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The role of neutral processes in alpine plant species distribution models on Mount Schrankogel (Tyrol, Austria)

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# Contents

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## Abstract

Alpine plant species distributions are mostly discussed through the lens of environmental gradients, niches, and competitive and facilitative interactions. A contrasting perspective views these plants as a metapopulation structured by disturbance-based extinctions, dispersal, and recruitment limitations. These and other processes are part of neutral theory, whose application to alpine environments has rarely been assessed. My thesis investigated the influence of neutral processes on community structuring of 45 alpine plant species in a high mountain landscape through a multi-step modeling approach. First, species distribution models (SDMs) were built for each species using 10 abiotic environmental predictor variables. The SDMs were used to make suitability projections that were then compared with observed species occurrences to calculate the model success and fail rates. Subsequently, these rates were analyzed using multiple regressions to test the effect of the density of suitable areas in the surroundings of a site (proportional suitability), and species mobility-related traits, including germination rate, anemochory, zoochory, and seed yield. The effects on projection accuracy were used to indirectly assess two neutral processes: source-sink dynamics, and dispersal limitations.

The results showed that proportional suitability has a significant positive effect on the likelihood that a species will be present in a site, even if the environmental conditions on site are projected as unsuitable. Furthermore, zoochory and germination rate were significantly linked to the likelihood of species to occur in unsuitable sites, according to the SDMs. These findings support a considerable role for dispersal limitations and source-sink dynamics in determining species distributions. However, the impact of seed yield was opposite than expected by dispersal limitation, since high seed yields had a significant negative effect on the likelihood of a species occurring in a suitable area. This is likely indicative of plant reproductive strategy trade-offs rather than neutral processes. Furthermore, germination rate effects could additionally be indirectly interpreted as evidence of establishment limitation – a niche-based process. The contrasting results highlight that while species niche explanations may serve as the foundation for understanding alpine species distributions, neutral processes are important for explaining the errors of niche-oriented models. The use of both approaches could yield the most precise and robust distribution models for these plants, which is especially relevant in the face of climate change and mounting threats in alpine habitats.

## Zusammenfassung

Die Verbreitung alpiner Pflanzenarten wird meist unter dem Blickwinkel von Umweltgradienten, Nischen sowie konkurrierenden oder förderlichen Interaktionen diskutiert. Eine andere Perspektive betrachtet diese Pflanzen als Metapopulation, die durch störungsbedingtes Aussterben, Verbreitung und Rekrutierungsbeschränkungen strukturiert ist. Diese und andere Prozesse sind Teil der neutralen Theorie, deren Relevanz für alpine Vegetation bisher kaum untersucht wurde. In meiner Masterarbeit untersuche ich den Einfluss neutraler Prozesse auf die Strukturierung auf die Verbreitung von 45 alpinen Pflanzenarten in einer Hochgebirgslandschaft durch einen mehrstufigen Modellierungsansatz. Zunächst wurden für jede Art unter Verwendung von 10 abiotischen Umweltvariablen Artenverteilungsmodelle (SDMs) erstellt. Die SDMs wurden zur Erstellung von Eignungsprognosen verwendet, die dann mit dem beobachteten Vorkommen der Arten verglichen wurden, um die Erfolgs- und Misserfolgsraten der Prognosen zu berechnen. Diese Raten wurden mit Modellen analysiert, um die Auswirkungen der Dichte geeigneter Gebiete in der Umgebung eines Standorts (proportionale Eignung) und der mit der Mobilität der Arten verbundenen Merkmale, einschließlich Keimungsrate, Anemochorie, Zoochorie und Samenertrag, auf die Inzidenz der Arten zu testen. Die Auswirkungen auf die Vorhersagegenauigkeit wurden genutzt, um zwei neutrale Prozesse indirekt zu bewerten: die Quelle-Senke-Dynamik und die Verbreitungsbeschränkungen.

Die Ergebnisse zeigten, dass die proportionale Eignung eine signifikante positive Auswirkung auf die Wahrscheinlichkeit hat, dass eine Art an einem Standort vorkommt, selbst wenn die Umweltbedingungen für sie ungeeignet sind. Darüber hinaus waren Zoochorie und Keimungsrate mit einem signifikanten Effekt verbunden, der die Wahrscheinlichkeit des Vorkommens von Arten an Standorten, die nach den SDM als ungeeignet eingestuft wurden, erhöhte. Diese Ergebnisse belegen, dass Ausbreitungsbeschränkungen und Quelle-Senke-Dynamik bei der Bestimmung der Verteilung von Arten eine wichtige Rolle spielen. Die Auswirkung des Samenertrags war jedoch entgegengesetzt zu den Erwartungen der Ausbreitungsbeschränkung, weil hohe Samenerträge eine signifikant negative Auswirkung auf die Wahrscheinlichkeit des Vorkommens einer Art in einem geeigneten Gebiet hatten. Dies ist eher ein Hinweis auf einen Kompromiss zwischen den Reproduktionsstrategien der Pflanzen als auf neutrale Prozesse. Darüber hinaus könnten die Auswirkungen auf die Keimungsrate indirekt als Beweis für einen Umweltfilter bei der Ansiedlung interpretiert werden, also einen nischenbasierten Prozess andeuten. Die Ergebnisse machen deutlich, dass nischenbasierte Erklärungen für Art-Verteilung zwar als Grundlage für das Verständnis der Anordnung alpiner Arten dienen können, neutrale Prozesse jedoch wichtig sind, um die Fehler nischenorientierter Modelle zu erklären. Die Verwendung beider Ansätze kann die präzisesten und robustesten Verbreitungsmodelle für diese Pflanzen liefern, was angesichts des Klimawandels und der zunehmenden Bedrohungen alpiner Lebensräume besonders wichtig ist.

## Introduction

As climate change advances and temperatures increase, mountain ecosystems and their cold-adapted plant species are expected to undergo significant changes, but the magnitude and distribution of these developments are unclear. Indeed, as the climate warms, formerly cold habitats on mountains will be invaded by lowland species, remaining cold habitats are predicted to shrink and shift to higher elevations, and mountain-top habitats may disappear entirely since low temperature extremes at the summits will no longer be available on many mountains (Rumpf et al., 2018; Hülber et al., 2016; Engler et al., 2010). For many species, this may mean losing most or the entirety of their suitable habitat on mountains in their current range, thus risking extinction. Considering these threats to alpine plants, it is important to understand the processes controlling their distribution and the composition of plant communities (e.g. Helm et al., 2024). Such efforts would help identify the status and trajectories of species threatened by climate change, and aid in conservation efforts.

Presently, there are two broad perspectives, each with their own model repertoires, regarding the future of alpine plant distributions. The microhabitat view emphasizes the importance of topographic complexity in mountain habitats, which provides a wide range of microclimatic conditions over a small area (Scherrer & Körner, 2010b). This complexity may form microrefugia where species can persist within or close to their current ranges in small sites, even if the surrounding areas become unsuitable (Scherrer & Körner, 2010a). The alternative perspective puts more emphasis on elevational lapse rates of temperature and understands the distribution of plants in an alpine landscape rather like a metapopulation, with the implication that species only occupy a fraction of the sites environmentally suitable to them at each elevational belt (Chytrý et al., 2024). In this scenario, alpine species are restricted by disturbance-based extinctions, low dispersal distances, and recruitment limitations that hinder (re-)colonization (see e.g. Dullinger & Hülber, 2011; Dullinger et al., 2012). While the first view highlights the key role of niche requirements and environmental conditions, the second view emphasizes the role of neutral processes, especially dispersal limitation and source-sink dynamics, for species distribution (Graae et al., 2018). To better understand how neutral theory may apply here and how it relates to other prevailing views of alpine plant distributions, it is important to briefly cover some developments in community ecology.

One of the fundamental debates in community ecology in recent decades has been about the relative influence of niche determinism versus neutral or stochastic processes on determining community composition. The long-established niche-based view of ecology described communities as being built by mechanisms such as biotic interactions (competition, mutualism, etc.), local adaptations, density dependence, and niche differentiation (Begon et al., 1996). Though this theory had been challenged over the course of the 20$^{th}$ century, one of the earliest and most comprehensive alternative views came in 1967 from MacArthur and Wilson's equilibrium theory of island biogeography (ETIB). The ETIB considered broader mechanisms that drove local community structuring, highlighting the impact of a regional metacommunity, species immigration and colonization, and local extinctions (MacArthur & Wilson, 1967). Though this theory was conceived to explain community structuring on islands and the impact of the associated mainland, eventually many of its principles were formulated for entirely

continental communities as well. Hubbell's 2001 book unified many ideas on the importance of metacommunity dynamics, stochasticity, and disequilibrium processes on determining community composition, which were all proposed in the aptly named Unified Neutral Theory of Biodiversity and Biogeography (UNTB). This neutral theory stated that, although species may have trait differences between each other, this fact is not enough to unequivocally connect traits to functional and ecological differences that are significant for determining community structure. Instead, random dispersal (within the local community but also from the metacommunity), speciation, and ecological drift (stochastic birth and death rate variations) are the key drivers of community structure, while species traits and environmental context are not significant (Hubbell, 2001). Given its radical departure from the niche-based view, it is no surprise that, since the formulation of the UNTB, much work has been done to prove, disprove, or otherwise investigate its explanatory power. Though there have been many, one of the main criticisms of the theory has been about the varying importance of species' environment-adapted traits, depending on the spatial scale. In many cases, such as tropical tree communities for example, adaptations have been shown to be significant for community structuring at fine spatial scales (Condit et al., 1996; Jabot & Shave, 2011). Despite its shortcomings, neutral theory has been viewed as beneficial for allowing better testing and predicting of community structure by providing a dynamic sampling theory of community assembly that uses the key processes of dispersal, speciation, birth, and death (Matthews & Whittaker, 2014). More importantly, neutral theory and niche theory have both been used to explain ecological reality, and it may be more appropriate to view the two as complementary approaches, one explaining the gaps of the other, rather than as a strict dichotomy (Leibold & McPeek, 2006; Adler et al., 2007).

By now, neutral processes are generally acknowledged as an important co-determinant of species distribution, especially at large, biogeographical scales (Soberón, 2007; Graae et al., 2018). Nonetheless, they are often neglected in distribution modelling, particularly at landscape or regional scales. Alpine plants are a good example here, as their distribution patterns are almost exclusively discussed in terms of steep environmental gradients in mountain terrain, and competitive and facilitative interactions (Körner, 2003; Callaway et al., 2002). As mentioned, however, there are some pieces of evidence that suggest that neutral processes also play a role at fine scales. Specifically, arguments in favor of the metapopulation view of alpine plant distribution offer insight into possible neutral processes. Some of these are, for example, the high disturbance frequency and strong year-to-year variation of weather conditions in alpine environments, which enhance stochastic extinctions, as well as low dispersal distances and considerable recruitment limitation, which hamper (re-)establishment (Dullinger & Hülber, 2011; Dullinger et al., 2012). Disturbance-related extinctions (i.e. demographic stochasticity and thus ecological drift), as well as dispersal and the associated establishment (or recruitment) limitations, are both key parts of neutral theory (Hubbell, 2001). A related concept to these neutral processes is mass effects, which are also predicted to play a significant role in climatically and physically heterogenous environments like mountains (Graae et al., 2018). Mass effects, or source-sink dynamics, occur when species flood unsuitable sites with propagules and thus foster the establishment of sink populations in unsuitable habitats which depend on the recurrent input of seeds for long-term persistence (Holt, 1993). As is the case for

other habitats whose community structures and distributions have been modeled, the ecological reality of mountainous alpine habitats likely lies in between neutral and niche theory, but currently the influence of neutral processes is far less understood.

## Research Questions and Hypotheses

I evaluate evidence for neutral processes playing a role for alpine plant distribution with an exceptional dataset. Specifically, the effect of dispersal limitation and source-sink dynamics or mass effects are considered. I assess two lines of indirect evidence: one via the density of suitable habitats in the surroundings of a site, and one via the traits of species. The rationale being that, first, denser suitable surroundings should increase propagule input and hence foster source-sink dynamics, i.e. result in species presence at environmentally unsuitable sites, and vice versa, for the same reason (higher propagule input), it should lead to more complete occupancy of suitable sites. Second, species with traits that foster mobility, like high dispersal distances and germination rate, should be more frequently present at unsuitable sites due to mass effects, and less frequently be missing from sites that are suitable.

General question:

- How important are neutral processes for alpine plant species distribution?

Specific questions:

- Is the occurrence of a species at a site related to the suitability of other sites in its surroundings?
- Do traits related to the mobility of a species explain the occupancy of suitable and unsuitable sites?

Hypotheses:

1. A higher frequency of suitable sites in the surroundings will increase the likelihood that a species occupies even an environmentally unsuitable site due to mass effects at play.
2. A higher frequency of suitable sites in the surroundings will decrease the likelihood that a species does not occupy an environmentally suitable site, because of reduced dispersal limitation.
3. High values in mobility-related traits will increase the likelihood that a species occupies even an environmentally unsuitable site due to mass effects.
4. High values in mobility-related traits will decrease the likelihood that a species does not occupy an environmentally suitable site because of reduced dispersal limitation.

These questions were tackled through a multi-step modeling process using environmental and species occurrence data of a mountain landscape in the Austrian Alps. First, I built species distribution models (SDM) that were used to make suitability projections for the study species based on abiotic, environmental variables. The resulting projections were compared with species occurrences to determine the success and fail rates. Finally, these rates of successful and failed projections of the SDMs were explained by a further series of models

that tested the effect of several species traits, as well as suitability densities in the surroundings of a site.

## Data and Methods

### Study area and species distribution data

The study site is located on Mount Schrankogel (3497 m a.s.l., 47°02′39.1″N, 11°05′56.0″E) in the western Austrian Alps. The climate of the region is characterized as temperate sub-continental, and the mean annual temperature is 2.5°C with an annual rainfall of 889 mm (meteorological station Obergurgl, 1950 m a.s.l., 20 km south of the study area). In 2021 and 2022, a system of 900 1 × 1 m-vegetation sampling plots has been established on this mountain by a larger research team as part of the MICROCLIM project (Chytrý et al., 2024; Helm et al., 2024) (Figure 1). The plots cover a landscape of ca. 5 km², span an elevational gradient from 1800 to 3497 m, and include all kinds of non-forest vegetation but mainly grasslands, dwarf shrub heath, as well as assemblages on scree, rock, and young moraines. In each plot, the occurrence of vascular plant species was recorded and their cover-abundance value estimated. These 45 study species (Appendix Table 1) were selected for their relative abundance, aiming at a representative sample of the overall flora of the area with respect to growth form, taxonomic coverage and habitat preferences.

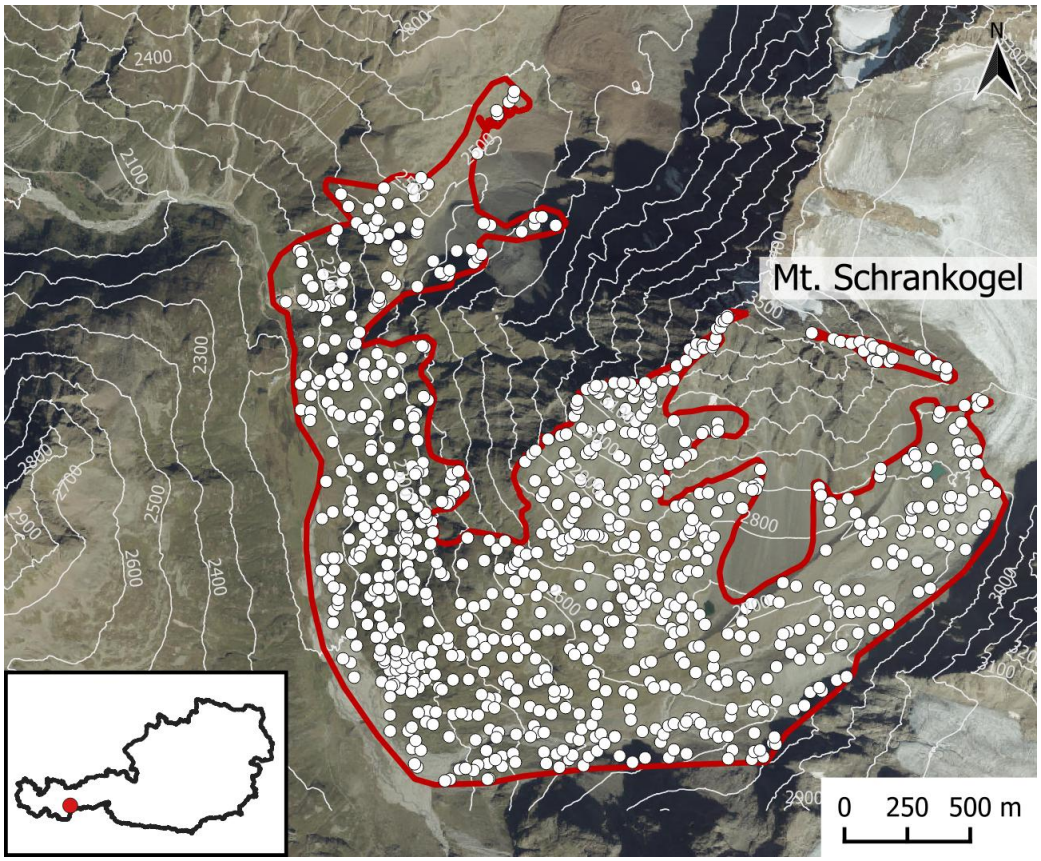


Figure 1. A map of the logger plots on Mount Schrankogel that were used in this study (© Norbert Helm, 2025). Though more plots in a separate valley to the west were part of the MICROCLIM project, these were not part of the analysis in this thesis and are thus not depicted here. Orthophoto source: basemap.at.

## Environmental data

In each of the 900 sampling plots, a temperature logger was installed at 10 cm soil depth and temperatures have been measured at an hourly rate since summer 2021. In addition, soil probes were taken at each plot in 2022 and 2023 and a number of variables, including carbon and nitrogen content, were subsequently determined in the lab (Eden, 2024). Based on the logger measurements, the mean annual temperature for 2022 and 2023 was calculated for each of the 900 plots (Chytrý et al., 2025). These metrics, as well as the measured soil properties, were then extrapolated across the entire Mt. Schrankogel landscape at 1 × 1 m resolution, using correlations with terrain variables, derived from a Digital Terrain Model (DTM), and vegetation productivity (NDVI). Data handling and all described analyses were done in R, version 4.4.1 (R Core Team, 2024), and specific packages are cited when relevant.

## Data on germination, seed yield and dispersal

To derive germination rates of the study species, five experimental sites in the larger area around the village of Obergurgl, around 20 km south of Mt. Schrankogel, had been established in September 2021. Sites were placed along an elevational and microclimatic gradient (1989 to 2650 m a.s.l.). At each site, five areas of approximately 15 × 15 m, differing in environmental conditions (local topography, soil conditions, vegetation types), were selected. The experimental areas were fenced during the growing season to reduce damage by cattle and sheep grazing in the region. In each area, four plots of 1 × 1 m were installed for sowing seeds of the 45 study species. Plots were subdivided in 10 × 10 cm cells and 20 seeds per species were sown into randomly selected cells around a point marked by a wooden stick. Seeds were softly pressed into the soil to avoid them being washed away too easily. To account for annual fluctuation in weather conditions, half of the plots (1 plot per pair of rows) were sown in 2021, and the other half in 2022. Seeds were sampled immediately before sowing in regional populations near the peak elevation of each species (approximately in optimum habitats). The number of seedlings in each cell was determined at peak growing season of the subsequent year. The average germination rate per species was then calculated by dividing the sum of seedlings per species by the sum of sown seeds.

To estimate species-specific seed yield, we counted the number of seeds of 10 randomly chosen, spatially distinguishable fruiting individuals and derived the mean (Appendix Table 1). For some species, the collected material did not allow for the derivation of reliable assessments of seed yield, due to the dispersal of seeds before collection, pest infestation, herbivory, and so on. In these cases, the counted values were replaced by literature data derived from LEDA3 for *Geranium sylvaticum, Luzula spicata, Trifolium badium* and *Vaccinium vitis-idaea*; and from ECOFLORA (http://ecoflora.org.uk/) for *Vaccinium myrtillus*.

Species dispersal ability was calculated for two different vectors, namely, wind (anemochory) and large herbivores (zoochory). Wind dispersal kernels were parameterized using the WALD model (Katul et al., 2005) with required species-specific values derived from own measurements (Appendix Table 1). Wind speed data was collected for the last decade (2015 – 2024), containing average wind speeds in 10-minute intervals during the shedding season (August – October). This data was measured at the closest weather station to

Schrankogel, named Brunnenkogel (10°51’42’ E, 46°54’46’’ N, 3437 m asl.), and downloaded from https://dataset.api.hub.geosphere.at/app/frontend/station/historical/klima-v2-10min. Since seeds in alpine habitats are most effectively dispersed under strong wind conditions (Tackenberg & Stöcklin, 2008), only the top 1/6 of windspeed values was used. This was corrected from measurement height (10 m) to seed release height by integrating over a logarithmic wind profile according to Skarpaas & Shea (2007), and other necessary parameters were set as done by Dullinger et al. (2012). The final wind dispersal values used for modeling were those calculated as the logarithm (base 10) of the probability of a seed to disperse a distance between 20 and 20.1 m (just beyond the buffer area) with the wind kernel.

For animal dispersal, we selected the chamois (*Rupicapra rupicapra* L.) as the principal animal vector because this species is the most common large herbivore in the European Alps, so it is probably the most effective long-distance dispersal agent. We generated kernels for both exozoochoric and endozoochoric dispersal using random walks (Morales et al., 2004) derived from chamois movements according to literature. Thus, walks remained mostly within a home range of about 1 km² (Boschi & Nievergelt, 2003; Hamr, 1984) but also included occasional home range movements up to 5 km in length (Fankhauser & Enggist, 2004). During the simulated walks, seeds were attached to the animals’ fur at a random starting location and then detached following species-specific detachment rates (Appendix Table 1). Likewise, seeds were ingested at random locations and defecated according to a normal probability density function, with a 30 hour mean and a 5 hour standard deviation. Dispersal kernels were calculated as the empirical probability densities of the distance between recorded attachment/ingestion and detachment/defecation location in each random walk, of which there were 10,000 done per study species. The detachment rates were modelled in dependence on species’ seed mass and surface structure (Appendix Table 1), according to a regression equation by Römermann et al. (2005). Because no function is published for chamois, we used those for sheep and cattle furs and used the average of the resulting detachment rates. Losses during gut passage were accounted for by weighing the endozoochoric kernel by species-specific gut survival probabilities that were calculated from seed weights (Appendix Table 1) using a regression equation parameterized by Mouissie (2004). In our analysis we eventually used an aggregated zoochoric dispersal value that included both the endozoochorous and exozoochorous kernels. Specifically, the aggregate value at the 0.99 quantile was used, representing the distance in meters until which 99% of the seeds are dispersed and therefore capturing long distance dispersal events that are especially important for zoochoric dispersal. For the calculation and analysis of the dispersal kernels, the packages shape (Soetaert, 2024) and circular (Agostinelli & Lund, 2024) were used.

## Species Distribution Modelling

### *Model fitting*

For each species, an SDM was built using the presence-absence data collected at 854 plots (46 plots could not be used due to problems in environmental data collection) as response, and a set of environmental descriptors as predictor variables. From the entire set of available

predictors, I chose 10 that are mechanistically relevant for alpine plant species, do not correlate too highly (|Pearson correlation coefficient| < 0.7), and that are at the highest available spatial resolution (mostly 3 × 3 m). Table 1 shows the 10 predictors used, and their source, which was mostly from or calculated from previously available governmental digital terrain models, or satellite data of the area. Furthermore, the full correlation table of predictors used can be found in Appendix Table 4.

To reduce model bias and increase the accuracy of the SDMs, an ensemble model and 10-fold cross-validation were used. This ensemble was composed of a random forest model (RF), generalized linear model (GLM), and a generalized additive model (GAM), all three of which used the 10 predictors outlined earlier. To make the ensemble, the R package tidymodels (Kuhn & Wickham, 2020) was used to make the RF model, while the mgcv package (Wood, 2010) was used for the GAM, and the GLM was built with the base R stats package (R Core Team, 2024). RF models were tuned for each species by optimizing two hyperparameters using a 75-25 training-testing data split. These hyperparameters were the mtry, meaning the number of predictors that was sampled in each tree split, and min_n, being the minimum number of data points in a node needed before further splitting. The hyperparameters that yielded the highest accuracy of projections were stored and used when running the random forest component of the ensemble model. Furthermore, the predictors in the GAM were smoothed with splines of third order, while the predictors in the GLM were used as second order polynomials, and for both regression techniques a binomial family was used.

For each species, the data set (presence-absence data) was divided into 10 equally sized folds, so that each fold contained a roughly equal number of presences. To project species occurrence probabilities onto each of these folds, an ensemble model was built using the remaining nine folds, resulting in ten ensemble model projections on the respective fold for every species. The match between projections and observations was quantified using the true skill statistics (TSS) value.

*Model projections and characterization of plot surroundings*

Occurrence probabilities for all 1 × 1 m cells within 20 m circular buffer areas around each of the 854 logger points were projected using the ensemble model that was parameterized without the fold that contains the focal logger point. The resulting occurrence probabilities were transformed into a presence or absence determination for each species by applying the threshold that maximizes the TSS value. The application of the circle buffer can be seen in Figure 2, and the final remaining area for modeling is depicted in Figure 3, amounting to 1,083,248 cells. I used these buffer areas to reduce computational load of projections while retaining the possibility to relate model errors to the suitability of the wider surrounding of a site. The R packages used to handle and transform this raster data were sf (Pebesma & Bivand, 2023) and terra (Hijmans, 2024).

From the projections, I derived two predictors used in downstream analysis: first, the distance of the projected occurrence probability of the logger cell to the occurrence threshold used for translation into binary presence-absence projections (henceforth called threshold distance); and second, the proportion of cells in each buffer where a species is projected to be

present, i.e. where the projected probability of occurrence is higher than this threshold (henceforth called proportional suitability).

## Linking model projections with traits and characteristics of plot surroundings

Ensemble-model projections could be categorized as being true or false negatives and true or false positives. My aim was to evaluate the rate of errors, therefore, the rate of false absence and false presence projections was related to the suitability of the surrounding landscape and to traits of the species.

To assess the relationship with the suitability of the surroundings, I fitted two generalized logistic mixed models (GLMM), one for probability of a true absence-projection and one for the probability of a true presence-projection as the response variable. In both models, proportional suitability was used as a fixed predictor variable. The threshold distance was used as an additional fixed predictor variable to filter out model errors that are mainly due to marginal transgression of the binary threshold. Such minor transgressions are likely an important source of model errors and can mask the effect of other variables if not considered. Both fixed-effect predictors were scaled to a mean of zero and a standard deviation of one. In addition to the fixed effects, I foresaw a random intercept for species identity in both models.

To evaluate the relationship between model errors and traits, I used the proportion of correct absence and correct presence projections per species as the response and the traits - germination rate, wind dispersal at 20 m, animal dispersal, and seed yield – as additive predictors in two logistic models (one for false absences and one for the false presences). All trait values were scaled beforehand. For all models I furthermore derived marginal and conditional $R^2$ using the package performance (Lüdecke et al., 2021).

Table 1. Environmental predictors used in modeling.

| Predictor | Full name | Source | Note |
|---|---|---|---|
| carbon | Soil carbon content | Measured at logger plots; spatially interpolated | |
| DEM_1 | Digital elevation model at 1 × 1 m resolution | Digital terrain model (DTM) derived from airborne laser scanning point cloud data | DTM from the Department of Geoinformation of the Federal State of Tyrol |
| MAT | Mean annual soil temperature | Measured at logger plots; spatially interpolated | Mean calculated from 2022 and 2023 data |
| pH | Soil pH | Measured at logger plots; spatially interpolated | |
| SLP_3 | Slope at 3 × 3 m resolution | Derived from DTM | |
| SLR_3 | Solar radiation at 3 × 3 m resolution | Derived from DTM | |
| SNW | Number of days under snow cover | Mountain camera data; interpolated to fill gaps | Mean calculated from 2022 and 2023 data; camera data comes from the MICROCLIM project |
| TPI_3 | Topographic position index at 3 × 3 m resolution | Derived from DTM | Degree of exposure/sheltering compared to surroundings |
| TWI_3 | Topographic wetness index at 3 × 3 m resolution | Derived from DTM | Measure of how much water is collected in the site |
| VRM_3 | Vector ruggedness measure at 3 × 3 m resolution | Derived from DTM | Measure of terrain ruggedness |

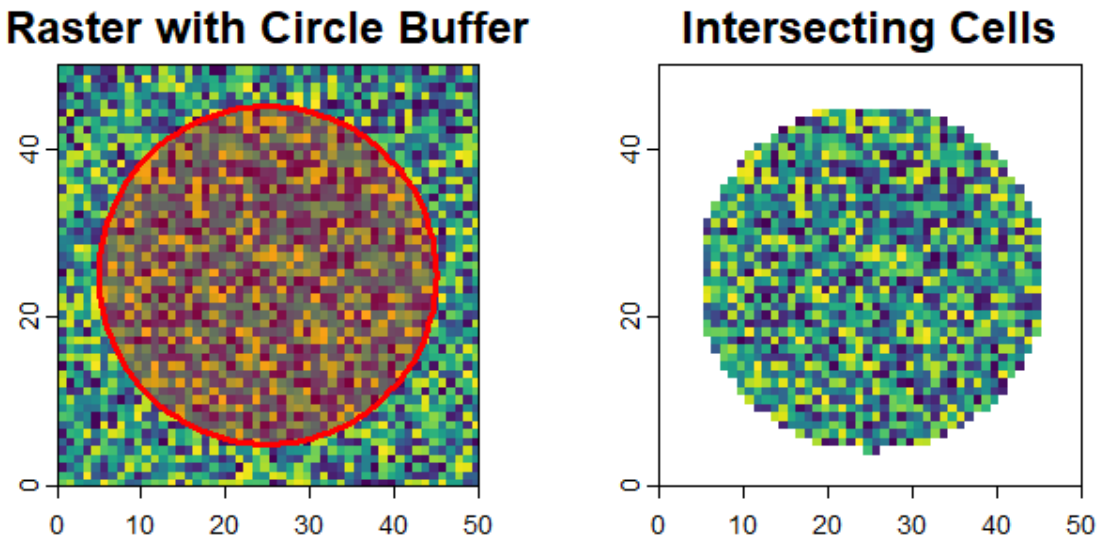


Figure 2. Effect of the circular 20 m buffer on raster cell selection with the use of the buffer function of the terra package in R. The raster used here is purely exemplary, and the logger point is in the center of the circle, at 25, 25.

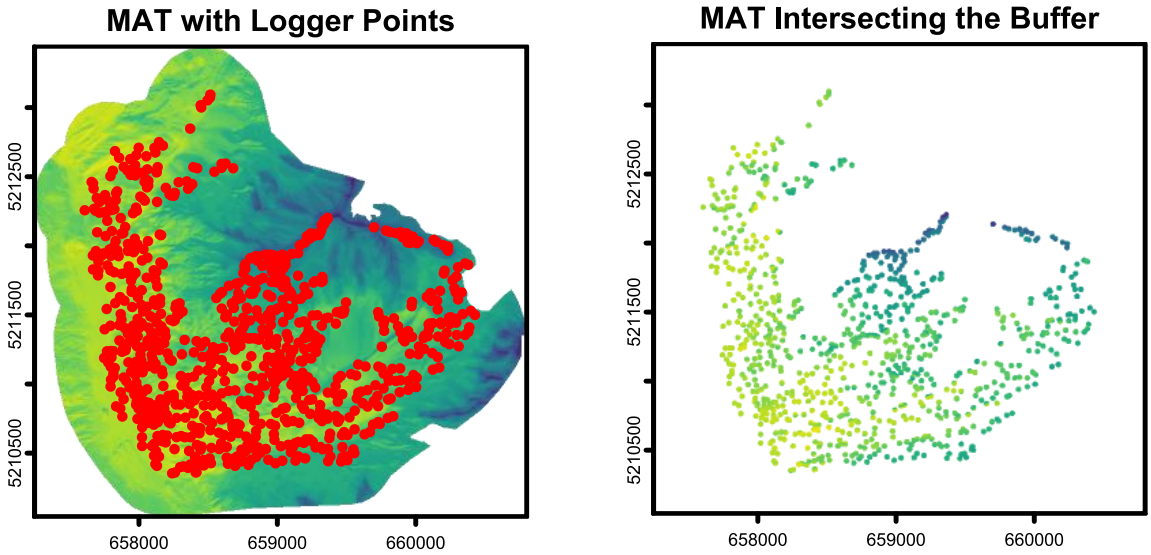


Figure 3. Remaining area used for modeling after buffer application. The left panel shows the positions of the 854 loggers, while the panel on the right only displays the cells within the 20 m buffer around each logger point. The raster used for illustration is the mean annual temperature for Mount Schrankogel.

## Results

### Species distribution models

Most SDMs showed a high degree of accuracy with high TSS values (Appendix Table 3), with a mean TSS of 0.63, and a standard deviation (SD) of 0.09. The mean specificity (true negative rate) across all models was ~0.77 (SD = 0.07) and the mean sensitivity (true positive rate) was ~0.86 (SD = 0.08), indicating that the models tended to make more false absence than false presence projections per species (Figure 4). The species with the highest TSS value, and thus the most accurate overall SDM, was *Oxyria digyna* (TSS = 0.79), while the species with the lowest model TSS was *Poa alpina* (TSS = 0.42). The SDM of *Geum reptans* had the highest sensitivity of 0.98, while *Poa alpina* had the lowest, at 0.66. The highest specificity was seen in the model of *Kobresia myosuroides*, measuring 0.89, while the lowest model specificity was observed for *Juncus trifidus*, at only 0.61. The high average TSS-value is mirrored in a clear distinction of correct absence and presence projections below and above the binary threshold (Figure 5). The variable importance (VI) of every predictor was calculated for every species' RF model, and the table of results can be found in Appendix Table 2. For almost all species, carbon and elevation (DEM_1) were among the top three most important variables by VI score ranking. Mean annual temperature was similarly important, being in the top three for two thirds of the study species. Thus, the average species' occurrence was largely determined through a combination of the carbon content of the soil, the elevation, and the temperature. The only other predictors that were in the top three more than two times were snow cover duration (SNW, highly important for 9 species) and pH (highly important for 12 species). Conversely, the predictors that were least important, meaning in the bottom three by VI score ranking, for four fifths of the species were those describing the exposure or sheltering of the terrain (TPI_3), and the ruggedness of the terrain (VRM_3). For over half the study species, the measure of water collection at the site (TWI_3) was also one of the least important predictors.

### Model errors and suitability of the surrounding landscape

A clear relationship between the error rate and the suitability of the landscape is already visible in the 'raw data'. True absences and presences are associated with much lower, respectively higher proportional suitability than false absences and presences (Figure 6). The GLMMs corroborate this visual impression: the rate of true absences decreases with proportional suitability while the rate of true presence projections increases, and this effect can be observed at both low and high threshold distances (Figures 7 and 8). However, as projections were made closer to the threshold value, the models were more likely to make an error. Furthermore, proportional suitability and threshold distance are both highly statistically significant (p-value < 0.001) predictors for the GLMMs.

### Model errors and traits

Only two traits had a significant effect on the likelihood of correct absence projections: both a higher average germination rate and a higher animal dispersal distance decreased this

likelihood (Figure 9). Conversely, species with a low germination rate or a low dispersal ability through animals are more likely to be correctly projected as absent in the logger plots.

For the presence projections of the model, three trait effects were significant - average germination rate, animal dispersal, and the average seed yield (Figure 10). In this case, both a higher germination rate and wider animal dispersal increased the true presence rate. So, species with a high value in either trait were more likely to be found where the model predicted an occurrence, while species with low values in these traits were more likely to be incorrectly projected as present. On the other hand, species with a high average seed yield were less likely to be correctly projected as present in logger plots, but those with a low seed yield were more likely to be correctly assessed as present.

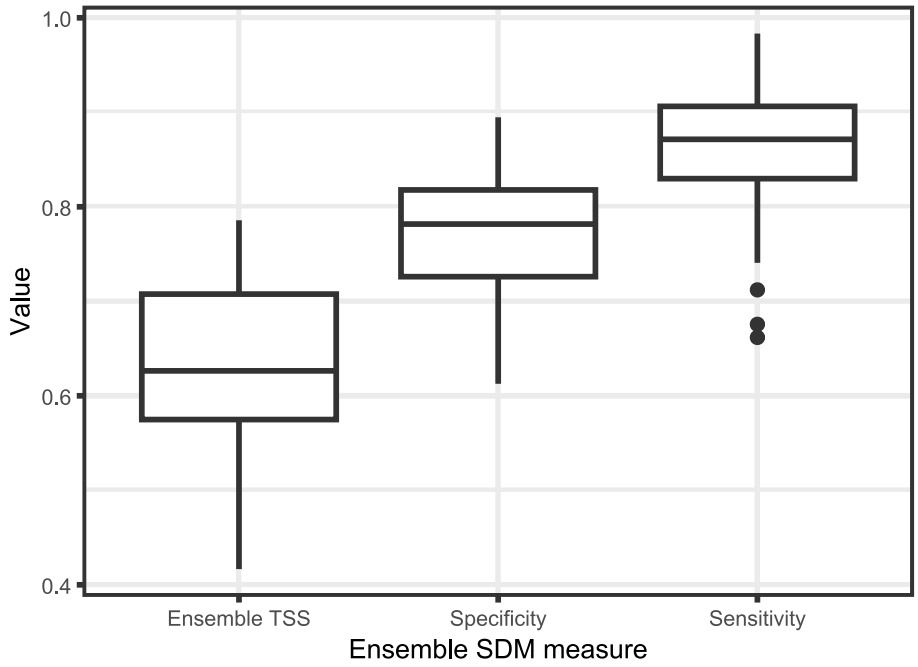


Figure 4. Ensemble SDM measures of true skill statistic (TSS), specificity, and sensitivity for all 45 study species.

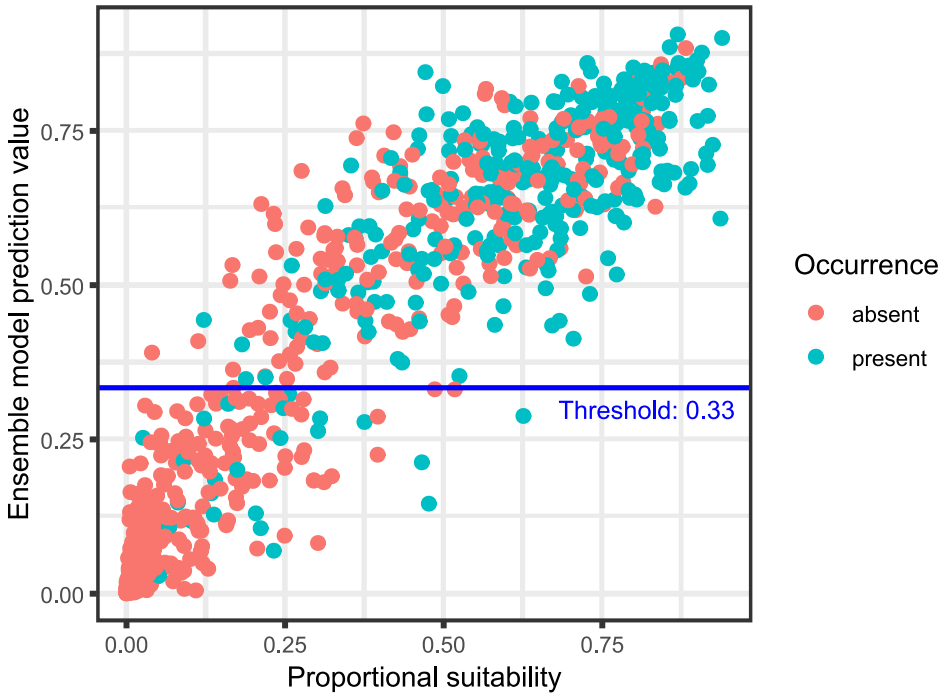


Figure 5. Ensemble SDM projection probabilities for *Persicaria vivipara* against the proportional suitability of each logger's buffer area. The blue line is the threshold of occurrence as derived from the model's TSS. In logger points above the line, *P. vivipara* was projected as present, and below the line it was projected as absent. Points are colored by observed occurrence (absences in red and occurrences in blue, respectively). This model had a specificity of ~0.70 and a sensitivity of ~0.90, with a TSS value of ~0.60.

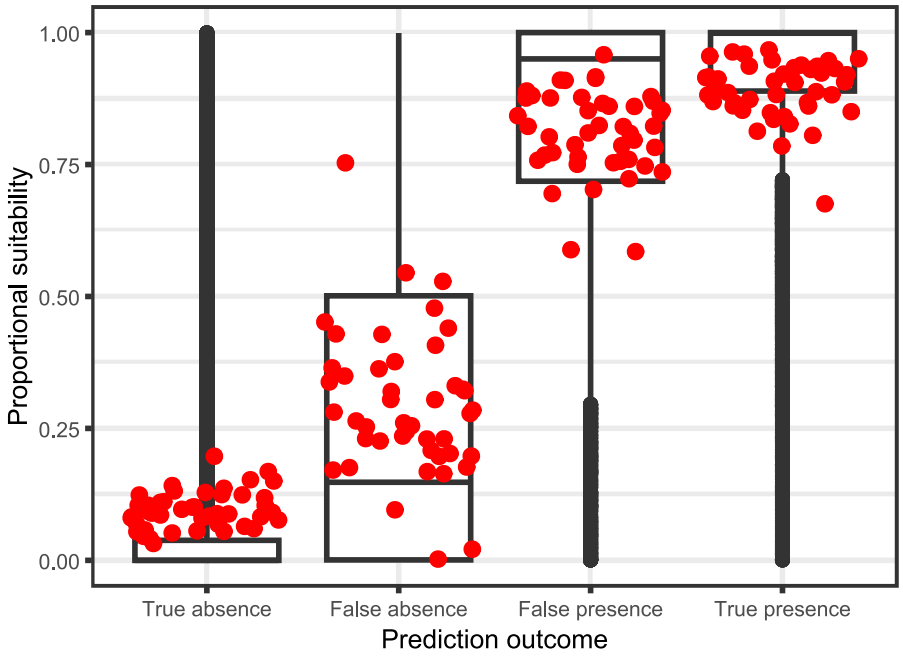


Figure 6. Ensemble SDM projection outcomes compared to proportional suitability of logger points' buffers. Every boxplot is composed of data from all 854 logger plot projections, while each red dot indicates the mean proportional suitability for a species across all logger buffers whose projection results fit into that outcome category.

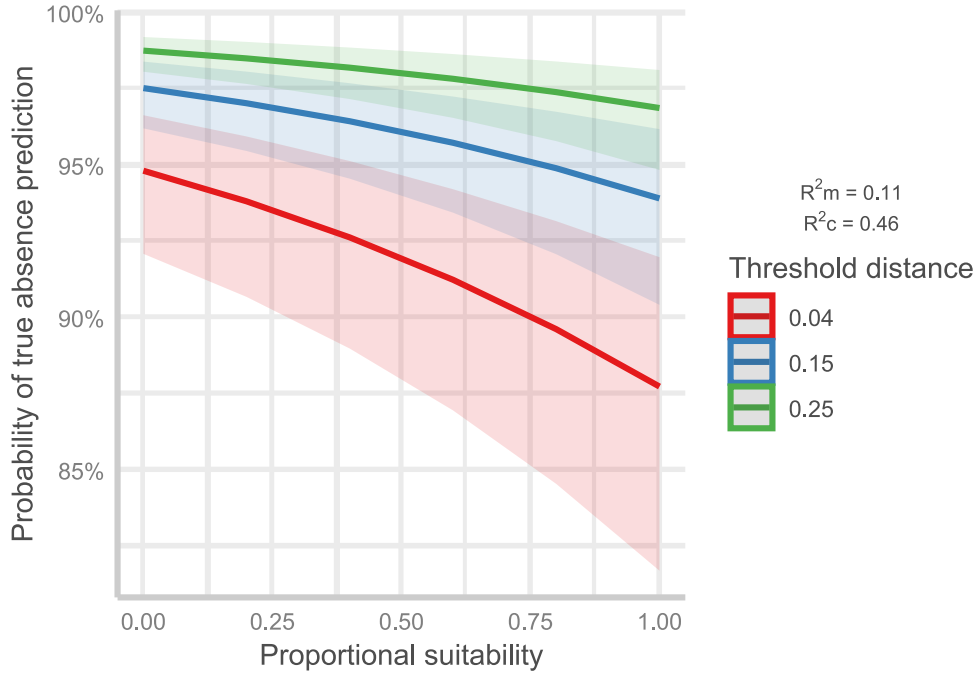


Figure 7. GLMM results of the probability of a true absence projection from the ensemble SDM based on the effect of proportional suitability and the projection values' distance to the occurrence threshold. The $R^2$m refers to the marginal $R^2$, while $R^2$c is the conditional $R^2$ value. The confidence intervals (95%) show the standard error of the model's fixed effects.

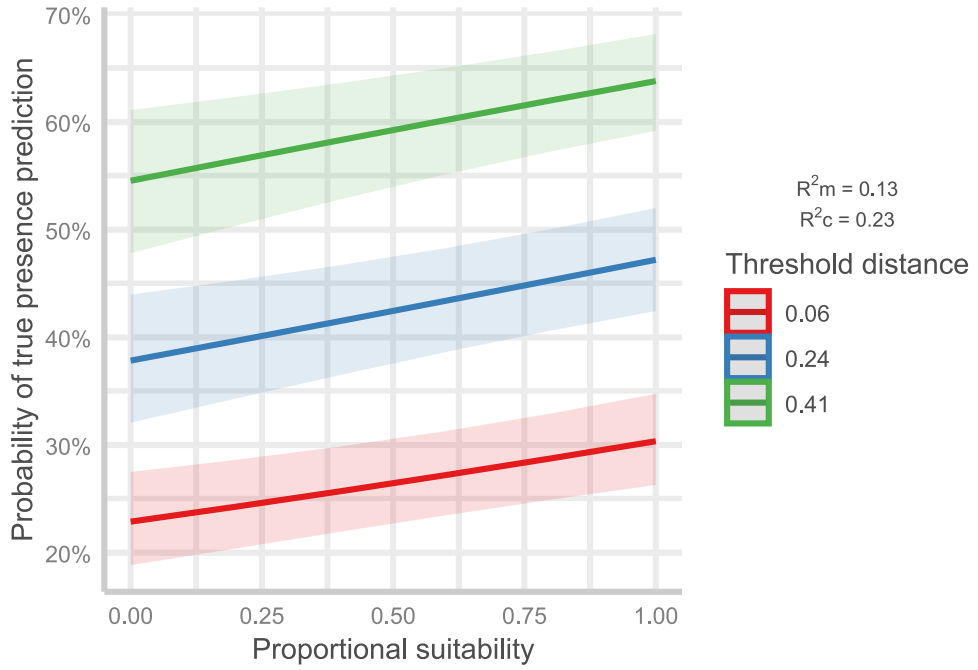


Figure 8. GLMM results of the probability of a true presence projection from the ensemble SDM based on the effect of proportional suitability and the projection values' distance to the occurrence threshold. The $R^2$m refers to the marginal $R^2$, while $R^2$c is the conditional $R^2$ value. The confidence intervals (95%) show the standard error of the model's fixed effects.

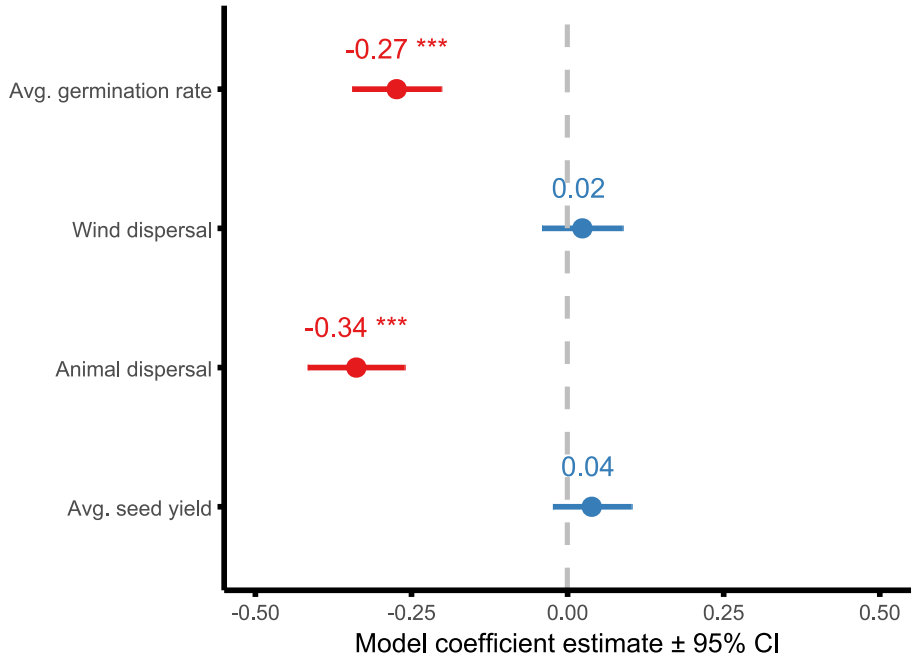


Figure 9. Trait effects on the rate of true absence projections made by the ensemble SDM. Red indicates a negative effect, while blue indicates a positive one. *** indicates a p-value between 0 and 0.001.

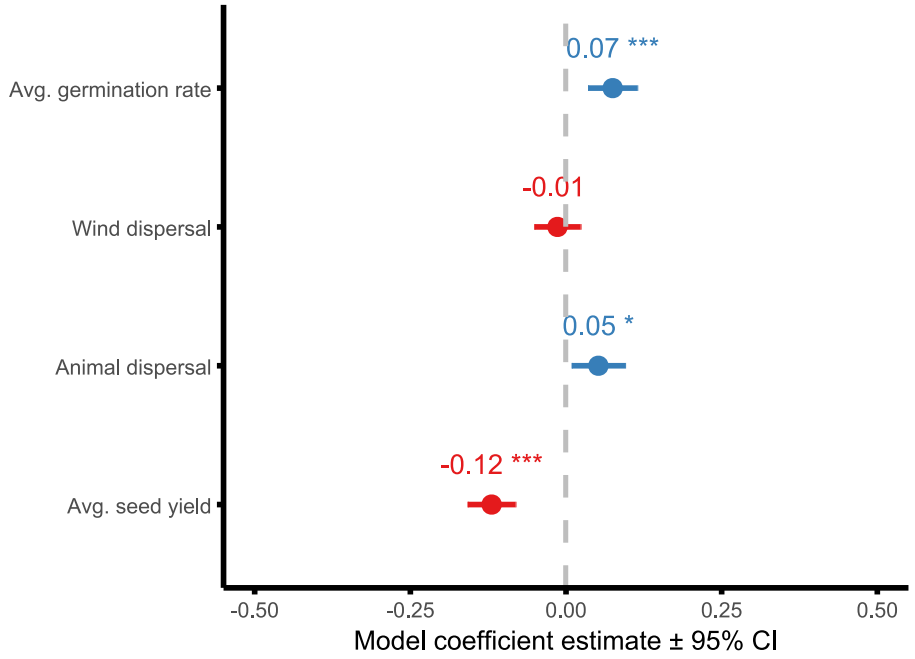


Figure 10. Trait effects on the rate of true presence projections made by the ensemble SDM. Red indicates a negative effect, while blue indicates a positive one. *** indicates a p-value between 0 and 0.001, and * indicates a p-value between 0.01 and 0.05.

## Discussion

### Neutral Processes and Environmental Suitability

When considering the absence projections of the model, we can analyze the effect of changing environmental suitability on the chances to make a true or false absence projection. The model was less likely to be correct when predicting an absence for a logger point in a buffer area with a high proportion of suitable cells (see Figure 7). This can be seen as an indication of source-sink dynamics, where species from nearby and suitable surrounding areas are able to colonize an unsuitable habitat and maintain a population there through constant seed input (Holt, 1993). When many individuals of a particular species surround an unsuitable site, they act as a large source of seeds or propagules, some of which, by chance, will be able to overcome the unfavorable conditions and establish themselves in the unfavorable site – the sink. At low threshold distances, some false absences could be explained by the model making a classification error due to borderline unsuitable conditions. At high threshold distances, however, there is still a decrease in correct absence projections with increasing proportional suitability. In these cases, the environmental conditions are far outside the range of where the species occurs on the mountain, and yet it has been empirically determined to be present. Thus, given the relationship with increasing environmental suitability, it can be concluded that source-sink dynamics are partially at play. However, the establishment of adult plants at unsuitable, but well-seed-supplied microsites may also be facilitated by nursing effects, known to be important in alpine environments (Callaway et al., 2002; Cavieres et al., 2014).

With increasing proportional suitability, we observe an increased probability of true presence projections (see Figure 8). Meaning, the more cells in a buffer are predicted as being suitable for a particular species, the more likely it is that the species truly occurs at the logger point when it is predicted to do so. The effect of increasing proportional suitability can thus be interpreted as the species overcoming dispersal limitations and dispersing to all cells in the buffer that have favorable environmental conditions for it. Dispersal limitation in Hubbell's 'Unified Theory' (UNTB) broadly refers to the isolation of a community from the source pools of metacommunity members, which especially implies a lack of seed input and can also be termed source limitation (Clark et al., 2007). Specifically, when there are many individuals growing in the surroundings, as is likely the case when there are many suitable sites projected, they produce enough seeds or propagules that the species can disperse and occupy every suitable site nearby. While the overall results for the 45 study species suggest this dynamic, it is worth noting that for specific alpine plants, the lack of suitable sites may be limiting their distribution instead of insufficient seed input (Dullinger & Hülber, 2011). The actual occupancy of suitable sites is also directly related to the source-sink effect described earlier, since complete or near complete filling of suitable sites fosters the recruitment to unsuitable sites. Thus, species that can overcome dispersal limitations are also more likely to form sink populations.

### Neutral Processes and Trait Effects

The effect of mobility-related traits on absence projections is straightforward; species with high germination rates and high animal dispersal distances are more likely to be present

in sites where they are projected as absent based on the local environment (Figure 9). Connecting with earlier results, it can be said that a high germination rate and long animal dispersal are what make species good dispersers, allowing them to establish sink populations (more false absences), in accordance with mass effects. On the other hand, average seed yield and wind dispersal do not have a significant effect on a species' likelihood to be found in unsuitable areas. These results indicate that high species-specific seed yields do not foster sink populations, as would be expected if many seeds are produced in a community under mass effects. One reason might be a trade-off between seed size and seed yield, which would convey an establishment advantage to species that produce less seeds that are better equipped with resources (Jakobson & Eriksson, 2000), and this is discussed later. Finally, the non-significance of anemochory for both absence and presence projections does not come as a surprise, as the dispersal values were small and very similar for all species.

For the presence projections, the opposite effect of germination rate and animal dispersal can be seen, as high values in these traits are significant for increasing the chance of a true presence projection (Figure 10). In other words, these traits allow for better range filling, i.e. more true presences, because species can overcome dispersal limitations. Low values in germination and animal dispersal would mean that the species is not found in all its suitable sites. This again indicates that species with low germination rates and whose seeds are unlikely to be dispersed far by animals are also less likely to have sink populations, since adequate filling of suitable sites fosters establishment in unsuitable sites, as discussed before. Just as source limitation was used as a more specific term for the effect of seed input from suitable surroundings, the effect of animal dispersal can be more accurately identified as disperser limitation (sensu Dent & Estrada-Villegas, 2021). This concept covers the interactions between a seed and any vector that allows its movement, but with the study species, only the animal vector is limiting as wind dispersal is not significant. In other literature, dispersal limitation can be used to refer to the vector-related barriers to seed dispersal, or as a general term when describing drivers of plant distribution. To avoid confusion, disperser limitation here specifically refers to the limits imposed by vectors, and dispersal limitation is used in the general, metacommunity sense as in Hubbell's UNTB.

*Seed yield effects*

While the results so far fit with prior expectations of the impact of neutral processes, the effect of average seed yield on projections does not. As Figure 10 shows, species with high seed yield have a lower rate of true presence projections. Logically, one would expect that species that produce a high number of seeds can occupy more sites suitable to them, but the results suggest the opposite is true, which goes against source-sink dynamics and the idea of source limitation as identified through the effect of proportional suitability. Interpreting this trait alone is difficult, because although this model assesses the effects of germination rate and seed yield separately, a potential indirect interaction and relationship between these traits should also be considered. Germination rate specifically and seed production are not known to have a direct relationship observable across plant groups, and indeed no significant interaction between these as predictors of species occurrence was observed with the data from Mt. Schrankogel either. However, it is well-established that seed size and seed number are a trade-

off in plant reproduction (Harper et al., 1970; Harper, 1977). A plant that produces many seeds compared to few is investing less resources in each seed, meaning they have less mass and nutrients, and therefore a lower chance of successfully establishing themselves and reaching the adult stage (Jakobsson & Eriksson, 2000). Conversely, the seeds of low-yield species would have more resources, making them more robust and allowing them to establish themselves more effectively in a broader variety of conditions. This trade-off, in combination with site conditions, could be used to explain how high seed yields do not necessarily mean that more suitable sites will be occupied. However, the available data only shows a weak negative correlation (Spearman: -0.18) between seed mass and seed yield. Furthermore, a GLM with log seed mass as a predictor of log seed number shows a marginally significant negative effect (p-value = 0.04) that only explains about 0.5% of the variance (adj. $r^2 = 0.073$). Initially, it appears that the seed mass-yield trade-off is not strong for the plants on Mt. Schrankogel. However, it is worth noting that seed nutrient content, like nitrogen (N) and phosphorus (P), was not measured, yet it could possibly be a better predictor of seed output, as mineral nutrient values have been shown to be a stronger driver of seed production than dry seed mass (Henery & Westoby, 2001). Also important is that the seed mass values calculated for the study species come from a mean of 100 seeds collected from plants near the average elevation of occurrence of each species. However, seed mass can vary intra-specifically, and for alpine plants, a decrease in mean seed mass with increasing altitude has been shown, both within and between species (Baker, 1972; Bu et al., 2007). Thus, with a combination of nutrient analysis and a wider altitudinal range of seed sampling, it is possible that a future study could show that the seed mass and seed yield trade-off is more prominent, especially across the elevational gradient.

It is important to remember that the environmental data for two key predictors, mean annual soil temperature and snow cover duration, were calculated from only two years of data. These values can fluctuate over longer periods of time and are especially affected by climate change, which will lead to temperature increases and snowfall reductions in the European Alps (Kotlarski et al., 2023). Thus, it is likely that many sites projected as marginally suitable or unsuitable have only recently become so, and their suitability could be in flux from year to year. It is also known that alpine plant seeds' germination is driven by a variety of abiotic factors like light, cold stratification, warm temperature cues, and temperature alterations (Fernández-Pascual et al., 2021), of which only light (SLR predictor) was included in the environmental predictors used in the modeling. Therefore, there is a degree of variability in the suitability or non-suitability for many sites which could make seed mass and resources a key factor for establishment. If the seeds of a high-yield species are resource-poor and can only survive and germinate under a longer period of suitable conditions, then they will display less range filling compared to hardier and resource-rich seeds of a low-yield species that could tolerate periods of unsuitable conditions and thrive at the edges of suitability. To properly test this, it would be necessary to model large in-situ germination experiments with more detailed and dynamic environmental data.

*Germination rate effects and establishment limitation*

Earlier, the effect of increasing suitability on presence projections was identified as evidence of source limitation, but because germination rate has a significant impact on true presence rates, it is important to consider whether establishment limitation also plays a role. Establishment limitation describes a plant population whose distribution is limited by the number and quality of sites, rather than the seed input as in the case of source limitation (Clark et al., 1998). This limitation is imposed by factors and processes that take place after a seed has arrived at a site, and include intrinsic seed properties (senescence, viability), abiotic conditions (temperature, light, nutrients, etc.) and biotic interactions (predation, pathogens, competition, facilitation) (Clark et al., 2007). My models could not account for any post-arrival processes, because the germination rate I worked with only accounts for first-year survival and is an average per species across all site conditions included in the experiment. Nevertheless, varying establishment limitation may still be reflected in the results. Namely, while both are highly significant, the positive effect of germination rate on presence projections (+0.07, see Figure 10) is much smaller than the negative effect on absence projections (-0.27, see Figure 9). Essentially, a high germination rate has a greater impact on whether a species will be found in an unsuitable area, than if it will be found in a suitable one. This discrepancy could be partially explained by the seed post-arrival processes listed before; just because a seed has dispersed to a suitable site, does not mean it will establish itself and reach the adult stage. Thus, because there are more steps and obstacles to reach adulthood (variations in abiotic conditions, biotic interactions, intrinsic seed properties), a high germination rate has a greater effect by enabling a species to colonize an unsuitable site than ensuring a suitable site will be occupied. Therefore, it is more accurate to say that the study species on Mt. Schrankogel are beholden to both source limitations in the dispersal stage, and establishment limitations post-arrival. This finding is in accordance with previous research on the relative influences of seed limitation (source and disperser) and site limitation (establishment) that conclude both play a role for various plant groups and that the two can be viewed as opposites on a gradient, though one is stronger than the other for most species (Clark et al., 2007; Muller-Landau et al., 2002; Turnbull et al., 2000). Furthermore, my results are congruent with the findings of Dullinger & Hülber (2011) that alpine plant distribution is similarly determined by a combination of establishment and seed limitations.

It is crucial to add that establishment limitation is a non-neutral process because it implies seeds and seedlings will compete within the sites where conditions for germination are met, i.e. their regeneration niche, and that the best competitor will end up winning in the limited number of suitable sites (Grubb, 1977; Muller-Landau et al., 2002). On the other hand, the aforementioned source and disperser limitations (together termed seed limitation) can be considered neutral processes because they are less determined by competition but instead by the stochastic arrival and recruitment of seeds at suitable sites; whatever species have dispersed there will grow, rather than the most competitive ones (Hubbell, 2001; Cornell & Lawton, 1992). Therefore, species mobility-related traits can be used to identify the influence of neutral processes on model errors, but in the case of germination rate, the effects also indirectly indicate establishment limitation – a niche-based process.

### Ecological Drift

As discussed, the two lines of inquiry into neutral processes acting on the alpine plant community on Mt. Schrankogel were the effect of the density of suitable habitats in site surroundings, and the effect of species mobility-related traits. These were intended to directly address the impact of mass effects or source-sink dynamics, and dispersal limitation, respectively. However, the third neutral process that was not directly assessed but underlies the other two is ecological drift. This dynamic describes a community that shifts over time due to stochastic, local disturbance-based extinctions that leave physical and resource gaps in the habitat that can then be occupied by the same or different species from the local or metacommunity (Hubbel, 2001). Following local extinction, the arrival of the next individual can be determined by dispersal limitations and mass effects. In alpine environments, plants are exposed to a variety of disturbance-based extinctions, since debris flow, rockfall, and extreme weather events can dramatically change the physical environment of alpine habitats, covering or destroying microhabitats (Chambers, 1995; Gentili et al., 2015). Moreover, climate change is increasing the risks of these geomorphological processes as glacier and permafrost changes influence slope and rock stability (Deline et al., 2015). Indeed, even over the course of the MICROCLIM project on Mt. Schrankogel, 15 logger plots were at least partially affected, and 9 logger plots were destroyed by disturbances, including rockfall and flooding (N. Helm, personal communication, May 27, 2025). While the impact of ecological drift on community composition has been difficult to quantify and directly study (Gilbert & Levine, 2017), it is likely to play a role in disturbance-prone mountainous environments that could be identified through future studies.

## Outlook and Conclusion

While neutral processes revolving around dispersal have been considered in analyses of alpine plant distributions before, my results more specifically identify and characterize these and other neutral dynamics that play considerable roles in community structuring. Source-sink dynamics in particular seem to be important for determining distributions, allowing species with enough individuals in an area to occur in sites beyond their suitable range, especially in harsh alpine landscapes where microhabitats only meters apart can differ greatly in conditions. Through the effects of mobility-related species traits, further support was observed for neutral processes including dispersal limitations (specifically seed limitations, identified through both source and disperser limitation) and consequent mass effects. However, not all results pointed towards neutral processes, as the effect of seed-yield appears to be more connected to plant reproductive strategy trade-offs, rather than stochasticity. Furthermore, non-neutral establishment limitations could also be identified as playing a role, highlighting the topographic and climatic complexity of mountainous environments where seed fitness and niche theory retain much explanatory power in community-structuring frameworks. In the future, it would be valuable to continue to more precisely quantify the relative importances of neutral and niche processes for alpine plants, as has been done with seed limitations. Of particular interest would be studies on the role of ecological drift, which could potentially be more readily observed and studied in dynamic and extinction-prone mountainous environments compared to other landscapes. Unfortunately, mortality rates for alpine plants are difficult to calculate, but by

aggregating results from projects like MICROCLIM that do contain data for sampling plots lost due to environmental hazards or weather events, it may be possible to create a base of knowledge from which drift could be approached in a study.

As has been shown for many other landscapes, it is also true for alpine environments that the best understanding of species distributions can be achieved with the use of both neutral and niche theories and processes. While alpine plant distributions have mostly been seen through the lens of environmental gradients and microhabitats, my results contribute to landscape-scale views of these plants acting also as a metacommunity that can be partially described with neutral processes. The implications are that neutral theory can be used to fill the gaps and explain the discrepancies of more complex microhabitat and niche-oriented models, allowing for overall more accurate and robust models. Such study frameworks that combine niche and neutral approaches have been done for plants of other habitats before, and my results indicate that this would also be applicable for alpine plants. Ultimately, more precise and multi-faceted modeling efforts will be invaluable in regularly (re-)assessing the impacts of climate change and a continuously changing world on alpine plants.

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# Appendix

Appendix Table 1. Fitness parameters of the study species used in dispersal modelling. The values were derived from own measurements.

| | *Wald[1)] dispersal kernels* | | | | | | *Demographic traits* | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **species** | **H0** | **h** | **SM** | **SS** | **GS** | **DR** | **n_seeds_o** | **n_seeds_m** | **Germ_rate** | **Wind_disp** | **Animal_disp** |
| *Achillea moschata* | 0.09 | 0.054 | 0.25 | n | 0.039 | 55.32 | 7.3 /i | 39.0 /s | 0.132 | -13.666 | 2475.7 |
| *Agrostis agrostiflora* | 0.41 | 0.120 | 0.07 | e | 0.087 | 65.47 | 237.0 /s | 237.0 /s | 0.063 | -5.142 | 2947.1 |
| *Agrostis alpina* | 0.15 | 0.058 | 0.14 | e | 0.056 | 64.45 | 37.9 /s | 37.9 /s | 0.097 | -6.320 | 2702 |
| *Agrostis rupestris* | 0.11 | 0.045 | 0.13 | e | 0.059 | 64.68 | 27.3 /s | 27.3 /s | 0.09 | -10.323 | 2875.1 |
| *Anthoxanthum alpinum* | 0.25 | 0.079 | 0.82 | e | 0.018 | 52.31 | 23.7 /s | 23.7 /s | 0.151 | -6.924 | 2341 |
| *Avenula versicolor* | 0.26 | 0.066 | 1.47 | e | 0.012 | 46.47 | 18.6 /s | 18.6 /s | 0.121 | -9.020 | 2203.7 |
| *Carex curvula subsp. curvula* | 0.15 | 0.045 | 2.59 | ba | 0.009 | 27.26 | 0.9 /s | 0.9 /s | 0.066 | -13.277 | 1677.5 |
| *Carex sempervirens* | 0.33 | 0.083 | 2.05 | ba | 0.010 | 29.86 | 14.4 /s | 14.4 /s | 0.098 | -6.990 | 1820.2 |
| *Cerastium uniflorum* | 0.03 | 0.024 | 0.23 | n | 0.041 | 56.32 | 26.1 /f | 26.1 /f | 0.044 | 0.000 | 2629 |
| *Crepis aurea* | 0.23 | 0.109 | 0.84 | e | 0.018 | 52.05 | 18.4 /s | 18.4 /s | 0.263 | -7.525 | 2276.8 |
| *Deschampsia cespitosa subsp. cespitosa* | 0.48 | 0.108 | 0.50 | e | 0.025 | 56.86 | 177.8 /s | 177.8 /s | 0.156 | -5.074 | 2350.3 |
| *Festuca nigrescens* | 0.55 | 0.121 | 0.73 | e | 0.02 | 53.48 | 54.6 /s | 54.6 /s | 0.187 | -5.723 | 2311.7 |
| *Festuca nigricans* | 0.38 | 0.106 | 1.01 | e | 0.016 | 50.29 | 65.1 /s | 65.1 /s | 0.305 | -7.042 | 2216.9 |
| *Geranium sylvaticum* | 0.26 | 0.122 | 6.61 | n | 0.005 | 18.06 | 3.3 /f | 3.3 /f | 0.201 | -11.728 | 1446.6 |
| *Geum montanum* | 0.16 | 0.075 | 1.33 | e | 0.013 | 47.53 | 38.6 /f | 38.6 /f | 0.224 | -13.185 | 2163.2 |
| *Geum reptans* | 0.09 | 0.054 | 1.68 | e | 0.011 | 45.09 | 111.8 /f | 111.8 /f | 0.046 | 0.000 | 2069.8 |
| *Gnaphalium supinum* | 0.02 | 0.035 | 0.08 | e | 0.080 | 65.49 | 13.2 /i | 13.2 /i | 0.064 | 0.000 | 2752.8 |
| *Homogyne alpina* | 0.20 | 0.084 | 1.63 | e | 0.012 | 45.44 | 32.5 /s | 32.5 /s | 0.115 | -5.739 | 2094.3 |
| *Juncus trifidus* | 0.16 | 0.088 | 0.17 | n | 0.050 | 59.84 | 2.1 /s | 2.1 /s | 0.049 | -9.713 | 2551.6 |
| *Kobresia myosuroides* | 0.15 | 0.054 | 0.64 | ba | 0.021 | 43.72 | 8.4 /s | 8.4 /s | 0.038 | -9.495 | 2135.8 |
| *Leucanthemopsis alpina* | 0.07 | 0.040 | 0.58 | n | 0.023 | 45.00 | 39.6 /s | 39.6 /s | 0.216 | 0 | 2065.2 |
| *Luzula alpino-pilosa* | 0.20 | 0.066 | 0.19 | n | 0.046 | 58.32 | 63.3 /s | 63.3 /s | 0.026 | -11.521 | 2650.1 |
| *Luzula lutea* | 0.24 | 0.068 | 0.35 | n | 0.031 | 51.26 | 19.0 /s | 19.0 /s | 0.015 | -10.793 | 2379.8 |
| *Luzula spicata* | 0.08 | 0.026 | 0.25 | n | 0.040 | 55.56 | 37.1 /s | 37.1 /s | 0.059 | 0 | 2447.6 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Mutellina adonidifolia* | 0.18 | 0.082 | 2.90 | f | 0.008 | 10.26 | 65.0 /i | 65.0 /i | 0.24 | -9.339 | 1342.8 |
| *Nardus stricta* | 0.21 | 0.086 | 0.42 | e | 0.028 | 58.25 | 17.3 /s | 17.3 /s | 0.064 | -8.630 | 2294.4 |
| *Oreochloa disticha* | 0.12 | 0.038 | 0.69 | ba | 0.020 | 42.74 | 8.7 /s | 8.7 /s | 0.137 | -10.475 | 2092.1 |
| *Oxyria digyna* | 0.09 | 0.058 | 0.76 | f | 0.019 | 20.03 | 49.6 /s | 49.6 /s | 0.081 | -8.999 | 1767.3 |
| *Persicaria vivipara* | 0.14 | 0.076 | 2.66 | n | 0.008 | 26.96 | 40.4 /s | 40.4 /s | 0.016 | 0 | 1784.3 |
| *Phyteuma hemisphaericum* | 0.09 | 0.057 | 0.08 | n | 0.079 | 67.22 | 206.1 /s | 206.1 /s | 0.126 | -12.796 | 2870 |
| *Poa alpina* | 0.22 | 0.060 | 0.49 | ba | 0.025 | 46.96 | 94.6 /s | 94.6 /s | 0.138 | -6.848 | 2193.4 |
| *Poa laxa* | 0.07 | 0.023 | 0.23 | ba | 0.041 | 56.21 | 42.7 /s | 42.7 /s | 0.083 | -13.541 | 2607.7 |
| *Primula glutinosa* | 0.06 | 0.031 | 0.19 | n | 0.047 | 58.87 | 17.8 /s | 5.2 /f | 0.019 | 0 | 2564.5 |
| *Ranunculus glacialis* | 0.07 | 0.020 | 0.68 | h | 0.020 | 57.18 | 10.7 /f | 10.7 /f | 0.032 | -12.019 | 2433.3 |
| *Ranunculus villarsii* | 0.17 | 0.094 | 1.95 | h | 0.010 | 50.75 | 27.3 /f | 27.3 /f | 0.182 | -11.741 | 2224.3 |
| *Saxifraga bryoides* | 0.04 | 0.029 | 0.03 | n | 0.155 | 74.65 | 47.0 /f | 47.0 /f | 0.005 | 0 | 3510 |
| *Scorzoneroides helvetica* | 0.15 | 0.073 | 1.61 | e | 0.012 | 45.52 | 43.1 /s | 43.1 /s | 0.274 | -11.033 | 2031.7 |
| *Sedum alpestre* | 0.02 | 0.028 | 0.02 | n | 0.189 | 75.81 | 72.5 /f | 72.5 /f | 0.018 | 0 | 3454.3 |
| *Sibbaldia procumbens* | 0.02 | 0.040 | 0.43 | n | 0.027 | 48.62 | 3.2 /f | 3.2 /f | 0.084 | 0 | 2339.3 |
| *Solidago virgaurea subsp. minuta* | 0.18 | 0.113 | 0.84 | e | 0.018 | 52.12 | 341.5 /s | 36.8 /i | 0.14 | -8.827 | 2239.5 |
| *Trifolium badium* | 0.13 | 0.095 | 1.41 | n | 0.013 | 34.11 | 40.3 /i | 40.3 /i | 0.212 | 0 | 1805.7 |
| *Vaccinium myrtillus* | 0.12 | 0.111 | 0.27 | n | 0.037 | 54.22 | 19.4 /f | 19.4 /f | 0.026 | 0 | 2524.1 |
| *Vaccinium vitis-idaea* | 0.07 | 0.090 | 0.42 | n | 0.028 | 48.89 | 6.3 /f | 6.3 /f | 0.008 | 0 | 2301.4 |
| *Veronica alpina* | 0.06 | 0.041 | 0.04 | n | 0.128 | 73.09 | 351.7 /s | 92.3 /f | 0.018 | 0 | 3352.4 |
| *Veronica bellidioides* | 0.10 | 0.046 | 0.12 | n | 0.064 | 64.01 | 289.4 /s | 48.4 /f | 0.093 | -10.221 | 2855.3 |

**H0** – seed release height (m): the straight distances from the base of the flowering shoot to the most distal point of the inflorescence measured for the highest inflorescence of a target individual averaged across target individuals.

**h** – vegetation height (m): the vegetative height (i.e., the height of maximum leaf density) of the vegetation in the 20x20 cm neighbourhood of a target individual, determined as the species cover-weighted mean of the tallest individual of each species, averaged across all target individuals. Cover was assessed according to abundance classes (< 1, 1-3, 3-5, 5-15, 15-25, 25-50, 50-75, 75-100 %) and transformed to the class means (0.5,2,4,10,20,37.5,62.5,87.5) for weighting. Dead leaves were considered only when attached to a living ramet.

**SM** – seed mass (mg) of a single seed measured as the mean of 100 seeds per species.

**SS** – seed surface structure was classified from collected seeds of all species following Römermann et al. (2005) as hooks [h], elongated appendages [e], flat appendages [f], balloon structures [ba] and no appendages [n]. For the berries of *Vaccinium* species we assumed no appendage as there is no class provided for fleshy fruits.

**GS** – probability to survive the gut passage of a large mammal (the chamois: *Rupicapra rupicapra*) as calculated from the seed mass by the regression equation in Mouissie (2004).

**DR** – hourly detachment rate (%) of seeds from chamois fur; assumed to be equal to the mean of the detachment rates from sheep and cattle fur as calculated from the seed mass and surface structure by the regression equations in Römermann et al. (2005).

**n_seeds_o** – number of seeds counted for a species-specific reproductive unit (flower [f], inflorescence [i] – i.e., corymb for Asteraceae, flower head for Fabaceae, catkin for Salicaceae, umbel for Apiaceae – or stalk [s]) averaged across 10 individual plants (one reproductive unit each) per species collected in the field. For some species collected material did not allow to derive reliable assessments of the seed yield (due to dispersal of seeds before collecting, pest infestation, etc.). In these cases, the counted values were replaced by literature data derived from LEDA3 for *Geranium sylvaticum, Luzula spicata, Trifolium badium* and *Vaccinium vitis-idaea*; and from ECOFLORA (http://ecoflora.org.uk/) for *Vaccinium myrtillus*.

**n_seeds_m** – number of seeds for the species-specific reproductive unit (flower [f], inflorescence [i] or stalk [s]). In case of having a different reproductive unit compared to n_seeds_o, values were adjusted based on the number of counted reproductive units (i.e., averaged for all reproductive target individuals of a species).

**Germ_rate** – germination rate calculated from the number of observed seedlings divided by the number of sown seeds in germination experiments. See Methods section “Data on germination, seed yield and dispersal” for details.

**Wind_disp** – wind dispersal value, calculated as log base 10 of the probability of a seed to disperse between 20 and 20.1 m using the wind kernel. See Methods section “Data on germination, seed yield and dispersal” for details..

**Animal_disp** – animal dispersal value representing the distance in meters at which 99% of the seeds are dispersed using the aggregated zoochoric dispersal kernel that includes endozhoochory and exozoochory. See Methods section “Data on germination, seed yield and dispersal” for details.

Appendix Table 2. Variable importance values of environmental predictors used in the random forest model component of the ensemble SDM.

| | carbon | | DEM_1 | | MAT | | pH | | SLP_3 | | SLR_3 | | SNW | | TPI_3 | | TWI_3 | | VRM_3 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **species** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** | **m_vi** | **sd_vi** |
| *A. moschata* | 0.0372 | 0.0029 | 0.0346 | 0.0022 | 0.0690 | 0.0054 | 0.0245 | 0.0028 | 0.0111 | 0.0009 | 0.0215 | 0.0018 | 0.0053 | 0.0011 | 0.0067 | 0.0008 | 0.0045 | 0.0007 | 0.0048 | 0.0008 |
| *A. agrostiflora* | 0.0114 | 0.0012 | 0.0140 | 0.0014 | 0.0096 | 0.0007 | 0.0096 | 0.0007 | 0.0096 | 0.0012 | 0.0028 | 0.0009 | 0.0069 | 0.0012 | 0.0062 | 0.0008 | 0.0055 | 0.0007 | 0.0033 | 0.0007 |
| *A. alpina* | 0.0283 | 0.0026 | 0.0267 | 0.0022 | 0.0216 | 0.0013 | 0.0113 | 0.0011 | 0.0120 | 0.0011 | 0.0084 | 0.0009 | 0.0153 | 0.0014 | 0.0069 | 0.0013 | 0.0058 | 0.0012 | 0.0056 | 0.0011 |
| *A. rupestris* | 0.0930 | 0.0060 | 0.0669 | 0.0028 | 0.0415 | 0.0052 | 0.0152 | 0.0028 | 0.0058 | 0.0013 | 0.0109 | 0.0019 | 0.0257 | 0.0033 | 0.0051 | 0.0014 | 0.0066 | 0.0018 | 0.0024 | 0.0012 |
| *A. alpinum* | 0.0450 | 0.0048 | 0.0438 | 0.0025 | 0.1080 | 0.0054 | 0.0330 | 0.0032 | 0.0076 | 0.0007 | 0.0052 | 0.0011 | 0.0177 | 0.0018 | 0.0043 | 0.0007 | 0.0153 | 0.0013 | 0.0074 | 0.0012 |
| *A. versicolor* | 0.0602 | 0.0033 | 0.0171 | 0.0013 | 0.0152 | 0.0009 | 0.0426 | 0.0032 | 0.0081 | 0.0011 | 0.0038 | 0.0003 | 0.0211 | 0.0016 | 0.0059 | 0.0013 | 0.0077 | 0.0011 | 0.0043 | 0.0007 |
| *C. curvula* | 0.0532 | 0.0029 | 0.0729 | 0.0038 | 0.0500 | 0.0030 | 0.0448 | 0.0027 | 0.0063 | 0.0007 | 0.0244 | 0.0025 | 0.0101 | 0.0009 | 0.0030 | 0.0004 | 0.0074 | 0.0011 | 0.0024 | 0.0003 |
| *C. sempervirens* | 0.0417 | 0.0021 | 0.0281 | 0.0019 | 0.0269 | 0.0016 | 0.0115 | 0.0009 | 0.0086 | 0.0010 | 0.0062 | 0.0009 | 0.0107 | 0.0011 | 0.0012 | 0.0002 | 0.0033 | 0.0007 | 0.0023 | 0.0005 |
| *C. uniflorum* | 0.0352 | 0.0017 | 0.0358 | 0.0019 | 0.0488 | 0.0027 | 0.0287 | 0.0018 | 0.0070 | 0.0007 | 0.0099 | 0.0010 | 0.0104 | 0.0012 | 0.0064 | 0.0008 | 0.0081 | 0.0011 | 0.0091 | 0.0006 |
| *C. aurea* | 0.0027 | 0.0005 | 0.0035 | 0.0003 | 0.0039 | 0.0004 | 0.0026 | 0.0005 | 0.0007 | 0.0003 | 0.0021 | 0.0003 | 0.0020 | 0.0002 | 0.0004 | 0.0002 | 0.0024 | 0.0004 | 0.0002 | 0.0001 |
| *D. cespitosa* | 0.0144 | 0.0019 | 0.0241 | 0.0014 | 0.0113 | 0.0007 | 0.0062 | 0.0012 | 0.0052 | 0.0009 | 0.0048 | 0.0008 | 0.0067 | 0.0013 | 0.0022 | 0.0004 | 0.0138 | 0.0016 | 0.0022 | 0.0003 |
| *F. nigrescens* | 0.0017 | 0.0005 | 0.0127 | 0.0015 | 0.0071 | 0.0015 | 0.0010 | 0.0005 | 0.0022 | 0.0003 | 0.0021 | 0.0005 | 0.0005 | 0.0002 | 0.0009 | 0.0004 | 0.0013 | 0.0004 | 0.0015 | 0.0003 |
| *F. nigricans* | 0.0202 | 0.0016 | 0.0224 | 0.0008 | 0.0168 | 0.0014 | 0.0118 | 0.0011 | 0.0081 | 0.0006 | 0.0076 | 0.0009 | 0.0046 | 0.0003 | 0.0070 | 0.0009 | 0.0066 | 0.0010 | 0.0025 | 0.0005 |
| *G. sylvaticum* | 0.0050 | 0.0012 | 0.0053 | 0.0007 | 0.0014 | 0.0006 | 0.0007 | 0.0006 | 0.0032 | 0.0007 | 0.0015 | 0.0005 | 0.0025 | 0.0006 | 0.0023 | 0.0004 | 0.0025 | 0.0007 | 0.0025 | 0.0004 |
| *G. montanum* | 0.0193 | 0.0016 | 0.0260 | 0.0013 | 0.0352 | 0.0015 | 0.0230 | 0.0014 | 0.0118 | 0.0017 | 0.0207 | 0.0012 | 0.0103 | 0.0012 | 0.0041 | 0.0011 | 0.0061 | 0.0008 | 0.0059 | 0.0008 |
| *G. reptans* | 0.0096 | 0.0012 | 0.0108 | 0.0011 | 0.0058 | 0.0007 | 0.0144 | 0.0013 | 0.0030 | 0.0003 | 0.0026 | 0.0003 | 0.0079 | 0.0010 | 0.0021 | 0.0006 | 0.0010 | 0.0003 | 0.0009 | 0.0003 |
| *G. supinum* | 0.0551 | 0.0030 | 0.0782 | 0.0053 | 0.0553 | 0.0052 | 0.0062 | 0.0008 | 0.0118 | 0.0011 | 0.0132 | 0.0018 | 0.0590 | 0.0037 | 0.0127 | 0.0015 | 0.0100 | 0.0016 | 0.0041 | 0.0008 |
| *H. alpina* | 0.0403 | 0.0018 | 0.0285 | 0.0022 | 0.0203 | 0.0015 | 0.0354 | 0.0018 | 0.0078 | 0.0007 | 0.0065 | 0.0007 | 0.0126 | 0.0012 | 0.0053 | 0.0005 | 0.0044 | 0.0005 | 0.0022 | 0.0005 |
| *J. trifidus* | 0.0588 | 0.0067 | 0.0227 | 0.0024 | 0.0134 | 0.0024 | 0.0570 | 0.0078 | 0.0004 | 0.0005 | 0.0039 | 0.0008 | 0.0066 | 0.0009 | 0.0013 | 0.0006 | 0.0012 | 0.0008 | 0.0000 | 0.0004 |
| *K. myosuroides* | 0.0153 | 0.0015 | 0.0183 | 0.0013 | 0.0121 | 0.0009 | 0.0084 | 0.0011 | 0.0067 | 0.0008 | 0.0077 | 0.0008 | 0.0176 | 0.0016 | 0.0052 | 0.0005 | 0.0040 | 0.0007 | 0.0035 | 0.0005 |
| *L. alpina* | 0.0664 | 0.0048 | 0.0932 | 0.0038 | 0.0340 | 0.0022 | 0.0065 | 0.0013 | 0.0129 | 0.0022 | 0.0120 | 0.0013 | 0.0169 | 0.0017 | 0.0043 | 0.0004 | 0.0067 | 0.0011 | 0.0044 | 0.0015 |
| *L. alpino-pilosa* | 0.0151 | 0.0015 | 0.0248 | 0.0014 | 0.0170 | 0.0012 | 0.0143 | 0.0010 | 0.0033 | 0.0007 | 0.0082 | 0.0005 | 0.0180 | 0.0015 | 0.0041 | 0.0006 | 0.0108 | 0.0011 | 0.0052 | 0.0004 |
| *L. lutea* | 0.0142 | 0.0013 | 0.0096 | 0.0011 | 0.0093 | 0.0006 | 0.0108 | 0.0019 | 0.0014 | 0.0003 | 0.0037 | 0.0007 | 0.0046 | 0.0005 | 0.0008 | 0.0004 | 0.0026 | 0.0008 | 0.0091 | 0.0018 |
| *L. spicata* | 0.0502 | 0.0027 | 0.0378 | 0.0020 | 0.0300 | 0.0012 | 0.0226 | 0.0018 | 0.0081 | 0.0010 | 0.0163 | 0.0018 | 0.0107 | 0.0009 | 0.0033 | 0.0006 | 0.0102 | 0.0012 | 0.0057 | 0.0006 |
| *M. adonidifolia* | 0.0582 | 0.0028 | 0.0149 | 0.0019 | 0.0257 | 0.0019 | 0.0230 | 0.0012 | 0.0012 | 0.0003 | 0.0039 | 0.0006 | 0.0252 | 0.0024 | 0.0054 | 0.0007 | 0.0042 | 0.0005 | 0.0017 | 0.0005 |
| *N. stricta* | 0.0191 | 0.0017 | 0.0274 | 0.0033 | 0.0268 | 0.0023 | 0.0141 | 0.0020 | 0.0024 | 0.0005 | 0.0075 | 0.0009 | 0.0074 | 0.0011 | 0.0012 | 0.0005 | 0.0013 | 0.0005 | 0.0018 | 0.0005 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *O. disticha* | 0.0253 | 0.0017 | 0.0300 | 0.0024 | 0.0740 | 0.0044 | 0.0274 | 0.0020 | 0.0030 | 0.0005 | 0.0066 | 0.0008 | 0.0145 | 0.0020 | 0.0026 | 0.0005 | 0.0022 | 0.0005 | 0.0036 | 0.0004 |
| *O. digyna* | 0.0058 | 0.0008 | 0.0071 | 0.0010 | 0.0066 | 0.0006 | 0.0034 | 0.0005 | 0.0015 | 0.0002 | 0.0036 | 0.0005 | 0.0050 | 0.0007 | 0.0018 | 0.0003 | 0.0017 | 0.0003 | 0.0014 | 0.0003 |
| *P. vivipara* | 0.0728 | 0.0056 | 0.0432 | 0.0023 | 0.0282 | 0.0032 | 0.0224 | 0.0021 | 0.0043 | 0.0007 | 0.0085 | 0.0012 | 0.0143 | 0.0017 | 0.0036 | 0.0010 | 0.0076 | 0.0014 | 0.0017 | 0.0005 |
| *P. hemisphaericum* | 0.0338 | 0.0021 | 0.0282 | 0.0031 | 0.0264 | 0.0017 | 0.0394 | 0.0023 | 0.0171 | 0.0015 | 0.0075 | 0.0010 | 0.0160 | 0.0024 | 0.0099 | 0.0012 | 0.0122 | 0.0014 | 0.0054 | 0.0008 |
| *P. alpina* | 0.0390 | 0.0037 | 0.0213 | 0.0015 | 0.0291 | 0.0022 | 0.0173 | 0.0031 | 0.0159 | 0.0021 | 0.0054 | 0.0012 | 0.0258 | 0.0016 | 0.0063 | 0.0011 | 0.0065 | 0.0015 | 0.0048 | 0.0011 |
| *P. laxa* | 0.0258 | 0.0013 | 0.0435 | 0.0029 | 0.0279 | 0.0022 | 0.0125 | 0.0016 | 0.0047 | 0.0004 | 0.0041 | 0.0005 | 0.0055 | 0.0004 | 0.0016 | 0.0004 | 0.0033 | 0.0003 | 0.0030 | 0.0005 |
| *P. glutinosa* | 0.0251 | 0.0013 | 0.0279 | 0.0017 | 0.0431 | 0.0031 | 0.0141 | 0.0013 | 0.0064 | 0.0006 | 0.0047 | 0.0009 | 0.0105 | 0.0012 | 0.0037 | 0.0007 | 0.0044 | 0.0006 | 0.0025 | 0.0005 |
| *R.s glacialis* | 0.0066 | 0.0010 | 0.0151 | 0.0009 | 0.0108 | 0.0010 | 0.0017 | 0.0004 | 0.0044 | 0.0004 | 0.0045 | 0.0004 | 0.0025 | 0.0004 | 0.0021 | 0.0004 | 0.0036 | 0.0007 | 0.0017 | 0.0003 |
| *R. villarsii* | 0.0232 | 0.0015 | 0.0521 | 0.0024 | 0.0687 | 0.0040 | 0.0168 | 0.0023 | 0.0043 | 0.0004 | 0.0082 | 0.0011 | 0.0137 | 0.0019 | 0.0052 | 0.0006 | 0.0157 | 0.0011 | 0.0043 | 0.0008 |
| *S. bryoides* | 0.0493 | 0.0030 | 0.0610 | 0.0033 | 0.0714 | 0.0039 | 0.0294 | 0.0030 | 0.0074 | 0.0010 | 0.0098 | 0.0008 | 0.0106 | 0.0010 | 0.0058 | 0.0006 | 0.0059 | 0.0007 | 0.0071 | 0.0007 |
| *S. helvetica* | 0.0389 | 0.0022 | 0.0449 | 0.0025 | 0.0651 | 0.0026 | 0.0561 | 0.0037 | 0.0134 | 0.0014 | 0.0087 | 0.0008 | 0.0087 | 0.0011 | 0.0054 | 0.0008 | 0.0084 | 0.0012 | 0.0045 | 0.0006 |
| *S. alpestre* | 0.0310 | 0.0031 | 0.0317 | 0.0039 | 0.0270 | 0.0036 | 0.0123 | 0.0011 | 0.0035 | 0.0005 | 0.0095 | 0.0022 | 0.0325 | 0.0030 | 0.0030 | 0.0006 | 0.0045 | 0.0009 | 0.0019 | 0.0005 |
| *S. procumbens* | 0.0152 | 0.0013 | 0.0257 | 0.0019 | 0.0185 | 0.0015 | 0.0139 | 0.0009 | 0.0047 | 0.0004 | 0.0101 | 0.0012 | 0.0116 | 0.0015 | 0.0070 | 0.0007 | 0.0069 | 0.0009 | 0.0074 | 0.0007 |
| *S. minuta* | 0.0092 | 0.0008 | 0.0130 | 0.0010 | 0.0103 | 0.0008 | 0.0056 | 0.0009 | 0.0051 | 0.0006 | 0.0048 | 0.0004 | 0.0036 | 0.0006 | 0.0029 | 0.0003 | 0.0022 | 0.0005 | 0.0048 | 0.0006 |
| *T. badium* | 0.0098 | 0.0011 | 0.0146 | 0.0008 | 0.0080 | 0.0008 | 0.0129 | 0.0010 | 0.0037 | 0.0006 | 0.0057 | 0.0006 | 0.0044 | 0.0004 | 0.0044 | 0.0004 | 0.0037 | 0.0006 | 0.0022 | 0.0007 |
| *V. myrtillus* | 0.0240 | 0.0016 | 0.0185 | 0.0011 | 0.0069 | 0.0008 | 0.0145 | 0.0014 | 0.0024 | 0.0003 | 0.0036 | 0.0003 | 0.0051 | 0.0007 | 0.0008 | 0.0004 | 0.0042 | 0.0005 | 0.0010 | 0.0002 |
| *V. vitis-idaea* | 0.0205 | 0.0017 | 0.0178 | 0.0011 | 0.0097 | 0.0009 | 0.0154 | 0.0009 | 0.0041 | 0.0005 | 0.0037 | 0.0005 | 0.0172 | 0.0008 | 0.0038 | 0.0004 | 0.0065 | 0.0005 | 0.0027 | 0.0003 |
| *V. alpina* | 0.0347 | 0.0030 | 0.0251 | 0.0025 | 0.0476 | 0.0036 | 0.0141 | 0.0015 | 0.0030 | 0.0009 | 0.0083 | 0.0010 | 0.0409 | 0.0025 | 0.0040 | 0.0008 | 0.0116 | 0.0016 | 0.0038 | 0.0008 |
| *V. bellidioides* | 0.0093 | 0.0010 | 0.0130 | 0.0011 | 0.0063 | 0.0008 | 0.0056 | 0.0005 | 0.0044 | 0.0006 | 0.0077 | 0.0004 | 0.0040 | 0.0005 | 0.0026 | 0.0005 | 0.0026 | 0.0004 | 0.0030 | 0.0005 |

**m_vi** – mean variable importance value for the specified predictor. The mean is taken across all 10 folds used to generate the random forest model for each species.

**sd_vi** – standard deviation of the variable importance value for the specified predictor. This value is taken across all 10 folds used to generate the random forest model for each species.

Descriptions and further information about each predictor used can be found in Table 1 of the Methods section.

Appendix Table 3. Ensemble SDM results and statistics for each species.

| *species* | *sensitivity* | *specificity* | *ens_TSS* | *occurences* |
|---|---|---|---|---|
| *Achillea moschata* | 0.7407 | 0.8595 | 0.6003 | 135 |
| *Agrostis agrostiflora* | 0.9615 | 0.6133 | 0.5749 | 104 |
| *Agrostis alpina* | 0.8343 | 0.7007 | 0.5350 | 169 |
| *Agrostis rupestris* | 0.8007 | 0.7312 | 0.5319 | 296 |
| *Anthoxanthum alpinum* | 0.8494 | 0.7953 | 0.6447 | 385 |
| *Avenula versicolor* | 0.8587 | 0.7601 | 0.6187 | 283 |
| *Carex curvula subsp. curvula* | 0.9078 | 0.8555 | 0.7633 | 141 |
| *Carex sempervirens* | 0.8298 | 0.8468 | 0.6766 | 188 |
| *Cerastium uniflorum* | 0.9194 | 0.8323 | 0.7517 | 186 |
| *Crepis aurea* | 0.9773 | 0.6432 | 0.6205 | 44 |
| *Deschampsia cespitosa subsp. cespitosa* | 0.8112 | 0.8143 | 0.6255 | 143 |
| *Festuca nigrescens* | 0.8529 | 0.8415 | 0.6944 | 34 |
| *Festuca nigricans* | 0.8667 | 0.7102 | 0.5769 | 150 |
| *Geranium sylvaticum* | 0.9063 | 0.8152 | 0.7214 | 64 |
| *Geum montanum* | 0.8758 | 0.8146 | 0.6904 | 153 |
| *Geum reptans* | 0.9833 | 0.8023 | 0.7856 | 60 |
| *Gnaphalium supinum* | 0.9261 | 0.7003 | 0.6264 | 230 |
| *Homogyne alpina* | 0.8869 | 0.8379 | 0.7248 | 274 |
| *Juncus trifidus* | 0.9444 | 0.6127 | 0.5572 | 162 |
| *Kobresia myosuroides* | 0.7600 | 0.8947 | 0.6547 | 75 |
| *Leucanthemopsis alpina* | 0.8390 | 0.6520 | 0.4910 | 354 |
| *Luzula alpino-pilosa* | 0.7626 | 0.7180 | 0.4806 | 198 |
| *Luzula lutea* | 0.8571 | 0.6631 | 0.5202 | 112 |
| *Luzula spicata* | 0.7572 | 0.8385 | 0.5957 | 173 |
| *Mutellina adonidifolia* | 0.8626 | 0.8087 | 0.6713 | 211 |
| *Nardus stricta* | 0.9459 | 0.7436 | 0.6896 | 148 |
| *Oreochloa disticha* | 0.8952 | 0.8091 | 0.7043 | 105 |

| | | | | |
|---|---|---|---|---|
| *Oxyria digyna* | 0.9000 | 0.8857 | 0.7857 | 40 |
| *Persicaria vivipara* | 0.8997 | 0.6971 | 0.5968 | 329 |
| *Phyteuma hemisphaericum* | 0.7707 | 0.7704 | 0.5411 | 266 |
| *Poa alpina* | 0.6618 | 0.7549 | 0.4166 | 340 |
| *Poa laxa* | 0.8811 | 0.8509 | 0.7320 | 143 |
| *Primula glutinosa* | 0.9722 | 0.7442 | 0.7165 | 72 |
| *Ranunculus glacialis* | 0.8714 | 0.8610 | 0.7324 | 70 |
| *Ranunculus villarsii* | 0.9005 | 0.8072 | 0.7076 | 211 |
| *Saxifraga bryoides* | 0.8299 | 0.8179 | 0.6478 | 294 |
| *Scorzoneroides helvetica* | 0.8805 | 0.7214 | 0.6019 | 452 |
| *Sedum alpestre* | 0.8354 | 0.7710 | 0.6064 | 164 |
| *Sibbaldia procumbens* | 0.6757 | 0.7897 | 0.4654 | 74 |
| *Solidago virgaurea subsp. minuta* | 0.9100 | 0.7679 | 0.6779 | 100 |
| *Trifolium badium* | 0.9000 | 0.7260 | 0.6260 | 40 |
| *Vaccinium myrtillus* | 0.9032 | 0.8178 | 0.7210 | 124 |
| *Vaccinium vitis-idaea* | 0.9360 | 0.7750 | 0.7110 | 125 |
| *Veronica alpina* | 0.8131 | 0.7454 | 0.5586 | 198 |

**ens_TSS** – the TSS score of the ensemble model as a whole.

**occurrences** – the number of times this species was recorded as present across all logger plots.

Appendix Table 4. Pearson correlation table for the 10 predictors used in the ensemble SDM.

| | carbon | DEM_1 | MAT | pH | SLP_3 | SLR_3 | SNW | TPI_3 | TWI_3 | VRM_3 |
|---|---|---|---|---|---|---|---|---|---|---|
| **carbon** | 1.0000 | -0.6009 | 0.5440 | -0.6604 | 0.1552 | -0.2593 | -0.1228 | 0.0246 | 0.0284 | 0.0521 |
| **DEM_1** | -0.6009 | 1.0000 | -0.8364 | 0.4276 | 0.2928 | 0.4026 | -0.2698 | 0.2034 | -0.3917 | 0.2235 |
| **MAT** | 0.5440 | -0.8364 | 1.0000 | -0.4354 | -0.2239 | -0.0901 | 0.2800 | -0.2499 | 0.3724 | -0.3328 |
| **pH** | -0.6604 | 0.4276 | -0.4354 | 1.0000 | -0.1945 | 0.1697 | 0.0918 | 0.0374 | 0.0262 | -0.0015 |
| **SLP_3** | 0.1552 | 0.2928 | -0.2239 | -0.1945 | 1.0000 | -0.3856 | -0.3292 | -0.0571 | -0.3947 | 0.2199 |
| **SLR_3** | -0.2593 | 0.4026 | -0.0901 | 0.1697 | -0.3856 | 1.0000 | -0.1151 | 0.1445 | 0.0654 | -0.2136 |
| **SNW** | -0.1228 | -0.2698 | 0.2800 | 0.0918 | -0.3292 | -0.1151 | 1.0000 | -0.4899 | 0.4324 | -0.3357 |
| **TPI_3** | 0.0246 | 0.2034 | -0.2499 | 0.0374 | -0.0571 | 0.1445 | -0.4899 | 1.0000 | -0.3787 | 0.4451 |
| **TWI_3** | 0.0284 | -0.3917 | 0.3724 | 0.0262 | -0.3947 | 0.0654 | 0.4324 | -0.3787 | 1.0000 | -0.3680 |
| **VRM_3** | 0.0521 | 0.2235 | -0.3328 | -0.0015 | 0.2199 | -0.2136 | -0.3357 | 0.4451 | -0.3680 | 1.0000 |