

Accounting for confounders reveals that ecosystems vary considerably in susceptibility 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 plantations to model the relationship between ecosystem type and wildling abundance — accounting for seed rain, climate, and other sources of variation between sites. Furthermore, we tested whether differences in susceptibility between individual ecosystem types could be generalized based on broad, shared characteristics.
3. We found that ecosystem susceptibility, modeled as relative establishment likelihood, varied more than the raw densities of wildlings in these ecosystems. Moreover, the rank order of ecosystems by susceptibility differed from their rank order by 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. Plantations hemmed in by agriculture or other unsusceptible ecosystems will result in relatively few wildlings, while plantations 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 contribute to the presence of alien conifers in protected areas, and 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).

How many wildlings are present and how far they are from the plantation varies a lot from site to site, even among conspecific plantations of similar age (Nygaard and Øyen 2017, Fernandes et al. 2018), which makes it harder to predict and manage their spread. To begin to understand this variation, we need to consider both dispersal and establishment (where establishment comprises germination and survival). These jointly generate patterns of wildling abundance and spatial distribution. Dispersal at a given site is affected by conditions related to a species' dispersal syndrome — for instance wind exposure and site topography, in the case of a wind-dispersed species. Likewise, establishment is affected by biotic and abiotic conditions where seeds arrive. In theory, conditions inhibiting either process may be exploited to suppress wildling spread.

Reducing 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, becomes: 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 that is most likely to regulate wildling germination and survival — 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 vulnerable the surroundings of an unobserved plantation are, based on its composition of ecosystems.

Determining which ecosystems are most vulnerable so that interventions can be prioritized objectively is among the most urgent objectives for invasion science (Pyšek et al. 2020). Plantations 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 plantations 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 and delineated plantations manually — using aerial imagery — aiming for plantations that were isolated from other plantations of the same species. Only plantations with cone-bearing

individuals were included in the sample. 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).

In the field, wildlings and ecosystems were mapped comprehensively within a 500x500 m plot framing the plantation of interest. Except in the 2016 field campaign, we also mapped as polygons any additional plantations of the same species within a larger 2x2 km plot. 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 implies that all polygons with a size over 250 m² were 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 plantations we measured the height of a representative individual in the plantation by clinometer. We also estimated the age of the plantation at the time of the field campaign, either by contacting land owners or municipal officials, or by counting growth rings. Details for all 82 plantations are provided in the Appendix (table 3).

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 field plots. Because conspecific plantations were sometimes located nearby the central plantation, we considered all plantations within a 1 km radius 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 plantations 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

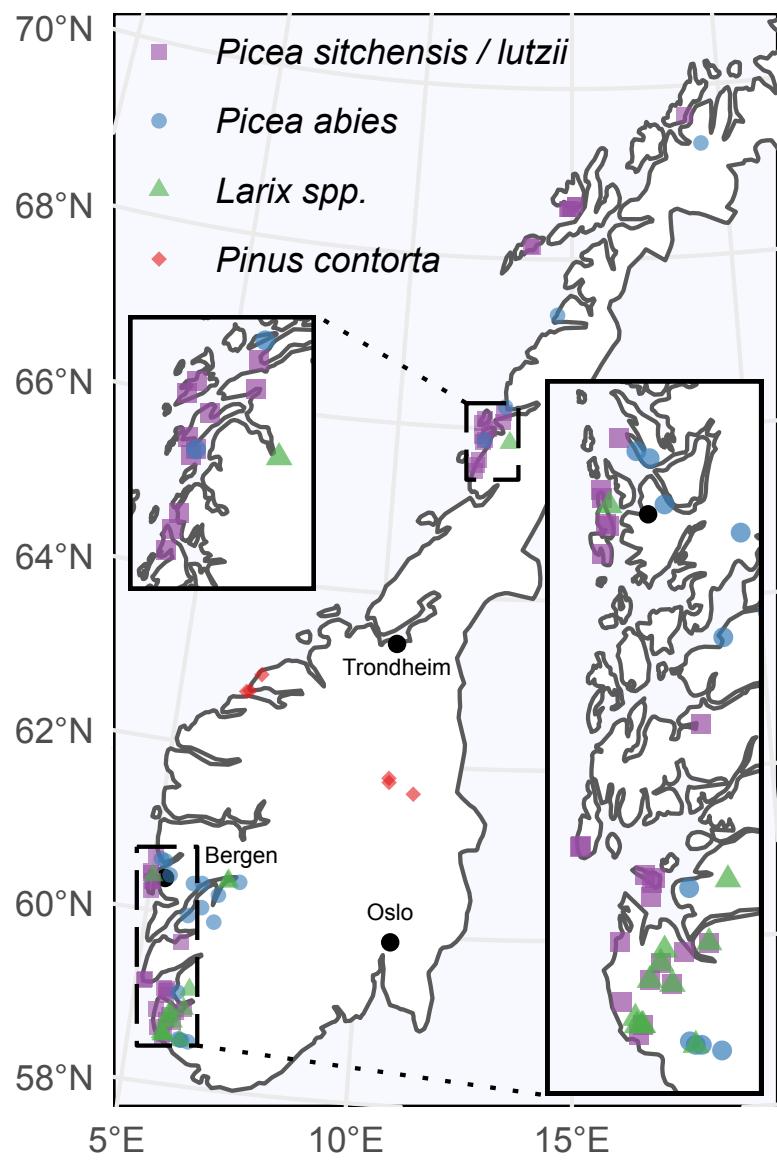


Figure 1: Locations of the 82 plantations in the data set.

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 plantation 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 m^{-2} for the first model and 0.01 m^{-2} for the second model (to reduce computation time). Then we applied our two dispersal models to estimate the distribution of 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 to try to 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 — establishment likelihood and seed rain — are descendants of variables that we could observe or model. We included an effect of elevation from plantation on seed rain because neither of our models of seed dispersal account for uneven terrain. To estimate the causal influence of ecosystem on wildlings, the DAG dictated that we adjust for site, climate, elevation from plantation, and relative seed rain in our regression model (McElreath 2020, Textor et al. 2016). We did not need to adjust for plantation age (with site in the model), but we included it as a covariate anyway because it reduced the unexplained variance associated

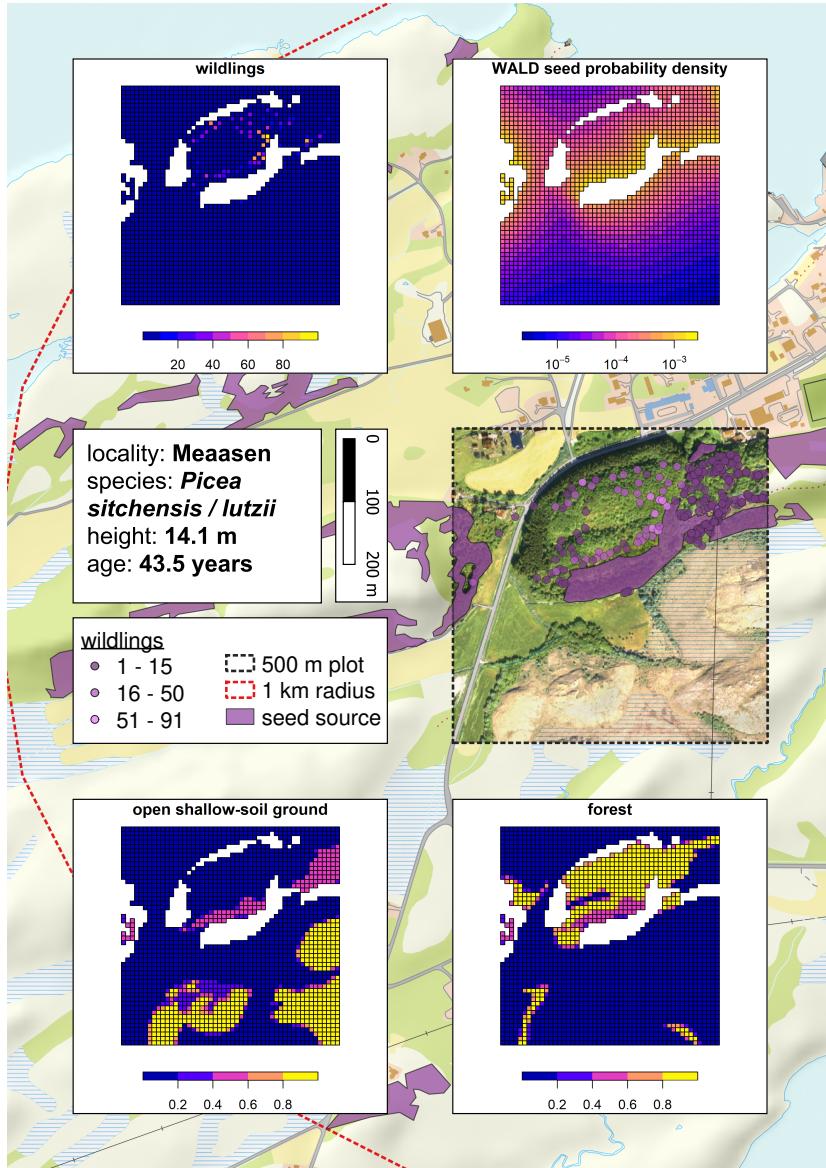


Figure 2: An illustration of one of the 82 plantation sites: Meaasen. The background map shows the surroundings of the plantation, and the 500x500 m plot is overlaid with an aerial photograph. The middle row of panels shows the data as registered in the field (but without ecosystem type polygons). The 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).

with the random effect of site, and because our assumed causal structure would allow us to interpret its coefficient as an (unconfounded) total effect on wildling abundance (Westreich and Greenland 2013). Climate entered the regression model 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 plantation was taken with respect to the highest point of the central plantation, from digital elevation models at 1 or 10 m resolution (Norwegian Mapping Authority).

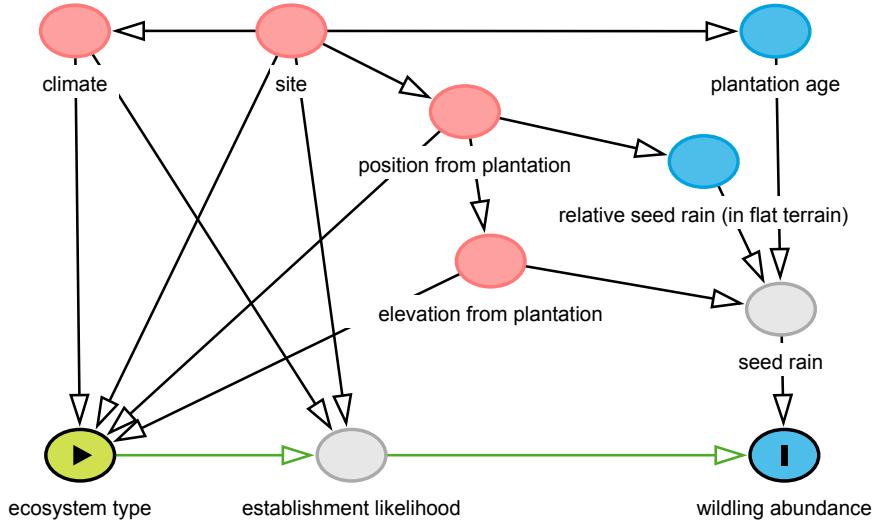


Figure 3: A directed acyclic graph showing the causal relationships motivating our statistical model of ecosystems' effects on wildling establishment. Red variables causally affect both the ecosystem type and wildling establishment, blue variables causally affect only wildling establishment, and grey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

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, negative binomial (ZINB) generalized linear models (Zuur et al. 2009). These regard zeros as the mixed product of a binomial process as well as a (conditional) count process. We modeled the binomial process as dependent on plantation age and site. We expected that younger plantations would exhibit more cells without wildlings than predicted under a constant rate of establishment, 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 summarize, we modeled:

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

where π is the probability of a zero from the binomial process, while μ and ϕ are the mean and dispersion of the negative binomial distribution, respectively (eq. 11.21 in Zuur et al. 2009). Subscripts i , j , and k index sites, cells, and ecosystems.

We standardized variables (except ecosystems, which were [0,1]) and fitted models with the glmmTMB package (version 1.0, Brooks et al. 2017) in R (version 3.6, R Core Team 2020). For each species we dropped ecosystems that were completely free of wildlings (to avoid model convergence issues stemming from complete separation). We fitted three parallel models for each species, containing one of our two seed rain variables (derived from empirical or WALD dispersal kernels) or neither of them, and selected the model with the best AIC. For lodgepole pine, only the model with the WALD-derived seed rain variable converged without warnings, and we proceeded with this one. 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. The Norway spruce model showed residual underdispersion, so we replaced the negative binomial distribution with the generalized Poisson distribution, which solved the issue (Brooks et al. 2019). Relative establishment likelihoods among ecosystems were calculated as predictions from the conditional part of the zero-inflation 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 vulnerability, 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 4). We then refitted our (otherwise unchanged) models with these eight strata replacing ecosystems — and obtained estimates of relative establishment likelihood for each category and structuring process.

6 Results

Estimated establishment likelihoods varied by up to five orders of magnitude among ecosystems (fig. 4). The pattern of establishment likelihood among ecosystems was modestly similar between species, with positive rank correlations in four of six species pairs (tab. 1).

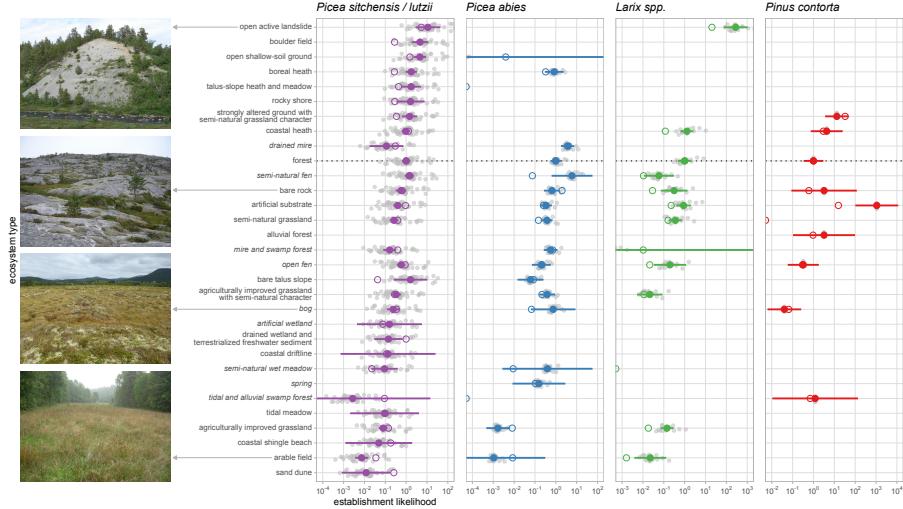


Figure 4: Relative densities (unfilled points) and relative establishment likelihoods (filled points) of four alien conifer species groups in various ecosystem types, using ‘forest’ as the reference level. Zero density is plotted at the lower limit of the x-axis. Estimates of relative establishment likelihood 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.

Wildling densities across all ecosystems ranged 0-211/ha for Sitka spruce, 0-49/ha for Norway spruce, 0-1045/ha for larch, and 0-219/ha for lodgepole pine. Relative establishment likelihoods varied more than the corresponding set of densities, in all species (fig. 4). The ranking of ecosystems by establishment likelihood also differed from their ranking by wildling density. For instance, Sitka/Lutz spruce showed higher densities in “artificial substrate” than “boreal heath”, but was more likely to establish in “boreal heath”.

Table 1: Rank correlations of relative establishment likelihoods in ecosystem types, between pairs of species.

	Picea abies	Larix	Pinus contorta
Picea sitchensis / lutzii	0.11	0.62	0.26
Picea abies		0.12	-0.2
Larix			0.5

Across species, the most consistently important covariates in the relationship between ecosystems and wildling abundance (by effect size) were: relative seed rain, precipitation, and site. For all species, seed rain estimates from the WALD seed dispersal model predicted wildling abundance better than estimates derived from the empirical seed dispersal kernel (Appendix, table 5). Omitting seed rain altogether produced the worst model fits. The direct effect of relative elevation on establishment — not including its effect mediated by ecosystems — was modest and acted in different directions for different species (Appendix, tables 6-9). The direct effect of climate on establishment — not including its effect mediated by ecosystems — was negligible for Sitka/Lutz spruce and Norway spruce. For larch there was a negative direct effect of precipitation (Bio19), with a 50 mm increase in coldest-quarter precipitation estimated to decrease establishment six-fold. Likewise for lodgepole pine, the model estimated a 175 mm increase in coldest-quarter precipitation to decrease establishment by a factor of 50. For Sitka/Lutz spruce and lodgepole pine, establishment likelihood varied strongly between sites, such that it swamped much of the variation between ecosystems.

Variation in establishment likelihoods shrank when ecosystems were aggregated (by category or structuring process; fig. 5). No more than two orders of magnitude separated the different groups. Sitka/Lutz spruce and Norway spruce established at higher rates in wetland ecosystems than terrestrial ecosystems, while the opposite was true for larch and lodgepole pine. Sitka/Lutz spruce and Norway spruce did not generally colonize disturbance-structured ecosystems at higher rates than ecosystems without disturbance structuring. For larch and lodgepole pine, structuring by natural disturbance and anthropogenic disturbance, respectively, were associated with the highest establishment likelihoods. Yet despite larger sample sizes, the mean establishment likelihood in any particular group was rarely clearly distinguishable from that in other groups.

7 Discussion

7.1 Ecosystem vulnerability

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

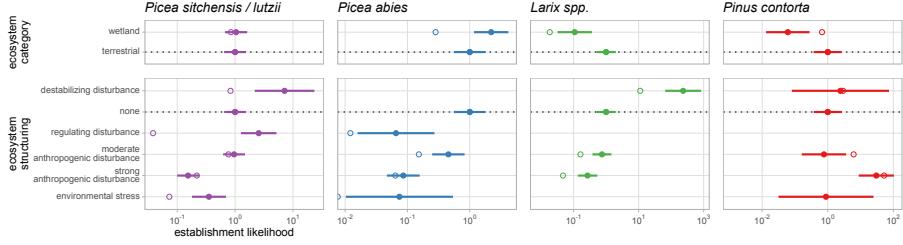


Figure 5: Relative densities (unfilled points) and relative establishment likelihoods (filled points) of four alien conifer species groups among categories of ecosystem types (top) or structuring processes in ecosystem types (bottom). Estimates of relative establishment likelihood are shown with 95 % 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.

conifer species we examined — perhaps with the exception of lodgepole pine — do not conform to these broader trends in ecosystem invasibility. Lodgepole pine establishment is relatively well 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), “coastal heath” (a short shrubland) facilitated more establishment than grassland-like ecosystems (Taylor et al. 2016), all ecosystems with canopy cover were among those with lowest establishment (Taylor et al. 2016, Langdon et al. 2010), and ecosystems with high establishment were frequently structured by anthropogenic disturbance (Richardson et al. 1994).

It is difficult to evaluate our ecosystem vulnerability 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 twice as likely to establish in wetland ecosystems as in terrestrial ecosystems. Yet it also established in “open shallow-soil ground” with very high likelihood, 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 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 plantations where surrounded by high proportions of ecosystems with low establishment likelihood. In particular, “arable fields” harbor very few wildlings of any species and are common near existing plantations, 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 plantations 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 vulnerability. Prioritizing ecosystems that are highly vulnerable 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 vulnerability (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 point of introduction).

7.2 Estimating vulnerability

Confounding of the relationship between ecosystem and wildling abundance caused wildling density to underestimate and sometimes completely mischaracterize differences in establishment likelihood between ecosystems. The underestimation implies that confounding variables counteracted differences in ecosystem establishment in our sample — for instance that vulnerable ecosystems were concentrated at sites predicted to show limited establishment. We caution, there-

fore, that direct inference from observations of wildling abundance misguides intuition about relative ecosystem vulnerability. For example, the density of Sitka spruce wildlings was about equal in “boreal heath” and “sand dunes”, but we estimate that establishment likelihood is actually about 100 times larger in “boreal heath”.

The effect size of WALD-modeled relative seed rain was estimated close to one for all species except Norway spruce, which indicates that spatial patterns of wildling abundance around plantations were captured satisfactorily by this variable. We take this as evidence that the WALD model describes seed dispersal well in our system, but recognize that survivorship bias prevents rigorous assessment of this relationship with our data. For example, the empirical seed dispersal model we tested generally showed a steeper decline in seed rain away from seed sources than the WALD model, so negative density dependence in seedling survival could skew the spatial distribution of wildling abundance towards the WALD model. That this important covariate was modeled and not measured is a limitation of our method, and it makes the establishment likelihoods we estimate less certain. Nevertheless, the mechanistic nature of the WALD model makes us more confident in its estimates across species and sites than we would be in a purely phenomenological model (Bullock et al. 2018). Relative elevation’s inconsistent effects on wildling abundance suggests that either terrain does not strongly affect seed dispersal or — more likely — vertical distance alone does a poor job of representing its effect. In any case, there is no rule of thumb for management that wildlings tend to move up or down slopes.

We reiterate that our models do not estimate the total causal effect of climate on wildling abundance, because they set aside climate’s influence on ecosystems (Westreich and Greenland 2013). Therefore, we interpret the estimated climate effects with respect to physiological constraints within a given ecosystem. The lack of a direct climate effect on Sitka/Lutz spruce wildling abundance is consistent with Sitka spruce’s wide climatic tolerance relative to climatic variation in Norway (Peterson et al. 1997, Vollering et al. 2019, Appendix F). Norway spruce seedling recruitment has previously been found to increase towards the wetter end of Norwegian climate (Tingstad et al. 2015), but most of our Norway spruce sites circumscribed a narrow part of that range. We are not confident that lodgepole pine responds strongly to precipitation, as estimated, because 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 establishment likelihood between sites. Our ability to predict these species’ magnitude of spread at a specific site, relative to other sites, is still limited. Ecosystem comparisons can nevertheless guide management. Bianchi et al. (2019) struggled to predict regeneration density within Sitka spruce plantations from bare ground cover, moss cover, plantation age, and plantation density. The inadequacy of plantation 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 at some sites, or (2) differing demographic characteristics among plantations (Taylor et al. 2016), potentially as a result of provenance.

7.3 Generalizing vulnerability

The overarching characteristics that we used to aggregate ecosystems did a poor job of generalizing differences in vulnerability. That is, groups of ecosystems belonging to the same hydrological category, or structured by the same form of disturbance, showed heterogeneous establishment likelihoods. We note that slightly different sets of ecosystems comprised the groups for each species, depending on their presence in the data. 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 vulnerability of an individual ecosystem frequently diverges from those it is classified with. Thus, we did not find any broad commonalities between vulnerable ecosystems that could help guide wildling management where data are scarce.

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 anthropogenically disturbed, which lowers the relative establishment likelihood of these two groups. Our results do not imply, for example, that any particular anthropogenic disturbance event will decrease establishment likelihood of Sitka/Lutz spruce relative to an ecosystem’s prior state (indeed, Vikane et al. (2013) show that burning in coastal heathland increases Sitka spruce establishment). Rather, we find that ecosystems structured by anthropogenic disturbance, on the whole, are no more vulnerable 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 vulnerability can be leveraged to reduce the rate of wildling establishment (potentially by orders of magnitude) through deliberate site selection for new plantations or targeted interventions around existing plantations. However, managers should be cautious judging ecosystem vulnerability based on descriptions of the species’ autecology, wildling densities, or generalizations about vulnerability across ecosystems.

One of main novelties of this study is that we inferred vulnerability/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 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 underlined variation in 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 of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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11 Appendix

The WALD model takes the form of an inverse Gaussian distribution whose mean (μ) and shape (λ) 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 σ is a wind turbulence parameter. We set H to the height of the central plantation, estimated U from a computed vertical wind profile, obtained F from literature, and calculated σ 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 4). 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 2: 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 plantation composition (e.g. in Olsen et al. 2019) were used with their point source density adjusted accordingly. For example, a plantation identified as composed of Sitka spruce and Norway spruce was assigned a seed source point density half that of a pure Sitka spruce plantation. Likewise, ‘mixed forest’ plantations (e.g. in Appelgren 2018) were assigned 0.1 times the seed source point density of a pure plantation. 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 3: Plantations

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
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 3: Plantations (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
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 [†]	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 3: Plantations (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
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 3: Plantations (*continued*)

reference	species group	site	easting	northing	height	age	bio01 ^a	bio19 ^b
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>	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 other plantations of the same species, inversely weighted by difference in age

† interpolated as the mean age of other plantations of the same species in the same region

Table 4: 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
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 4: Ecosystem types (*continued*)

type	code	category	structuring	vegetation height ^a
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

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

Table 5: Comparison of models with different seed dispersal estimates

species group	seed dispersal estimate	AIC	dAIC	df
Picea sitchensis / lutzii	WALD	53221.357	0.0000	39
	Exponential Power	54607.707	1386.3495	39
	none	54984.938	1763.5812	38
Picea abies	WALD	9573.258	0.0000	27
	Exponential Power	9774.782	201.5239	27
	none	9781.127	207.8688	26
Larix	WALD	9986.405	0.0000	22
	Exponential Power	10308.055	321.6503	22
	none	10380.688	394.2837	21
Pinus contorta	WALD	3421.620	0.0000	18
	Exponential Power	NA	NA	18
	none	NA	NA	17

Table 6: Model summary for Picea sitchensis / lutzii. The conditional submodel is glmmTMB's nbinom2 family with dispersion parameter phi = 0.244.

Mixture component	Term	Fixed effects		Random effects	
		Estimate	95% CI	SD (Intercept)	N
	(Intercept)	-0.41	-0.87, 0.05		
	seeds.WALD	0.95	0.89, 1		
	age	0.13	-0.32, 0.58		
	bio01	0.21	-0.32, 0.73		
	bio19	-0.58	-1.08, -0.07		
	relelev	-0.35	-0.42, -0.28		
	T45	-2.53	-2.74, -2.33		
	artificial	-0.93	-1.18, -0.69		
	T44	-4.91	-5.52, -4.3		
	T32	-1.34	-1.56, -1.12		
	V9	0.34	0.05, 0.63		
	T34	-0.04	-0.24, 0.16		
	V12	-2.17	-4, -0.35		
	V1	-0.55	-0.79, -0.32		
	T13	0.48	-1.34, 2.29		
	T41	-1.10	-1.45, -0.76		
	T1	-0.56	-0.98, -0.15		
	V2	-1.82	-2.39, -1.25		
	T2	1.52	0.97, 2.07		
	T40	0.39	-0.37, 1.15		
	V10	-2.39	-3.8, -0.98		

	T27	1.53	0.69, 2.37		
	T17	2.40	1.1, 3.7		
	T29	-3.02	-6.68, 0.64		
	T16	0.55	-0.44, 1.54		
	V8	-5.90	-14.47, 2.67		
	T31	0.57	0.09, 1.05		
	V3	-1.43	-1.98, -0.88		
	T6	0.49	-1.01, 1.98		
	V13	-1.84	-5.4, 1.72		
	T12	-2.38	-6.16, 1.4		
	T24	-2.00	-7.23, 3.23		
	T21	-4.41	-7.07, -1.75		
	T36	-1.95	-3.45, -0.46		
	site			1.37	42
Zero-inflation model	(Intercept)	1.04	0.37, 1.71		
	age	-0.82	-1.47, -0.16		
	site			2.12	42

Table 7: Model summary for Picea abies. The conditional submodel is glmmTMB’s genpois family with dispersion parameter phi = 2.6.

Mixture component	Term	Fixed effects		Random effects	
		Estimate	95% CI	SD (Intercept)	N
	(Intercept)	-1.12	-1.71, -0.53		
	seeds.WALD	0.39	0.34, 0.44		
	age	-0.11	-0.59, 0.37		
	bio01	-0.32	-0.94, 0.29		
	bio19	0.51	-0.05, 1.08		
	relelev	0.27	0.18, 0.37		
	T45	-6.40	-7.53, -5.27		
	artificial	-1.07	-1.4, -0.74		
	T44	-6.85	-12.51, -1.19		
	T32	-0.97	-1.24, -0.7		
	V9	1.79	-0.44, 4.02		
	V12	1.30	0.84, 1.75		
	V1	-1.60	-2.46, -0.75		
	T13	-2.79	-4.11, -1.47		
	T41	-0.95	-1.62, -0.28		
	T1	-0.42	-1.1, 0.26		
	V2	-0.58	-1.05, -0.11		
	T2	-10.73	-35.37, 13.91		
	V10	-0.92	-5.91, 4.07		
	T31	-0.18	-1.06, 0.71		

	V4	-1.86	-4.74, 1.01		
	V3	-0.29	-2.76, 2.18		
	site			0.62	19
Zero-inflation model	(Intercept)	1.86	0.89, 2.83		
	age	0.38	-0.47, 1.23		
	site			1.73	19

Table 8: Model summary for Larix. The conditional submodel is glmmTMB's nbinom2 family with dispersion parameter phi = 0.203.

Mixture component	Term	Fixed effects		Random effects	
		Estimate	95% CI	SD (Intercept)	N
	(Intercept)	-2.08	-2.81, -1.36		
	seeds.WALD	0.82	0.73, 0.92		
	age	-0.96	-2.04, 0.12		
	bio01	-0.87	-1.69, -0.06		
	bio19	-1.82	-2.96, -0.67		
	relelev	0.22	0.1, 0.34		
Conditional Model	T45	-1.95	-2.46, -1.43		
	artificial	-0.12	-0.56, 0.33		
	T44	-3.79	-5.47, -2.11		
	T32	-1.02	-1.36, -0.69		
	V9	-2.83	-4.4, -1.27		
	T34	0.26	-0.29, 0.82		
	V1	-1.62	-3.35, 0.12		
	T41	-3.85	-5.07, -2.62		
	T1	-1.16	-2.49, 0.17		
	V2	-8.42	-26.75, 9.91		
	T17	5.64	4.4, 6.87		
	site			0.97	15
Zero-inflation model	(Intercept)	1.03	0.14, 1.93		
	age	-1.07	-1.81, -0.33		
	site			1.19	15

Table 9: Model summary for Pinus contorta. The conditional submodel is glmmTMB's nbinom2 family with dispersion parameter phi = 0.031.

Mixture component	Term	Fixed effects		Random effects	
		Estimate	95% CI	SD (Intercept)	N
	(Intercept)	-3.36	-4.45, -2.27		
	seeds.WALD	1.07	0.7, 1.45		
	age	1.04	0.71, 1.37		
	bio19	0.23	-1.05, 1.5		

	relelev	0.02	-0.45, 0.49		
Conditional Model	artificial	6.98	4.94, 9.03		
	T34	1.46	-1.31, 4.23		
	V1	-1.13	-3.85, 1.6		
	T1	1.17	-2.83, 5.17		
	T40	2.58	1.91, 3.25		
	T30	1.17	-2.05, 4.38		
	V8	0.19	-4.38, 4.75		
	V3	-3.22	-4.84, -1.59		
	site			0.00	6
Zero-inflation model	(Intercept)	-0.58	-5.54, 4.38		
	age	0.69	-3.2, 4.59		
	site			4.16	6

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