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„Limited prospects to identify suitable unoccupied sites
for snowbed plant species using environmental
parameters.“

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Abstract

Identifying suitable unoccupied sites is relevant to understand if the distribution of a plant species is mainly determined by environmental conditions or rather by dispersal limitation. Although transplantation experiments can provide direct evidence if a site is suitable for a given plant species, indirect methods such as Species Distribution Models (SDMs) are supposed to be more advantageous as they are less laborious. However, studies comparing the performance of direct and indirect methods are scarce, especially those considering long-lived plant species.

The present work sets out to predict suitable unoccupied sites for four long-lived plant species (*Achillea atrata*, *Achillea clusiana*, *Arabis caerulea* and *Gnaphalium hoppeanum*) occurring in snowbed sites in the north-eastern Calcareous Alps of Austria, by means of models based on the following sets of environmental variables: i) abiotic factors (bioclimatic and topographic conditions); ii) parameters derived by species composition (mean Ellenberg indicator values); iii) a combination of the above mentioned variables. Model predictions were evaluated using seven performance traits obtained from a 4-years transplantation experiment carried out at the same sites.

Our results showed that models based on environmental variables have limited ability to predict suitable but unoccupied sites for snowbed species, as the number and identity of predicted sites varied largely among models. However, models relating parameters derived by species composition to the occurrence pattern of species showed a better fit than those based on abiotic factors as they integrate information about actual and past habitat conditions.

The predicted probability of occurrence showed only weak correspondence to long-term results from transplantation experiments. This result underlies the importance of integrating dispersal abilities in the model to predict the distribution of long-lived species in fragmented landscapes. We therefore suggest the use of variables describing the dispersal abilities of species (e.g. seed mass, seed number) for the determination if an unoccupied site is suitable. Our study offered valuable insights for predicting new suitable sites for rare plant species,

highlighting the necessity of embedding additional relevant factors in the models to obtain accurate predictions.

Introduction

The distribution of a plant species depends on the availability of environmentally suitable habitats (niche) and the probability of seeds reaching those sites (Pulliam 2000, Münzbergova and Herben 2005). Therefore a suitable habitat can be unoccupied because of dispersal limitations and, on the other hand, unsuitable habitats can be occupied by remnant populations when environmental conditions change due to extinction debt (Eriksson 1996, Kuussaari et al. 2009, Hylander and Ehrlén 2013). The identification of suitable unoccupied sites is hence necessary for the understanding of landscape dynamics and is used for conservation and restoration of endangered species and for management of invasive species (Elmendorf and Moore 2008).

The most convincing technique to prove if occupied or unoccupied sites are suitable is through experimental transplantations (Ehrlén and Eriksson 2000, Turnbull et al. 2000, Ehrlén et al. 2006, Moore and Elmendorf 2006, Dullinger and Hülber 2011, Hemrová and Münzbergová 2012). Although it may seem an easy task to sow seeds in the soil and check if they germinate, there are some issues to be considered. Firstly, for a successful establishment a plant has to complete a whole lifecycle, as population bottlenecks may occur in later life stages. So, when applying such experiments on plants, one has to observe the reproduction success in order to verify the site suitability, and such process may need several years (Turnbull et al. 2000, Ehrlén et al. 2006). Secondly, the success of germination and establishment is weather dependent and may vary between years. Thirdly, a negative performance due to demographic stochasticity may occur if an insufficient amount of seeds is utilized (Clark et al. 2007). Fourthly, there is a potential risk of introducing invasive species. Lastly, testing site suitability everywhere with transplantation experiments is too time consuming, costly and inefficient in terms of human resources employed.

A more efficient way to detect suitable but unoccupied sites is by means of indirect approaches. Indirect approaches commonly used in ecology are the so called species distribution models (SDMs, niche models) which predict the probability of occurrence of species in a spatially explicit manner (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Carlson et al. 2013). The predicted probability for species occurrence needs to be transformed into suitable/unsuitable and compared with the occurrence in the sites to identify those sites that are suitable but unoccupied. The quality of models depends on an appropriate selection of model parameters, i.e. environmental variables with high predictive power. Widely used variables are abiotic predictors obtained from large-scale maps and databases. The abiotic predictors usually include bioclimatic and topographic conditions and in rarer cases parameters describing geology and soil (Ehrlén and Eriksson 2000). Another way to identify suitable sites is based on species composition of sites as co-occurring species have similar environmental requirements (Dupre and Diekmann 1998). In spite of the large amount of collected data on community composition, to date only a few studies have explored the use of species assemblages for the development of models, predicting species distribution (Münzbergová and Herben 2004). In these models biotic interactions might be included to some degree as the species composition is co-determined by competitive and facilitative effects e.g. mediated by accumulating litter (Niederfriniger Schlag and Erschbamer 2000). Another advantage is that temporarily fluctuating environmental factors, such as ground water level or light are integrated (Dupre and Diekmann 1998). In contrast, co-occurring species may be influenced by dispersal limitations in the same way as target species and therefore the method has limits in predicting suitable but unoccupied sites.

A few studies compared the predictive performance of models based on species composition vs models based on abiotic factors and used transplantation experiments as a reference for model performances validation (Ehrlén et al. 2006, Moore and Elmendorf 2006, Hemrová and Münzbergová 2012). In particular, Hemrova and Münzbergova (2012) employed a short-lived species to test the performance of SDMs using long-term transplantation experiments as reference, suggesting that SDMs embedding species composition fit better than SDMs based on environmental predictors only. The use of short-lived species in transplantation experiments has the advantage of requiring less time to detect the reproduction success. Short-lived species are better indicators of environmental conditions as they give a faster

response to habitats modifications. On the other hand, it is a common knowledge that long-lived species like *Festuca* spp. or *Silene acaulis* can survive for longer periods under unsuitable conditions forming remnant populations, which can act as false presence in the model predictions. This reason may explain the scarcity of transplantation experiments employing long-lived species. On the other hand, the persistence of long-lived species may be an advantage as they have a lower probability for stochastic extinctions in a suitable habitat (Eriksson 1996). Yet, if long-lived plants are also highly specialized, they represent the core community of habitats and thus advancing the knowledge on their environmental requirements is of utmost importance.

At present, no study has validated yet the predictive power of direct against indirect approaches in detecting suitable but unoccupied sites for alpine long-lived species. To fill this gap, we predicted the probability of occurrence for four long-lived, clonally propagating species (*Achillea atrata*, *Achillea clusiana*, *Arabis caerulea* and *Gnaphalium hoppeanum*) characterized by a different occurrence frequency and present in isolated alpine habitat patches (snowbed patches). Predictions were made by relating species occurrence to abiotic factors (i) or parameters obtained from species composition (ii) or a combination of all factors (iii). After running the three types of models, we evaluated the predicted probability of occurrence using data on plant performance derived from extensive transplantation experiments (Dullinger and Hülber 2011). We aimed to ascertain whether it is possible to identify suitable but unoccupied sites for long-lived species using indirect approaches. In particular we asked:

- (i) Do models based on species composition predict suitable unoccupied sites better than those based on abiotic factors? Is there a positive effect when combining both groups of factors in a single model?
- (ii) Do the model ability for identification differ among species and performance traits derived from transplantation experiments?
- (iii) Do our three models predict the same suitable unoccupied habitat sites?

Methods

Study area

Data were collected on four different mountain ranges (Mt. Schneeberg, Mt. Rax, Mt. Schneealpe, and Mt. Hochschwab, 15° to 16°E, and 47°30' to 47°50'N) of the northeastern Calcareous Alps of Austria. All four mountains have a similar bedrock substrate (Mesozoic limestone and dolomites) and are geomorphologically characterized by displaced plateaus of different altitudes. The climatic conditions are temperate humid. Mean annual temperature is approximately 0 – 2 °C and the annual precipitation between 1500 and 2500 mm in the summit region. The upper subalpine zone is mainly covered by a krummholz belt of prostrate pine *Pinus mugo* up to ca 1850 m a.s.l. Above the krummholz line, alpine grasslands and rock faces predominate. Within the grassland matrix, snowbed habitats are patchily distributed on sites with a particularly long lasting snow cover (~ 8 to 10 months on average). The snowbeds of the study area typically have a sparse vegetation cover (31% on average across all surveyed sites), and a high proportion of coarse scree material and rocks (49%). Organic and mineral soil horizons are shallow, if present, with the latter usually being of sandy texture. The species composition of these habitats is quite distinctive with small, rosette forming perennials representing the dominant life form (Englisch 1993)

Study species

Achillea atrata (Asteraceae), *Arabis caerulea* (Brassicaceae), *Achillea clusiana* (Asteraceae) and *Gnaphalium hoppeanum* (Asteraceae) are insect-pollinated, clonally growing and rosette forming perennial. All study species are restricted to snowbed habitats, with a subalpine to subnival distribution and are widespread on calcareous bedrock throughout the Alps, except for *A. clusiana* which is endemic to the northeastern-most Calcareous Alps.

Study design and data collection

To identify suitable unoccupied sites for the study species, we used a dataset with abiotic factors and a dataset with species composition. Abiotic factors for our sites were obtained from spatially explicit raster data (resolution of 20 m) of the study area describing topography (altitude, slope, erosion and wetness indices), micro-climate (degree days, solar radiation income for June, July and August, water balance in August topographically modified wind velocities, snow cover probability). To avoid collinearities we excluded degree days and solar radiation income for June and August. A correlation matrix and an overview on the abiotic factors employed are provided in the Appendix; a detailed description of how the predictors were calculated is provided in Dirnböck et al. (2003). In 2014 species composition was recorded in 131 sites (43 on Mt. Hochschwab, 33 on Mt. Rax, 31 on Mt. Schneealm and 24 on Mt. Schneeberg). We selected site positions such that vegetation cover and substrate conditions were representative for those prevailing within the snowbed (but avoided solid rocks and coarse scree material which are hardly colonizable by our study species). Selection was done from a distant point at the patch margin, which allowed an overview of the whole snowbed but not of the distribution of individual species. After localizing the site we recorded the coordinates with a hand-held GPS (Garmin e-trex). Each site was represented as an area of 20 x 20 m to match the spatial resolution of abiotic factors. We recorded all vascular plant species along two 20 x 1 m transect forming a cross fitted within the site. The number of occupied sites by the study species was variable (27 for *A. atrata*, 122 for *A. clusiana*, 10 for *A. caerulea* and 87 for *G. hoppeanum*). Based on the species composition we calculated mean Ellenberg indicator values for light, temperature, moisture, nutrients, soil and reaction (Ellenberg et al. 1992, Englisch 1999) for each habitat. Ellenberg indicator values for continentality were *a priori* excluded from the models because of the small extent of the study area. A moderate collinearity among light and temperature (correlation value = 0.62) was accepted and both variables were used in the models. A correlation matrix is provided in the Appendix.

From the total of 131 snowbeds, 54 (15 on Mt. Schneeberg, 15 on Mt. Rax, 14 on Mt. Hochschwab and 10 at Mt. Schneealpe) were used in a former 4-years transplantation experiment. Also in this case the number of occupied snowbeds varied among the study species (23 for *A. atrata*, 50 for *A. clusiana*, 8 for *A. caerulea* and 35 for *G. hoppeanum*).

Within each of these 54 sites, a plot of 3.0 x 2.5 m was localized and the corners permanently marked. The following seven performance traits were derived from data collected during repeated observation of transplanted seeds, juveniles and adult: Germination; Seedling, Juvenile and Adult survival; Juvenile and Adult growth; and flowering frequency of experimental plants transplanted from outside the study area into the snowbed patches. We used regression models regarding for the complex experimental design (spatial clustering and temporal dependencies) to predict the mean performance of individuals within a snowbed separately for each trait. A detailed description of the transplantation experiment can be found in Dullinger and Hülber (2011).

Data analysis

The probability of occurrence was calculated with a generalized linear model (GLM) and the occurrence of one study species as binomial distributed independent variable. As predictor variables we used abiotic factors in model **Abiot**, mean Ellenberg indicator values in model **Ellen** and both abiotic factors and mean Ellenberg values in the model **Full**. Variable selection for GLMs was based on comparing candidate models by means of the Akaike information criterion (AIC) using a combined forward and backward selection procedure as implemented in the function “step” in R (R Development Core Team 2008). The importance of individual predictor variables in the fitted GLMs is provided in Table 1. Each site was classified as suitable or unsuitable based on the predicted probability using the threshold value where the sum of sensitivity (i.e. the proportion of correctly predicted presences) and specificity (i.e. the proportion of correctly predicted absences) is maximized (Liu et al. 2005). The performance of each model was evaluated both by calculating the area under the receiver operating characteristic curve (AUC, Swets 1988) and by comparing the probability of occurrence with the seven performance traits derived from the transplantation experiments. Then, a further comparison between the models was done by averaging parameter estimates from those models whose difference for corrected Akaike values (AICc; Hurvich, 1995) was < 2 units and subsequently by computing Akaike weights (AICcWt) across all models (Burnham and Anderson 2002). These weights express the level of support for each model.

For the sites where the transplantation experiments were carried out we tested the model predictions vs performance traits using a linear model. The fitted values of performance for each experiment were used as the dependent variable, while the predicted probability of occurrence from the models Abiot, Ellen and Full were used as independent variables. For all study species, we tested the three models using all selected performance traits (Table 2). Furthermore, the occurrence of the study species in the experimental plots were regressed against the performance traits using a GLM. All analyses were performed in R 3.2.2 (R Development Core Team 2015).

Results

For all species it was possible to develop the three models (Abiot, Ellen and Full) for predicting suitable habitat sites. The importance of the different factors used to fit GLMs varied largely among species (Table 1). There was no dominant single factor explaining the occurrence of all four study species. Erosion, water balance index and wetness index were not significantly related to the species occurrence (Table 1). All mean Ellenberg indicator values were significant for at least one species; in particular, temperature was strongly positively related to the occurrence of *A. clusiana* but strongly negatively related to the occurrence of *A. caerulea* (Table 1). In the model Full, only *A. clusiana* was explained by Ellenberg values alone, while the other study species were related to at least two of the abiotic factors, although not always significantly (Table 1).

All models revealed reasonable AUC values ($AUC > 0.7$, Table 2), except the model Abiot for *A. clusiana* ($AUC = 0.61$) and the model Ellen for *G. hoppeanum* ($AUC = 0.57$). A very good discrimination capacity was indicated for models of *A. caerulea* ($AUC \geq 0.94$). Only *G. hoppeanum* had lower AUC value for the model Ellen than the one for the model Abiot. Model Full showed slightly higher AUC values for all four study species.

Looking at corrected Akaike weights (AICcWt; Table 2), only for *G. hoppeanum* the model Abiot was more supported than the model Ellen. Furthermore, the performance of the model Full was higher for *A. caerulea* and *G. hoppeanum* (Table 2). Interestingly, for three study species the most supported models (those with the highest AICcWt) corresponded to

an average number of suitable unoccupied sites, except for *G. hoppeanum* where the model with the highest AICcWt was associated to the lowest number of suitable unoccupied sites (Table 2). On the other hand, the least supported models identified the highest number of suitable unoccupied sites. Focusing on the most supported models, 7.4% of unoccupied sites were predicted as suitable for *A. caerulea* (Full), 9.0% for *A. clusiana* (Ellen), 17.4% for *G. hoppeanum* (Full) and 19.2% for *A. atrata* (Ellen) respectively (Table 2).

For all study species not only the predicted number of suitable unoccupied sites (Table 2, Fig. 1) but also their identity (Fig. 2) varied largely among the models. For three species (*A. atrata*, *A. clusiana* and *G. hoppeanum*), all the suitable unoccupied sites predicted by the model Full coincided with those selected either by models Abiot or Ellen, according to their performance. Model Full predicted 4 unshared suitable unoccupied sites for *A. caerulea* only (Fig. 2). The performance traits derived from transplantation experiments proved unsuitable for testing the model predictions, as suggested by the low adjusted R^2 values (Table 2).

For both models Ellen and Full for *A. atrata* and model Abiot for *G. hoppeanum* no significant relationships with any performance trait were found (Table 2). All the other models were significantly related to at least one performance trait. Generally, there was no simultaneous correspondence between the performance traits and both model Abiot and model Ellen, if we exclude *A. caerulea* for Juvenile growth, Adult survival and Reproduction and *A. clusiana* for Adult survival (Table 2).

The occurrence of the four study species was weakly related to performance traits. In fact, only for *A. caerulea* we found significantly higher traits in occupied sites, namely Adult survival ($p = 0.01$, coef. = 16.58 ± 6.64) and Juvenile growth ($p = 0.01$, coef. = 7.9 ± 3.09), while for all the other cases no positive association was found.

Table 1 - Habitat characteristics used in the three models (Abiot - abiotic factors, Ellen - Ellenberg indicator values and Full - a combination of Abiot and Ellen's parameters) to predict suitable sites for four snowbed species. Coefficients (coef, together with their standard errors - SE), z- value and p- value are shown for variables included in the model after a stepwise selection algorithm (function "step" in R, R Development Core Team 2008).

Habitat characteristics	<i>Achillea atrata</i>			<i>Achillea clusiana</i>			<i>Arabis caerulea</i>			<i>Gnaphalium hoppeanum</i>		
	coef ± SE	z	p	coef ± SE	z	p	coef ± SE	z	p	coef ± SE	z	p
Model Abiot												
Abiotic factors												
Altitude	0.7±0.27	2.54	0.01	-0.51±0.35	-1.45	0.15	3.63±1.07	3.39	<0.01			
Slope Inclination							1.86±0.67	2.78	0.01			
Solar Radiation Income	-0.44±0.22	-1.96	0.05							1.24±0.31	4.03	<0.01
Water Balace August										0.47±0.27	1.76	0.08
Wetness Index										-0.36±0.21	-1.69	0.09
Wind speed	-0.4±0.28	-1.44	0.15							-0.71±0.25	-2.81	<0.01
Erosion							0.67±0.35	1.89	0.06			
Snow Cover Probability							2.91±1.01	2.88	<0.01			
Model Ellen												
Ellenberg indicator values												
Light	10.34±2.49	4.15	<0.01				-7.46±5.22	-1.43	0.15	1.48±1.01	1.47	0.14
Moisture	5.01±1.92	2.62	0.01									
Soil Reaction				2.28±0.82	2.77	0.01	7.06±2.66	2.66	0.01	0.73±0.48	1.51	0.13
Nutrients							7.16±2.90	2.47	0.01			
Temperature				21.05±6.53	3.22	<0.01	-23.19±8.44	-2.75	0.01			
Model Full												
Abiotic factors												
Altitude							5.59±2.45	2.28	0.02			
Slope Inclination							-2.17±1.24	-1.74	0.08			
Solar Radiation Income										1.37±0.32	4.24	<0.01
Water Balace August							-1.66±1.18	-1.41	0.16	0.64±0.29	2.18	0.03
Wetness Index												
Wind speed	-0.59±0.4	-1.47	0.14				-6±3.01	-2	0.05	-0.57±0.24	-2.41	0.02
Erosion												
Snow Cover Probability	-0.59±0.33	-1.77	0.08									
Ellenberg indicator values												
Light	10.96±2.61	4.21	<0.01				-19.24±9.65	-1.99	0.05			
Moisture	5.49±2.02	2.71	0.01									
Soil Reaction				2.28±0.82	2.77	0.01	13.84±5.23	2.64	0.01	1.23±0.57	2.17	0.03
Nutrients										2.72±1.31	2.08	0.04
Temperature				21.05±6.53	3.22	<0.01						

Table 2 – Comparison of Abiot, Ellen and Full models. The number of suitable unoccupied sites, AUC values, the number of parameters in fitted models (K), corrected Akaike information criterion (AICc), corrected Akaike Weights (AICcWt) and correspondence of model predictions with seven performance traits derived from transplantation experiments (Adjusted R² are shown only for significant relations with P < 0.05). Abbreviations: unoc. sites = unoccupied sites, Abiot = environmental based model, Ellen = species composition based model, Full = including variables from Ellen and Abiot; a dash indicates non-significant tests; highly significant relations (P < 0.001) are shown in bold.

Model	Suitable unoccupied sites	AUC	K	AICc	AICcWt	Germination	Seedling survival	Juvenile survival	Juvenile growth	Adult survival	Adult growth	Reproduction
<i>A. atrata</i>												
(104 unoc. sites)												
Abiot	34	0.71	3	131.14	0.00	-	-	-	-	-	0.12	-
Ellen	20	0.82	2	109.06	0.60	-	-	-	-	-	-	-
Full	8	0.83	4	109.84	0.40	-	-	-	-	-	-	-
<i>A. clusiana</i>												
(11 unoc. sites)												
Abiot	2	0.61	1	77.37	0.00	-	-	-	-	0.17	-	-
Ellen	1	0.88	2	59.81	0.50	-	-	-	0.10	0.16	0.06	-
Full	1	0.88	2	59.81	0.50	-	-	-	0.10	0.16	0.06	-
<i>A. caerulea</i>												
(121 unoc. sites)												
Abiot	16	0.94	4	47.85	0.01	-	-	0.12	0.26	0.08	-	0.22
Ellen	4	0.95	4	47.35	0.01	0.28	-	-	0.32	0.20	-	0.15
Full	9	0.98	6	37.78	0.99	0.09	-	-	0.36	0.19	-	0.22
<i>G. hoppeanum</i>												
(46 unoc. sites)												
Abiot	14	0.76	4	152.70	0.26	-	-	-	-	-	-	-
Ellen	33	0.57	2	172.64	0.00	-	-	0.06	0.16	0.08	0.15	-
Full	8	0.80	5	150.60	0.74	-	-	0.13	-	-	-	-

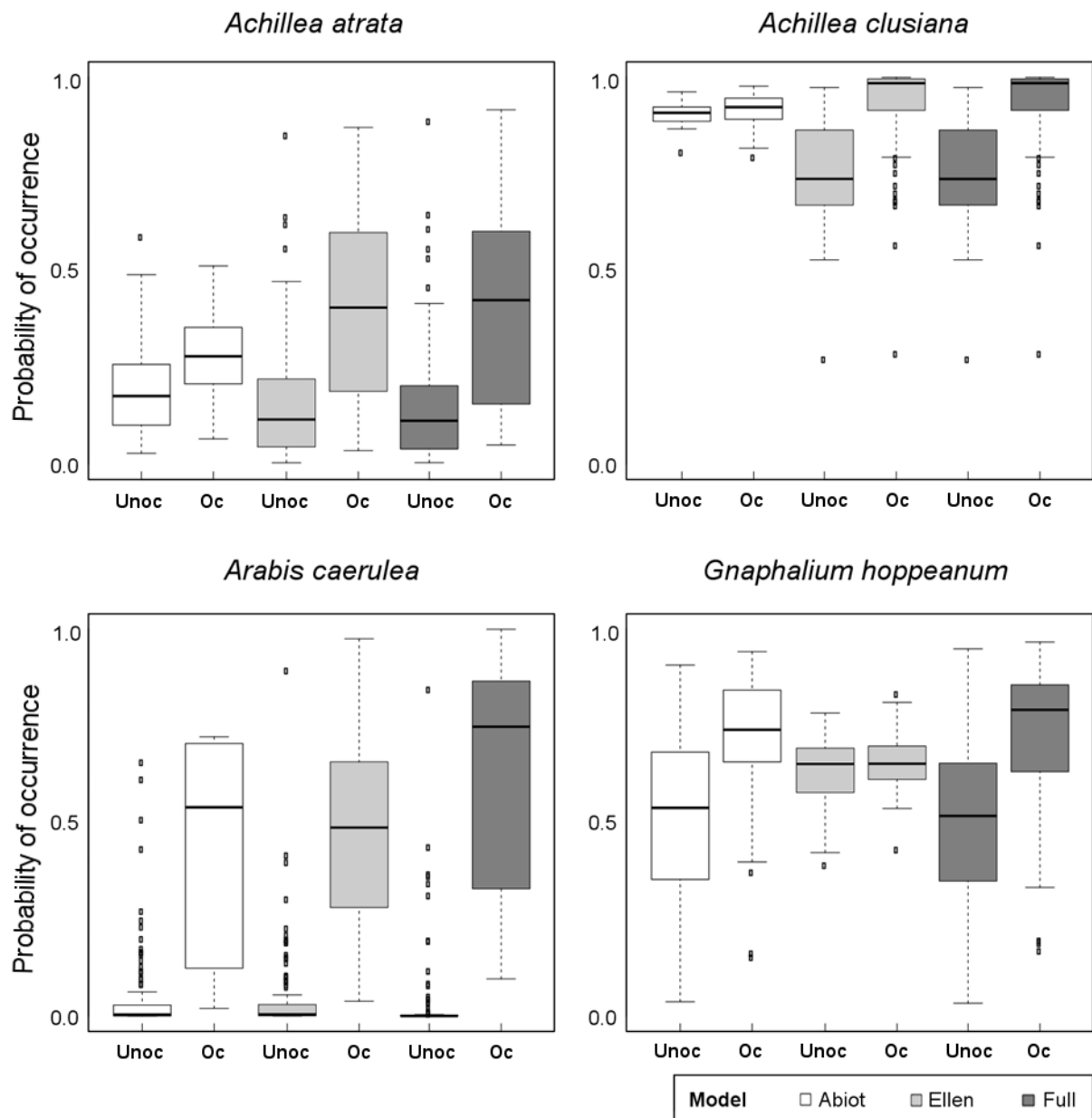


Fig. 1 – Probability of occurrence predicted for unoccupied (Unoc) or occupied (Oc) sites by the four study species according to different models: Abiot (using abiotic variables), Ellen (using Ellenberg indicator values) and Full (using combinations of habitat characteristics). Median, 25% and 75% quartiles are shown; whiskers indicate the 10% and 90% percentiles and dots are outliers.

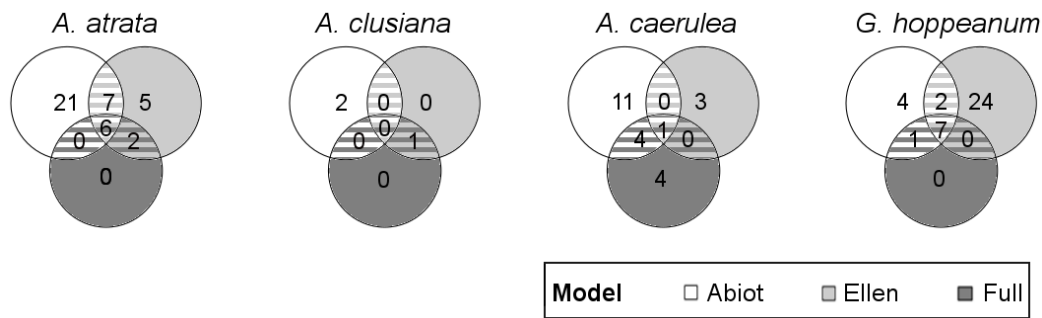


Fig. 2 – Number of suitable unoccupied sites predicted exclusively by one model, by two models and by all models. Striped areas indicate shared suitable unoccupied sites.

Discussion

Identifying suitable unoccupied sites is relevant to understand if the distribution of a plant species is determined mainly by environmental conditions or rather by dispersal limitation (Eriksson 1996, Ehrlén and Eriksson 2000, Guisan and Zimmermann 2000, Münzbergová and Herben 2005). Although detecting suitable unoccupied habitats is fundamental for conserving endangered species (Elmendorf and Moore 2008, Frei et al. 2011), there is still need of further investigation as to the methods that allow accurate predictions.

Generally, direct methods such as transplantation experiments provide clear evidence of habitat suitability through successful recruitment (Hemrová and Münzbergová 2012). However, using indirect methods to identify suitable habitats should be preferred over transplantation experiments due to their inefficiency in terms of both costs involved and time employed. Based on this assumption, our study explored the performances of three models (based on abiotic factors, or parameters obtained from species composition, or a combination of all factors) and compared them with a set of performance traits derived by transplantation experiments, in order to offer a comprehensive verification of the diverse approaches currently in use.

Overall, our results suggest that both abiotic factors and parameters derived from species composition show only limited capacity to identify suitable unoccupied sites for our long-lived study species. Nonetheless, in all cases higher probability of occurrence was predicted

for occupied sites compared to unoccupied sites. Also the discrimination between suitable and unsuitable sites was accurately for each of the four study species, at least for the most supported model.

For three species (*A. atrata*, *A. clusiana* and *A. caerulea*), parameters derived from species composition are more reliable than abiotic factors in predicting suitable unoccupied sites. The advantage of Ellenberg indicator values based on the species composition of sites compared to abiotic factors representing bioclimatic conditions or topography more directly is that they are integrating habitat conditions over several years. A combination of abiotic factors and species composition improve the predictions in two species (*A. caerulea*, *G. hoppeanum*), as shown also in previous studies (Tájek et al. 2011, Hemrová and Münzbergová 2012). Since no environmental parameter was used for all species (Table 1), it may be difficult to pre-select factors to be integrated in the models. The different importance of environmental parameters for different plant species was also shown by (Hemrová and Münzbergová 2012).

We assume that the identification of suitable unoccupied sites is limited in our study system because the probability of occurrence and the results from the transplantation experiments showed weak accordance. Only the probability of occurrence of *A. caerulea* was highly significantly related with performance traits. Some performance traits were significantly related to the occurrence predictions of none of the study species. In those cases where a significant relation was detected between model predictions and measured performance traits the correspondence was low ($0.11 < \text{Adj. } R^2 > 0.36$). This weak accordance might suggest that some important habitat characteristics are not included in our models. For instance, we know from a previous study (Hülber et al. 2011) that neighbourhood densities can strongly modify the performance of snowbed plants. In addition, dispersal limitation should be included in models predicting a species' probability of occurrence.

The performance in transplantation experiments of our study species showed a correlation to species occurrence in the case of *A. caerulea* only (Dullinger and Hülber 2011). This might be the reason why an evaluation of the models with performance traits showed low accordance. On one hand the duration of transplantations experiments might be too short for our study species. The study species showed only in some cases reproduction success

which should be considered for a successful recruitment (Ehrlén et al. 2006). On the other hand, model predictions were representative for adult populations, while some performance traits refer to very early life stages (e.g. Germination, Seedling survival). Therefore, a successful germination could be possible at unsuitable sites when conditions are favourable during the time of the experiment. In addition, a previous study by (Hülber et al. 2011) showed that inside a particular snowbed different abiotic conditions are responsible for suitable and unsuitable microhabitats, with the effect that suitable conditions exist only in a very small extent inside the snowbed and species are subjected to dispersal limitations – not habitats. This evidence is also supported by a study about seed sowing experiments with alpine plant species (Niederfriniger Schlag and Erschbamer 2000).

In addition to the low accordance between probabilities of occurrence to the performance traits, the variable number of suitable unoccupied sites recorded for the different models offered a further proof of inaccuracy. Moreover, many of the suitable unoccupied sites predicted by models based on abiotic factors did not overlap with those using Ellenberg indicator values.

In our study system it was difficult to identify suitable unoccupied sites for long-lived species with indirect approaches (Ehrlén et al. 2006). Although, our study species are not occurring in every suitable habitat as it is considered in metapopulation theory (Levins 1969, Hanski and Gilpin 1991, Pulliam 2000). However, it might be possible for other systems as the transferability of our results is limited. That's because, beside abiotic factors other important influences which are not detectable with Ellenberg indicator values may play a major role. These might be historical events like local stochastic extinctions and recolonizations (Eriksson 1996). The time for recolonization is dependent on patch configuration (i.e. size and connectivity of the snowbed patch) and the dispersal abilities of the study species (Dullinger et al. 2011). The information of dispersability is included in species compositions (as co-occurring species may be limited by the same dispersal barriers) but not shown by mean Ellenberg indicator values. Perennials with clonal growth like our study species have high abilities to persist but are not effective in long-distance dispersal, which is necessary for colonisation of isolated patches + in contrast to the surrounding vegetation covered by grassland species and generalists of the alpine vegetation. We suppose, the wider the

ecological gradient e.g. from snowbeds to exposed ridges, the more meaningful the model and the more defined are the differences in performance between the investigated sites. For instance, *A. caerulea* is restricted to those snowbeds with especially long-lasting snow cover (Hülber et al. 2011) and therefore models can more easily distinguish suitable from unsuitable sites.

Furthermore, a spatial resolution of 20 x 20m might be inadequate for our study system as snowbed patches are often much smaller ($< 3 \text{ m}^2$) with the consequence that different habitats from outside of the snowbed can be included in the surveyed site. However, species composition obtained on a smaller scale (3.0 x 2.5 m) did not improve model-performance and were therefore not used for further explorations.

Conclusion

Our results showed that the identification of suitable unoccupied sites for long-lived snowbed species with abiotic factors or parameters derived by species composition has a low accordance to measured performance traits. This might be because dispersal limitations are more important factors influencing snowbed species occurrence than environmental conditions. However, parameters derived by species composition performed better than abiotic factors in predicting suitable unoccupied sites, as they integrate information on habitat conditions from several years. Therefore, we suggest that parameters describing the dispersal abilities of species would improve the identification of suitable unoccupied sites for perennial plant species.

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Appendix

Appendix 1 - Correlation matrix of habitat characteristics. A detailed description about the calculation of abiotic predictors is given in Dirnböck et al. (2003) and Dullinger et al. (2011)

	L ¹	T ¹	F ¹	R ¹	N ¹	Altitude ²	Slope Inclination ²	Degree Days ³	SRI_Mai ⁴	SRI_July ⁴	SRI_Sept ⁴	Water Balance August ⁵	Wetness Index ⁶	Erosion Index ⁷	Wind Speed ⁸	Snow Cover Probability
L	1	-0.62	-0.07	0.25	-0.53	-0.162	0.069422	0.1869	-0.161	-0.1651	-0.1524436	0.0508549	-0.0163777	-0.00048561	-0.00552421	-0.014789
T	-0.62	1	-0.36	-0.14	0.25	0.2875	-0.21326	-0.2379	0.2128	0.21489	0.16675272	-0.1826296	0.1057726	0.1057698	-0.02554024	0.030840
F	-0.07	-0.36	1	-0.14	0.22	-0.0419	0.055626	0.0116	-0.004	0.03525	-0.0432874	0.0809695	-0.1272088	-0.24753444	0.09549126	-0.02683
R	0.25	-0.14	-0.14	1	-0.34	-0.1461	0.040042	0.226	0.043	0.03724	0.0528595	-0.1887522	-0.058651	0.02742697	-0.18659835	0.143345
N	-0.53	0.25	0.22	-0.34	1	0.0316	-0.02957	-0.0131	-0.025	-0.0083	-0.05275585	0.0016801	0.0030396	0.03123357	0.05717015	-0.055642
Altitude	-0.16	0.29	-0.04	-0.15	0.03	1	-0.29787	-0.906	0.1286	0.16656	0.02678832	-0.1724908	0.0205391	-0.10867481	0.36286492	-0.18265
Slope Inclination	0.07	-0.21	0.06	0.04	-0.03	-0.2979	1	0.321	-0.369	-0.4373	-0.15057221	0.1581603	-0.4464894	-0.16909917	-0.15922352	-0.187299
Degree Days	0.19	-0.24	0.01	0.23	-0.01	-0.906	0.320991	1	-0.132	-0.1697	-0.02285367	-0.1376429	-0.023633	0.14369328	-0.35592769	0.173682
SRI_Mai	-0.16	0.21	-0	0.04	-0.02	0.1286	-0.36935	-0.132	1	0.98876	0.95124353	-0.6258235	0.0785476	-0.02239669	0.14228437	0.030487
SRI_July	-0.17	0.21	0.04	0.04	-0.01	0.1666	-0.43731	-0.1697	0.9888	1	0.91106169	-0.6080888	0.1100789	-0.00499618	0.15528229	0.05575
SRI_Sept	-0.15	0.17	-0.04	0.05	-0.05	0.0268	-0.15057	-0.0229	0.9512	0.91106	1	-0.6576705	-0.0547195	-0.05489266	0.08819731	-0.04514
Water Balance August	0.05	-0.18	0.08	-0.19	0	-0.1725	0.15816	-0.1376	-0.626	-0.6081	-0.65767048	1	-0.0075632	-0.06484467	-0.09240971	-0.001140
Wetness Index	-0.02	0.11	-0.13	-0.06	0	0.0205	-0.44649	-0.0236	0.0785	0.11008	-0.05471954	-0.0075632	1	0.39230464	-0.20923364	0.627043
Erosion Index	-0	0.11	-0.25	0.03	0.03	-0.1087	-0.1691	0.1437	-0.022	-0.005	-0.05489266	-0.0648447	0.3923046	1	-0.05616685	0.159542
Wind Speed	-0.01	-0.03	0.1	-0.19	0.06	0.3629	-0.15922	-0.3559	0.1423	0.15528	0.08819731	-0.0924097	-0.2092336	-0.05616685	1	-0.607231
Snow Cover Probability	-0.01	0.03	-0.03	0.14	-0.06	-0.1827	-0.1873	0.1737	0.0305	0.05575	-0.0451492	-0.0011408	0.6270435	0.15954217	-0.60723112	

¹ Mean Ellenberg Indicator Values (Ellenberg et al. 1992). For some species adjusted Ellenberg values for the Northeastern Calcareous Alps were obtained from Englisch (1999). Abbreviations: L = Light; M = Moisture; S = Soil reaction; N = Nutrients; T = Temperature

² Derived from a digital elevation model (DEM; resolution: 20 × 20 m), provided by the Austrian Mapping Agency (Österreichisches Bundesamt für Eich- und Vermessungswesen).

³ Number of days with a daily mean temperature > 0°C; measurements from 20 climate stations during the years 1995 - 1999 were integrated with altitude and geographical latitude.

⁴ Solar Radiation Income for 15 Mai, 15 July, 15 September, derived from a solar radiation model, SOLARFLUX (Rich et al. 1995) on the DEM¹.

⁵ Precipitation less potential evapotranspiration (Turc 1961), for calculation Solar Radiation Income⁴, temperature and precipitation derived from regression measurements from 20 climate stations against altitude and geographical latitude was used.

⁶ Spatial distribution of zones of saturation as well as runoff generation, calculated from the DEM using the software TAPES-G (Gallant and Wilson 1996).

⁷ Spatial distribution of soil loss, erosion and deposition potential, calculated from the DEM using the software TAPES-G (Gallant and Wilson 1996).

⁸ Topographical modification of near-surface wind velocity, calculated with the diagnostic wind field model NUATMOS (Version 5N, 07/31/91; Ross et al. 1988, integrated in a GIS by Bachmann 1998).

⁹ Probability of snow cover, calculated by relating snow melt date as derived from a series of 11 SPOT scenes to altitude, slope, cumulative solar radiation income (SOLARFLUX), topographically modified wind velocity (calculated by NUATMOS), wetness and erosion indices and plant cover type (krummholz versus grasslands, screes and rocks, derived from a vegetation map). The relationship was established by means of a classification tree, and the measure derived was the mean probability of a cell to be covered by snow across all days from which SPOT scenes were available.

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Zusammenfassung

Die Identifizierung von geeigneten unbesetzten Standorten ist notwendig um zu verstehen ob für die Verteilung einer Pflanzenart entweder vorherrschende Umweltbedingungen oder limitierte Ausbreitungseigenschaften entscheidend sind.

Als direkter Nachweis für die Eignung eines Standortes gelten Transplantationsexperimente, im Gegensatz dazu sind indirekte Methoden wie sogenannte Habitatmodelle (Species Distribution Models) weit aus ökonomischer und liefern schneller Ergebnisse.

Vergleichsstudien zwischen direkten und indirekten Methoden bezüglich der Fähigkeit geeignete Standorten vorauszusagen gibt es wenige, insbesondere für mehrjährige Arten.

In dieser Studie wurden geeignete unbesetzte Standorte von vier mehrjährigen auf Schneeböden spezialisierten Pflanzenarten (*Achillea atrata*, *Achillea clusiana*, *Arabis caerulea* und *Gnaphalium hoppeanum*) mit Vorkommen in den Nordöstlichen Kalkalpen mittels auf Umweltvariablen basierenden Modellen vorausgesagt. Als Umweltvariablen dienten entweder abiotische Faktoren (abgeleitet aus Klimadaten und der Topographie) oder aus der Artenzusammensetzung abgeleitete Parameter (gemittelte Ellenberg Zeigerwerte) oder einer Kombination aus allen eben genannten Faktoren. Ein Vergleich der verschiedenen Modelle wurden angestellt und anschließend die Güte der prognostizierten Vorkommenswahrscheinlichkeiten mit der auf denselben Standorten gemessenen Leistungsfähigkeit der Pflanzen in 4-jährigen Transplantationsexperimenten geprüft.

Unsere Ergebnisse zeigen, dass die Identifizierung von geeigneten unbesetzten Standorten für mehrjährige Schneebodenarten nur begrenzt möglich ist, da die Anzahl und die Identität der prognostizierten Flächen zwischen den Modellen stark abweicht.

Jedenfalls sind die auf Artenzusammensetzung basierenden Parameter meist verlässlicher, um geeignete unbesetzte Standorte vorauszusagen, als abiotischen Faktoren. Eine Erklärung dafür ist, dass die Artenzusammensetzung die Umweltbedingungen über mehrere Jahre widerspiegelt. Bei zwei Arten trat durch die Kombination aller Faktoren eine Verbesserung der Voraussagen ein.

Eine Evaluierung der prognostizierten Vorkommenswahrscheinlichkeiten mit der Leistungsfähigkeit der Pflanzen in den Langzeit-Transplantationsexperimenten zeigte nur einen schwachen Zusammenhang. Diese Erkenntnis unterstützt die Bedeutung der Ausbreitungsfähigkeit für das Vorkommen von langlebigen Pflanzenarten in fragmentierten Landschaftskomplexen. Für weitere Untersuchungen empfehlen wir deshalb Eigenschaften bezüglich der Ausbreitungsfähigkeit (z.B. Samengewicht, Samenanzahl), bei der Bestimmung von geeigneten unbesetzten Standorten miteinzubeziehen. Unsere Studie liefert nützliche Hinweise für die Voraussage von neuen unbesetzten Standorten für gefährdete Pflanzenarten und weist auf die Notwendigkeit weiterer relevanter Faktoren für eine zuverlässige Prädiktion hin.

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