Article

Fl. Medit. 31(Special Issue): 43-53
https://doi.org/10.7320/FlMedit31SI.043
Version of Record published online on 16 July 2021

Otto Wildi

Searching for hidden site factors – species pool and land use blurring Swiss forest vegetation types

Abstract

Wildi, O.: Searching for hidden site factors – species pool and land use blurring Swiss forest vegetation types. — Fl. Medit. 31(Special Issue): 43-53. — ISSN: 1120-4052 printed, 2240-4538 online.

A numerical analysis of data more than 50 years old shows that two zones of particularly high fuzziness appear in the as yet valid classification of forest vegetation in Switzerland. This raises the question of the causes of the phenomenon, but also that of a possible correction. The results show that the crispness of the classification is significantly improved by bypassing some dominant tree species. This is true for *Fagus sylvatica* in lower altitudes of the country, but especially for the beech forests in general. *Picea excelsa*, probably the most frequently tree species planted in the past, predominantly blurs the subalpine forest classification. For some less frequent tree species (*Castanea sativa*, *Larix decidua*) it can be shown that rare plantings were often made in locations unsuitable for the species. Many analyses are only possible with the help of a more recent, systematically collected data set, which also includes numerous environmental variables. This is now already 25 years old, which means that the species composition known today is not up do date. The general species poverty of all forests of Central Europe is likely to make them particularly vulnerable to drought events, storms and insect infestation.

Key words: classification, forest management, group similarity, heat colors,potential vegetation.

Introduction

Semi-natural vegetation is of particular interest because, in the absence of management without human control, it develops in compliance with ecological laws. This results in a new species-specific diversity, which on the one hand is highly dependent on the local "species pool" and on the other hand is modified by interactions between species such as competition and mutual support (Connell & Slatyer 1977). To what extent the vegetation cover encountered in the real world is natural is difficult to determine, because sites without human influence no longer exist on earth. In the case of forests, therefore, one speaks of "potential natural vegetation" addressing a fictitious stable final state (Tüxen 1956; Neuhäusl 1984; Kowarik 1987; Küchler 1988; Brzeziecki & al. 1993; Lindacher 1996). However, Chiarucci & al. (2010), for example, consider this concept to be too rigid and therefore fundamentally question its validity. In fact, there is no single definition of potential natural vegetation, but most authors agree that if no management is undertaken, the plant cover will generally develop in the direction of greater proximity to nature. This is not valid if irreversible environmental changes occur in the meantime, such as soil erosion or climate change. In these cases, a new species combination that has never been observed before can be expected.

There is hardly any alternative to the narrative of potential natural vegetation, as will be illustrated below using the relatively well researched forests of Switzerland as an example. With the publication of Ellenberg and Klötzli (1972) a nationwide classification exists, which is still in use after half a century - for lack of alternatives. It is based on vegetation records that are now more than fifty years old and that were made by various authors. For many of them, the place and time of the survey are unknown and the taxonomies used can hardly be reconciled with the current one. The classification method used at that time is purely heuristic and thus also not verifiable (de Caceres & al. 2015). Some recent local additions and attempts at correction hardly contribute to the nationwide representation.

A serious gap in the data situation is the lack of comprehensive data on management intensity and management type, both past and present, although a national forest inventory has been compiled in Switzerland since the 1980s. It is currently in its fourth edition (Brändli & al. 2020). This inventory provides information on the shrub and tree layer of the forests, but does not include a survey of the herb layer or an analysis of the soil. Thanks to the systematic sampling, the data allow at least an extrapolation to the whole country.

In the 1990s, a vegetation survey was carried out on a square sub-network of the National Forest Inventory, using a mesh size of 4 by 4 kilometres (Wohlgemuth & al. 2008; Wildi 2017). Despite the limited sample size of 726, it provided for the first time a representative picture of the forest ecosystem, both of the vegetation and of some environmental factors, in contrast to previous surveys. Thanks to proven interpolation methods, good quality climate data are available for all plots (Zimmermann & Kienast 1999). Of the soils, there is only a single pH measurement from the first national forest inventory. Again, data on current and historical forest management is missing, which has never been collected in a uniform way across the whole country and which is likely to significantly affect existing classifications.

The aim of the present analysis is to find and explain weaknesses in the existing vegetation classification using appropriate models. A first systematic disturbance factor could have arisen from the fact that forests at lower and flatter altitudes were more intensively managed and modified than those at higher altitudes for purely practical reasons (Brändli & al. 2020). A second factor, the general species poverty of forests in Central Europe, could have led to the fact that the ecological niches realized by some tree species are wider than those of other species due to a lack of competition (Latham & Ricklefs 1993). This could be the case for *Fagus sylvestris*, which extends like a veil over numerous vegetation types, or *Picea excelsa*, probably the most frequently planted species. And thirdly, there are a few tree species that, thanks to their efficient propagation mechanism, spread very quickly and reach less suitable sites, such as *Fraxinus excelsior*, *Acer platanoides* or *Acer pseudoplatanus*.

Data

The 2533 vegetation relevés used by Ellenberg & Klötzli (1972) and the corresponding group affiliations were first published by Keller & al. (1999). They are included in the R-package "dave" (R Development Core Team 2017) and further analysed by Wildi (2017). The vegetation data are in the file "EKv", the corresponding group numbers in "EKs". For these data, there is no complete information about the authors, the location and the year of recording. The classification is, as usual at that time, purely heuristic. The tree species were each treated as three independent descriptors according to their occurrence in the tree, shrub and herb layer.

The data collected in the 1990s in a systematic grid and initially analysed by Wohlgemuth & al. (2008) are also included in the package "dave", under the object names "ws30", "ws200" and "ws500" for the plot sizes of 30, 200 and 500 square meters respectively. The file "wssit" contains the corresponding site factors described in Wildi (2017). The sample size is n=726. Again in this data set, tree species are described by three descriptors each according to their occurrence in the tree, shrub and herb layer.

Methods

In the absence of spatial, temporal or environmental data, as is the case with the data set of Ellenberg & Klötzli (1972), the interpretability of a classification can be evaluated by comparing the similarities of equal group membership with those between groups. The resulting matrix resembles a similarity matrix, but its elements are mean values of all pairwise groups involved. Such a representation can be found in Wildi (2017), p. 51 (Fig. 1, upper right). The method scales the similarity values to a range from 0 to 1 and converts them into heat colors. The highest value occurring in the matrix becomes a dark red, medium values become yellow and the lowest becomes white. Ideally, the diagonal of the matrix is red, which indicates a high similarity of relevés within a vegetation unit. Red cells outside the diagonal mean that vegetation units are similar and therefore difficult to distinguish.

In the graphic in Fig. 1, upper right, there are two noticeable areas besides some local problems. The units 1 to 21, upper left, are more similar than average among themselves, as can be seen from an intense red colored square. They are beech forests, which dominate in lower altitudes of the alpine country. Could it be that one species dominates all units, for example *Fagus sylvatica* or the often planted *Picea excelsa*? Or is it just a weakness of the classification method?

A similar phenomenon is to be observed in the forest communities 45 to 60, which are subalpine forests where spruce (*Picea excelsa*) probably also naturally dominates, while it can be assumed that management is less intensive.

I have decided to leave the classification unchanged, because a critical evaluation by means of environmental factors is not possible. Instead, I try to eliminate one or more tree species (always in the tree, shrub and herb layer simultaneously) in the expectation that the overly high similarity of the block will partially or completely disappear. In the results I show the influence of *Fagus sylvatica*, *Picea excelsa*, *Abies alba* and the two species *Fraxinus excelsior* and *Acer pseudoplatanus* with their particularly far-reaching wind distribution.

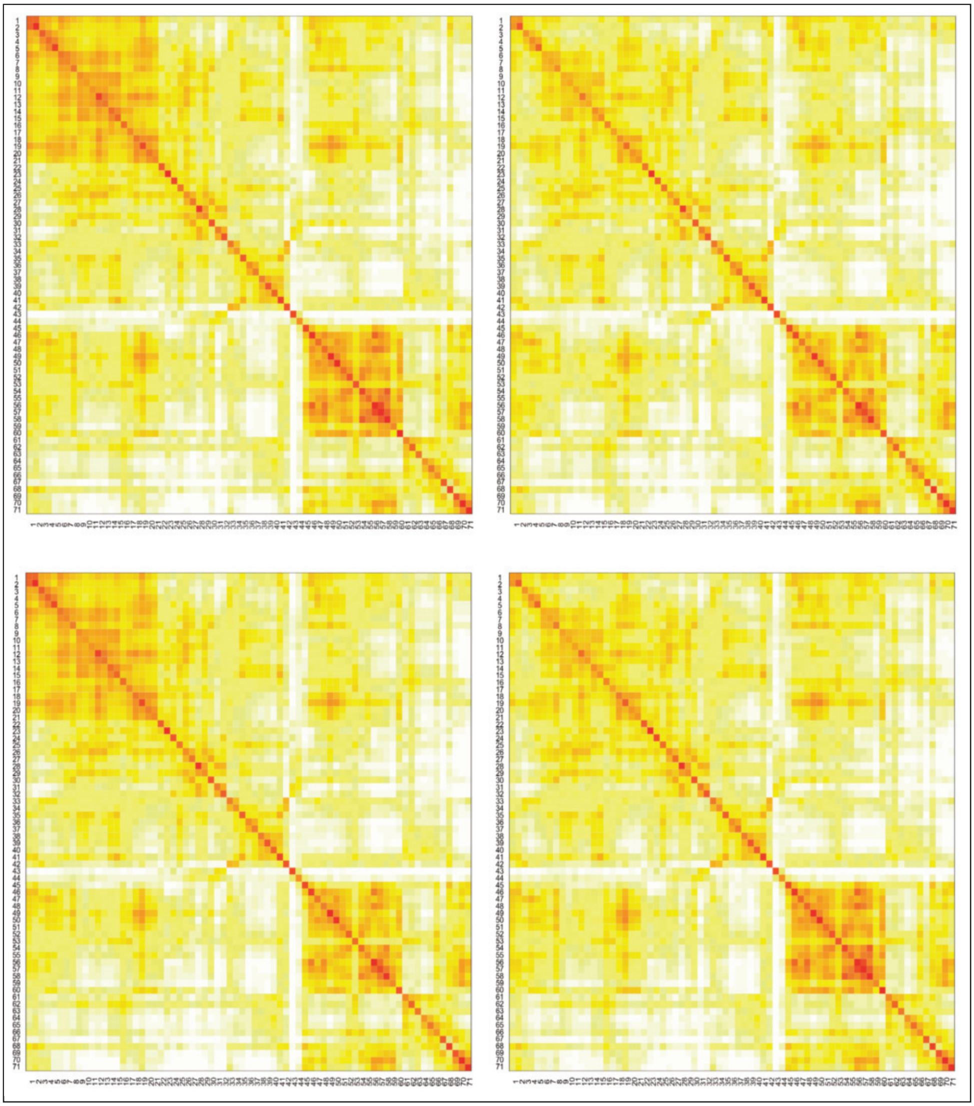

Fig. 1. Within and between similarity of 71 vegetation types of Swiss forests (Ellenberg & Klötzli 1972; Wildi 2017). Upper left: full data set. Upper right: *Fagus sylvatica, Picea abies, Acer pseudoplananus, Fraxinus excelsior* and *Abies alba* removed. Lower left: *Picea excelsa* removed. Lower right: *Fagus sylvatica* removed.

The systematically collected data set now allows to verify a possible influence of dominant tree species independently from the old classification, but also to compare the potential vegetation with the current one. No official classification of this data set exists so far. Since the sample size is very limited, I first generate a coarse classification with eight vegetation types using the total sample of 726 relevés and applying a numerical method (Ward's method, based on correlations transformed to distances), as already shown in Wildi (2017). From this I derive a matrix of mean similarities within and between the vegetation types, with and without the dominant tree species.

Since the localities of all relevant species are known, the vegetation types can be displayed as distribution maps. For this purpose I use a multinomial regression (Venables & Ripley 2010, R package "nnet") with the site factors elevation, yearly precipitation, yearly degree-days, and pH (soil), which have proven to be particularly good predictors in a previous analysis (Wildi 2017).

Tree plantations play a central role in forest management. Preference is given to planting species whose wood is economically interesting. To identify unfavourable plantations, I compare the occurrence probabilities of some species with their actual distribution. An indication for artificial occurrence are populations that can be observed on unsuitable sites. However, the method can only work if plantings are not too frequent (e.g. in *Larix decidua* or *Castanea sativa*), because otherwise they influence the determination of the potential distribution too much. To determine the probability of occurrence I use a generalized linear model (Venables & Ripley 2010; Wildi 2017) with the same site factors as in the multinomial regression.

Results

Fig. 1 shows that the two blurred areas, the forest communities 1 to 21 and 45 to 60 respectively (graph upper right) largely disappear when the species *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Fraxinus excelsior* and *Acer pseudoplatanus* are eliminated from the data set (graph upper left). The raw data for the graphs (not shown here) indicate, as expected, that the similarities of all forest communities are reduced when species are omitted, but that those between them (outside the diagonal) are reduced more strongly than those within (diagonal elements). If only *Picea excelsa* is suppressed, the crispness in the range of forest types 45 to 60 is improved (Fig. 1, bottom left). If only *Fagus sylvatica* is suppressed, crispness improves in the range 1 to 21.

Fig. 2 shows the same effects in the much smaller, systematic sample. The classification involved is generated numerically (Ward's method). If the full data set is used (graphic above left), for example, units 1, 2 and 3 are difficult to distinguish from each other, but also units 5 to 7. The resolution improves considerably if the above-mentioned 5 tree species are omitted (Fig. 2, graph upper right). If only Picea excelsa is suppressed (graphic bottom left), the crispness improves in the lower right part of the matrix with the forests of the subalpine area. The lower right graphic again shows that it is primarily the suppression of *Fagus sylvatica* improving the crispness of the classification.

The systematic sampling data set not only allows generating a coarse classification of forest types, but also the spatial distribution of occurrence probability (Fig. 3). Just by coincidence the first 3 forest types encompass the natural range of Fagus sylvestris. Then follow the ones of the higher altitudinal zones and ending with the same of the Southern Alps. Fig. 3 also suggests the similarity pattern being a continuum in which the edges of the forest types are arbitrary.

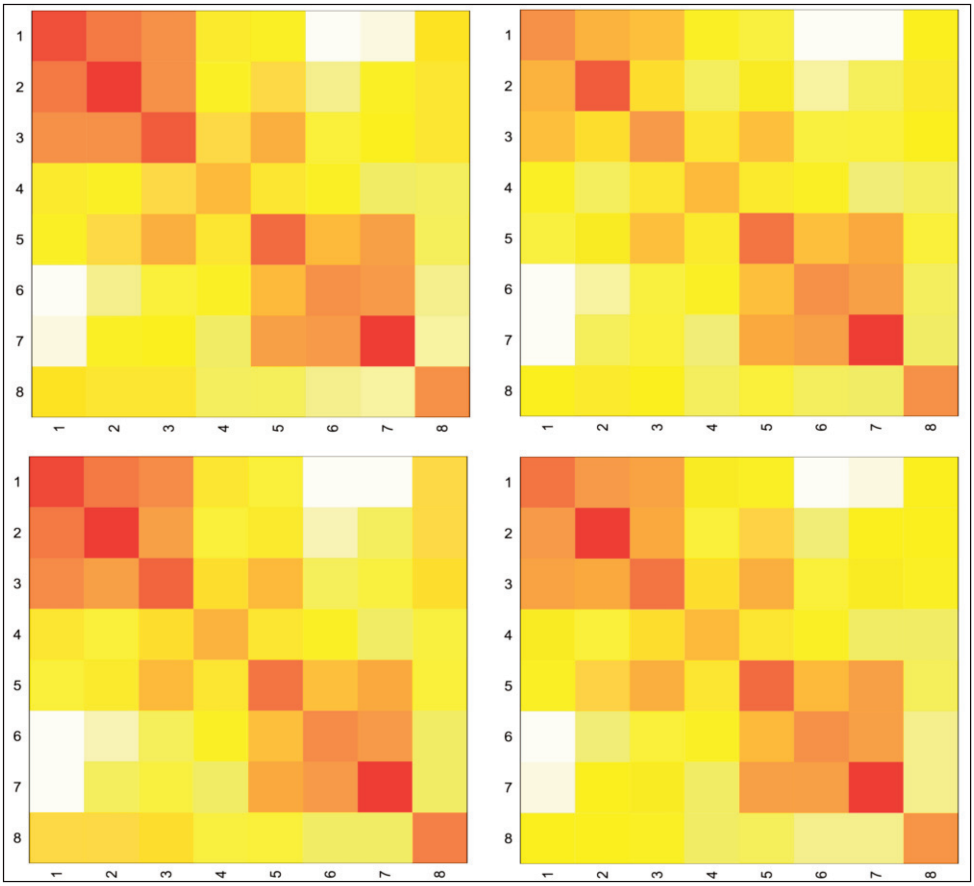

Fig. 2. Within and between similarity of 8 vegetation types derived from the systematic Swiss forests survey (Wohlgemuth & al. 2008; Wildi 2017). Upper left: full data set. Upper right: *Fagus sylvatica, Picea abies, Acer pseudoplananus, Fraxinus excelsior* and *Abies alba* removed. Lower left: *Picea abies* removed. Lower right: *Fagus sylvatica* removed.

Fig. 4 shows the observed (left column) and potential distribution (right column) of 4 selected tree species. *Fagus sylvatica* (first row) is distributed over the whole country, with the exception of the high subalpine areas and the southern side of the Alps. *Picea excelsa* (second line) is very dominant, probably planted in the lower altitudes, but naturally occurring in the higher ones. In *Larix decidua* (third line) the artificial plantings north of the Alps are recognizable (Fig. 4). The species occurs mainly in the central Alps. The few populations north of the Alps are on ecologically unsuitable sites. An analogous situation is shown by *Castanea sativa*, which is normally restricted to southern Switzerland, but occasionally occurs in western Switzerland as well. Here, too, it is evident that the ecological conditions are not really suitable.

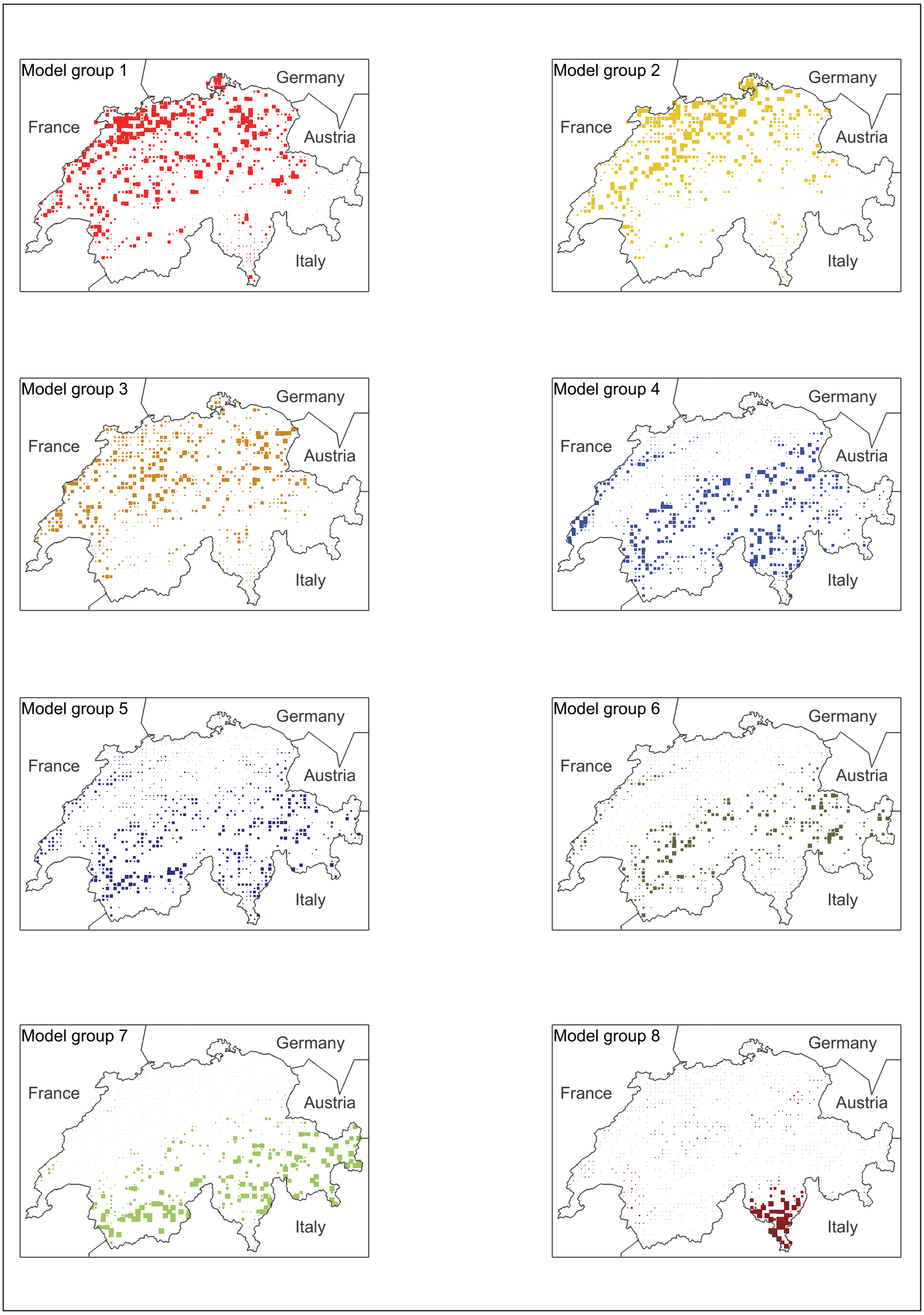

Fig. 3. Spatial distribution of 8 vegetation types derived by numerical classification of the Swiss systematic survey. The occurrence probability bases on 5 site variables (Wildi 2017, p. 291).

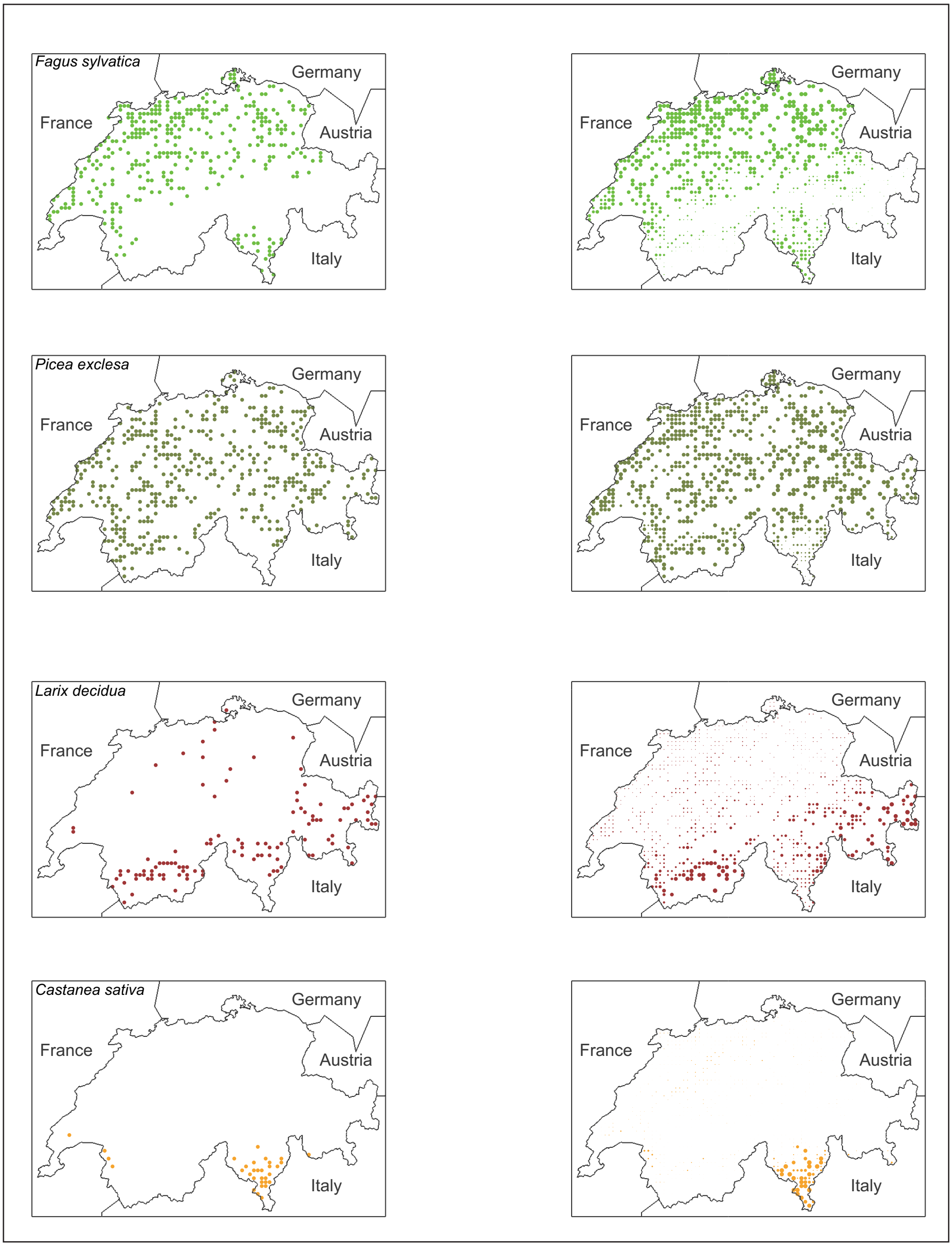

Fig. 4. Occurrence of 4 selected tree species (left hand row) compared to the occurrence probability of the same based on a generalized linear model using 5 site factors. *Fagus sylvatica* (first row) is hardly ever planted, but it has a wide ecological niche. *Picea excelsa*, second row, has been planted almost everywhere for economic reasons. *Larix decidua*, typical for central Alps, has frequently been planted in the northern parts of the country and the few populations hit by the sampling grid all occur on unsuitable sites. The same holds for *Castanea sativa* with suitable sites only south of the Alps.

Conclusion

The issue of the analysis is the occurrence of inconsistencies in the classification of Swiss forest types. Traditionally, shilouette plots are used to identify contradicting delineation of vegetation types (Everitt & al. 2011). These offer a more compact representation of group structure than dendrograms, but they are still too voluminous for overviewing very large data sets. With the proposed visualization of mean similarities within and between groups, even extensive classification systems can be surveyed. Trying to evaluate classification methods with this method is not recommended (nor would it be by silhouette plots), because the mean similarity coefficients are transformed to a range from zero to one and thus may encompass a very narrow range. However, entire blocks of groups that differ from all others with respect to consistency are detected. In the present case this concerns the very widespread beech and spruce forest types.

Whether an overall improvement in the crispness of the classification can be achieved by omitting certain species is one more question not further explored here. As Feoli & Ganis (2019) mention, different analyses of variance could provide answers, alternatively also the evenness of the eigenvalues of the similarity of the groups.

Although it can be shown that the shrub and herb layer of the examined forests behave differently than the tree layer, I have merged all three for the purpose of the analysis. Seedlings can also occur more frequently when their mother trees are found under unsuitable conditions. This is true for many changed stands, some of which dating back far into the past, because forestry has always focused on the promotion of economically interesting tree species (Brändli & al. 2020). This fact is evidenced by the wide distribution of *Picea excelsa* (Ellenberg & Klötzli 1972), but also of *Fagus sylvatica*, which has a broad realized niche by nature. If five frequently occurring tree species from all layers are removed from the data set, the zone of blurring between the forest communities disappears to a high extent.

Thanks to a systematically collected sample from recent times (Wohlgemuth & al. 2008; Wildi 2017), it can be shown that the influence of dominant species on the classification of forests is general. Thus, the observed uncertainties are not due to a lack of data quality or an insufficient grouping analysis by Ellenberg & Klötzli (1972). However, the interpretation that the undifferentiated behavior of common tree species is due to centuries of cultivation is difficult to prove. Historical sources on tree plantations are only available sporadically, on a local to regional scale.

In favourable individual cases (*Larix decidua*, *Castanea sativa*) it can be shown that tree plantings were occasionally made on unsuitable sites. Thanks to the availability of numerous site factors, the systematically collected data set allows the regression-based simulation of the regional distribution of potentially suitable sites. Tree groups planted at unsuitable sites can thus be identified. However, if a tree species is very common and plantations are widespread (*Picea excelsa*, *Fagus silvatica*), this method is not applicable because the tree species-site model is distorted by the uncontrolled management.

Fig. 1 suggests that the classification of Ellenberg & Klötzli (1972) in the realm of beech forests is somewhat too high in resolution, because different plant communities show a low degree of homogeneity internally, recognizable by rather light red coloured diagonal elements. If one merges very similar forest communities, the zone of blurring does not disappear. And in the systematic sample, where the majority of beech forests is represented by only three groups, the influence of *Fagus sylvatica* and *Picea excelsa* is equally visible. This in turn indicates that the causes of the blurring are not to be found either in the classification method or in the data quality.

The dominance of few tree species, and thus the lack of diversity of tree species overall, represents one of the risks associated with climate change (Gehrig-Fasel & al. 2005). In the case of beech, it is the susceptibility to drought in extreme sites (Brändli & al. 2020), while in the case of spruce it is the susceptibility to pests such as bark beetle as well as storm damage. A preventive measure would involve reducing this species poverty by changing the cultivation regime. The recipe is to narrow the realized niche of *Fagus* and *Picea*. This might be difficult due to the lack of better suited species.

As Latham & Ricklefs (1993) explain, the relative poverty of tree species applies to the whole of Europe. To confirm this would require a statistically satisfactory survey of the forest vegetation combined with adequate ecological information. However, as shown for Switzerland, the data situation is unsatisfactory throughout the whole continent. There is a lack of a sufficiently large sample, which would have to be up-to-date to reflect changes.

References

Brändli, U. B., Abegg, M., Allgaier Leuch, B. (eds) 2020: Schweizerisches Landesforstinventar. Eidgenössische Anstalt für Wald, Schnee und Landschaft WSL. – Bern.

Brzeziecki, B., Kienast, F. & Wildi, O. 1993: A simulated map of the potential natural forest vegetation of Switzerland. – J. Veg. Sci. **4:** 499-508.

De Cáceres, M., Chytrý, M., Agrillo E., Attorre, F., Botta-Dukát, Z., Capelo, J., Czúcz, B., Dengler, J., Ewald, J. & Wiser, S. K. 2015: A comparative framework for broad-scale plot based vegetation classification. – Appl. Veg. Sci. **18:** 543-560.

Chiarucci, A., Araújo, M. B., Decocq, G., Beierkuhnlein, C. & Fernández-Palacios, J. M. 2010: The concept of potential natural vegetation: an epitaph? – J. Veg. Sci. **21:** 1172-1187.

Connell, H. J. & Slatyer, R. O. 1977: Mechanisms of succession in natural communities and their role in community stability and organisation. – Amer. Naturalist **111:** 1119-1144.

Ellenberg, H. & Klötzli, F. 1972: Waldgesellschaften und Waldstandorte der Schweiz. – Mitteilungen der Eidgenössischen Anstalt für das forstliche Versuchswesen, **48.** – Zürich.

Everitt, B. S., Landau, S., Leese, M. & Stahl, D. 2011: Cluster Analysis, 5° Ed. – Chichester.

Feoli, E. & Ganis, P. 2019: The Use of the Evenness of Eigenvalues of Similarity Matrices to Test for Predictivity of Ecosystem Classifications. – Mathematics **7:** 245.

Gehrig-Fasel, J., Zimmermann, N., Guisan, A. & Brändli, U. B. 2005: Climate change or land abandonment? Analysis of treeline change in the Swiss Alps. – 90th ESA Annual Meeting / IX International Congress of Ecology, Montreal, Canada.

Kowarik, I. 1987: Kritische Anmerkungen zum theoretischen Konzept der potentiellen natürlichen Vegetation mit Anregungen zu einer zeitgemässen Modifikation. – Tüxenia **7:** 53-67.

Küchler, A. W. 1988: Mapping dynamic vegetation. – In: Küchler, A.W. & Zonneveld, I. S. (eds), Vegetation Mapping. Handbook of Vegetation Science **10:** 13-23.

Latham, R. E. & Ricklefs, R. E. 1993: Continental Comparisons of Temperate-Zone Tree Species Diversity. – In: Ricklefs, R. E. & Schluter, D. (eds). Species Diversity in Ecological Communities: Historical and Geographical Perspectives: 294-317. – Chicago .

Lindacher, R. 1996: Verifikation der potentiellen natürlichen Vegetation mittels Vegetationssimulation am Beispiel der TK 6434 "Hersbruck". – Hoppea **57:** 5-143.

Neuhäusl, R. 1984: Umweltgemässe natürliche Vegetation, ihre Kartierung und Nutzung für den Umweltschutz. – Preslia **56:** 205-212.

R Development Core Team 2017: A Language Environment for Statistical Computing. – R version 3.3.3. R Foundation for Statistical Computing 2017, Vienna.

Tüxen, R. 1956: Die heutige potentielle Vegetation von Oberfranken. – Angewandte Pflanzensoziologie (Stolzenau) **13:** 5-42.

Venables, W. N. & Ripley, B. D. 2010: Modern Applied Statistics with S*,* 4th Ed. – Berlin.

Wildi, O. 2017: Data Analysis in Vegetation Ecology. – 3rd Ed., Boston.

Wohlgemuth, T., Moser, B., Brändli, U.-B., Kull, P. & Schütz, M. 2008: Diversity of forest plant species at the community and landscape scales in Switzerland. – Pl. Biosyst. **142:** 604-613. https://doi.org/10.1080/11263500802410975

Zimmermann, N. E. & Kienast, F. 1999: Predictive mapping of alpine grassland in Switzerland: species versus community approach. – J. Veg. Sci. **10:** 469-482.

Address of the author:
Otto Wildi,
WSL Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland. E-mail: otto.wildi@wsl.ch