estimated relative establishment likelihoods when relative seed rain (from the WALD dispersal model) is included in the model as a covariate rather than an offset. Arrows point from the models with offsets to the models with covariates.

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