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# *Integration of species distribution models and field assessment for evaluating the dynamics of mountain forests under climatic change. Analysis over a 20 years time scale.*

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## ABSTRACT

**Aim:** This project offers the opportunity to evaluate the quality of the models predictions and the ecological shifts in the distribution of plants over the last 20-25 years. For this purpose, we used an earlier inventory (done by Sylvain Meier, 1998-2002) and climatic data to realise a current projection of the floristic distribution under present climate. In summer 2014, fieldwork contributed to collect a resampling of forest species among areas that may have changed according to the predictions. We postulated that the dynamics of plant distributions may be influenced in part by global warming.

**Location:** Temperate mountain forests in the Alps of Canton de Vaud, Switzerland.

**Questions:** Does the species composition change over 20-25 years? Are models able to predict efficiently floristic shifts? Is a potential modification in vegetation distribution influenced by climate change? What are the other factors, albeit climate, that have significant impacts on species distribution dynamics?

**Methods:** We used modelling in order to generate ancient models with a past floristic dataset from 1998 to 2002 and climatic data from 1960 to 1990. Then, a calibration with the current climate (temperature and precipitation) was conducted to build a random-stratified sampling for selected areas, predicted to have changed over the last 20-25 years. In summer 2014, we revisited 92 phytosociological surveys of 314 $m^2$ in the Swiss Alps at different elevation belts. Models evaluation and floristic analyses were executed to study changes in vegetation's distributions.

**Results:** The modelling of species and communities obtained generally good performances. Although models can sufficiently predict shifts in species richness and community composition, they are not yet able to define geographically where these occur. Results of vegetation analysis showed both land use and climate change as potential drivers of changes. A forest densification caused by the anthropic land management is observed with an increasing frequency of more shadow-tolerant species. Some clues revealed possible impacts of global warming in medium and high elevation belts (shifts in vegetation composition and distribution).

**Main conclusions:** In the Swiss Alps forests, the major driver influencing new establishments of vegetation is the abandonment of land management. Impacts of climate change are currently relatively rare to perseive. Modelling and field observations are useful to understand the floristic distribution dynamics, to anticipate the invasive species expansion and to protect the extinction of certain species and biodiversity. For this purpose, it is important to optimize the quality of models to be able to better predict floristic changes. Although it takes time, field observations are still very essential to study and understand the vegetation dynamics.



**Keywords:** Western Swiss Alps, Switzerland, mountain forests, species distribution models, modelling, climate change, forest densification, species richness and land abandonment.


## RESUME

**Objectif:** L'objectif principal de ce projet a été de réaliser des prédictions de distribution d'espèces végétales des forêts des Alpes vaudoises sur une échelle de temps de 20-25 ans sous l'influence des changements climatiques, afin d'en évaluer la qualité et de découvrir l'évolution de la flore à l'aide d'une étude de terrain. Cette dernière a été constituée d'une analyse comparative entre d'anciens relevés forestiers (dirigés par Sylvain Meier, 1998-2002) et d'un ré-échantillonnage de terrain réalisé en été 2014.

**Lieu:** Les forêts tempérées de montagne dans les Alpes du Canton de Vaud, Suisse.

**Questions:** La composition de la végétation forestière a-t-elle changé sur 20-25 ans ? Les modèles sont-ils capables de prédire correctement ces changements ? Les changements climatiques sont-ils en partie responssables de ces modifications de distribution d'espèces ? Quels autres facteurs peuvent influencer cette dynamique ?

**Méthodes:** Des modèles prédictifs d'espèces et de comunautés ont été générés afin d'observer les potentiels changements dans la composition floristique. Ces derniers ont été réalisés à partir d'une base de données de végétation datant de 1998 à 2002 et de mesures climatiques (1960-1990) calibrés sur le climat actuel (température et pluviométrie). Un échantillonnage aléatoire et stratifié a sélectionné des zones susceptibles d'avoir changé en 20-25 ans, en vue d'une nouvelle récolte de données de terrain. L'été 2014 a permis de réaliser un ré-échantillonnage composé de 92 relevés phytosociologiques de 314 $m^2$ à différentes altitudes dans les Alpes suisses. Les analyses de ces données ont permis de comparer la prédiction des modèles aux changements floristiques réels.

**Résultats:** La performance de la modélisation d'espèces et de communautés a été dans l'ensemble bonne. Bien que les modèles aient pu prédire de manière satisfaisante les changements dans la diversité en espèces et dans la composition de communautés, ils n'ont pas été capables de définir géographiquement où ces derniers sont apparus. Les analyses des modèles et de la végétation observée (actuelle et passée) ont montré que le premier facteur principal dirigeant les changements floristiques était la densification des forêts. Ce phénomène est soutenu par la réduction d'activités anthropiques amenant à une augmentation en fréquence d'espèces plus tolérantes à l'ombre. Quelques autres indices ont démontrés un potentiel impact du réchauffement climatique dans les altitudes intermédiaires et hautes (changement dans la composition végétale et dans la distribution d'espèces).

**Conclusions:** Dans les forêts des Alpes vaudoises, le principal facteur influençant la végétation est l'abondant de l'utilisation du territoire par l'homme. L'impact du rechauffement climatique est encore relativement peu visible. La modélisation et l'étude sur le terrain sont vraiment essentielles afin de comprendre la dynamique des ecosystèmes, d'anticiper l'expansion d'espèces invasives, de protéger la biodiversité et d'éviter l'extinction de certaines espèces. Dans ce but, il est important de mettre tout en oeuvre afin d'optimiser la qualité des modèles pour qu'ils puissent mieux générer des prédictions. Bien qu'il demande beaucoup de temps, le travail de terrain reste actuellement fondamental pour étudier la végétation et sa dynamique sous l'influence des changements globaux.

**Mots clés:** Alpes vaudoises, Suisse, forets de montagne, modèles de distribution d’espèces, modélisation, changements climatiques, densification des forêts, diversité en espèces et abondant anthropique des terres.

# 1. INTRODUCTION

## 1.1. Dynamics of the mountain vegetation

A lot of previous studies expected shifts in plant distributions around the globe due to some impacts of astronomic (solar cycles; Delmas et al., 2007; Jambon & Thomas, 2009), intrinsic (climate; Kiehl & Trenberth, 1997) and anthropic factors (Watson et al., 1998; Muller-Dombois, 1992; Vergès et al., 2005). On a large scale, these disturbances participate to change the trajectory of winds (extratropical storms), to expand areas of drought and to increase the frequency of heavy rainfall accelerating the weathering of soils (G.I.E.C., 2007). In mountainous regions, a lot of studies observed changes in vegetation patterns (Pearson & Dawson, 2003). For instance, some researchers detected shifts in the community composition and the distribution of plants (Walther, 2003; Lenoir et al., 2008; Vittoz et al., 2008; Lenoir et al., 2010), others perceived many new establishments of forest species (Mather & Fairbairn, 2000; Gherig-Fasel et al., 2007; Brändli & Abegg, 2009; DGE, 2011) and a rise upwards of the tree line has been measured (Szerencsits, 2012; Carcaillet & Brun, 2000).

The first possible explanation of these major shifts in floristic could be the changing climate. The end of the last ice age was on a time scale of thousand years, however the impacts of current climate change is happening in a few decades on ecosystems. Thus, profound perturbations can be observed faster, especially in mountain areas, where temperature is the main drive of the species composition along elevation gradients (Vergès et al., 2005). For example, the optimum temperature for maintaining the glaciers and the perennial snow will ascend in altitude (Haeberli & Hoelzle, 1995). Although this phenomenon creates more accessible areas for the growth of vegetation (Beniston, 2005), melting snow increases in parallel rivers flow and seas level, principally in summer (increased flood and inundation).

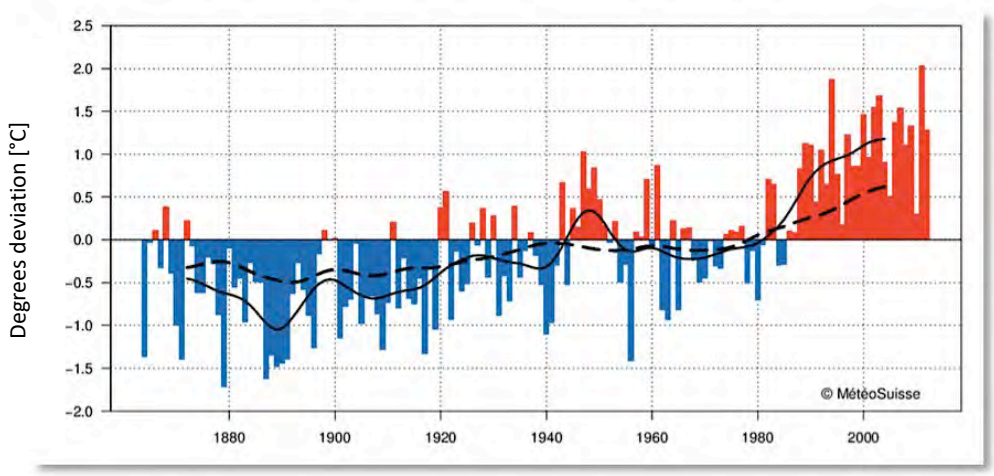



***Figure 1*** *– Variation of the mean annual temperatures around the 1961 to 1990 mean. The black line illustrates the average of temperatures in Switzerland, while the dotted line illustrates the average of continental temperatures (weighted average over 20 years, MeteoSwiss, 2014).*

In Switzerland, global warming is observable with an increase of annual temperatures between 1864 and 2011 reaching on average 1.7°C (*Fig. 1;* 0.12°C per decade; Filliger et al, 2013). Furthermore, an increase of approximately 0.57°C per decade was recorded between 1978 and 2008 (0.38°C in winter and 0.86°C in summer; Rebetez & Reinhard, 2008). At the same time, a reduction of rainfall was estimated and predicted to be more important in future (*Fig. 2*; 8 to 40% in summer, G.I.E.C., 2007) improving the risk of drought, heat waves and heavy rains (OcCC, 2008; Schär et al., 2004). In the coming decades, the Swiss climate is going to evolve towards Mediterranean conditions with higher contrasts, across years, and between summer and winter (Beniston, 2005). In the Swiss Alps, summers could be warmer and drier than 2003 with five times more heat waves after 2070. Winters are going to be warmer with an increase of temperature reaching from 1 to 3°C and a reduction of precipitation ranging from 5 to 25% in 2050 (Shardul, 2007).

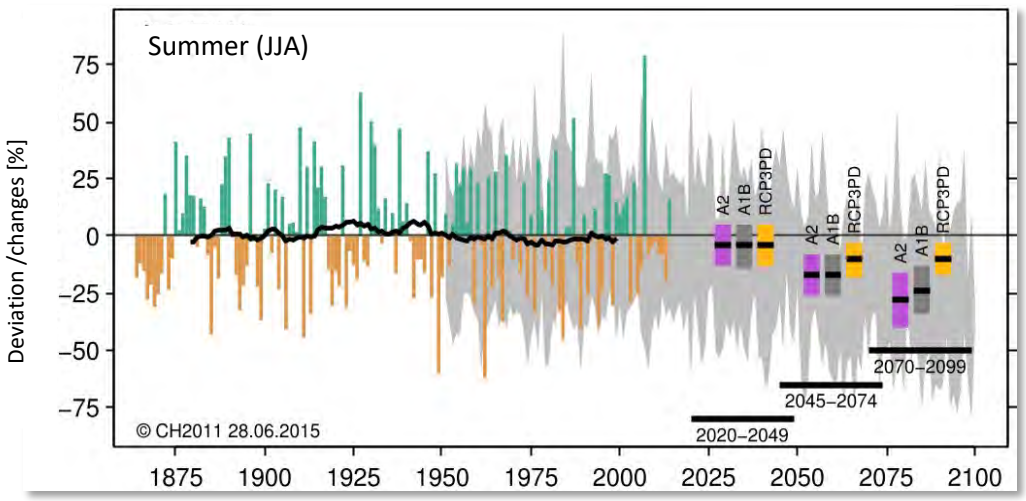



***Figure 2*** *– Variation between the average of annual precipitation calculated on the 1980-2009 mean. The black line illustrates the average of precipitation in Switzerland. Precipitation predictions are given for three periods and according to three climatic scenarios correlated with the quantity of greenhouse gases released in the atmosphere (A2: strong increased emission, A1B and RCP3PD (reduction of emission) (MeteoSwiss, 2014*).

As temperature is the main factor limiting the growth and the different life stages of trees in Swiss mountains (Vittoz et al., 2008), mountain forests may also be strongly disrupted by current global warming. For instance, nowadays the milder temperatures observed in spring stimulate plant flowering to be earlier than expected (Walther, 2003). According to Defila & Clot (2001), the growing period of vegetation in Alps is 13.3 days longer in 2000 than it was in 1951. Moreover, global warming can promote the expansion of invasive or thermophilous species (Lenoir et al., 2010; Lenoir et al., 2008; Carcaillet & Brun 2000), which could have several consequences on biodiversity (Vittoz et al., 2013). However, in Swiss forests, the observed changes in climate might explain only 4% of tree distributions' dynamics around the tree line (Gehrig-Fasel et al., 2007). Actually, the majority of vegetation changes could be highly influenced by the anthropic

land abandonment, the habitat fragmentation and the anthropic pollutions such as the growing use of fertilizers or atmospheric nitrogen releases (Peter et al., 2009; Mather & Fairbairn, 2000; DGE, 2011; Vittoz et al., 2013).

### 1.2. Models of floristic distributions

Von Humboldt & Bonpland (1807) are the pioneers of linking environmental factors to the distribution of species (biogeography). Since their work, a lot of researchers have optimized their studies by taking into account more accurate and various ecological factors to predict species and communities distribution (Guisan et al., 1998; Guisan et al., 2005; Scherrer & Körner, 2011; Dubuis et al., 2011; Guisan & Zimmermann, 2000). Ecologists and conservation managers create now predictive models to have an estimation of species distributions (SDMs) and a pattern of community illustrating the relationship between an organism and its habitat (Guisan & Theurillat, 2000; Loyn et al., 2001; Vaughan & Ormerod, 2003). Nowadays, technology brings the opportunity to use both computer modelling and statistical analysis to predict the vegetation composition and ecological changes in the future (*Fig. 3*; Engler et al., 2009). However, it is often difficult to check the prediction's validity with field observations when datasets are not available - with a waiting time reaching decades or centuries.

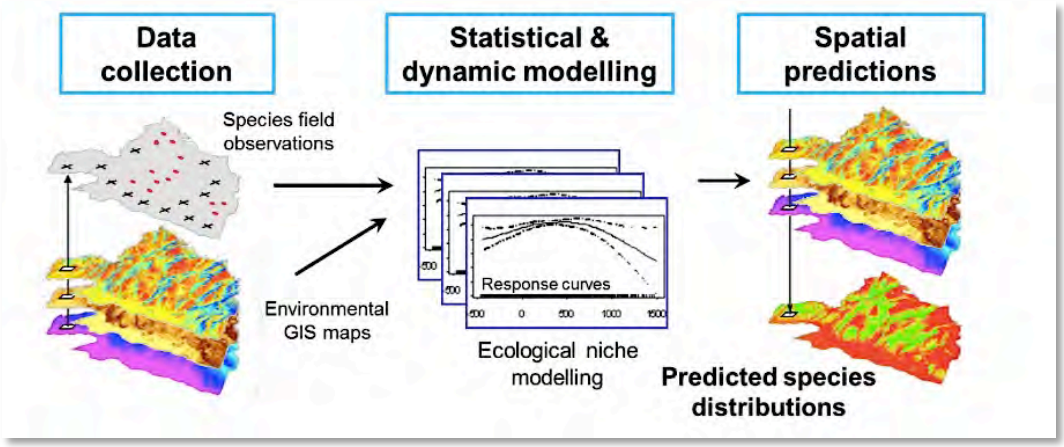



***Figure 3*** *– Summary of the method used to generate a model from a dataset and its environmental factors. A new model can be useful to make a predictive map, on which we can see presence and absence of a species. Guisan & Thuiller, 2005; Ecospat, 2015).*

In this study, we have thus the opportunity to evaluate the models predictions and the vegetation evolution between an earlier inventory from 1988 to 2002 (directed by the forestry engineer Sylvain Meier) and a similar forest species resampling realised during the summer of 2014. This latter was selected through modelling among areas in the past dataset that may have changed over the last 20-25 years. We expected that the potential plants distribution modification, between past and current conditions, is caused by impacts of warmer temperature and small rainfall reduction estimated in Switzerland. To investigate this, we used two approaches, one on modelling and the

other on vegetation analysis, to answer the following questions: Does the species composition change over 20-25 years? Are models able to predict efficiently floristic shifts? Are the observed modifications in species distribution influenced by climate change? What are the other factors, that have significant impacts on species distribution dynamics?

# 2. MATERIAL AND METHODS

## 2.1 Study area

The study area is situated in the Western Swiss Alps of the canton Vaud (46°10´ to 46°30´ N; 7° to 7°´10 E; *Fig. 4*) and covers a surface of ca. 700 km$^2$. This environment is characterized by a temperate climate with mean temperatures from -5 to 4°C in December (-0.44°C per 100 m of elevation) and from 11 to 23°C in July (-0.68°C per 100 m of elevation; averaged over the period of 1981-2010; MeteoSwiss, 2014). Rainfall could be consequent, about 1366 to 1644 mm of rain in 140 days per year (1'445 m of altitude; Serquet & Rebetez, 2013).

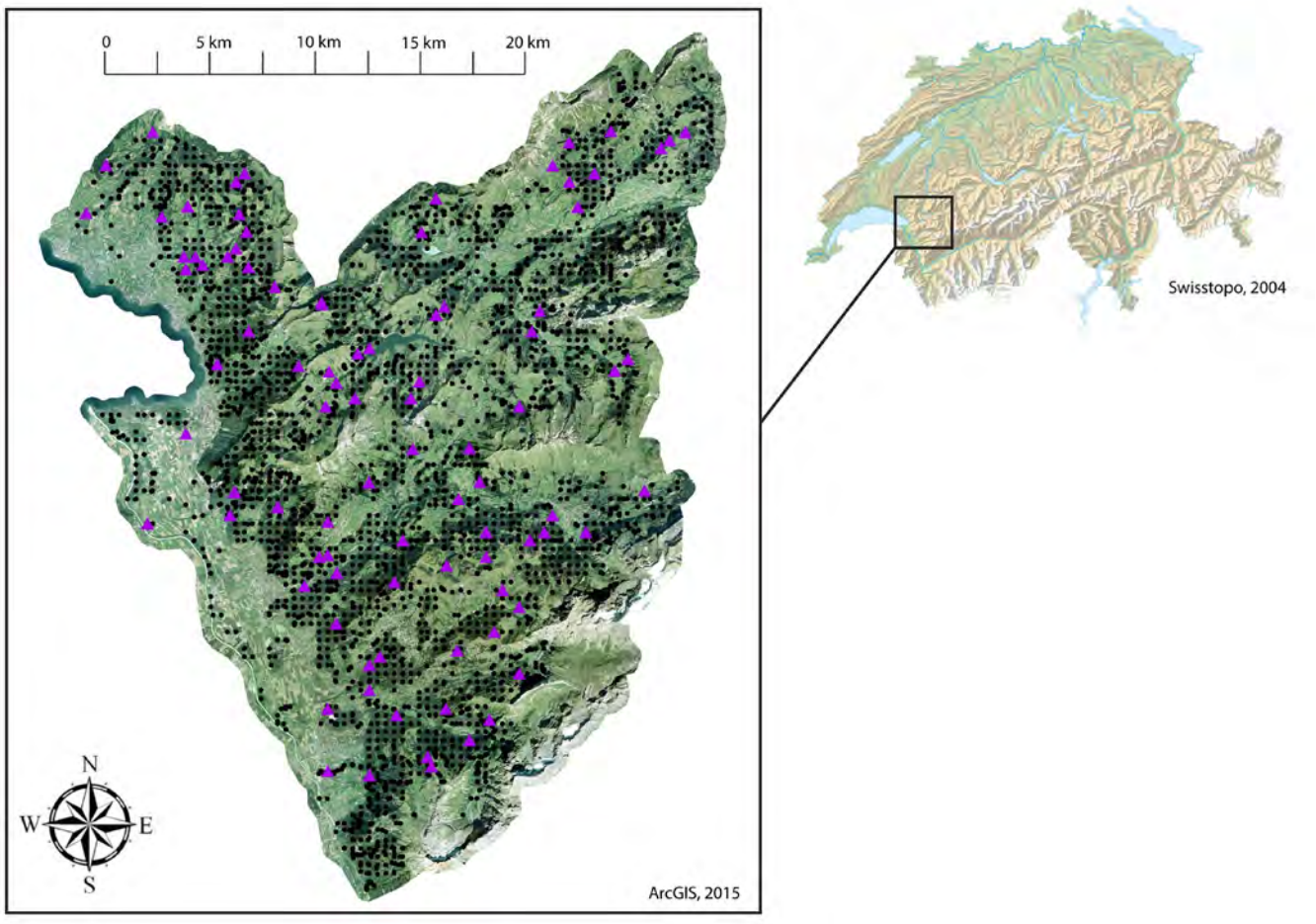
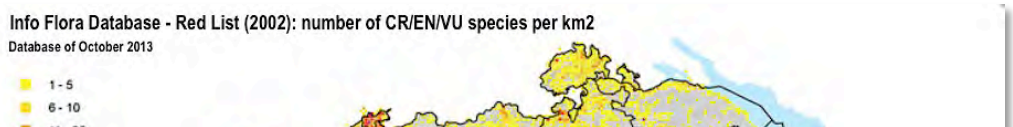



***Figure 4*** *– Illustration of the study area (Western Alps of Switzerland). Black points are the forest inventory from 1988 to 2002 realised by Sylvain Meier. Purple triangles display current resurveys sampling from 2014.*

The elevation within the study area ranges from 375 to 3210 m, but forests are mainly located at low and medium elevations (400 – 1800 m). In mountainous areas, the steep altitudinal gradients and the fine scale topography create a mosaic of temperatures, precipitations and soil properties providing micro-habitats for a large number of species (Scherrer & Körner, 2011). Consequently, the Western Swiss Alps show an exceptionally high biodiversity of plant associations (*Fig. 5;* DGE, 2011).



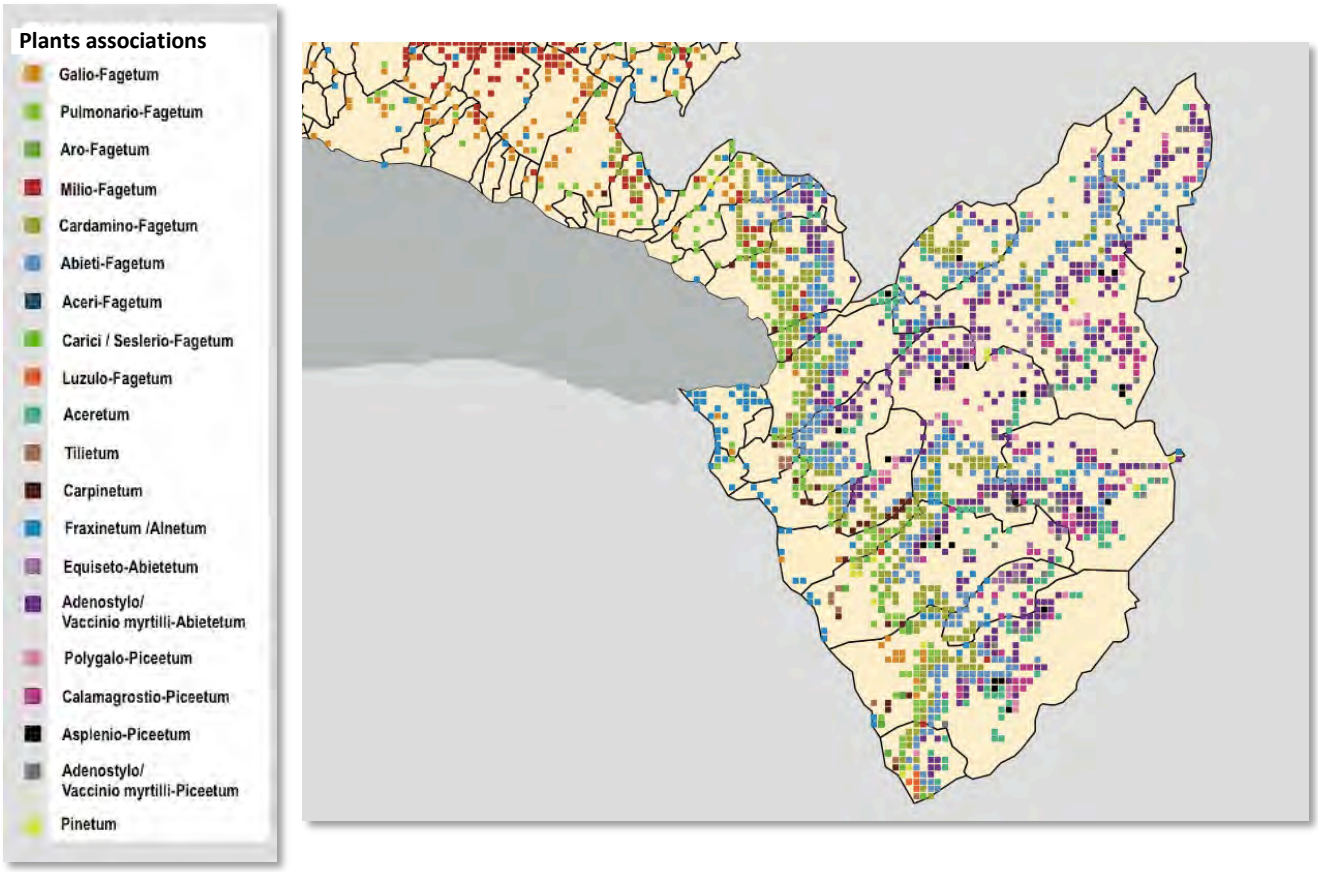



***Figure 5*** *– The map on the top illustrates the diversity of plant species from the Red list per km$^2$ in Switzerland (Info-Flora, 2013). The figure on the bottom shows plant associations that are present in the Western Swiss Alps (DGE, 2011).*

## 2.2 Initial sampling

This earlier dataset is composed of 3076 forests surveys and is part of a cantonal forest inventory from 1988 to 2002 realised by the forestry engineer Sylvain Meier. Every plot had a circular surface of 314 $m^2$ (r = 10 m) and was distributed on a 400 m grid all across the studied area (Neet et al., 2009). The phytosociological investigations was conducted after the Braun-Blanquet method (Braun-Blanquet, 1964), which estimates the cover of each species by an abundance-dominance coefficient separately for each of the three strata: tree (>6 m), shrub (0.5-6 m) and herbaceous (<0.5 m). In total, 347 taxa (including subspecies) were recorded in the forests of the studied area, but only 290 (83.6 %) had enough occurrences for modelling purposes (see *Appx. 1* and *2* for species lists).

## 2.3 Environmental data

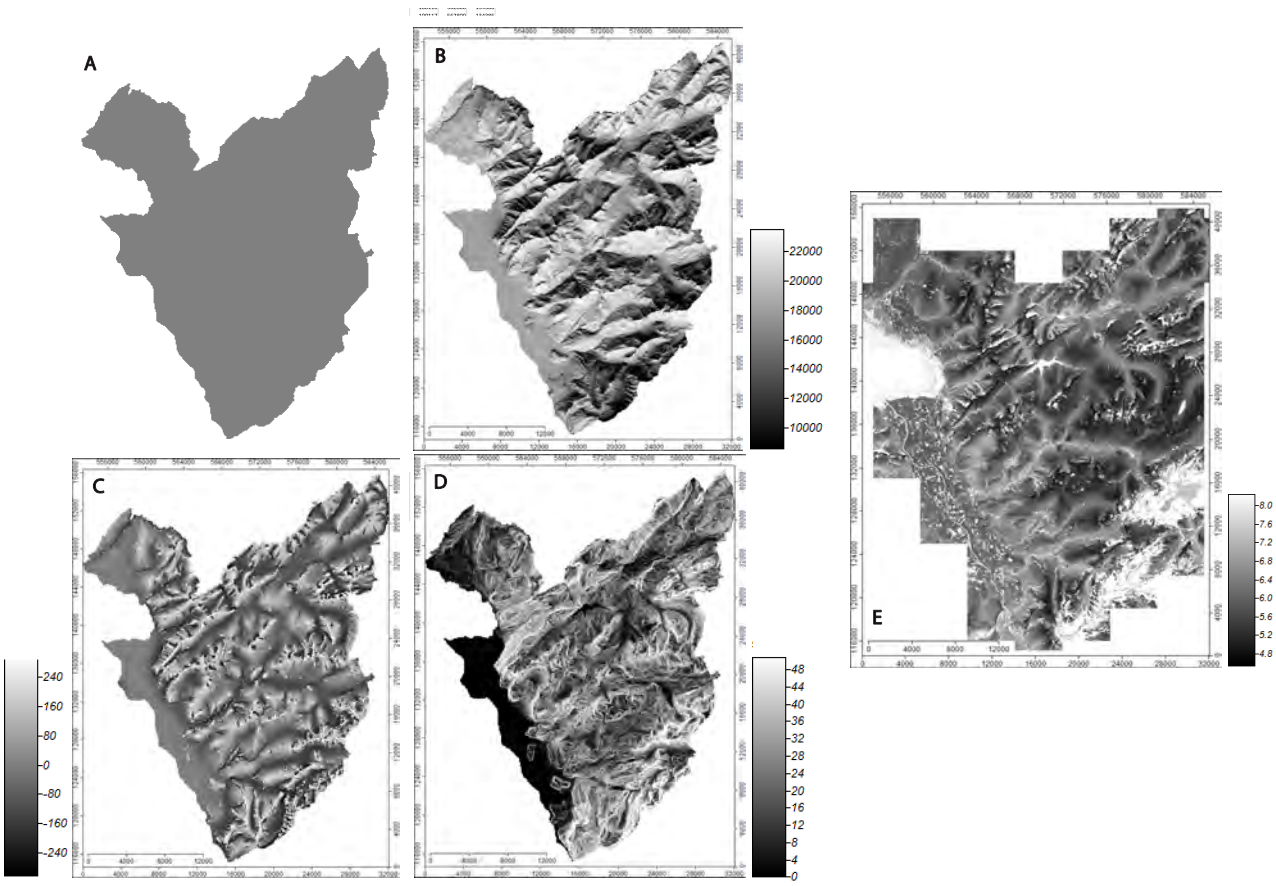



***Figure 6*** *– Figures illustrating predictors used for the sampling modeling. A shows the area. B, C, D and E are respectively global solar radiation, topography, slope and soil pH.*

The major climatic factors affected by atmospheric changes are temperature and precipitation. The observed changes on these two dominant climatic variables over a few decades (Vergès et al., 2005; Guisan & Thuiller, 2005; Pereira et al. 2010) might have an impact on species distributions and community composition. In this study we used two different sets of environmental variables: one for the current (2014) and one for the past (1990) climate. These factors reflect changes on the

long-term values of temperature and precipitation. Monthly average temperature [°C] and precipitation [mm] maps for both current and past climate were calculated based on 30 years (1961-1990) and 25 years (1991-2015) of meteorological data from national weather stations and extrapolated to each pixel according to the method described in Zimmermann & Kienast (1999). Additionally, a digital elevation model was used to calculate the global solar radiation [$Wh/m^2$], the slope [°] and the topographic position. For soil properties, we used a map of modeled soil pH established by Burri et al. (2009). All environmental data had a spatial resolution of 25 m, closely matching the plot size of the field sampling (d = 20 m, see *Fig. 6* for predictors examples).

### 2.4 Species distribution and community modelling

#### *2.4.1 Species Distribution Models (SDMs)*

Six environmental predictors were selected for species distribution modelling: annual mean temperature, annual sum of precipitation, annual sum of solar radiation, topographic position, slope and soil pH. These variables were selected because they cover the main factors necessary for plants life (energy, water, light and nutrients). They are therefore expected to be of ecophysiological significance (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Austin & Van Niel, 2011). They are not highly cross-correlated (<0.75; Dorman et al., 2013) and have been shown to allow reasonable predictions for a large number of different species and taxonomic groups. As the time between current and past conditions reaches only 20-25 years, we considered annual sum of radiation, soil's pH, slope and topographic position to be unaffected by climate change.

SDMs were run with the R package biomod2 (Thuiller et al., 2009; Thuiller et al., 2013) in R 3.1.2 (R Development Core Team, 2014). The modelling was calibrated with species presence/absence and climatic data from the past dataset (1988 to 2002), using generalized linear models (GLM; R library: 'glm'; McCullagh & Nelder, 1989), general additive models (GAM; R library: 'gam'; Hastie & Tibshirani, 1990), generalized boosted regression models (GBM; R library: 'gbm'; Ridgeway, 2006) and random forest (RF, R library: 'random- Forest'; Breiman, 2001). The calibration data was split randomly (70% / 30%) to allow repeated cross-validation (N=25) and a threshold of 0.7 (AUC; Fielding & Bell, 1997) was calculated and used to create a weighted ensemble model (Araújo & New, 2007). Finally, we used an ensemble forecast with both current and past climates data to create the probability maps for each species and time period.

#### *2.4.2 Community assemblage*

A transformation of continuous probabilities into presence/absence data is necessary to construct maps of species communities. As for the methods used to create these presence/absence data are known to influence the resulting species communities, we decided to use the following eight different thresholding methods (see section "*2.4.3*"): maximizing accuracy (max Accuracy),

maximizing Cohens Kappa factor (max Kappa), maximizing True Skill Statistic (max TSS), sensitivity equal specificity (Sens=Spec), sensitivity against 1-specificity (max ROC), maximal commission error of 5% (MCE5), prevalence approach (preval) and the sum of raw probabilities (pS-SDM). Based on these community maps, we calculated for each thresholding method the Accuracy, the deviation of species richness and the Sørensen similarity index between the predicted and observed communities with the past and current models.

*2.4.3 Threshold techniques*

The **Sens=Spec** technique selects the threshold, where the sensitivity and the specificity values are equal. In other words, this technique finds the threshold where positive observations are just as likely to be wrong as negative observations (Freeman & Moisen, 2008).

The **max Accuracy** method maximises the correct prediction of presences and absences (Percent Correctly Classified; Liu et al., 2011). Nevertheless, this method is known to be highly influenced by the proportion of presences and absences in the dataset.

The **max Kappa** threshold is selected to maximize Cohens Kappa factor assessing the improvement over chance prediction (Cohen, 1968).

The **max TSS** method selects the highest average success rates of net prediction of presences and absences calculated by the True Skill Statistic (TSS, sensitivity + specificity -1). This technique is a recent method in ecology that has the same advantages as the Kappa method. However, it is not influenced by variations in prevalence between absences and presences (Allouche et al., 2006).

The **max ROC** threshold corresponds to the point on Receiver Operating Characteristic (ROC) curve (sensitivity against 1-specificity), which has the shortest distance from the top-left corner (0,1) in ROC plot.

The minimal commission error technique (**MCE5**) promotes a manual selection of a desired threshold through a minimum acceptable error (maximal commission error established: 0.05; Fielding & Bell, 1997) and the max ROC technique maximises AUC value.

The prevalence technique (**preval**) selects as threshold defining the predicted prevalence as equal to the observed prevalence in the calibration data.

The probability stacked species distribution modelling approach (**pS-SDM**) sums up the probability for all the species in a given plot in order to create a species richness map. This map is then used to select the species in each plot according to a probability ranking rule (Dubuis et al. 2011).

## 2.5 Evaluation of the predictive models with fieldwork

### *2.5.1 Selecting plots for the current sampling*

As we did not have enough time to resurvey all 3076 sites, we followed a random stratified sampling strategy to select plots, using the following strata: (1) elevation, (2) modelled changes in site species richness and (3) site specific species turnover (Sørensen similarity). As we expected stronger climate change impacts at higher elevation sites, we decided to stratify our sampling by low (<1000 m), medium (1000-1500 m) and high elevation (>1500 m).

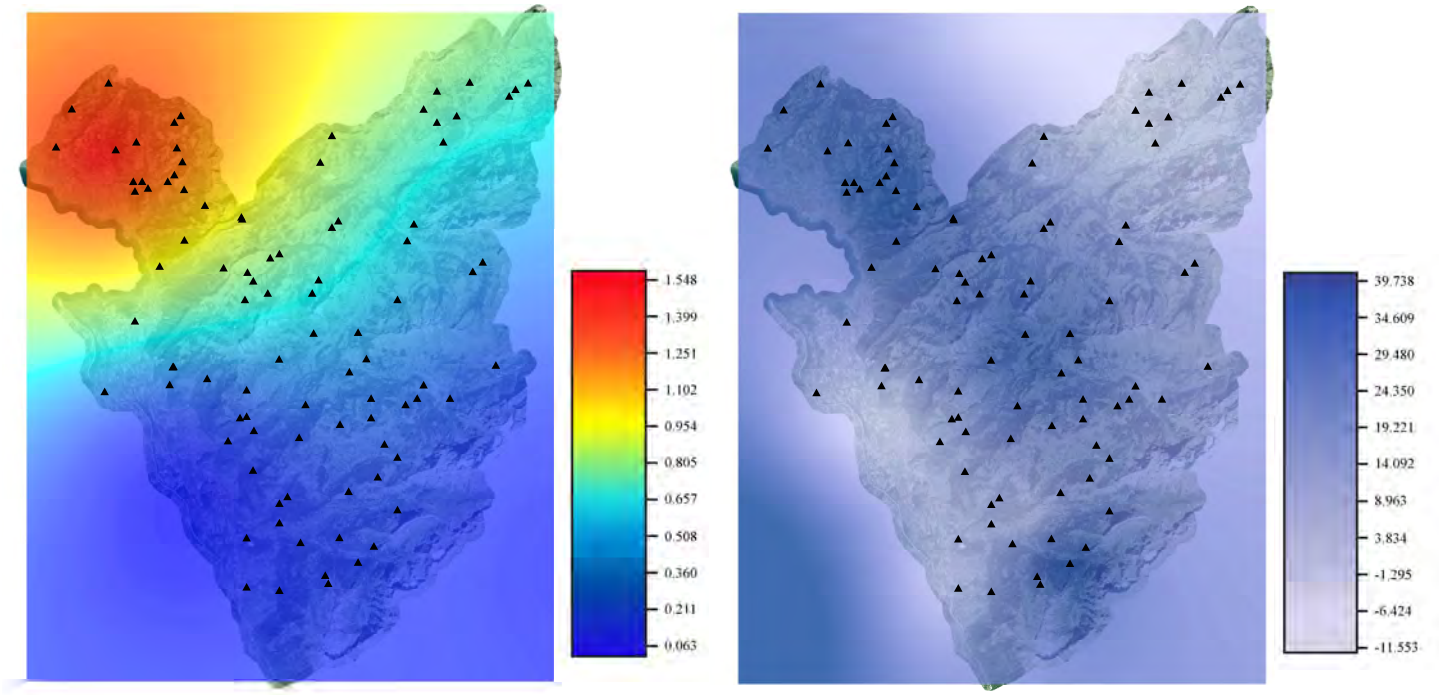



***Figure 7*** *– Maps showing changes between past (1960-1990) and current (2014) climatic conditions for temperature [°C/year] (left) and precipitations [mm/year] (right) through a subtraction of pixel raster maps. Black triangles display current resurveys sampling from 2014.*

Based on the predicted shifts in species richness (past vs. current), we divided the plots into the following three categories: increased (+5 or more), static (+5 to -5) and decreased species richness (-5 or more). We classified the sites according to their Sørensen similarity between past and current projections in three categories to account for predicted changes in species composition (turnover) rather than species number: low (<0.5), medium (0.5-0.75) and high similarity (>0.75). Visiting four sites in each possible strata combination would result in a total of 108 sites (3x3x3x4). However, not all combinations occurred in our simulation and plots that were located on a slope ≥ 40° were excluded from the selection, because they were unreachable or dangerous. Therefore, we ended up with a total of 92 sites, which were illustrated thought maps showing the interpolated changes in climate conditions between the past and current time period (*Fig. 7*).

### *2.5.2 Current forest surveys*

The 92 forest plots selected by random stratified sampling were revisited during the summer 2014

(mid July to the end of August 2015). First, plots' center were located by GPS (Garmin ETrex 10 with 3-5 m accuracy) and the location was verified by comparing the arborescent stratum (> 6 m) of past surveys with the current vegetation assuming that most of the dominant trees from 20 years ago should still be present. For each plot, we took photos of the vegetation structure, measured the slope and the topographic position with a compass Recta containing a clinometer and measured the canopy closure with a densitometer (measure forest density from unobstructed sighting positions).

The phytosociological surveys were conducted with the same Braun-Blanquet based field method employed by Sylvain Meier for the past data sampling to ensure optimal comparability (area was defined by a 10 m radius circle). Braun-Blanquet codes used were r = 1 - 3 individual(s), + = <1%, 1 = 1 -5%, 2 = 6-25%, 3 = 25-50%, 4 = 51-75% and 5 = 76-100% (Braun-Blanquet, 1964). Before leaving the survey, an aluminum plate was buried to relocate more easily the plot in the future.

### 2.6 Statistical analysis

#### *2.6.1 Processing data*

First, the tree layer was removed from the phytosociological dataset, as it is impossible to observe climate driven changes in the composition of well-established large trees (> 6 m) within 20 years. Then, Braun-Blanquet codes were transformed into two different kinds of numerical values: presence/absence (binary) and numerical dominance according to Wildi (2010) (*Table 1*). We obtained numerical dominance values through a substitution of the Braun-Blanquet codes by numbers from 0 to 8. Then, a square-root transformation was added to give more weight to species with low cover (Güsewell & Le Nédic, 2004).

**Braun-Blanquet codes**

| Braun-Blanquet codes | Presence/absence | Numerical dominance [a] | Numerical dominance [b] |
|---|---|---|---|
| absence | 0 | 0 | 0 |
| r | 1 | 1 | 1 |
| + | 1 | 2 | 1.41 |
| 1 | 1 | 3 | 1.73 |
| 2 | 1 | 4 | 2.12 |
| 3 | 1 | 6 | 2.45 |
| 4 | 1 | 7 | 2.65 |
| 5 | 1 | 8 | 2.83 |

***Table 1*** *– Table containing possible transformations for numerical analysis according to Wildi (2010). Numerical dominance* $_a$ *represents the substitution of Braun-Blanquet codes (1964) and numerical dominance* $_b$ *is the square root transformation on these last values.*

These two types of data were organized in Excel tables containing the species cover values (columns) per surveys (lines) for the past and recent datasets. Binary values were selected for the modelling to compare the observed changes with the models predictions. The cover data substituted by the numerical dominance values allowed to study the observed species composition with Principle Component Analysis (PCA).

*2.6.2 Analysing model predictions of species and communities*

The first aim of this study was to compare models predictions with real observed shifts. First, the indices of AUC, TSS, overprediction, underprediction, sensitivity and specificity were calculated to estimate the validity of the modelled species distributions in the past. This step was important to see if our models are well suited for prediction. Overprediction results represent the proportion of false predicted presences ($F_{alse}P_{ositif}$ / $T_{rue}N_{egatif}$ + $F_{alse}P_{ositif}$). This explains the overestimation in species distribution from the model. The underprediction results are the proportion of false predicted absences, meaning that the true vegetation distribution is underestimated ($F_{alse}N_{egatif}$ / $T_{rue}P_{ositif}$ + $F_{alse}N_{egatif}$). Furthermore, sensitivity is the probability that the model has correctly predicted an observation, while the specificity corresponds to a correct prediction of absence (Liu et al., 2011).

Then, to analyse the community distribution and ecological changes, two different analyses comparing the past and current field observations with models predictions were executed. The first one, using the cover data transformed in binary values, studied changes in species richness (past - current values) and the similarity of Sørensen. Species richness deviation are the number of plants that have been either lost or won between past and current surveys and the similarity of Sørensen measures the similarity in species composition between past and current surveys (turnover; Sørensen, 1948). These indices were evaluated and compared through statistical tests (Wilcoxon test) and illustrated in boxplots with R 3.1.2 tools, regarding the three elevation belts and the specific stratification used for the sampling modelling. Finally, to evaluate past and current ecological conditions, the second analysis was based on Landolt's indicators (Landolt et al., 2010; Swiss geographic alternatives from Ellenberg's indicator values; Ellenberg, 1992), to show if modelling can correctly predict the ecological conditions and thereby the species pool right. Actually, these ordinal variables are often relevant for the quantitative analysis of the vegetation to describe, analyse or modelize ecological niche of species, taxa or ecosystems (Landolt et al., 2010).

Landolt's values are separated into three groups: ecological indicators (climate and soil indicators), biological attributes (salt and heavy metal tolerance) or growth and life strategies (leaf duration, growth forms, etc.; Landolt et al., 2010). Therefore, we chose indicators which have potentially changed in accordance with the species distribution modified by climate change. Thus, we selected temperature T, soil moisture F, light L and humus H content in soil. Then, we calculated averages of these values per surveys for past and current predictions (Preval threshold method) and observations to see the potential ecological changes and to evaluate the models predictions. To display our results, we plotted them on graphics per elevation belt. Although a lot of ecologists employed means of indicator values to determine the ecology of areas (e.g., Bodin et al., 2013;

Grytnes et al, 2014), these manipulations must be employed with precaution. Indeed, according to Zelený & Schaffers (2012), this tends to explain more variance than the real observed change.

*2.6.3 Analysing the evolution of vegetation dynamics*

The second aim of this study was to compare recent species surveys with the past one in order to evaluate floristic changes over the last 20-25 years. To evaluate this dynamics, we used Principle Component Analysis. Ecologists often use this method, because they can analyse a set of species data with environmental variables by combining multiple regressions with Principal Component Analysis (PCA). Therefore, this constrained linear ordination method allowed to extract and summarise variations in a studied data (abundance of species), which can be identified by explanatory correlated variables (Borcard et al., 2011).

Three steps were followed to obtain Principle Component Analysis. Firstly, we divided the full cover matrix in three sets containing plots localised in three different elevation belts (24 surveys: <1000 m, 32 surveys: 1000-1500 m and 36 surveys: >1500 m). This splitting takes into account that the temperature variable would explain most of the variance with the complete gradient, masking possible effects of climate change. Indeed, the elevation gradient is highly correlated with a decrease in temperature averages of -0.56°C to -0.57°C per 100 m of mountain elevation in the Swiss Alps (Ozenda, 1985; Lachat et al., 2011). Secondly, as this dataset has semi-quantitative values, which zero means absence, a common standardization for ecological analysis was executed with the function 'decostand ()' from 'vegan' package (method: Hellinger; Borcard et al., 2011). Indeed, according to Legendre & Legendre (1998), Hellinger transformation is used when statistical exploration is a linear ordination and offers the best compromise between resolution and linearity to adapt the cover data to the analysis (Legendre & Gallagher, 2001).

Finally, we used Landolt's indicators (Swiss geographic alternatives to Ellenberg's indicator values; Ellenberg, 1992) as explanatory variables to give an ecological estimation about the patterns displayed on the PCA graphics. We selected eight ecological indexes: light L, temperature T, continentatily K, soil moisture F, soil reactivity R (pH), nutrients N, humus H and soil aeration D. Our approach was to find corresponding ecological factors for each plant present in our dataset in order to calculate weighted averages per plots for Principle Component Analysis.

Then, according to a more specific analysis, these values were gathered into three tables to study the general past and current ecology trend per elevation belt (*Table 2*) and weighted averages from species frequency and cover, which are different between the associated pairs of past and current surveys (*Tables 6* and *8*). Student tests (Bailey, 1995) were also calculated to evaluate differences in Landolt's indicators averages (*Tables 3,5,6 and 8).*

# 3. RESULTS

## 3.1 Variables evaluation

The most important predictor included in the majority of species distribution models was annual mean temperature (median: 0.65), followed by annual sum of radiation (median: 0.21), annual sum of precipitation (median: 0.19), slope (median: 0.13) and soil's pH (median: 0.098) (*Fig. 8*).

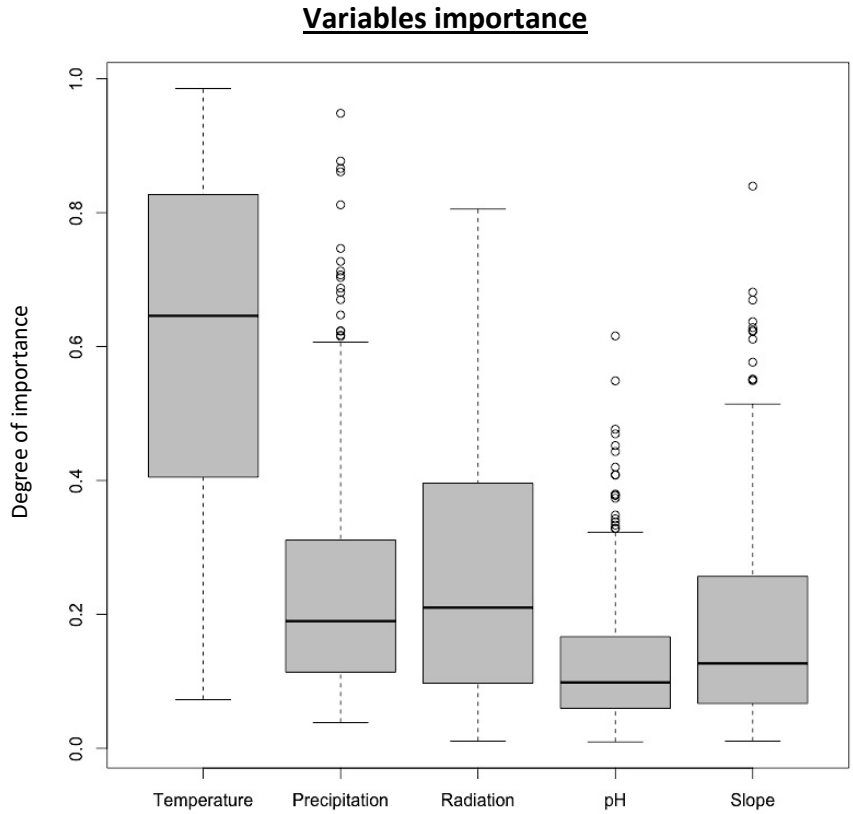



***Figure 8*** *– Boxplots illustrating the relative importance of predictors, which were used for species distribution modelling.*

## 3.2 Performance of species distribution models

### *3.2.1 Model performance for past predictions of species*

The predictive capacity of the models generated from past conditions had excellent AUC values reaching an average of 0.952 (standard deviation: 0.055; median: 0.967; *Fig. 9*). The species such as *Listera ovata* (0.700), *Carex ornithopoda* (0.705) and *Agrostis capillaris* (0.709) had the lowest AUC values and *Trifolium medium*, *Ranunculus repens* and *Globularia nudicaulis* obtained the highest score (1.000). The median values for accuracy and TSS strongly depended on the chosen thresholding method and ranged from 0.880 (average: 0.873 ± 0.092; max TSS method; *Appx. 3*) to 0.967 (average: 0.947 ± 0.058; max Accuracy method; *Fig. 10*) for an accuracy between 0.239 (average: 0.299 ± 0.314; pS-SDM method; *Appx. 3*) and 0.862 (average: 0.806 ± 0.178; max TSS method; *Fig. 10*) for TSS scores.

## Evaluation of predictions

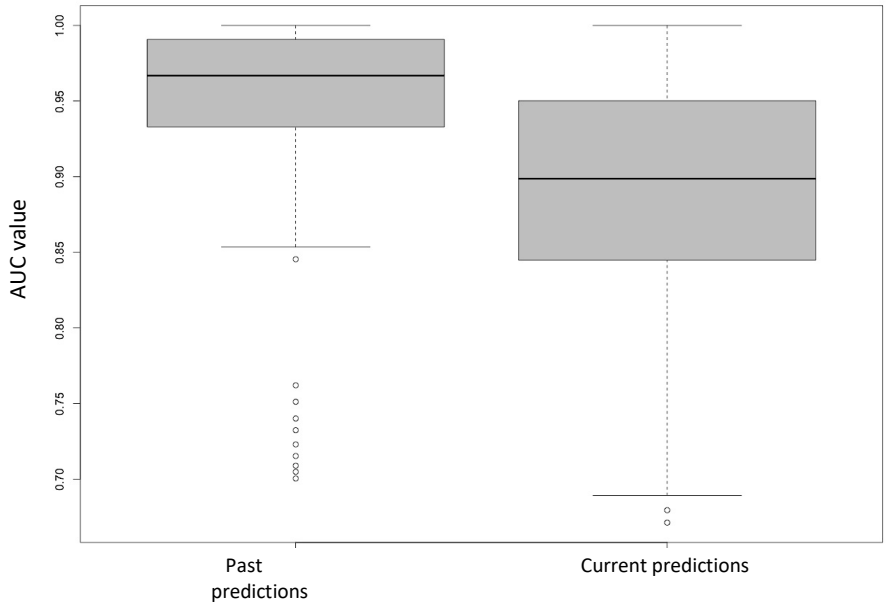



***Figure 9*** *– Boxplots of the AUC values for past and current predictions.*

## The best model of prediction

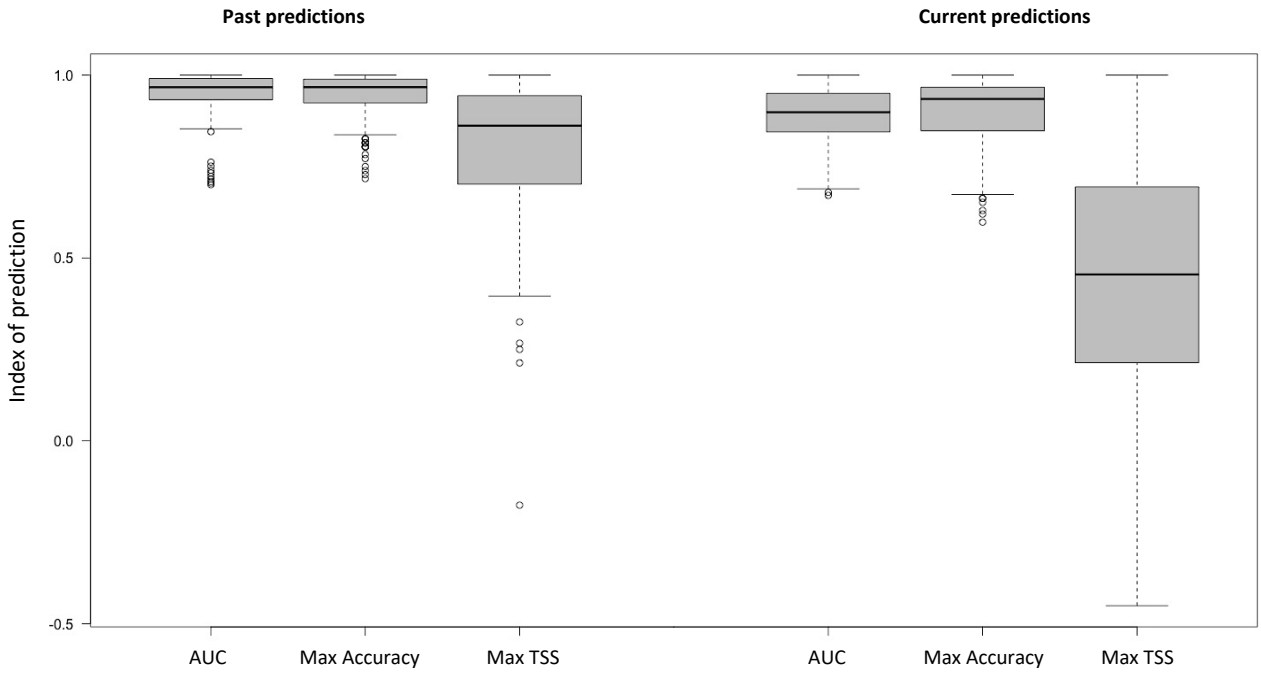



***Figure 10*** *– Boxplots of AUC, Max Accuracy and TSS for past and current predictions.*

The methods have correctly predicted, on average, 36.3% (sd: ± 37.3%; pS-SDM method) to 94.1% (sd: ± 11.7%; max TSS method) of presence values (general average of sensitivity: 73.2% ± 20.1%) and 86.8% (sd: ± 9.7%; max TSS method) to 97.5% (sd: ± 5.7%; max Accuracy method) of absence values (general average of specificity: 92.7% ± 4%). Indeed, a general bias was observable through averages reaching from 2.5% (sd: ± 5.7%; max Accuracy method) to 13.2% (sd: ± 9.7%; max TSS method) per models in cases of overestimation (general average:

7.3% ± 4%) and from 5.9% (sd: ± 11.7%; max TSS method) to 63.7% (sd: ± 37.3%, pS-SDM method) in cases of underestimation (general average: 26.8% ± 20.1%).

*3.2.2 Models performance for the current predictions of species*

The performance of current predictions had as good AUC values as the past predictions, with an average of 0.893 (standard deviation: 0.073; median: 0.899; *Fig 9*). The lowest AUC values were for *Carex ornithopoda* (0.671), *Agrostis capillaris* (0.679) and *Fragaria vesca* (0.689). The highest AUC values corresponded to *Cardamine impatiens*, *Ranunculus repens* and *Trifolium medium* with a score between 1.000 and 1.000. Median values obtained for accuracy scores were between 0.815 (average: 0.815 ± 0.103; max TSS method; *Appx. 3*) and 0.935 (average: 0.899 ± 0.090; max Accuracy; *Fig. 10*) and the TSS values ranged from 0.000 (average: 0.189 ± 0.270; pS-SDM method; *Appx. 3*) to 0.455 (average: 0.436 ± 0.327; max TSS method; *Fig. 6*). The methods have correctly predicted averages ranging from 27.1% (sd: ± 34.2%; pS-SDM method) to 60.5% (sd: ± 34.1%; max TSS method) of the presence values (general average of sensitivity: 43.6% ± 12.9%) and from 83.1% (sd: ± 10.8%; max TSS method) to 95% (sd: ± 6.8%; max Accuracy method) for absence values (general average of specificity: 90% ± 4.5%). The general bias observable was between 5% (sd: ± 6.8%; max Accuracy method) to 16.9% (sd: ± 11%; max TSS method) for the overestimation (general average: 10.4% ± 4.5%) and from 39.5% (sd: ± 34.1%; max TSS method) to 72.9% (sd: ± 34.2%; pS-SDM method) for the underestimation (general average: 56.4% ± 12.9%).

**3.3 Performance of community distribution models**

The predictive capacity of community models for past conditions showed good accuracy values reaching between 0.877 (sd: ± 0.038; median: 0.883; max TSS method) and 0.954 (sd: ± 0.025; median: 0.954; max Accuracy method) for the average values. The deviation of species richness obtained avergage values ranging from -4.815 (sd: ± 8.283; median: -4; max Accuracy method) to 29.207 (sd: ± 12.218; median: 29.5; max TSS method) and the similarity reached scores between 0.529 (sd: ± 0.144; median: 0.555; max TSS method) and 0.664 (sd: ± 0.121; median: 0.684; max Kappa method) (*Table 2*).

The current community predictions also acquired high accuracy scores with averages per model method reaching values between 0.831 (sd: ± 0.040; median: 0.828; max TSS method) and 0.911 (sd: ± 0.0307; median: 0.914; max Accuracy method). The species richness deviation obtained average values ranging from -4.750 (sd: ± 13.607; median: -6; max Accuracy method) to 30.772 (sd: ± 15.586; median: 31; max TSS method) and from 0.330 (sd: ± 0.124; median: 0.323; MCE5 method) to 0.518 (sd: ± 0.117; median: 0.522; pS-SDM method) for the similarity scores (*Table 2*).

| Past prediction of the communities | | | | |
|---|---|---|---|---|
| Elevation belts | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | -4 | 0.959 | 0.652 |
| | Max Kappa | 4 | 0.952 | 0.668 |
| | Max ROC | 23 | 0.897 | 0.515 |
| | Max TSS | 27 | 0.885 | 0.487 |
| | MOE5 | 6 | 0.933 | 0.551 |
| | Preval | 1 | 0.953 | 0.657 |
| | pS-SDM | 4 | 0.944 | 0.610 |
| | Sens=Spec | 21 | 0.903 | 0.526 |
| | General average | 10 | 0.928 | 0.583 |
| | Median | | | |
| | Max Accuracy | -3 | 0.957 | 0.667 |
| | Max Kappa | 4 | 0.957 | 0.707 |
| | Max ROC | 21 | 0.902 | 0.509 |
| < 1000 m | Max TSS | 25 | 0.890 | 0.477 |
| | MOE5 | 4 | 0.941 | 0.572 |
| | Preval | 2 | 0.961 | 0.710 |
| | pS-SDM | 5 | 0.942 | 0.625 |
| | Sens=Spec | 19 | 0.910 | 0.524 |
| | General average | 9 | 0.932 | 0.599 |
| | Standard deviation | | | |
| | Max Accuracy | 7 | 0.018 | 0.095 |
| | Max Kappa | 9 | 0.022 | 0.112 |
| | Max ROC | 13 | 0.037 | 0.140 |
| | Max TSS | 13 | 0.037 | 0.142 |
| | MOE5 | 14 | 0.034 | 0.113 |
| | Preval | 9 | 0.020 | 0.110 |
| | pS-SDM | 8 | 0.019 | 0.151 |
| | Sens=Spec | 14 | 0.036 | 0.132 |
| | General average | 11 | 0.028 | 0.124 |
| Elevation band | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | -5 | 0.946 | 0.652 |
| | Max Kappa | 4 | 0.935 | 0.626 |
| | Max ROC | 22 | 0.897 | 0.560 |
| | Max TSS | 26 | 0.887 | 0.543 |
| | MOE5 | -2 | 0.936 | 0.605 |
| | Preval | 1 | 0.939 | 0.637 |
| | pS-SDM | 3 | 0.920 | 0.550 |
| | Sens=Spec | 20 | 0.900 | 0.564 |
| | General average | 8 | 0.920 | 0.592 |
| | Median | | | |
| | Max Accuracy | -4 | 0.952 | 0.667 |
| | Max Kappa | 6 | 0.938 | 0.629 |
| | Max ROC | 22 | 0.903 | 0.559 |
| 1000 - 1500 m | Max TSS | 26 | 0.890 | 0.555 |
| | MOE5 | -3 | 0.947 | 0.608 |
| | Preval | 3 | 0.941 | 0.635 |
| | pS-SDM | 4 | 0.924 | 0.552 |
| | Sens=Spec | 21 | 0.907 | 0.575 |
| | General average | 9 | 0.925 | 0.597 |
| | Standard deviation | | | |
| | Max Accuracy | 9 | 0.031 | 0.122 |
| | Max Kappa | 9 | 0.027 | 0.139 |
| | Max ROC | 12 | 0.039 | 0.162 |
| | Max TSS | 12 | 0.039 | 0.164 |
| | MOE5 | 10 | 0.035 | 0.144 |
| | Preval | 9 | 0.030 | 0.131 |
| | pS-SDM | 11 | 0.025 | 0.121 |
| | Sens=Spec | 11 | 0.039 | 0.164 |
| | General average | 10 | 0.033 | 0.143 |
| Elevation band | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | -5 | 0.947 | 0.694 |
| | Max Kappa | 6 | 0.938 | 0.694 |
| | Max ROC | 29 | 0.877 | 0.571 |
| | Max TSS | 34 | 0.863 | 0.546 |
| | MOE5 | 3 | 0.921 | 0.604 |
| | Preval | 3 | 0.937 | 0.680 |
| | pS-SDM | 2 | 0.926 | 0.627 |
| | Sens=Spec | 27 | 0.884 | 0.581 |
| | General average | 12 | 0.912 | 0.625 |
| | Median | | | |
| | Max Accuracy | -5 | 0.952 | 0.694 |
| | Max Kappa | 7 | 0.940 | 0.700 |
| | Max ROC | 29 | 0.879 | 0.615 |
| > 1500 m | Max TSS | 34 | 0.868 | 0.600 |
| | MOE5 | 2 | 0.928 | 0.604 |
| | Preval | 3 | 0.938 | 0.667 |
| | pS-SDM | 2 | 0.928 | 0.675 |
| | Sens=Spec | 27 | 0.952 | 0.694 |
| | General average | 12 | 0.923 | 0.650 |
| | Standard deviation | | | |
| | Max Accuracy | 8 | 0.022 | 0.090 |
| | Max Kappa | 8 | 0.020 | 0.101 |
| | Max ROC | 11 | 0.034 | 0.133 |
| | Max TSS | 11 | 0.033 | 0.123 |
| | MOE5 | 13 | 0.035 | 0.139 |
| | Preval | 9 | 0.021 | 0.096 |
| | pS-SDM | 9 | 0.020 | 0.081 |
| | Sens=Spec | 12 | 0.034 | 0.131 |
| | General average | 10 | 0.027 | 0.112 |
| | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | -5 | 0.950 | 0.669 |
| | Max Kappa | 4 | 0.940 | 0.664 |
| | Max ROC | 25 | 0.889 | 0.552 |
| | Max TSS | 29 | 0.877 | 0.529 |
| | MOE5 | 2 | 0.929 | 0.591 |
| | Preval | 2 | 0.942 | 0.659 |
| | pS-SDM | 3 | 0.928 | 0.596 |
| | Sens=Spec | 23 | 0.894 | 0.561 |
| | General average | 10 | 0.919 | 0.603 |
| | Median | | | |
| | Max Accuracy | -4 | 0.883 | 0.555 |
| | Max Kappa | 2 | 0.895 | 0.565 |
| | Max ROC | 3 | 0.900 | 0.583 |
| All elevation | Max TSS | 3 | 0.931 | 0.596 |
| | MOE5 | 6 | 0.938 | 0.604 |
| | Preval | 23 | 0.941 | 0.667 |
| | pS-SDM | 26 | 0.947 | 0.672 |
| | Sens=Spec | 30 | 0.954 | 0.684 |
| | General average | 11 | 0.924 | 0.616 |
| | Standard deviation | | | |
| | Max Accuracy | 8 | 0.025 | 0.105 |
| | Max Kappa | 9 | 0.024 | 0.121 |
| | Max ROC | 12 | 0.037 | 0.145 |
| | Max TSS | 12 | 0.038 | 0.144 |
| | MOE5 | 13 | 0.035 | 0.135 |
| | Preval | 9 | 0.025 | 0.113 |
| | pS-SDM | 9 | 0.023 | 0.120 |
| | Sens=Spec | 12 | 0.037 | 0.144 |
| | General average | 11 | 0.031 | 0.128 |

| Current prediction of the communities | | | | |
|---|---|---|---|---|
| Elevation belts | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | 4 | 0.920 | 0.397 |
| | Max Kappa | 14 | 0.896 | 0.377 |
| | Max ROC | 36 | 0.829 | 0.304 |
| | Max TSS | 40 | 0.819 | 0.296 |
| | MOE5 | 23 | 0.853 | 0.256 |
| | Preval | 11 | 0.904 | 0.391 |
| | pS-SDM | 10 | 0.917 | 0.454 |
| | Sens=Spec | 35 | 0.834 | 0.304 |
| | General average | 21 | 0.871 | 0.347 |
| | Median | | | |
| | Max Accuracy | 4 | 0.917 | 0.418 |
| | Max Kappa | 14 | 0.893 | 0.421 |
| | Max ROC | 34 | 0.823 | 0.314 |
| < 1000 m | Max TSS | 38 | 0.817 | 0.319 |
| | MOE5 | 25 | 0.852 | 0.240 |
| | Preval | 12 | 0.900 | 0.433 |
| | pS-SDM | 9 | 0.919 | 0.444 |
| | Sens=Spec | 33 | 0.830 | 0.323 |
| | General average | 21 | 0.869 | 0.364 |
| | Standard deviation | | | |
| | Max Accuracy | 14 | 0.026 | 0.134 |
| | Max Kappa | 15 | 0.034 | 0.143 |
| | Max ROC | 18 | 0.044 | 0.114 |
| | Max TSS | 17 | 0.042 | 0.114 |
| | MOE5 | 20 | 0.043 | 0.102 |
| | Preval | 15 | 0.032 | 0.149 |
| | pS-SDM | 9 | 0.019 | 0.139 |
| | Sens=Spec | 18 | 0.044 | 0.113 |
| | General average | 16 | 0.035 | 0.126 |
| Elevation band | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | -7 | 0.909 | 0.434 |
| | Max Kappa | 2 | 0.895 | 0.449 |
| | Max ROC | 22 | 0.847 | 0.406 |
| | Max TSS | 26 | 0.837 | 0.399 |
| | MOE5 | -2 | 0.879 | 0.377 |
| | Preval | -1 | 0.902 | 0.459 |
| | pS-SDM | 2 | 0.911 | 0.530 |
| | Sens=Spec | 20 | 0.851 | 0.410 |
| | General average | 8 | 0.879 | 0.427 |
| | Median | | | |
| | Max Accuracy | -7 | 0.903 | 0.422 |
| | Max Kappa | 3 | 0.893 | 0.462 |
| | Max ROC | 22 | 0.847 | 0.476 |
| 1000 - 1500 m | Max TSS | 25 | 0.836 | 0.426 |
| | MOE5 | -2 | 0.871 | 0.304 |
| | Preval | -1 | 0.899 | 0.458 |
| | pS-SDM | 2 | 0.909 | 0.519 |
| | Sens=Spec | 21 | 0.847 | 0.439 |
| | General average | 8 | 0.875 | 0.432 |
| | Standard deviation | | | |
| | Max Accuracy | 13 | 0.034 | 0.147 |
| | Max Kappa | 12 | 0.033 | 0.134 |
| | Max ROC | 13 | 0.042 | 0.128 |
| | Max TSS | 13 | 0.043 | 0.131 |
| | MOE5 | 16 | 0.041 | 0.127 |
| | Preval | 12 | 0.034 | 0.133 |
| | pS-SDM | 11 | 0.024 | 0.112 |
| | Sens=Spec | 12 | 0.043 | 0.134 |
| | General average | 13 | 0.037 | 0.131 |
| Elevation band | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | -8 | 0.907 | 0.478 |
| | Max Kappa | 3 | 0.891 | 0.497 |
| | Max ROC | 25 | 0.844 | 0.464 |
| | Max TSS | 29 | 0.834 | 0.454 |
| | MOE5 | -2 | 0.878 | 0.382 |
| | Preval | -1 | 0.897 | 0.499 |
| | pS-SDM | 0 | 0.907 | 0.551 |
| | Sens=Spec | 22 | 0.849 | 0.461 |
| | General average | 9 | 0.876 | 0.473 |
| | Median | | | |
| | Max Accuracy | -9 | 0.909 | 0.484 |
| | Max Kappa | 2 | 0.897 | 0.515 |
| | Max ROC | 25 | 0.845 | 0.460 |
| > 1500 m | Max TSS | 30 | 0.831 | 0.454 |
| | MOE5 | -2 | 0.886 | 0.388 |
| | Preval | -1 | 0.902 | 0.518 |
| | pS-SDM | 2 | 0.912 | 0.557 |
| | Sens=Spec | 24 | 0.952 | 0.694 |
| | General average | 9 | 0.892 | 0.509 |
| | Standard deviation | | | |
| | Max Accuracy | 12 | 0.031 | 0.116 |
| | Max Kappa | 12 | 0.032 | 0.095 |
| | Max ROC | 14 | 0.035 | 0.099 |
| | Max TSS | 14 | 0.036 | 0.101 |
| | MOE5 | 15 | 0.034 | 0.110 |
| | Preval | 13 | 0.030 | 0.093 |
| | pS-SDM | 10 | 0.024 | 0.089 |
| | Sens=Spec | 14 | 0.034 | 0.100 |
| | General average | 13 | 0.032 | 0.101 |
| | Methods | Species richness deviation | Accuracy | Similarity |
| | Average | | | |
| | Max Accuracy | -5 | 0.911 | 0.442 |
| | Max Kappa | 5 | 0.894 | 0.449 |
| | Max ROC | 27 | 0.841 | 0.402 |
| | Max TSS | 31 | 0.831 | 0.394 |
| | MOE5 | 5 | 0.872 | 0.330 |
| | Preval | 2 | 0.901 | 0.457 |
| | pS-SDM | 3 | 0.911 | 0.518 |
| | Sens=Spec | 25 | 0.846 | 0.402 |
| | General average | 12 | 0.876 | 0.424 |
| | Median | | | |
| | Max Accuracy | -6 | 0.828 | 0.323 |
| | Max Kappa | 1 | 0.838 | 0.402 |
| | Max ROC | 3 | 0.841 | 0.416 |
| All elevation | Max TSS | 4 | 0.871 | 0.422 |
| | MOE5 | 5 | 0.893 | 0.440 |
| | Preval | 24 | 0.900 | 0.464 |
| | pS-SDM | 25 | 0.914 | 0.477 |
| | Sens=Spec | 31 | 0.914 | 0.522 |
| | General average | 11 | 0.875 | 0.433 |
| | Standard deviation | | | |
| | Max Accuracy | 14 | 0.031 | 0.135 |
| | Max Kappa | 14 | 0.033 | 0.131 |
| | Max ROC | 16 | 0.040 | 0.129 |
| | Max TSS | 16 | 0.040 | 0.131 |
| | MOE5 | 20 | 0.040 | 0.124 |
| | Preval | 14 | 0.032 | 0.130 |
| | pS-SDM | 11 | 0.023 | 0.117 |
| | Sens=Spec | 16 | 0.040 | 0.131 |
| | General average | 15 | 0.035 | 0.128 |

***Table 2*** *– Table containing the evaluation of models capacity. Deviation of species richness, accuracy and similarity between community predictions and field observations are given for each elevation belt.*

In general, although past and current predictions obtained an excessive variation in species richness values, models predicted well the species richness of plots with deviations between observed and predicted communities being less than ± 2 species for 29% of the past plots and 20% of the current ones and ± 5 species for 86% (past) and 79% (current) of the surveys (*Table 2*). Furthermore, the similarity slightly increases along the elevation gradient with significant differences (Wilcoxon test p-values: <0.05: *, <0.01: ** and <0.001: ***). Indeed, max Kappa (*) and pS-SDM (**) methods showed differences between medium (1000-1500 m) and high (> 1500 m) belts for the past predictions. For the current predictions, the eight different threshold methods showed differences between low (< 1000 m) and high bands (max Accuracy: *; Preval and pS-SDM: **; max Kappa, ROC and TSS, MCE5 and Sens=Spec: ***) and a few of them indicated also variances between low and medium belts (MCE5 and pS-SDM: *; Sens=Spec, max Roc and TSS: **). However, there was no significant difference between the values of accuracy and species richness deviation for the communities according to the elevation belts (*Table 2*).

### 3.4 Evaluation of the predicted changes in species, communities and ecological conditions

Regarding changes in species richness and the similarity in species composition, the eight different threshold methods illustrated approximately similar tendencies. Therefore only four of them are illustrated on *Fig. 11* (Preval, max Accuracy, max Kappa and max ROC), the others are available in the *Appx. 4* (*MCE5, Sens=spec, max TSS and pS-SDM*).

#### *3.4.1 Shifts in species richness*

The predicted changes in species richness showed significant gradient of three different bands corresponding to the categories selected for the random stratified sampling (increased: +5 or more; static: +5 to -5; decreased in species richness: -5 or more) (*Fig. 11*; graphics A). Obviously, the lowest and the highest boxplots are significantly different from zero. Concerning the predicted changes distributed along the elevation belts, a trend to decrease in species richness with elevation is observable. More significant changes in species richness are visible in the lowest elevation than in medium and high bands (*Fig. 11*; graphics B). Regarding field observations, we can see a small similar tendency of species richness depending on the specific sampling stratification and an opposite trend according to the elevation belts, but the three strata were not significantly different from each other and from zero (*Fig. 11*; graphics A and B).

#### *3.4.2 Sørensen similarity in species composition (specific species turnover)*

The similarity between past and current predictions illustrated a significant gradient of three different belts, which corresponds to the categories of division selected for the random stratified sampling (low: <0.5, medium: 0.5-0.75 and high similarity: >0.75) (*Fig. 11*; graphics C).

## Species richness and similarity in plant composition according species distribution models

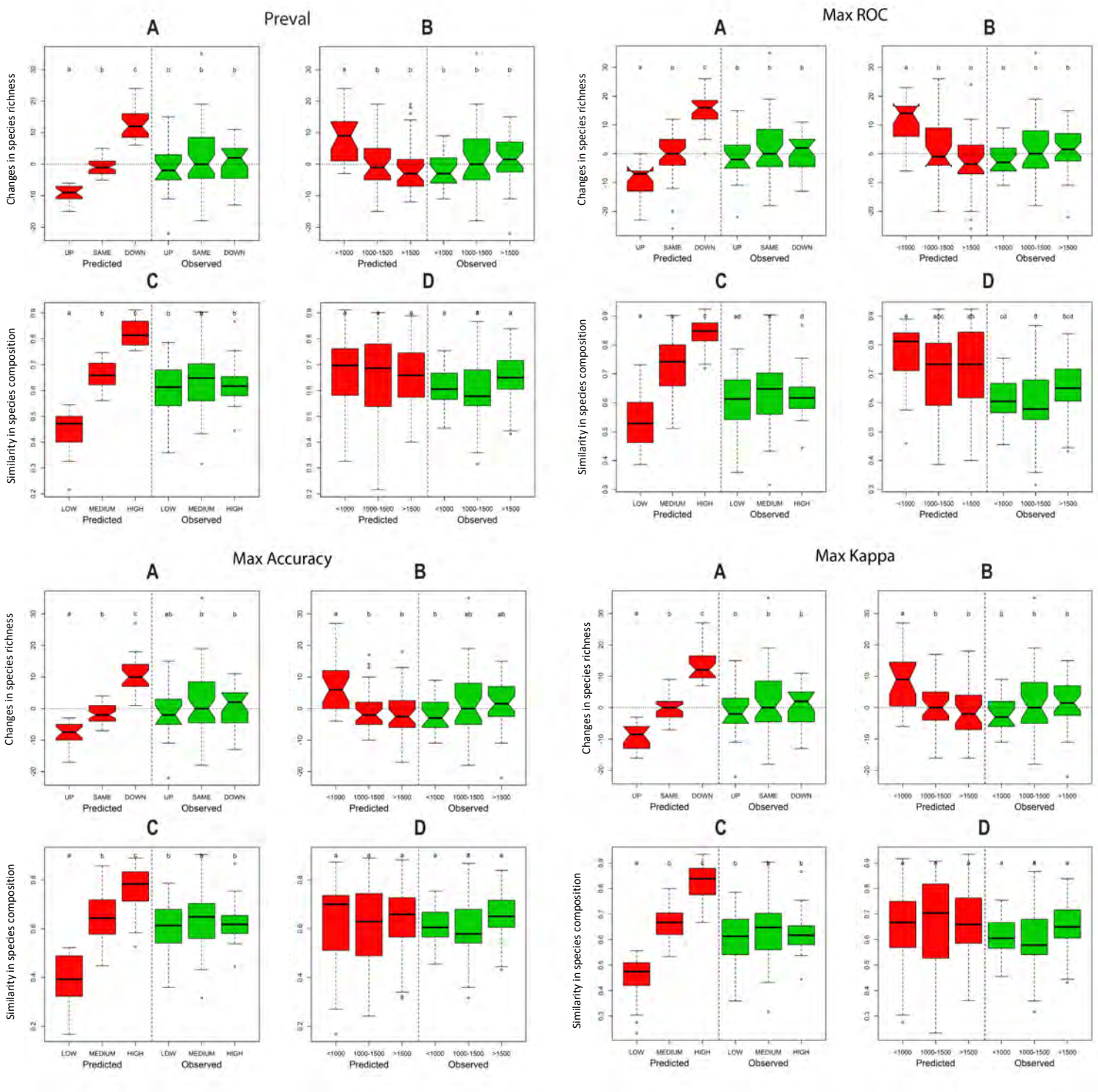



***Figure 11*** *– Boxplots illustrating changes in species richness and similarity in species composition between past and current conditions from predictions and observations depending on the division selected for the random stratified (graphics A and C) and elevation (graphics C and D) for Preval, max ROC, max Accuracy, max Kappa threshold methods. When they are different, small letters on top of boxplots illustrate significant differences between groups.*

## Ecological changes between past and current conditions

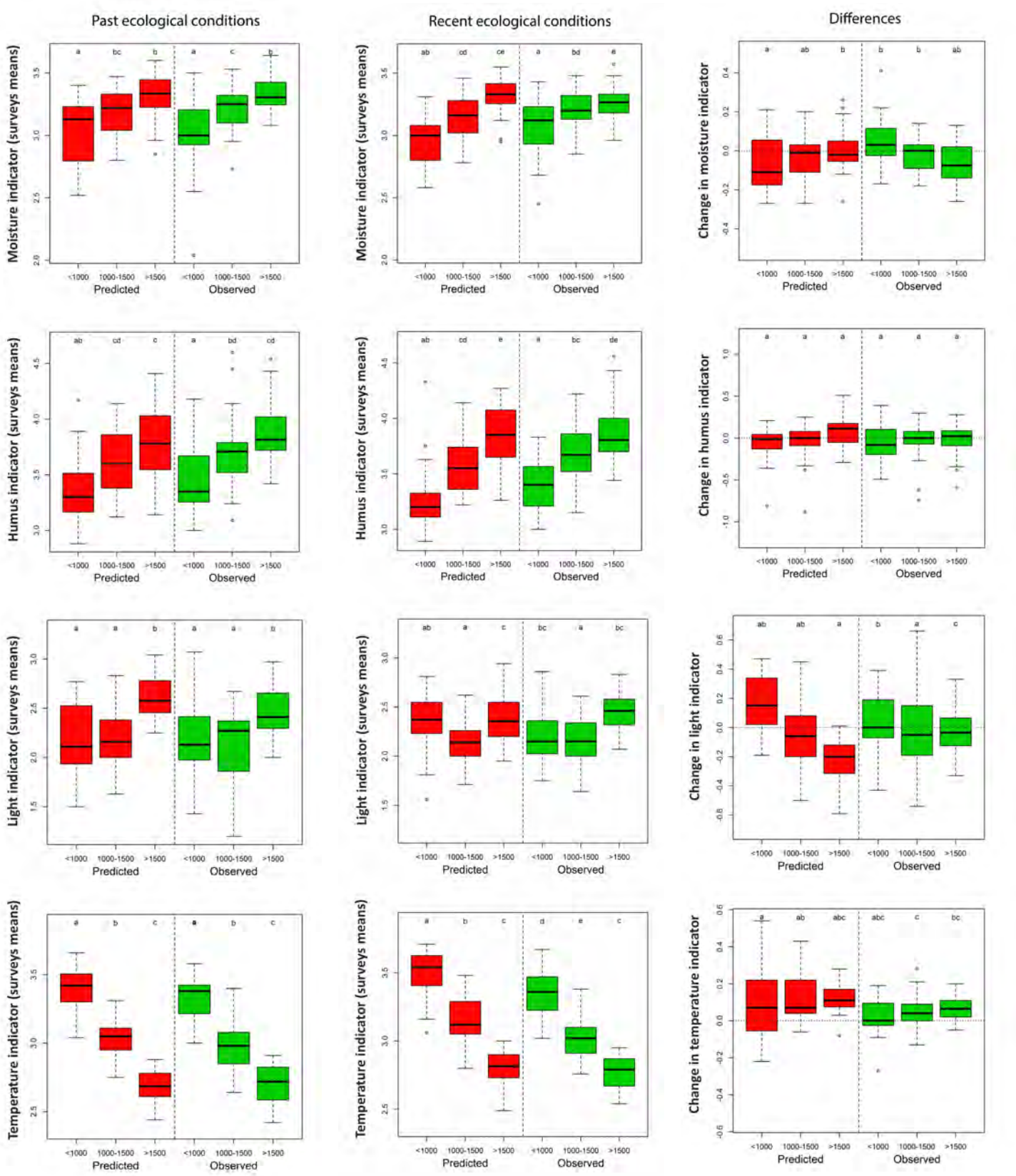



***Figure 12*** *– Graphics illustrating ecological indicators changes between predictions and field observations (past and current conditions). Boxplots on the right show ranges of shifts (past minus current conditions). When they are different, small alphabet letters on top of boxplots illustrate significant differences between groups.*

Along elevation, the predictive similarity of species composition obtained similar boxplots extended per band (*Fig. 11*; graphics D). Regarding field observations, no boxplot was significantly different from each other according to the sampling selection and as a function of the elevation belts (*Fig. 11*; graphics C and D). Nevertheless, overall species composition from field observations is more dissimilar between the two periods than for the predictions.

*3.4.3 Changes in ecological conditions (Landolt indicators)*

In general, the predicted ecological conditions matched the field observations according to soil moisture, humus, light and temperature indicators (*Fig. 12*). The predicted and observed temperature conditions illustrated significant degrees of reduction along the elevation belts, unlike humidity and humus, which increased towards the highest elevation belt. Moreover, light indicator was significantly higher at high elevation. Regarding past and current ecological indicators, several changes occurred such as a significant increase in temperature, especially in medium and high elevation belts (boxplot significant different to zero). Additionally, in these elevations, an important light reduction was observable between both inventories. A humidity reduction was also more important in field observations, at high elevation, than expected. The ecological predictions perceived an increase of light and a humidity reduction in the lowland. Unlike field ecology, which showed no significant change in light at low elevation and a humidity reduction at high elevation. Finally, the humus values have not changed during the last 20-25 years.

**3.5 Evolution of vegetation dynamics**

*3.5.1 Species richness dynamics (herbaceous and shrub strata)*

The analysis of species richness showed that current surveys obtained on average 2 to 3 species more than the past ones (average: 2.43; sd: 10.02; P-value: < 0.05; *Fig. 13*). At medium elevation, the current values have acquired significantly higher species richness than the past scores with an addition of 5 species (average: 5.10; sd: 12.97; P-value: < 0.05; *Fig. 13*). Along the elevation gradient, we can see significant differences between low and medium elevation belts reaching 7-8 species more according to the current conditions (average: 7.87; P-value: < 0.05).

*3.5.2 Principle Component Analysis of field observations*

Principle Component Analysis on the 92 past and current surveys showed various important changes in vegetation for each elevation belt (*Fig. 14*). Their amplitudes were not different depending on the year of the historical inventory (*Fig. 15*). According to Landolt's values along the elevation gradient, we observed a significant negative correlation between temperature and both light (P-value: <0.001; rho: -0.37) and soil moisture (P-value: <0.01; rho: -0.19; *Fig. 16*).

## Species richness analysis

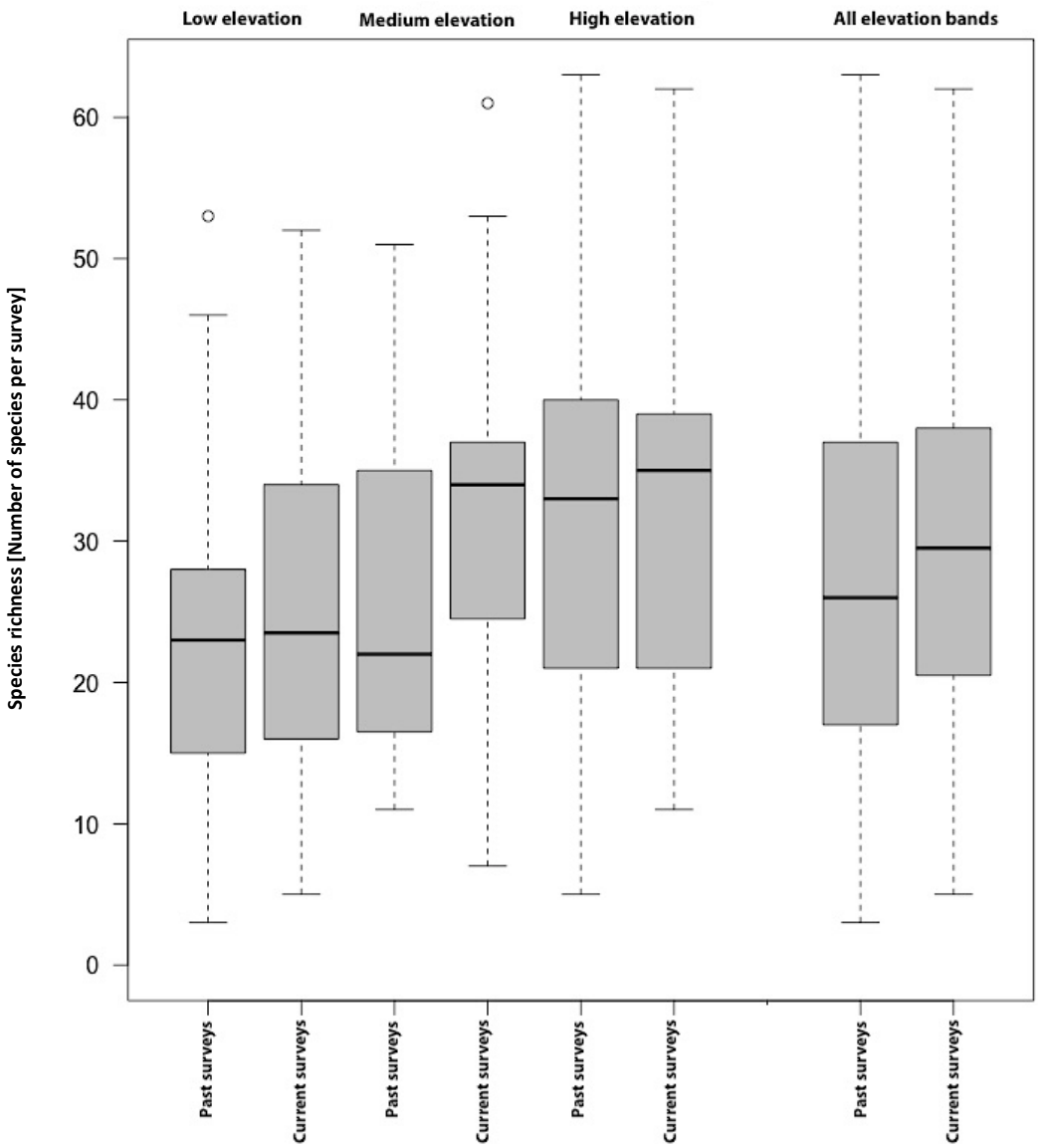
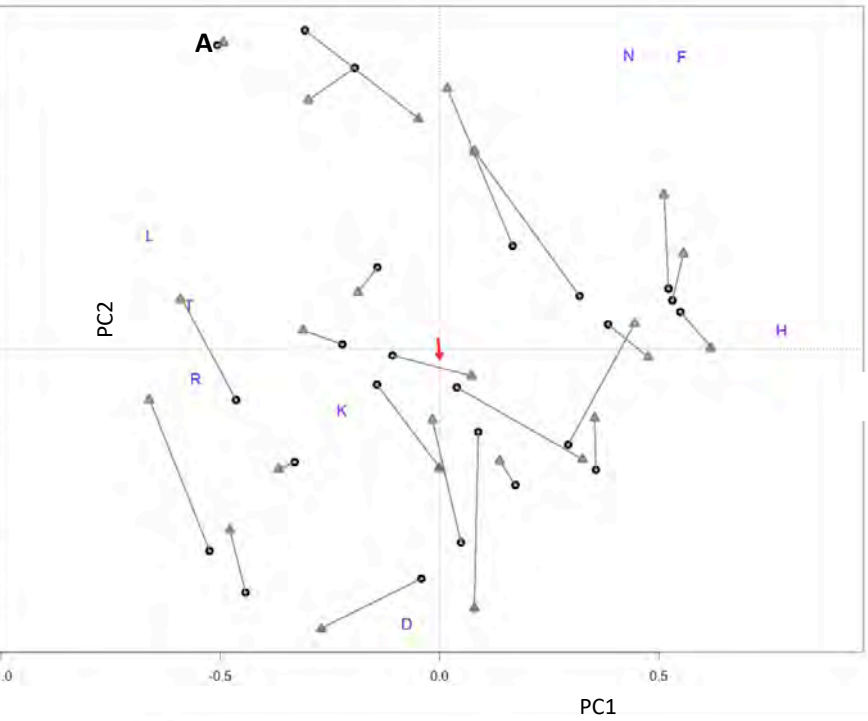
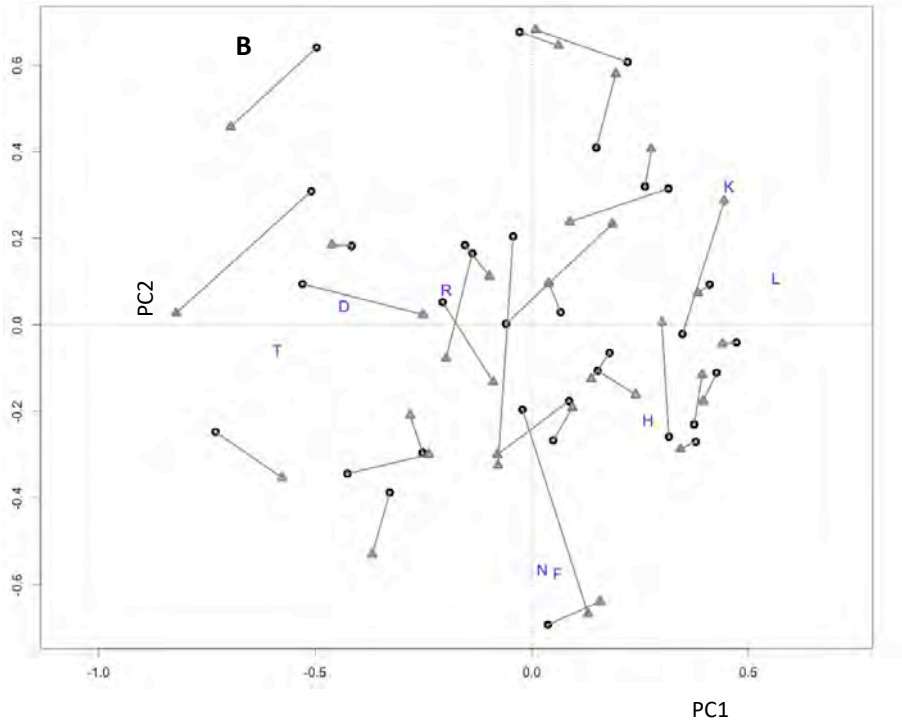



***Figure 13*** *– Boxplots illustrating past and recent species richness along elevation belts.*

## Principle Component Analysis (PCA)



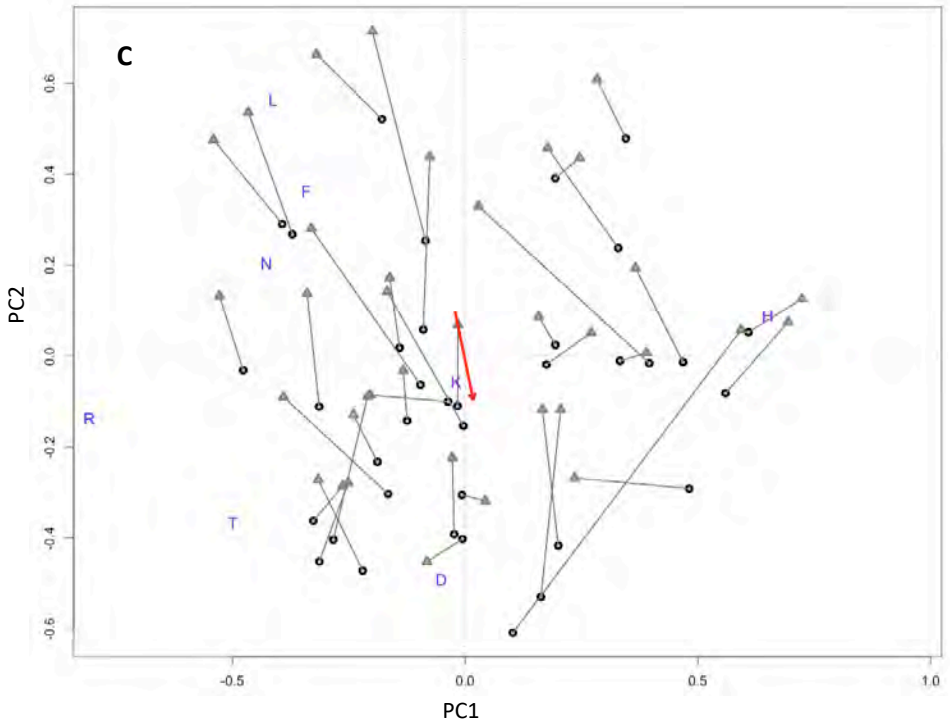




***Figure 14*** *– Graphics containing the Principle Component Analysis (PCA) on past and current field observations (A: low, B: medium and C: high elevation belts). Grey arrows represent changes between past (black circles) and recent (grey triangles) surveys. The red arrow summarizes the significant trend of all shifts. Letters correspond to the projection of Landolt's indicators (temperature T, humus H, soil moisture F, light L, reactivity R, continentality K, soil aeration D, nutrients N).*

## Ecological changes through time

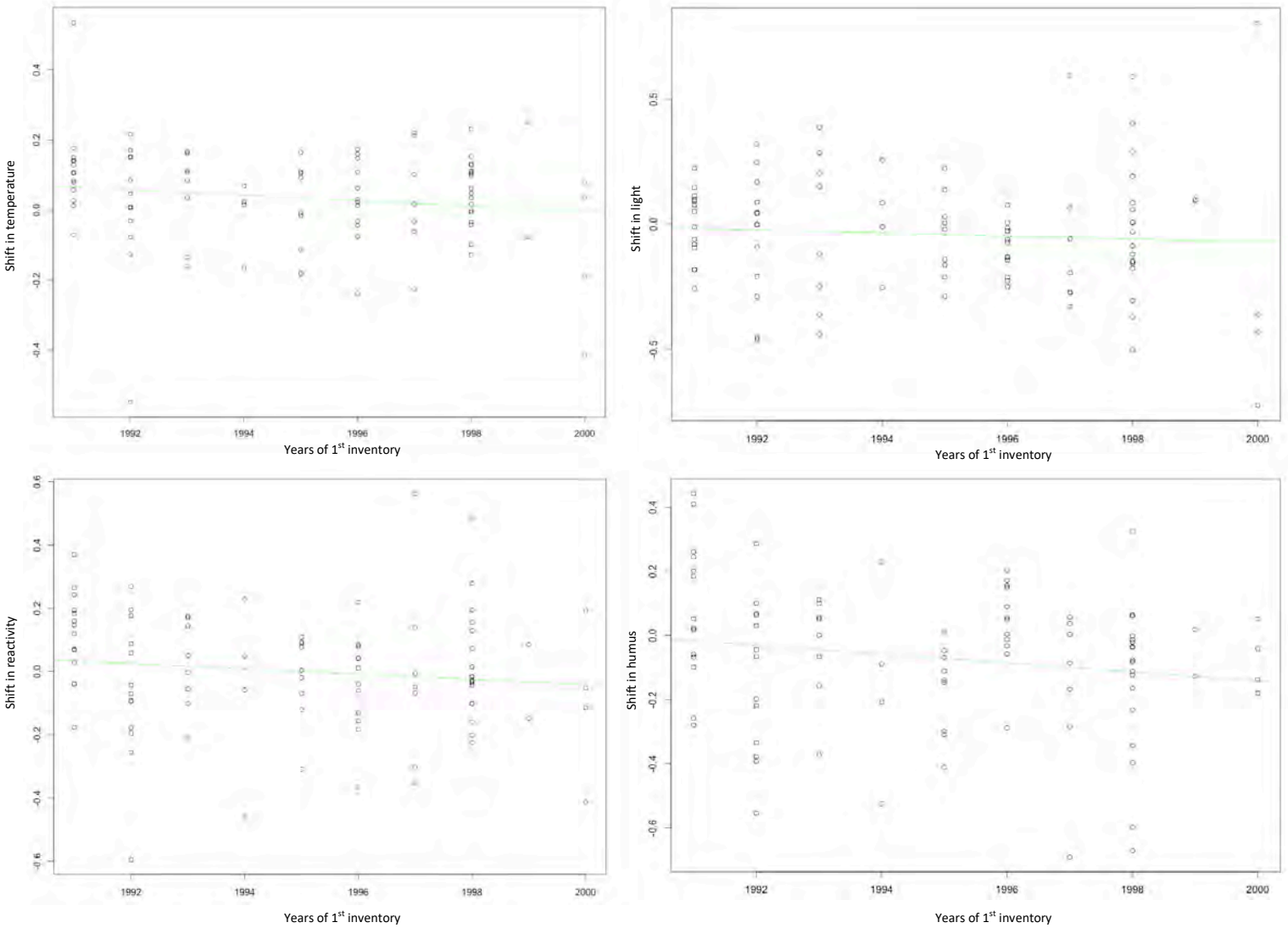



***Figure 15*** *– Linear regression of temperature, humus, reactivity and light changes, showing that according to the years of 1st inventory there is no significant trend within shifts.*

## Linear regression between temperature and light and soil moisture indicators

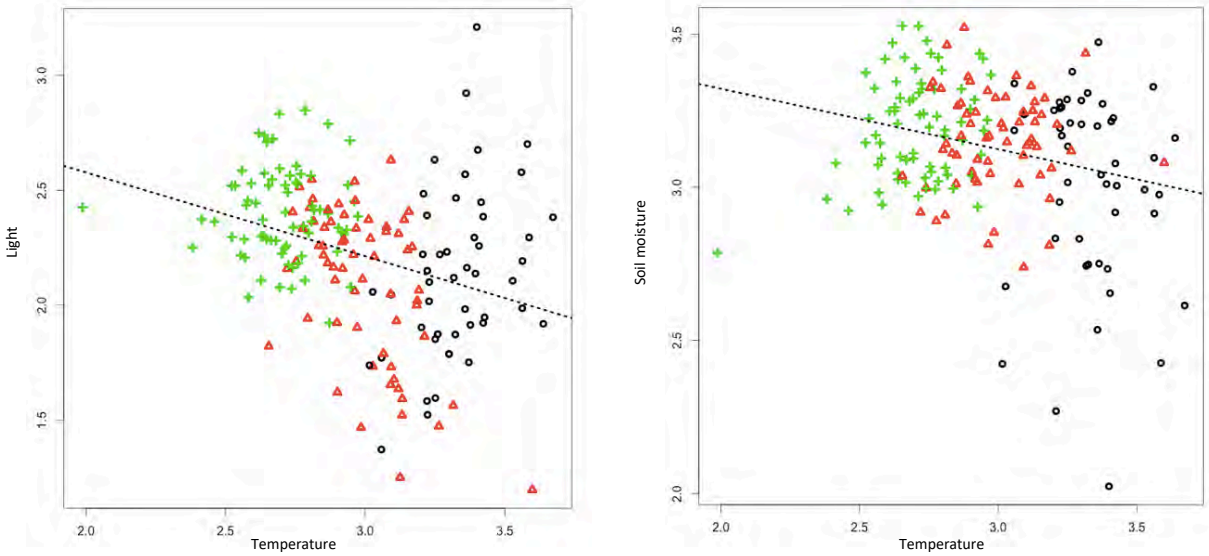



***Figure 16*** *– Graphics representing linear regressions calculated with weighted averages of Landolt's indicators (per current surveys), which are significantly correlated (temperature and light P-value: <0.001; temperature and soil moisture P-value: <0.01). Green crosses correspond to plots situated in high elevation, red triangles in medium elevation and black circles in low elevation.*

*3.5.3 Changes within the low elevation belt (<1000 m)*

At low elevation, the first axis of PCA represented a gradient of humus, with humus-poor forests appearing on the left and humus-affluent on the right (inertia ratio: 43.27%). Furthermore, light, temperature and reactivity factors (pH) obtained a gradient opposite to the humus's. The second axis represented a gradient of nutrients and moisture in opposed to aeration factor with aeration-poor soils appearing at the top and aeration-high soils at the bottom (inertia ratio: 23.86%) (*Fig. 14;* graphic A). The red arrow summarizing the significant trend between past and current conditions displayed in part a decrease of nutrients and light factors. Landolt's indicators analysis indicated that humus values obtained significant shifs (*Table 3*; P-value: <0.01).

**Analysis of past and current ecology**

| | Low elevation belt (< 1000 m) | | Medium elevation belt (1000 - 1500 m) | | High elevation belt (> 1500 m) | |
|---|---|---|---|---|---|---|
| **Landolt's indicators** | Past surveys | Current surveys | Past surveys | Current surveys | Past surveys | Current surveys |
| Temperature (T) | 3.330 | 3.332 | 2.979 | 3.004 | 2.673 | 2.739 ** |
| Continentality (K) | 2.621 | 2.544 | 2.641 | 2.650 | 2.638 | 2.665 |
| Light (L) | 2.180 | 2.093 | 2.106 | 2.086 | 2.416 | 2.378 |
| Moisture (F) | 2.998 | 3.006 | 3.175 | 3.133 | 3.242 | 3.149 *** |
| Reactivity (R) | 3.304 | 3.270 | 3.083 | 3.101 | 2.860 | 2.626 |
| Nutrients (N) | 2.887 | 2.924 | 3.028 | 3.008 | 2.982 | 2.938 |
| Humus (H) | 3.434 | 3.314 ** | 3.678 | 3.618 | 3.812 | 3.767 |
| Aeration (D) | 2.430 | 2.377 | 2.301 | 2.239 | 2.117 | 2.122 |

***Table 3*** *– Table showing averages of Landolt's indicators from past and recent species (weighted mean per survey according to the elevation belts and field observations). These values show a decrease of temperature and an increase of light, reactivity, humus, soil moisture and soil aeration along elevation belts. Significant differences are highlighted with following p-values:* * : *<0.05,* ** : *<0.01 and* *** : *<0.001 (Student test).*

*3.5.4 Changes within the medium elevation belt (1000-1500 m)*

At medium elevation, the first axis illustrated two opposite gradients in light and temperature (inertia ratio: 32.18%). Indeed, a condition with poor light and high temperatures was appearing on the left (*Fig. 14;* graphic B). A soil aeration gradient also distributed the data in the same direction than temperature indicator. Moisture and nutrients represented the second axis with higher values at the bottom and lower values at the top (inertia ratio: 28.77%). We did not obtain significant general shift in this elevation belt.

*3.5.5 Changes within the high elevation belt (>1500 m)*

At high elevation, the first axis characterised a gradient in humus with humus-poor forests appearing on the left and humus-affluent forests on the right (inertia ratio: 35.80%). An opposite gradient in reactivity (pH) was observable with more basic pH appearing on the right and more acidic pH on the left (*Fig. 14;* graphic C). The second axis was explained by a gradient in aeration, with high soils aeration appearing at the bottom and a low soil aeration at the top (inertia ratio: 22.71%). Regarding the red arrow showing differences between past and current conditions, a temperature increase and a soil moisture reduction was observed. Landolt's indicators analysis

was in agreement with this trend through significant scores (*Table 3*; temperature P-value: <0.01; soil moisture P-value: <0.001).

*3.5.6 Species frequency analysis according to the elevation belts*

At low elevation, past and current surveys displayed a predominance of deciduous forests with tree species such as *Fagus sylvatica, Acer pseudoplatanus* and *Fraxinus excelsior* overtopping herbaceous species (<0.5 m) such as *Mercurialis perennis, Viola reichenbachiana, Lamium galeobdolon, Dryopteris filix-mass* and *Hedera helix.* In the medium and high elevation belts, *Picea abies* and *Abies alba* occupied the most of past and current areas, followed by usual forest species like *Oxalis acetosela, Lamium galeobdolon, Hieracium murorum, Adenostyles alliariae, Athyrium filix-femina* and *Prenanthes purpurea* (Delarze & Gonseth, 2008*; Appx. 5*). The recent species frequency increased according to the elevation belts with significant values between low and medium elevations (average: 1.08; sd: 3.78; P-value <0.001) and medium and high elevations (average: 0.54; sd: 4.07; P-value < 0.01). Regarding the past surveys, the same trend was observable with significant values between low and medium elevations (average: 0.74; sd: 3.09; P-value <0.001) and medium and high elevations (average: 0.56; sd: 3.54; P-value < 0.001).

*3.5.7 Species frequency analysis between past and current surveys*

Along the elevation belts, the recent species frequency was significantly higher than the past one (average: 0.71; sd: 6.26; P-value: <0.05), especially in high elevation belt (average: 0.34; sd: 3.22; P-value: <0.05). Furthermore, 1219 case of local occurrence were measured between recent and past surveys, where 289 were different species. On the other hand, 995 case of local extinction were calculated between recent and past surveys, where 309 were dissimilar species.

*3.5.8 Species frequency changes in the low elevation belt (<1000 m)*

In the lowland, the majority of the species increasing in frequency, over the last 20-25 years, were forest plants such as tree seedlings of *Acer pseudoplatanus, Fagus sylvatica, Fraxinus excelsior* and *Corylus avellana,* accompanied by species growing in various forest areas such as *Hedera helix, Ilex aquifolium* and *Lamium galeobdolon.* Moreover, other species growing in more specific alliances like *Cephalanthero-Fagenion (Neottia nidus avis* and *Sorbus aria), Tilion platyphylli (Tilia platyphyllos), Lunario-Acerion (Cardamine pentaphyllos)* and *Galio-Fagenion (Lonicera xylosteum)* also appeared more frequently (Delarze & Gonseth, 2008*; Table 4*). However, averages of Landolt's indicator values, associated with these species, showed no significant ecological difference with the past conditions.

| The increased frequency of species between past and current conditions | | | | | |
|---|---|---|---|---|---|
| Low elevation (<1000 m) | | Medium elevation (1000-1500 m) | | High elevation (>1500 m) | |
| Species | Surveys (X/24) | Species | Surveys (X/32) | Species | Surveys (X/36) |
| *Hedera helix (H)* | 11 | *Acer pseudoplatanus (H)* | 13 | *Sorbus aucuparia (H)* | 17 |
| *Acer pseudoplatanus (H)* | 10 | *Sorbus aucuparia (H)* | 13 | *Acer pseudoplatanus (H)* | 13 |
| *Fagus sylvatica (H)* | 9 | *Fagus sylvatica (H)* | 12 | *Oxalis acetosella (H)* | 13 |
| *Fraxinus excelsior (H)* | 7 | *Picea abies (H)* | 11 | *Fragaria vesca (H)* | 12 |
| *Corylus avellana (H)* | 5 | *Fraxinus excelsior (H)* | 9 | *Rubus idaeus (H)* | 12 |
| *Hedera helix (B)* | 4 | *Lamium galeobdolon (H)* | 9 | *Phyteuma spicatum (H)* | 11 |
| *Lonicera xylosteum (H)* | 4 | *Oxalis acetosella (H)* | 9 | *Hieracium murorum (H)* | 10 |
| *Neottia nidus avis (H)* | 4 | *Galeopsis tetrahit (H)* | 7 | *Lonicera nigra (H)* | 10 |
| *Abies alba (H)* | 3 | *Lonicera nigra (H)* | 7 | *Abies alba (H)* | 8 |
| *Cardamine pentaphyllos (H)* | 3 | *Lonicera xylosteum (H)* | 7 | *Astrantia major (H)* | 8 |
| *Fraxinus excelsior (A)* | 3 | *Rubus idaeus (H)* | 7 | *Hieracium lachenalii (H)* | 8 |
| *Galeopsis tetrahit (H)* | 3 | *Viola reichenbachiana (H)* | 7 | *Homogyne alpina (H)* | 8 |
| *Hedera helix (A)* | 3 | *Abies alba (H)* | 6 | *Campanula rhomboidalis (H)* | 7 |
| *Ilex aquifolium (A)* | 3 | *Dryopteris filix mas (H)* | 6 | *Carex sylvatica (H)* | 7 |
| *Lamium galeobdolon (H)* | 3 | *Fragaria vesca (H)* | 6 | *Petasites albus (H)* | 7 |
| *Sorbus aria (A)* | 3 | *Hordelymus europaeus (H)* | 6 | *Ranunculus nemorosus (H)* | 6 |
| *Sorbus aucuparia (H)* | 3 | *Neottia nidus avis (H)* | 6 | *Ajuga reptans (H)* | 5 |
| *Tilia platyphyllos (B)* | 3 | *Ajuga reptans (H)* | 5 | *Knautia dipsacifolia (H)* | 5 |
| *Tilia platyphyllos (H)* | 3 | *Athyrium filix femina (H)* | 5 | *Picea abies (A)* | 5 |
| *Corylus avellana (B)* | 2 | *Carex sylvatica (H)* | 5 | *Blechnum spicant (H)* | 4 |
| *Fagus sylvatica (A)* | 2 | *Fraxinus excelsior (B)* | 5 | *Calamagrostis varia (H)* | 4 |
| *Fragaria vesca (H)* | 2 | *Helleborus foetidus (H)* | 5 | *Epipactis helleborine (H)* | 4 |
| *Galium odoratum (H)* | 2 | *Prenanthes purpurea (H)* | 5 | *Saxifraga rotundifolia (H)* | 4 |
| *Hepatica nobilis (H)* | 2 | *Rubus fruticosus aggr (H)* | 5 | *Solidago virgaurea (H)* | 4 |
| *Hordelymus europaeus (H)* | 2 | *Abies alba (B)* | 4 | *Veronica officinalis (H)* | 4 |
| *Ilex aquifolium (H)* | 2 | *Carex digitata (H)* | 4 | *Adenostyles alliariae (H)* | 3 |
| *Picea abies (H)* | 2 | *Corylus avellana (H)* | 4 | *Brachypodium pinnatum (H)* | 3 |
| *Sorbus aria (H)* | 2 | *Fagus sylvatica (B)* | 4 | *Carex digitata (H)* | 3 |
| *Taxus baccata (A)* | 2 | *Hieracium murorum (H)* | 4 | *Crepis pyrenaica (H)* | 3 |
| *Tilia platyphyllos (A)* | 2 | *Paris quadrifolia (H)* | 4 | *Euphorbia cyparissias (H)* | 3 |
| *Viburnum opulus (B)* | 2 | *Polygonatum verticillatum (H)* | 4 | *Festuca rubra (H)* | 3 |

| The decreased frequency of species between past and current conditions | | | | | |
|---|---|---|---|---|---|
| Low elevation (<1000 m) | | Medium elevation (1000-1500 m) | | High elevation (>1500 m) | |
| Species | Surveys (X/24) | Species | Surveys (X/32) | Species | Surveys (X/36) |
| *Phyteuma spicatum (H)* | -7 | *Carex montana (H)* | -7 | *Aster bellidiastrum (H)* | -6 |
| *Euphorbia dulcis (H)* | -4 | *Centaurea montana (H)* | -5 | *Carex ferruginea (H)* | -6 |
| *Arum maculatum (H)* | -3 | *Corylus avellana (B)* | -5 | *Rubus idaeus (B)* | -6 |
| *Cardamine heptaphylla (H)* | -3 | *Campanula rhomboidalis (H)* | -4 | *Salix appendiculata (B)* | -6 |
| *Oxalis acetosella (H)* | -3 | *Veronica chamaedrys (H)* | -4 | *Sambucus racemosa (B)* | -6 |
| *Rosa arvensis (H)* | -3 | *Geum rivale (H)* | -3 | *Anthoxanthum odoratum (H)* | -5 |
| *Viburnum lantana (B)* | -3 | *Heracleum sphondylium (H)* | -3 | *Hieracium prenanthoides (H)* | -5 |
| *Acer campestre (B)* | -2 | *Lonicera alpigena (B)* | -3 | *Abies alba (A)* | -4 |
| *Acer opalus (B)* | -2 | *Luzula pilosa (H)* | -3 | *Campanula cochleariifolia (H)* | -4 |
| *Acer platanoides (B)* | -2 | *Picea abies (B)* | -3 | *Ranunculus aconitifolius (H)* | -4 |
| *Carex flacca (H)* | -2 | *Polystichum lonchitis (H)* | -3 | *Alnus viridis (B)* | -3 |
| *Cornus mas (B)* | -2 | *Rosa pendulina (H)* | -3 | *Asplenium viride (H)* | -3 |
| *Cornus sanguinea (B)* | -2 | *Rumex alpestris (H)* | -3 | *Dryopteris dilatata (H)* | -3 |
| *Daphne mezereum (H)* | -2 | *Sambucus racemosa (B)* | -3 | *Epilobium angustifolium (H)* | -3 |
| *Deschampsia cespitosa (H)* | -2 | *Sorbus aria (B)* | -3 | *Geranium sylvaticum (H)* | -3 |
| *Melittis melissophyllum (H)* | -2 | *Veratrum album (H)* | -3 | *Geum rivale (H)* | -3 |
| *Paris quadrifolia (H)* | -2 | *Luzula luzulina (H)* | -2 | *Gymnocarpium dryopteris (H)* | -3 |
| *Polygonatum verticillatum (H)* | -2 | *Luzula sylvatica (H)* | -2 | *Heracleum sphondylium (H)* | -3 |
| *Primula acaulis (H)* | -2 | *Maianthemum bifolium (H)* | -2 | *Hypericum maculatum (H)* | -3 |
| *Prunus spinosa (B)* | -2 | *Melica nutans (H)* | -2 | *Rosa pendulina (B)* | -3 |
| *Rubus caesius (B)* | -2 | *Origanum vulgare (H)* | -2 | *Polygonatum verticillatum (H)* | -2 |
| *Rubus idaeus (B)* | -2 | *Picea abies (A)* | -2 | *Polygonum bistorta (H)* | -2 |
| *Sambucus nigra (B)* | -2 | *Poa nemoralis (H)* | -2 | *Polystichum aculeatum (H)* | -2 |
| *Taxus baccata (B)* | -2 | *Ribes petraeum (B)* | -2 | *Potentilla erecta (H)* | -2 |
| *Teucrium montanum (H)* | -2 | *Salix caprea (B)* | -2 | *Primula elatior (H)* | -2 |
| *Viburnum lantana (H)* | -2 | *Sambucus racemosa (H)* | -2 | *Ranunculus montanus (H)* | -2 |
| *Viburnum opulus (H)* | -2 | *Saxifraga rotundifolia (H)* | -2 | *Rosa pendulina (H)* | -2 |
| *Vincetoxicum hirundinaria (H)* | -2 | *Senecio ovatus (H)* | -2 | *Silene dioica (H)* | -2 |
| *Viola reichenbachiana (H)* | -2 | *Sorbus aucuparia (A)* | -2 | *Soldanella alpina (H)* | -2 |
| *Vicia sylvatica (H)* | -1 | *Ulmus glabra (A)* | -2 | *Thesium alpinum (H)* | -2 |
| *Viola hirta (H)* | -1 | *Vaccinium myrtillus (H)* | -2 | *Viola biflora (H)* | -2 |

***Table 4*** *– Tables showing species with the highest increase or decrease in frequency for past and current conditions. Letters in bracket correspond to the strata of plant height (A: tree >6 m, B: shrub 0.5-6 m and C: herbaceous <0.5 m).*

On the other hand, the species decreasing in frequency lived in similar alliances than previous plants. However, some species growing at forest edges such as *Viburnum opulus*, *Cornus sanguinea*, *Rubus caesius* and *Prunus spinosa* decreased too (*Pruno-Rubion*). The ecology of these species was significantly higher in continentality (P-value: <0.01) and light indicators (P-

value: <0.01) than the past conditions one (*Table 5*). Moreover, decreasing species had higher light indicator values than increasing species (P-value: <0.05; *Table 6*).

**Differences between current changes and past ecology**

| | Low elevation belt (< 1000 m) | | Medium elevation belt (1000 - 1500 m) | | High elevation belt (> 1500 m) | |
|---|---|---|---|---|---|---|
| **Landolt's indicators** | Increased frequency | Decreased frequency | Increased frequency | Decreased frequency | Increased frequency | Decreased frequency |
| Temperature (T) | x | x | + 0.089 * | x | + 0.216 *** | x |
| Continentality (K) | x | + 0.275 ** | + 0.173 ** | + 0.291 *** | + 0.155 *** | + 0.148 ** |
| Light (L) | x | + 0.357 ** | + 0.319 *** | + 0.555 *** | + 0.198 *** | + 0.371 *** |
| Moisture (F) | x | x | x | x | - 0.114 ** | x |
| Reactivity (R) | x | x | + 0.134 * | x | + 0.179 ** | + 0.177 * |
| Nutrients (N) | x | x | x | x | x | x |
| Humus (H) | x | x | x | x | x | x |
| Aeration (D) | x | x | x | x | x | x |
| **Landolt's indicators** | Increased cover | Decreased cover | Increased cover | Decreased cover | Increased cover | Decreased cover |
| Temperature (T) | x | x | x | x | x | + 0.126 * |
| Continentality (K) | x | x | x | x | x | + 0.117 * |
| Light (L) | x | + 0.367 ** | + 0.540 *** | + 0.421 *** | + 0.390 *** | + 0.380 *** |
| Moisture (F) | x | x | x | x | x | x |
| Reactivity (R) | x | x | x | + 0.197 * | + 0.264 ** | x |
| Nutrients (N) | x | x | x | x | x | x |
| Humus (H) | x | - 0.245 * | x | x | x | x |
| Aeration (D) | x | x | - 0.447 *** | - 0.290 * | x | x |

***Table 5*** *– Comparison between Landolt's indicators averages of past ecology and ecology of species, which had changes in frequency or cover (field observations). Positive values are an increase of current indicators and negative values are a decrease. Significant results are highlighted with following p-values:* * : *<0.05,* ** : *<0.01 and* *** : *<0.001 (Student test).*

**Ecology of species changing in frequency**

| | Low elevation belt (< 1000 m) | | Medium elevation belt (1000 - 1500 m) | | High elevation belt (> 1500 m) | |
|---|---|---|---|---|---|---|
| **Landolt's indicators** | Increased frequency (86/489 species) | Decreased frequency (119/489 species) | Increased frequency (123/489 species) | Decreased frequency (118/489 species) | Increased frequency (137/489 species) | Decreased frequency (113/489 species) |
| Temperature (T) | 3.377 | 3.402 | 3.068 | 2.935 *** | 2.889 | 2.665 *** |
| Continentality (K) | 2.781 | 2.896 | 2.814 | 2.932 ** | 2.793 | 2.786 |
| Light (L) | 2.331 | 2.537 ** | 2.425 | 2.661 *** | 2.614 | 2.787 *** |
| Moisture (F) | 3.015 | 2.971 | 3.103 | 3.128 | 3.128 | 3.321 *** |
| Reactivity (R) | 3.370 | 3.444 | 3.217 | 3.189 | 3.039 | 3.037 |
| Nutrients (N) | 3.018 | 2.879 | 3.074 | 3.058 | 2.985 | 2.985 |
| Humus (H) | 3.374 | 3.410 | 3.629 | 3.571 | 3.807 | 3.823 |
| Aeration (D) | 2.448 | 2.356 | 2.218 | 2.180 | 2.174 | 2.039 |

***Table 6*** *– Table showing averages of Landolt's indicators for species with increase or decrease in frequency between past and current conditions (weighted mean per survey according to the elevation belts and field observations). Significant results are highlighted with following p-values:* * : *<0.05,* ** : *<0.01 and* *** : *<0.001 (Student test).*

### *3.5.9 Species frequency changes in the medium elevation belt (1000-1500 m)*

At medium elevation, the most of species increasing in frequency grow in various forest areas such as tree seedling of *Acer pseudoplatanus*, *Sorbus aucuparia*, *Fagus sylvatica*, *Picea albies* and *Fraxinus excelsior*, accompanied by plants living in various forests like *Lamium galeobdolon*, *Oxalis acetosella*, *Drypoteris filix mas* and *Prenanthes purpurea*. Some other species are established in *Galio-Fagenion (Carex digitata)*, *Abieti-Fagenion (Hordelymus europaeus* and *Athyrium filix-femina)*, *Cephalanthero-Fagenion (Neottia nidus avis* and *Viola reichenbachiana)* and *Lonicero-Fagenion (Carex sylvatica* and *Polygonatum verticillatum)*. However, in current

conditions, *Ajuga reptans* (*Aegopodion/Alliarion*) was also detected more often in this elevation, although its optimal habitat is situated in the lower elevation belt (Delarze & Gonseth, 2008). The ecology represented by these species obtained significant higher values in temperature (P-value: <0.05), continentality (P-value: 0.01), light (P-value: <0.001) and reactivity indicators (P-value: <0.05) than past conditions (*Table 5*).

The plants decreasing in frequency live principally in grasslands, pastures or forest edges such as *Seslerion* (*Carex montana*), *Calthion (Geum rivale), Polygono-Trisetion (Campanula rhomboidalis, Rumex alpestris* and *Heracleum sphondylium), Caricion ferrugineae (Centaurea montana), Rumicion alpini (Veratrum album), Sambucuo-Salicion (Corylus avellana, Sambucus racemosa* and *Senecio ovatus)* and *Trifolion medii* (*Veronica chamaedrys* and *Origanum vulgare*) (Delarze & Gonseth, 2008). The ecology of these species obtained significantly higher factor of continentality (P-value: 0.001) and lower value of light indicator (P-value: 0.001) than the past ecological conditions (*Table 5*). Furthermore, these two last indicators' averages were significantly higher than scores of species increasing in frequency (continentality P-value: <0.01; light P-value: <0.001), unlike temperature factor, which obtained lower result (P-value: <0.001; *Table 6*).

*3.5.10 Species frequency changes in the high elevation belt (>1500 m)*

At high elevation, the majority of species increasing in frequency are observed in forest areas such as in *Abieti-Piceion (Lonicera nigra, Solidago virgaurea, Sorbus aucuparia* and *Calamagrostis varia), Vaccinio-Piceion (Homogyne alpine, Blechnum spicant* and *Picea albies)* and *Abieti-Fagenion (Acer pseudoplatanus, Phyteuma spicatum, Hieracium murorum,* and *Petasites albus).* Species growing in grasslands and pastures like in *Polygono-Trisetion (Campanula rhomboidalis, Astrantia major* and *Knautia dipsacifolia)* had also increased. However, *Carex sylvatica* (*Lonicero-Fagenion*) and *Ajuga reptans* (*Aegopodion/Alliarion*) were also more present in this elevation, although their habitat is situated in lower elevation (*Delarze & Gonseth, 2008*). Regarding ecological indicator values, these plants recorded significant higher averages in temperature (P-value: <0.001), continentality (P-value: 0.001), light (P-value: <0.001) and reactivity indicators than past dataset (P-value: <0.01) and a lower value in soil moisture (P-value: <0.01).

The observed species decreasing in frequency live in alliances of grasslands or pastures such as *Carex ferrunigea* (*Caricion ferrugineae*), *Ranunculus aconitifolius* (*Calthion*), *Heracleum sphondylium* and *Anthoxanthum odoratum* (*Polygono-Trisetion*), *Aster bellidiastrum* (*Caricion ferrugineae*), *Hypericum maculatum* (*Poion alpinae*) and *Epilobium angustifolium* (*Epilobion angustifolii*). A reduction of *Salix appendiculata*, *Rosa pendulina* and *Alnus viridis* (*Alnenion viridis*) was also percepted (*Table 4*). Furthermore, a decrease of species growing in an

environment with a strong presence of snow like in *Adenostylion (Geranium sylvaticum)* was highlighted (Delarze & Gonseth, 2008). Accordingly, averages of Landolt's indicators showed significantly higher scores in continentality (P-value: 0.001), light (P-value: <0.001) and reactivity indicators (P-value: <0.05) than past conditions (*Table 5*). Moreover, averages of light and soil moisture indicators were significantly higher than scores of species increasing in frequency (light P-value: <0.01; soil moisture P-value: <0.001), unlike temperature factor, which obtained lower result (P-value: <0.001; *Table 6*).

*3.5.11 Species cover analysis along the elevation belts*

A general increase of species cover was estimated between past and current conditions, especially for trees and shrubs (*App. 6*). Along the elevation gradient, medium elevation had higher species cover than low elevation (average: 0.09; sd: 1.02; P-value <0.05) and lower values than high elevation (average: 0.08 sd: 0.80, P-value < 0.05). Regarding past surveys, the same trend was detected, but it was not significant.

*3.5.12 Cover analysis in the low elevation belt (<1000 m)*

At low elevation, the current dataset showed a higher cover of herbaceous (< 0.5 m) and trees species (deciduous and coniferous) growing in *Carpinion* (*Prunus avium* and *Rosa arvenis*), *Tilion platyphylli* (*Ulmus glabra* and *Quercus petraea/robur*), *Lonicero-Fagenion* (*Abies alba, Acer pseudoplatanus, Hordelymus europaeus* and *Polygonatum verticulatum*), *Erico-Pinion mugo* (*Larix decidua* and *Picea albies*) and *Fraxinion* (*Primula elatior, Viburnum opulus* and *Quercus robur*), than perceived in the past conditions.

On the other hand, we detected an important decrease in cover of various forests herbaceous species such as *Petasites albus, Carex alba, Phyteuma spicatum* and *Vicia sepium* (*Table 7*). This floristic change was also illustrated by a significant reduction in cover of all species compared to the past conditions (average: 0.15; P-value: <0.001; *Table 7*). Moreover, the ecology related to the plants decreasing in cover obtained a significant higher value in light indicator (P-value: <0.01) and a lower score in humus factor (P-value: <0.05) than the past dataset (*Table 5*). Additionally, averages of light and soil aeration indicators were significant higher than scores of species increasing in frequency (light P-value: <0.01; soil aeration P-value: <0.01; *Table 8*).

| The increased cover of species between past and current conditions | | | | | |
|---|---|---|---|---|---|
| Low elevation (<1000 m) | | Medium elevation (1000;1500 m) | | High elevation (>1500 m) | |
| Species | Surveys (X/24) | Species | Surveys (X/32) | Species | Surveys (X/36) |
| *Prunus avium (A)* | 0.72 | *Carex ferruginea (H)* | 0.41 | *Cardamine heptaphylla (H)* | 0.41 |
| *Ajuga reptans (H)* | 0.41 | *Hypericum maculatum (H)* | 0.41 | *Elymus caninus (H)* | 0.41 |
| *Primula elatior (H)* | 0.41 | *Pteridium aquilinum (H)* | 0.41 | *Laburnum alpinum (B)* | 0.41 |
| *Ulmus glabra (B)* | 0.36 | *Ulmus glabra (H)* | 0.41 | *Ligusticum mutellina (H)* | 0.41 |
| *Picea abies (B)* | 0.35 | *Sorbus aucuparia (A)* | 0.33 | *Phyteuma orbiculare (H)* | 0.41 |
| *Juniperus communis (H)* | 0.32 | *Polygala chamaebuxus (H)* | 0.32 | *Sorbus chamaemespilus (H)* | 0.36 |
| *Quercus petraea (A)* | 0.32 | *Cirsium oleraceum (H)* | 0.27 | *Alnus incana (B)* | 0.36 |
| *Quercus robur (A)* | 0.32 | *Impatiens noli angere (H)* | 0.27 | *Ribes petraeum (B)* | 0.35 |
| *Acer pseudoplatanus (A)* | 0.32 | *Lonicera nigra (B)* | 0.26 | *Hepatica nobilis (H)* | 0.27 |
| *Abies alba (B)* | 0.29 | *Sorbus aria (A)* | 0.24 | *Sorbus aucuparia (A)* | 0.27 |
| *Larix decidua (A)* | 0.26 | *Dryopteris carthusiana (H)* | 0.21 | *Abies alba (A)* | 0.25 |
| *Hordelymus europaeus (H)* | 0.24 | *Equisetum sylvaticum (H)* | 0.21 | *Caltha palustris (H)* | 0.25 |
| *Ulmus glabra (A)* | 0.24 | *Luzula nivea (H)* | 0.21 | *Acer pseudoplatanus (A)* | 0.22 |
| *Viburnum opulus (B)* | 0.24 | *Vicia sylvatica (H)* | 0.21 | *Vicia cepium (H)* | 0.21 |
| *Daphne aureola (H)* | 0.21 | *Ulmus glabra (A)* | 0.19 | *Chaerophyllum villarsii (H)* | 0.21 |
| *Fagus sylvatica (B)* | 0.21 | *Sorbus aucuparia (B)* | 0.17 | *Melica nutans (H)* | 0.21 |
| *Actaea spicata (H)* | 0.21 | *Vaccinium vitis idaea (H)* | 0.16 | *Calamagrostis villosa (H)* | 0.20 |
| *Carex cutiformis (H)* | 0.20 | *Elymus caninus (H)* | 0.16 | *Larix decidua (A)* | 0.16 |
| *Cornus sanguinea (B)* | 0.20 | *Orthilia secunda (H)* | 0.15 | *Lonicera caerulea (B)* | 0.16 |
| *Convallaria majalis (H)* | 0.17 | *Corylus avellana (B)* | 0.15 | *Rhododendron ferrugineum (H)* | 0.16 |
| *Taxus baccata (B)* | 0.17 | *Cardamine pentaphyllos (H)* | 0.14 | *Senecio ovatus (H)* | 0.16 |
| *Sorbus aria (B)* | 0.16 | *Vaccinium myrtillus (H)* | 0.11 | *Alnus viridis (B)* | 0.16 |
| *Pinus sylvestris (B)* | 0.16 | *Ulmus glabra (B)* | 0.11 | *Oreopteris limbosperma (H)* | 0.14 |
| *Fagus sylvatica (H)* | 0.16 | *Fraxinus excelsior (A)* | 0.09 | *Alchemilla conjuncta (H)* | 0.14 |
| *Carex flacca (H)* | 0.14 | *Abies alba (A)* | 0.08 | *Hordelymus europaeus (H)* | 0.14 |
| *Polygonatum verticillatum (H)* | 0.11 | *Saxifraga rotundifolia (H)* | 0.08 | *Carex sylvatica (H)* | 0.13 |
| *Rosa arvensis (H)* | 0.10 | *Lonicera xylosteum (B)* | 0.08 | *Abies alba (B)* | 0.12 |
| *Acer opalus (A)* | 0.09 | *Carex flacca (H)* | 0.07 | *Crepis paludosa (H)* | 0.11 |
| *Picea abies (H)* | 0.07 | *Dactylis glomerata (H)* | 0.07 | *Aegopodium podagraria (H)* | 0.10 |
| *Helleborus foetidus (H)* | 0.07 | *Myosotis sylvatica (H)* | 0.07 | *Silene vulgaris (H)* | 0.10 |
| *Sorbus aria (A)* | 0.05 | *Lonicera alpigena (B)* | 0.06 | *Picea abies (A)* | 0.10 |

| The decreased cover of species between past and current conditions | | | | | |
|---|---|---|---|---|---|
| Low elevation (<1000 m) | | Medium elevation (1000;1500 m) | | High elevation (>1500 m) | |
| Species | Surveys (X/24) | Species | Surveys (X/32) | Species | Surveys (X/36) |
| *Petasites albus (H)* | ;0.73 | *Ranunculus aconitifolius (H)* | ;0.71 | *Gentiana purpurea (H)* | ;0.62 |
| *Carex alba (H)* | ;0.69 | *Allium ursinum (H)* | ;0.52 | *Euphorbia cyparissias (H)* | ;0.53 |
| *Sesleria caerulea (H)* | ;0.58 | *Melica nutans (H)* | ;0.47 | *Rubus saxatilis (H)* | ;0.52 |
| *Cephalanthera damasonium (H)* | ;0.57 | *Carduus defloratus (H)* | ;0.41 | *Campanula barbata (H)* | ;0.41 |
| *Acer campestre (H)* | ;0.41 | *Epilobium alpestre (H)* | ;0.41 | *Juncus effusus (H)* | ;0.41 |
| *Asplenium fontanum (H)* | ;0.41 | *Euphorbia dulcis (H)* | ;0.41 | *Myosotis scorpioides (H)* | ;0.41 |
| *Asplenium richomanes (H)* | ;0.41 | *Brachypodium pinnatum (H)* | ;0.36 | *Calamagrostis varia (H)* | ;0.39 |
| *Dryopteris carthusiana (H)* | ;0.41 | *Campanula rhomboidalis (H)* | ;0.34 | *Equisetum arvense (H)* | ;0.36 |
| *Euonymus europaeus (H)* | ;0.41 | *Campanula trachelium (H)* | ;0.32 | *Prenanthes purpurea (H)* | ;0.35 |
| *Juglans regia (H)* | ;0.41 | *Euphorbia cyparissias (H)* | ;0.32 | *Astrantia minor (H)* | ;0.32 |
| *Prunus avium (B)* | ;0.41 | *Hedera helix (H)* | ;0.32 | *Dryopteris affinis (H)* | ;0.32 |
| *Tamus communis (B)* | ;0.41 | *Homogyne alpina (H)* | ;0.32 | *Fagus sylvatica (B)* | ;0.32 |
| *Vicia cepium (H)* | ;0.41 | *Dactylorhiza maculata (H)* | ;0.31 | *Globularia cudicaulis (H)* | ;0.32 |
| *Rubus caesius (H)* | ;0.39 | *Cardamine heptaphylla (H)* | ;0.29 | *Tussilago farfara (H)* | ;0.32 |
| *Juniperus communis (B)* | ;0.39 | *Daphne mezereum (H)* | ;0.27 | *Gentiana lutea (H)* | ;0.24 |
| *Vinca minor (H)* | ;0.38 | *Sanicula europaea (H)* | ;0.26 | *Ranunculus nanuginosus (H)* | ;0.24 |
| *Polygala chamaebuxus (H)* | ;0.37 | *Ranunculus nanuginosus (H)* | ;0.24 | *Dactylorhiza maculata (H)* | ;0.24 |
| *Phyteuma spicatum (H)* | ;0.35 | *Rumex alpestris (H)* | ;0.24 | *Melampyrum sylvaticum (H)* | ;0.24 |
| *Aruncus dioicus (H)* | ;0.32 | *Aposeris foetida (H)* | ;0.23 | *Carex paniculata (H)* | ;0.24 |
| *Brachypodium sylvaticum (H)* | ;0.32 | *Lonicera alpigena (H)* | ;0.21 | *Veronica officinalis (H)* | ;0.24 |
| *Castanea sativa (H)* | ;0.32 | *Galium odoratum (H)* | ;0.21 | *Luzula luzulina (H)* | ;0.22 |
| *Clematis vitalba (B)* | ;0.32 | *Ajuga reptans (H)* | ;0.21 | *Viola biflora (H)* | ;0.22 |
| *Daphne aureola (B)* | ;0.32 | *Geranium sylvaticum (H)* | ;0.21 | *Carduus defloratus (H)* | ;0.21 |
| *Potentilla sterilis (H)* | ;0.32 | *Laburnum alpinum (B)* | ;0.21 | *Avenella flexuosa (H)* | ;0.21 |
| *Tilia cordata (B)* | ;0.32 | *Neottia nidus avis (H)* | ;0.21 | *Fagus sylvatica (H)* | ;0.21 |
| *Stachys sylvatica (H)* | ;0.31 | *Sorbus aria (H)* | ;0.21 | *Galeopsis tetrahit (H)* | ;0.21 |
| *Galeopsis tetrahit (H)* | ;0.31 | *Vicia cepium (H)* | ;0.21 | *Neottia nidus avis (H)* | ;0.21 |
| *Mercurialis perennis (H)* | ;0.31 | *Dryopteris filix mas (H)* | ;0.19 | *Salix appendiculata (H)* | ;0.21 |
| *Fragaria vesca (H)* | ;0.29 | *Dryopteris dilatata (H)* | ;0.18 | *Gymnocarpium dryopteris (H)* | ;0.20 |
| *Epipactis helleborine (H)* | ;0.27 | *Carex digitata (H)* | ;0.18 | *Primula elatior (H)* | ;0.19 |
| *Veronica urticifolia (H)* | ;0.27 | *Aegopodium podagraria (H)* | ;0.18 | *Cicerbita alpina (H)* | ;0.19 |

**Table 7** – *Table showing species with the highest increase or decrease in cover for past and current conditions. Letters in bracket correspond to the strata of plant height (A: tree >6 m, B: shrub 0.5-6 m and C: herbaceous <0.5 m).*

## Ecology of species changing in cover

| | Low elevation belt (< 1000 m) | | Medium elevation belt (1000 - 1500 m) | | High elevation belt (> 1500 m) | |
|---|---|---|---|---|---|---|
| **Landolt's indicators** | Increased cover (76/489 species) | Decreased cover (163/489 species) | Increased cover (107/489 species) | Decreased cover (149/489 species) | Increased cover (123/489 species) | Decreased cover (133/489 species) |
| Temperature (T) | 3.273 | 3.432 | 2.891 | 2.952 | 2.776 | 2.799 |
| Continentality (K) | 2.658 | 2.747 | 2.688 | 2.753 | 2.724 | 2.755 |
| Light (L) | 2.280 | 2.547 ** | 2.646 | 2.527 | 2.806 | 2.796 |
| Moisture (F) | 3.088 | 2.995 | 3.219 | 3.220 | 3.311 | 2.250 |
| Reactivity (R) | 3.309 | 3.453 | 2.958 | 3.280 ** | 3.124 | 2.939 |
| Nutrients (N) | 2.907 | 2.979 | 2.979 | 3.129 | 3.020 | 2.908 |
| Humus (H) | 3.351 | 3.189 | 3.875 | 3.581 * | 3.633 | 3.796 |
| Aeration (D) | 2.189 | 2.663 ** | 1.854 | 2.011 | 2.286 | 1.980 * |

***Table 8*** *– Table showing averages of Landolt's indicators for species with increase or decrease in cover between past and current conditions (weighted mean per survey according to the elevation belts and field observations). Significant results are highlighted with following p-values:* * : *<0.05,* ** : *<0.01 and* *** : *<0.001 (Student test).*

### *3.5.13 Cover analysis in the medium elevation belt (1000-1500 m)*

At medium elevation, deciduous trees and shrubs such as *Ulmus glabra, Sorbus aria*/*aucuparia*, *Lonicera nigra* and *Corylus avellana* increased in cover in parallel with some grassland species like *Carex ferruginea* and *Hypericum maculatum*. The ecology associated with these species reached a significant higher value in light indicator (P-value: <0.001) and a lower value in soil aeration factor (P-value: <0.001) than the past surveys.

We detected a decrease of various forests species such as *Cardamine heptaphylla*, *Melica nutans*, *Euphorbia dulcis*, *Ranunculus aconitifolium* and *Brachypodium pinnatum* and grassland species like *Campanula rhomboidalis* and *Euphorbia cyssparissias*. Landolt's indicators averages were significantly higher in both light (P-value: <0.01) and reactivity indicators than the past conditions (P-value: <0.05) and they were lower in soil aeration factor (P-value: <0.05; *Table 5*). Furthermore, average of reactivity indicator as significantly higher than the scores of species increasing in frequency (reactivity P-value: <0.01), unlike humus factor, which obtained lower result (P-value: <0.05; *Table 8*).

### *3.5.14 Cover analysis in the high elevation belt (>1500 m)*

Analysis indicated changes towards an increase in cover for species living in *Alnenion viridis* (*Alnus viridis*, *Ribes petraeum* and *Rhododendron ferrugineum*), *Lunario-Acerion* (*Acer pseudoplatanus*), *Alnion incanae* (*Alnus incarna*, *Aegopodium podagraria* and *Elymus caninus*) and species growing in coniferous forests (*Laburnum alpinum*, *Phyteuma orbiculare*, *Sorbus aucuparia*, *Abies alba*, *Larix decidua*, *Oreopteris limbosperma*, *Calamagrostis varia* and *Lonicera caerulea*). Regarding the ecology, we obtained significantly higher values in light (P-value: <0.001) and reactivity indicators (P-value: <0.01) than past surveys (*Table 5*).

Furthermore, we observed a decrease of various grassland species living in *Nardion* (*Gentiana purpurea* and *Campanula barbata*), *Mesobromion* (*Euphorbia cyparissias*), *Calthion* (*Myosotis*

*scorpioides* and *Juncus effusus*) and *Seslerion* (*Globularia nudicaulis*). The ecology of plants decreasing in cover was significantly higher in temperature (P-value: <0.05), continentality (P-value: <0.05) and light indicators (P-value: <0.001) than the past dataset (*Table 5*). Additionally, the average of soil aeration factor was lower than the result of plants increasing in cover (P-value: <0.05; *Table 8*).

Finally, several plants, living in a lower elevation belt than observed, obtained a higher current cover than the past one. Indeed, species such as *Carex sylvatica* (*Galio-Fagenion* and *Lonicero-Fagenion*), *Hepatica nobilis* (*Cephalanthero-Fagenion* and *Tilion platyphylli*), *Vicia sepium* (*Aegopodion*/*Alliarion*) and *Silene vulgaris* (*Arrhenatherion*) are growing at higher elevation than expected (Delarze & Gonseth, 2008). *Cardamine heptaphylla* and *Vicia sepium* decreased in cover at low and medium elevations in the same time that they increased at high elevation.

# 4. DISCUSSION

## 4.1 Variables evaluation

In our results, the temperature variable was the most important climatic driver, which explains the majority of floristic variation. It is followed by four additional indicators bringing additional variation (radiation, precipitation, slope and pH*; Fig. 8*). According to Woodward (1987) and Helmuth et al. (2005), temperature is the most fundamental predictor of species and population distribution, especially along the elevation gradient. However, in the study of Jeffree & Jeffree (1994) where they measured the potential geographical distribution of species with temperature, they found residual variance explained by other variables such as precipitation. This latter also play a significant part in determining species occurrence and abundance. Currently, researchers combine several climatic, edaphic and biotic factors influencing plants distributions with temperature variables (*Fig. 17*) for a projection in geographical space with greater ecological realism (Guisan & Thuiller, 2005). Modellers especially use statistical tools (SDMs, Guisan & Zimmermann, 2000) and high resolution numerical data depending the sampling scale and species mobility to study species ecological niche, with applications to ecology, biogeography, evolution, conservation biology and climate change (Guisan & Thuiller, 2005).

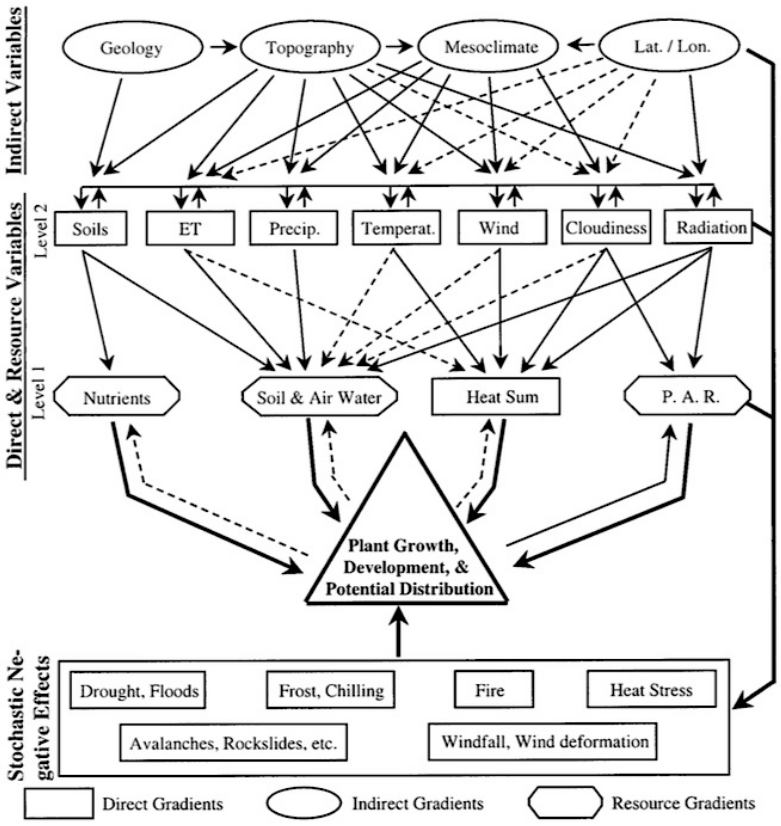



**Figure 17** – *Diagram of principal factors influencing vegetation distribution dynamics (Guisan & Zimmermann, 2000).*

## 4.2 Predicted changes

### *4.2.1 Predictions of species distributions*

Although the accuracy of current predictions (AUC averages: 0.89) was a little less good than that of past ones (AUC average: 0.95) due to calibration of current models generated from past models, SDMs proved able to predict past and current distributions of single species with generally good performances. As data used to fit the models take into account interspecific interactions, they implicitely predict the realized niche of species (*Fig. 18*). Yet some biases nevertheless appear. Indeed, a general low proportion of false predicted presences (past: 2.5 – 13.2%; current: 5 – 16.9%) and a slightly higher proportion of false predicted absences following some thresholding methods like pS-SDM (past: 5.9 – 63.7%; current: 39.5 – 72.9%) were calculated, meaning that true species occurrences were slightly underestimated.

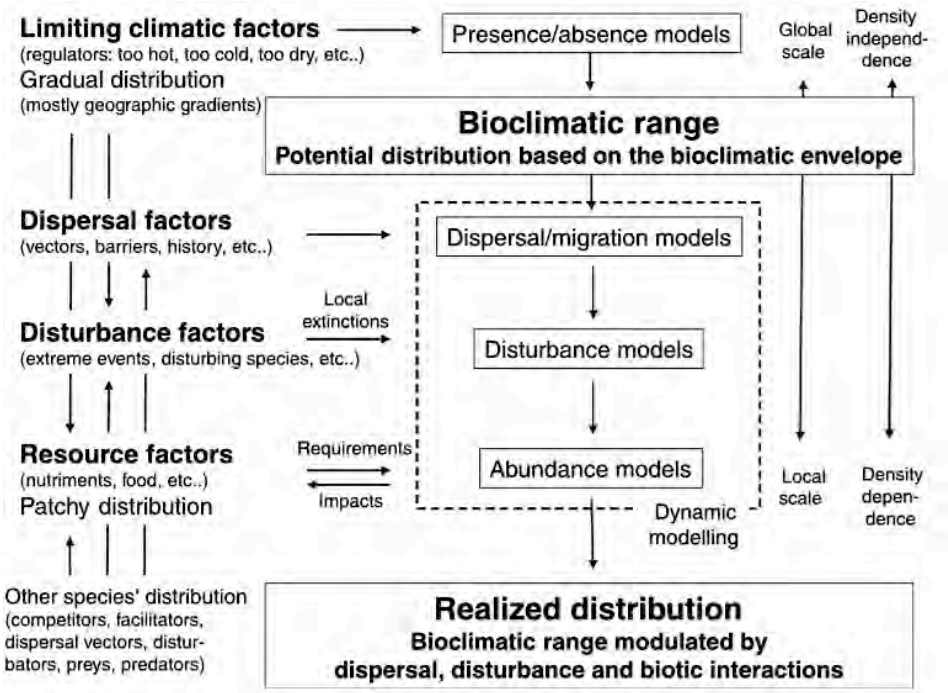



**Figure 18** – *Representation of principal factors generating the realized niche of species (Guisan & Thuiller, 2000).*

In addition, models rarely reach the best AUC values (1), perhaps because some non-homogenous effects such as the anthropic management (clearing and pasture) or the variability of dispersion and micro environments (perturbations and spatial dimensions; Lischke et al., 1998) can bring errors in modelling. For instance, the ability of some ubiquitous plants to live in many different environments such as *Oxalis acetosella*, *Carex sylvatica*, *Fragaria vesca*, *Abies alba* and *Rubus idaeus* produce poor models performance in our results. Currently, some researchers try to create predictors that take into account more biotic factors to improve modelling such as species and community dynamics, ecological migration and species' interactions (Guisan & Thuiller, 2005).

*4.2.2 Predictions of communities*

The model predictions of community distributions depend on the prediction of single species assemblages in the same way as species richness analysis (Guisan & Theurillat, 2000). In our results, we obtained good models performances for communities with high accuracy scores for past and current conditions. The high similarity scores between predictions and field observations confirm that models can basically predict species assemblages, especially for past predictions. Its significant increase along the elevation belts could be explained by a reduction of species richness towards mountain summits, which decreases identification errors or species omissions through lower detectability (*Table 2*). Moreover, low similarity values calculated between the current community predictions and the observations could indicate that models are less good at predicting community changes.

*4.2.3 Predictions of vegetation changes over the last 20-25 years*

Several studies used SDMs to support conservation decisions (Guisan et al., 2013, for instance species and communities dispersion (Jaberg & Guisan, 2001; Loyn et al., 2001), changes in biodiversity and species shifts due to climate change (Gottfried et al., 1999; Bakkenes et al., 2002; Thomas et al., 2004) or direct anthropic impacts (Collingham & Huntley, 2000). However, it is yet difficult to evaluate the modification of floristic distribution according to environmental changes, because the adaptation of communities from these perturbations can take decades or centuries. Some palaeoecological investigations have rather evaluated the predictions of ancient patterns with earlier data (Pearman et al., 2008), but very few have evaluated recent changes (Lenoir et al., 2010). In this study, we had thus the opportunity to investigate the ability of SDMs to predict current - species distributions from data from the past.

First, regarding the general average of species richness predictions and observations, we did not observe any tendency of changes in the Western Swiss Alps (average of field observations: 0.848; sd: ± 8.718). On a detailed scale analysis, however floristic changes occurred, but as some surveys obtained more species and others less, it is not surprising that the overall average reaches zero. Nevertheless, the distribution around zero in boxplots of field observations illustrate that models cannot predict exactly in which area these shifts appear (*Fig. 11;* graphics A and B). Mismatches can be a result of SDMs' limitations to make future predictions, because they generate a bias according to missing important predictors (spatial dimension and perturbations), sample size (Stockwell & Peterson, 2002) or some weaknesses in model parameterization (Guisan & Theurillat, 2000). Biotic interactions could also have evolved during the last 20-25 years and thus have increased error rates, especially for fast growing organisms (see Davis et al., 1998).

Concerning similarity in species composition, there is no significant difference between the boxplots from field observations along the sampling strata and the elevation belts (*Fig. 11*,

graphics C and D*; Appx. 4*) whereas models predicted differences. This means that we are not able to predict which areas are currently more or less similar than the past conditions. However, surprisingly we observed that more observed changes occurred than expected in the predictions (similarity average of field observations: 0.424; sd: ± 0.128; similarity average of predictions: 0.603; sd: ± 0.128; *Table 2*). As the climate change drove our sampling selection (temperature and precipitation), these additional shifts could indicate that other factors influence the floristic vegetation dynamics, such as forest densification (explained in the section *"4.3").*

*4.2.4 Predictions of the ecological dynamics over the last 20-25 years*

In our results on ecological indicators, the field observations obtained the same trend than predicted (*Fig. 12*). The reason could be the strong influence of steep altitudinal gradients on temperature and precipitation in mountain forests (Scherrer & Körner, 2011). These factors being the most important to explain species distribution and are influenced by climate change. The forests modification, along elevation driving the changes in humus and light indicators, was also strongly perceived (deciduous species reduction; *Fig. 12*). Nevertheless, regarding the differences between past and current ecological conditions, the temperature increase observed and predicted, especially at high elevation, and the light reduction perceived in the medium and high elevations could be influenced by other factors than the elevation gradient (*Fig. 12*). Indeed, global warming and forest densification, described in details in the section *"4.3"*, could also represent potential explanations.

In general, predictions showed often more extreme trends than field observations. The reason is perhaps that the composition of vegetation needs more time to evolve than predicted. Even if these results are poor, they are encouraging, because it is very remarkable to see changes in species distribution on a 20 years time scale. To conclude, although models are not yet perfect, they can be already very useful to evaluate biodiversity changes and species distributions (Engler et al., 2009), in a way to prevent plants from extinction (Randin et al., 2009) and to assess and monitor invasive species (Petitpierre et al, 2012). Current scientific challenges are to increase modelling power by developing models with more dynamic components and multi-specific patterns, and incorporate predictors such as population dynamics and dispersal, impact scale of global changes and soil indicators (Guisan & Thuiller, 2005).

## 4.3 Observed vegetation changes

*4.3.1 General species distribution in mountain forests (along the elevation belts)*

The field observations showed that both past and current plant distribution along the elevation gradient is essentially driven by temperature, light, pH and humus indicators. Soil aeration, soil humidity and nutrients ranked second (*Fig. 14*). This result is not surprising according to Körner (2000), who explains that the variability of environmental factors in mountains areas such as temperature, precipitation, slope, pH and soil resources, have an imposing impact on plants' growth, metabolism and reproduction. In the Swiss Alps, altitude and topography drive climatic conditions, especially temperature (decrease; Serquet & Rebetez, 2013) and precipitation (increase; Schwarb, 2000). Landolt's indicators analysis along the elevation could significantly confirm the strong influences of these two opposite scales on mountain forests distribution (temperature and soil moisture indicators; *Fig. 16*).

The negative correlation also observed between temperature and light indicators could correspond to forests density's and cover's decrease with elevation (*Fig. 16*). According to Horisberger & Clot (2009), the reduction of species shading the ground with their high cover and abundance such as *Fagus sylvatica* could offer sunnier areas promoting the expansion of heliophilous plants. The decrease of *Fagus sylvatica* frequency perceived in parallel with a significant cover and frequency increase of herbaceous and shrub species could confirm this hypothesis (*Appx. 5* and *6*). Moreover, grassland species occurrences increase significantly along the elevation gradient (see section *"3.5.6"*). At medium elevation, the high number of species detected could be explained by an important mix of forest and grassland plants, which have more present than in the lowland (see section "*3.5.5*").

However, according to many researchers, species richness has a linear decreasing trend closely connected to temperature reduction across elevation belts (Hamilton, 1975; Odland & Birks, 1999). Rahbek (1995) explained, in his study, that species richness could instead have a humped relationship along altitude with a peak corresponding to a hotspot in resources. The slope, geological perturbations, biotic interactions and the group of species considered co-determine different curve amplitudes following the micro and macro spatial scale. In our results, the significant increase of 7-8 herbaceous and shrub species observed between low and medium elevation belts (*Fig. 13*; section "*3.5.5*") could correspond to species richness values before the hotspot peak described by Rahbek (1995).

*4.3.2 General changes in the floristic distributions dynamics over the last 20-25 years*

At plots scale, we see important floristic changes per elevation belt between past and current conditions (*Fig. 14).* Communities' modification was perceived with an increase in species frequency over the last 20-25 years, especially in the high elevation belt (see section "*3.5.7*"). In

parallel, species richness increased by 2-3 herbaceous and shrub species between the current and the past surveys and reach 5 species more especially in medium elevation (*Fig. 13;* see section "*3.5.5*").

In the western Swiss Alps, an increase of forests species is revealed in the lowlands and especially at mid-elevations (DGE, 2011). Some other studies indicated the same trend according to an increase of plants occurrence and frequency in forests like in Canada, where Szeicz & MacDonald (1995) displayed an increase of species presences in the stand forests over 100-150 years. Shiyatov et al. (2005) observed the same tendency in Russian forests. Moreover, an increase in species richness in alpine and nival grasslands has been measured in parallel. For instance, in the European Alps, Grabherr et al. (1994) confirmed the increase of species richness observed at first by Braun-Blanquet (1957) and explained that they saw an upward distribution of vascular species, especially on the highest summits. In the Swiss Alps, the immigration of 15 to 20 plants towards the mountains top has been observed by Hofer (1992) and this trend gets an even more important rate since 1980s (Walther et al., 2005). In Norwegian mountains, Klanderud & Birks (2003) observed the same trend in species richness along the altitudinal gradient during a 68 years period. Recently, many other studies recorded such shift in the distribution of plants limits (Pauli et al 2007; Vittoz et al., 2009; Matteodo et al., 2013), even on a shorter time period (Pauli et al., 2012).

In Switzerland, variations in species richness are strongly influenced by environmental variables such as low precipitations and especially, temperature levels (Wohlgemuth, 1998). Regarding results of Landolt indicators, the observed shifts seem mainly related to this last statement with a temperature increase and a soil moisture reduction, especially in the high elevation belt (*Fig. 14; Table 3*). Furthermore, temperature corresponds to the major ecological factors modified by climate changing (G.I.E.C., 2007; Filliger et al., 2013). According to the study of Lenoir et al. (2008), climate change could induce strong ecological and biological responses, such as shifts in distribution and abundance of species. As its impacts on temperature and precipitation keeps evolving throughout the years, we expected that oldest past surveys (1991-1994 years) had more vegetation shifts than the most recent ones (1998-2000 years). However, we did not obtain any significant trend. This could be explained by a smaller sample size available, which downgrades the power of statistical tests (Kent, 2011), or by the complexity and variability of vegetation distribution hiding the information.

Parallel to the modification of temperature and soil moisture indicators, the significant reduction of humus indicator, saw especially in lowlands, may be explained by impacts of climate change too (*Fig. 14; Table 3*). Indeed, while humus rates depend principally on soil temperature and humidity (O'Connell, 1990), actual conditions, like higher temperatures or more heavy rain, might improve the degradation of organic matter and release nutritive elements (Niklińska et al., 1999;

Hart & Perry, 1999). The functioning ecosystem is fairly sensitive to these shifts in the soil, because nitrogen and phosphorus are growth-limiting nutrients influencing the primary production and can influence changes in species distributions (Verhoeven et al., 1996).

Regarding these general floristic changes in our results and in the literature, two main hypotheses can be considered to understand these shifts of natural biota: forest densification (Carraro, 1999) and changes in species distributions caused by climate change (Lenoir et al., 2008).

*4.3.3 Forests densification*

As we know, cattle grazing, agriculture and trees exploitation slowed down the forest expansion and the position of the tree line in the Alps for almost 4000 years (Holtmeier, 2003; Tinner & Theurillat, 2003). However, farming and pasture activities have been reduced since the 19$^{th}$ century leading to a forest expansion of 17% during the last 90 years (Mather & Fairbairn, 2000; DGE, 2011). Moreover, according to Gherig-Fasel et al. (2007), the Western Swiss Alps also obtained a rise of the forests cover between 1985 and 1997, correlated positively with elevation, reaching 3% from 1650 to 1750 m, and predicted to reach 19% between 2050 and 2150, and more than 49% after 2150 m. These changes represent, in general, a forest regrowth, and are especially important between 1400 and 2100 m, where forests can reach their initial treeline limit, between 1650 m and 2450 m (*Fig. 19*).

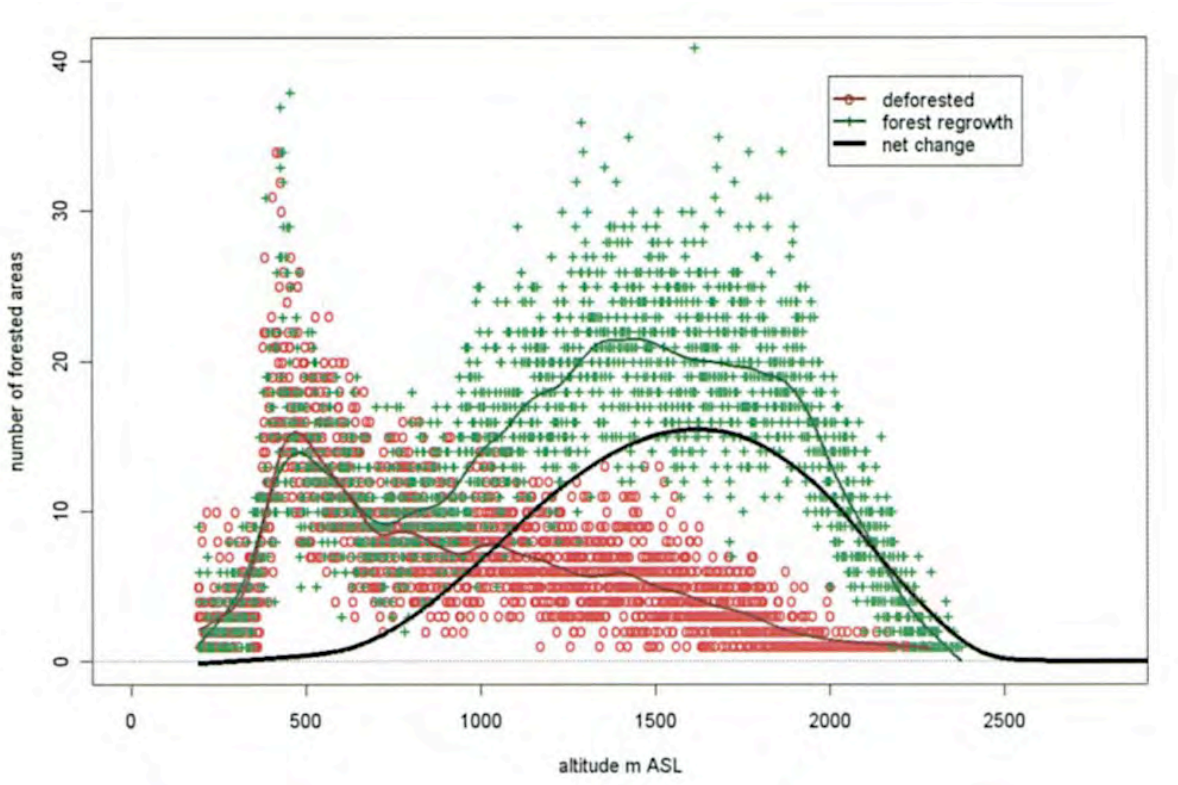



**Figure 19** – *Illustration of forests shifts (groves and shrubs) during 1985-1997. Red symbols (circles) symbolise a zone of 1 ha of disappeared forests and green ones (crosses) the forest regrowth (Gehrig-Fasel et al., 2007).*

*4.3.4 Forests densification in the low elevation belt (<1000 m)*

At low elevation, our first result supporting the forest maturation and closure hypothesis of 3% recorded in Swiss forests (Brändli & Abegg, 2009) is the significant cover increase shown by trees and shrubs (*Prunus avium, Ulmus glabra, Quercus petraea/robur, Abies alba*, etc.; see section "*3.5.12*"). Moreover, when forests become denser and darker, heliophilous and thermophilous species can be negatively affected in their vital rates, and disappear or reduce their presence. This observation is supported by our study, which showed a reduction of species living in scrubs (*Pruno-Rubion; see* section *"3.5.8"*) and a significant higher average of light indicator for the species decreasing in cover and frequency than the increasing one, and the ones in the past conditions. In parallel, in medium and high elevation belts, we statistically accounted the same trend for the frequency with very significant values (*Tables 5, 6* and *8*). According to Lenoir et al. (2010), modification in light penetration could be associated to management or natural disturbance. As we observed this phenomenon in all elevation, anthropic land abandonment could be the best explanation. The species decreasing in cover also indicated higher soil aeration than the increasing one, perhaps because they live in warmer and sunnier areas, with soils drying quicker and more aeration (*Table 8*).

The community changes observed at low elevation might also stimulate the recolonisation in small-scale of more adapted species. For instance, the low competition of herbaceous species with seedlings in dense forests could also promote shadow-tolerant seedlings (*Fagus sylvatica*; Löf & Welander, 2004). We perceived this singularity through an increased frequency of many forest species, especially shadow-tolerant trees seedlings (*Acer pseudoplatanus, Fagus sylvatica* and *Fraxinus excelsior*) (*Appx. 6*). This last analysis has to be interpreted with caution, because many other reasons could influence the tree seeds and seedlings survival such as warmer seasons with mild winters (deciduous species) or the presence of a snow cover for frost protection (Sykes et al., 1996). Furthermore, this could also depend on the waiting time between seeding too, which is specific for each species or on the humus quantity. Indeed, higher-humus rates could negatively influence the seedling (Pellissier & Trosset, 1992).

However, it remains difficult to fully understand the causes influencing the forest changes in this elevation belt, because many factors have multiple and linked impacts such as the reduction of anthropic land use, the regional influence of herbivore pressure (e.g. deer populations, Taverna et al., 2005), the impact of climate change or the current anthropic activities (fertilizers, atmospheric nitrogen deposition) (Vitousek et al., 1997; Gehrig-Fasel et al., 2007; Peter et al., 2008; Vittoz et al., 2013). For instance, a reduction of the forest exploitation can promote shade-tolerant species, but according to Smith & Huston (1989) the distribution of these plants also depends on water stress, which can be modified by global warming.

*4.3.5 Forest densification in the medium elevation belt (1000-1500 m)*

At medium elevation, the reduction in frequency of species living in forest edges, grasslands or pastures contrasting with increased presences of forest plants like various young trees (*Acer pseudoplatanus, Sorbus aucuparia, Fagus sylvatica* and *Picea abies*) and a cover increase of shrubs (*Ulmus glabra, Sorbus aria/aucuparia* and *Corylus avellana*) may reveal the forest regrowth (*Tables 4 and 7*). Moreover, the current cover expansion of species preferring a more acidic soil quality with higher humus mass than the plants decreasing in cover could be explained by an increase of species living in coniferous forests bringing acidic litter such as *Abieti-Piceion* and *Vaccinio-Piceion* (*Tables 5* and *8*).

According to Gehrig-Fasel et al (2007), the greater number of newly established forests is over 1400 m. At medium elevation, we statistically demonstrated a quick vegetation dynamics with current values of species richness (herbaceous and shrubs) greater than measured in the past conditions (*Fig. 13;* see section "*3.5.5*"). Theoretical analyses assumed that biotic regulations, such as competition, could stabilize community patterns with enough time. Thus, the high species richness observed currently will be reduced in the future with plants shifting upslope and others with a distribution not yet in equilibrium could be in extinction (Lenoir et al., 2010; Callaway & Walker, 1997).

*4.3.6 Forests densification in the high elevation belt (>1500 m)*

At high elevation, the same phenomenon of forest densification and vegetation turnover between grasslands and forest species observed in the medium elevation belt appears (*Tables 4* and *7).* Furthermore, regarding Landolt's indicators according to frequency shifts, significant changes in soil moisture (reduction) and temperature (increase) factors are perceived in addition (*Tables 3* and *6*). Moreover, the species increasing in cover obtained higher soil aeration than the decreasing ones, maybe because warmer conditions could reduce soil moisture and improve soil aeration (*Table 8*). These ecological shifts may reveal a vegetation dynamics partly influenced by the impacts of climate change, hidden by anthropic impacts and land recolonisation (Gehrig-Fasel et al., 2007; Vittoz et al., 2013). Atmospheric nitrogen released by anthropic activities would also bring a soil acidification (Verhoeven et al., 1996).

*4.3.7 Species distribution influenced by climate change*

According to Gherig-Fasel et al. (2007) and Vittoz et al. (2009), although the increases in forest density and species richness are principally due to land abandonment, climate change drives a small fraction of visible upward shifts. Indeed, 4% of forest colonisation above the tree line, but have currently a low impact in mountains areas. In the literature, some studies illustrated floristic changes influenced by impacts of global warning. For instance, in mountain forests, scientists reported a forest recolonisation increase around the tree line (Szerencsits, 2012; Carcaillet & Brun,

2000), an immigration of 171 forest species from lower elevations (Lenoir et al., 2008), a treeline shift up to 2500 m in the Central Alps (Vittoz et al., 2008) and a promotion on mountain summits of more thermophilous species such as *Pinus cembra L* (Vittoz et al., 2008; Walther, 2003).

In our research at high elevation, we can show three clues, which together might be in accordance with these tendencies showing climatic impacts: visible upward shifts of some species, increase of thermophilous species and *Picea abies* distribution.

*4.3.8 Upward shifts of species*

The first clue illustrating potential impacts of climate change on the distribution of plants was observed in medium elevation, where those species increasing in frequency obtained a lower continentality indicator than the decreasing ones (*Table 6*). This could be explained by upwards shifts of species living with more temperature variations and frost. However, this species substitution did not change significantly the general difference between past and current ecological conditions (*Table 3*), perhaps because we did not monitor a long-enough period of time (e.g. 20-25 years) to see significant shifts occurring on continentality factor.

At plots scale, some species changed their optimum elevation, especially at high elevation. For instance, Horisberger & Clot (2009) discovered that although *Phyteuma spicatum* often occur in all elevation gradients up to the tree line (1900-2000 m), this plant prefers fresh climate and can be more present at high elevation in the western Swiss Alps. Global warming could thus promote this species. Our study supports this observation with an increase in frequency of this plant in the medium (+3) and high elevation belt (+11) and a decrease in frequency (-4) and in cover (-0.35) at low elevation. Lenoir et al. (2008) also established that *Phyteuma spicatum* increased its optimum elevation over the 20$^{th}$ century (+273 m) with some other species such as *Hieracium murorum* (+162 m), *Acer pseudoplatanus* (+137 m), *Abies alba* (+214 m; significant P-value) and *Knautia dipsacifolia* (+200 m). In our study, these latter plants also increase in frequency at high elevation. In opposit, species like *Aster bellidiastrum* (-60 m), *Hieracium prenanthoides* (-259 m), *Drypoteris dilatata* (-235 m) and *Epilobium angustifolium* (-175 m), which reduced their optimum elevation according to Lenoir et al. (2008) and decreased in frequency in our results. Additionally, species increasing their optimum elevation such as *Cardamine heptaphylla* (+173 m), *Ribes petraeum* (+264 m), *Hepatica nobilis* (+498 m), *Abies alba* (+214 m), *Vicia septium* (+75 m) and *Senecio ovatus* (+300 m) in Lenoir et al. (2008), increased their cover in our study in contrast with plants like *Rubus saxitilis* (-73 m) and *Calamagrostis varia* (-94 m), which reduce their cover and their optimum elevation.

The major biological trait of colonisation categorizing these last species is the high potential for seed dispersal by wind (anemochorous). According to Ozinga et al. (2004), this capacity is positively correlated with light along elevation gradients and the decrease in seed weight observed

at the same time reflecting the species competition for light. Along the elevation gradient, the forest canopy becomes less high and dense with an important presence of open spaces increasing the wind effect (Grace, 1977; Pellissier et al., 2010). This could explain the higher presence of anemochorous plants observed with elevation. However, although climate changes could occur in a few decades, some biological traits of colonisation could be promoted before the others (e.g. diaspore morphology such as pappus; Vittoz et al., 2009; Matteodo et al., 2013).

Finally, at high elevation, an increase in frequency or cover of some species occupying habitats situated in lowland such as *Carex sylvatica*, *Ajuga reptans*, *Hepatica nobilis*, *Vicia sepium* and *Silene vulgaris* have been observed (see section "*3.5.10*"). *Vicia sepium* and *Ajuga reptans* normally live in the *Aegopodion/Alliarion* alliances with other species such as *Aegopodium podagraria* and *Geum urbanum*, which slightly increased in cover or frequency in our study too. These plant communities contain species living in a semi-shaded exposure with fresh and wet conditions such as in forest clearings and hemi-heliophilous forest edges (Terrisse, 2006). They naturally often recolonised by woody species reducing clearings and light under the canopy. Thus, the forest densification detected at low and medium elevations, in the same time with the reduction of *Vicia sepium* occurrence, might illustrate the decline of these communities. Nevertheless, the increased occurrence of species living in *Aegopodion/Alliarion* at high elevation could be promoted by better ecological conditions according to climate change.

*4.3.9 Increase of thermophilous species*

Global warming combined with the reduction of soil moisture in forests could promote the reproduction and performances of thermophilous plants (Lenoir et al., 2010). Indeed, in our results, species such as *Hepatica nobilis* (increase in cover), which lives in a warmer environment and survives with less soil moisture than the majority of species collected in the similar elevation (>1500 m) was observed. According to Carraro (1999) & Walther (2001), we can see in the Swiss forests an increase of thermophilous and laurophyllous species caused by milder winter, especially in *Fagus sylvatica* forests. In the low elevation belt, we also see this trend with an increased frequency of laurophyllous species such as *Hedera helix,* such as *Taxus baccata* and *Ilex aquifolium*.

*4.3.10 Reduction of Picea abies distribution*

Following a climate change scenario planned for 2100, an increased frequency of *Fagus sylvatica* and *Abies alba* is expected in parallel with a reduction of *Picea abies* (Vittoz et al., 2013). In our results, we displayed this tendency with a *Picea abies* substitution (-2) by an increase of *Fagus sylvatica* (+4) and *Abies alba* scrubs (+4) occurrences at medium elevation (*Table 4*). Additionally, the distribution of *Picea abies* is also limited by aridity conditions, mild winters and competition with tree species such as *Pinus sylvestris* (Sykes et al., 1996). Indeed, as tree growth

in dry soils strongly depend on precipitation (Rigling, 2002), the significant reduction of soil moisture indicators observed in this elevation could indirectly show an expansion of dry sites influencing *Picea abies* distribution. The development of parasites may be promoted with milder winters or warmer conditions in summers induced by global warming. For instance, the bark beetle *Ips typographus* (Wermelinger et al., 2008) could contribute to the death of pines, which is quickly affected by its increase. In our study at medium elevation, the reduction of *Picea abies* distribution (tree and shrub frequency) may be correlated with this last hypothesis.

In summary, the combination of these three last observations can illustrate a potential impact of climate change through our field observations. However, this climatic influence is not always visible on the floristic distribution, because each species has its own interspecific response of dispersion and many other biotic and abiotic factors may interact in an unknown way (Gleason, 1926; Hansen et al., 2001).

# 5. CONCLUSION AND PERSPECTIVES

In conclusion, the following findings can be reported for our study (see *App. 7* showing a synthesis of the project):

1) The modelling of species and communities has generally good performances, especially for the species with high prevalence in the calibration and evaluation dataset. They can predict a part of the ecological dynamics according to climate change concerning temperature indicators. Although models can predict shifts in species richness and community composition in a satisfactory way, they are not yet able to define geographically where these changes occur, and they sometime predict fewer shifts than observed. Hence the complexity of the ecosystem brings limitations in model predictions (Pearson & Dawson, 2003).
2) The observed vegetation changes are partly attributed to forests densification. This statement is justified by our field observations through a diminution of the light indicator along elevation gradients, with an increase in species richness between past and current conditions being especially pronounced at medium elevation. This phenomenon could explain the lower community similarity obtained in field observations (more floristic changes) than predicted by the models fitted on potential climate change.
3) In medium and high elevation belts, the hypothesis about the potential impact of global warming could be supported by some observations such as an increase of species frequency especially at high elevation, and various changes in the species distribution dynamics (upwards shifts in species distribution, increase of thermophilous species). These latter analysis should be viewed with caution, because our analyses are based on a limited number of observation and climate change could occur on many factors and at various scales in space and time.

Climate changes and anthropic land management are dynamic topics that transcends any time scale, and will continue to evolve in parallel. Future research will be useful to take into account both influences on vegetation dynamics to protect biodiversity (Zechmeister et al., 2003; Milad et al., 2011) and species habitats. For this purpose, promoting and improving the quality and spatial resolution of models and predictors (Pradervand et al., 2014) could be a key element to better understand and predict the floristic distribution dynamics, to faster anticipate any invasive species expansion (Petitpierre et al. 2015) and to protect the extinction of certain species. For instance, mountain species living in high elevation ecosystems must be protected because they have less and less escape path according to the elevation gradient, when climate changes promote an upward shift in distribution (Theurillat & Guisan, 2001). But in the end, modelling can deliver a first approximation of the natural system and its evolution through perturbation and the fieldwork is

still essential to check predictions and better understand species distribution dynamics (Pearson & Dawson, 2003).

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- OcCC, Organe consultatif sur les changements climatiques: http://www.occc.ch/index_f.html.
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## 8. Appendix - Species list N°1

| Species recorded in the study area | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Abies alba* | *Bromus benekenii* | *Crepis pyrenaica* | *Gymnadenia conopsea aggr.* | *Melampyrum sylvaticum* | *Melampyrum sylvaticum* | *Populus tremula* | *Solanum dulcamara* |
| *Acer campestre* | *Calamagrostis varia* | *Cystopteris fragilis* | *Gymnocarpium dryopteris* | *Melica nutans* | *Melica nutans* | *Potentilla erecta* | *Soldanella alpina* |
| *Acer opalus* | *Calamagrostis villosa* | *Dactylis glomerata* | *Gymnocarpium robertianum* | *Melica uniflora* | *Melica uniflora* | *Potentilla sterilis* | *Sorbus aria* |
| *Acer platanoides* | *Caltha palustris* | *Dactylorhiza maculata* | *Hedera helix* | *Melittis melissophyllum* | *Melittis melissophyllum* | *Prenanthes purpurea* | *Sorbus aucuparia* |
| *Acer pseudoplatanus* | *Campanula barbata* | *Daphne laureola* | *Helleborus foetidus* | *Mercurialis perennis* | *Mercurialis perennis* | *Primula acaulis* | *Sorbus chamaemespilus* |
| *Aceras anthropophorum* | *Campanula cochleariifolia* | *Daphne mezereum* | *Hepatica nobilis* | *Milium effusum* | *Milium effusum* | *Primula elatior* | *Sorbus mougeotii* |
| *Achillea macrophylla* | *Campanula rhomboidalis* | *Deschampsia cespitosa* | *Heracleum sphondylium aggr.* | *Moehringia muscosa* | *Moehringia muscosa* | *Prunella grandiflora* | *Stachys alpina* |
| *Aconitum lycoctonum aggr.* | *Campanula rotundifolia* | *Digitalis lutea* | *Hieracium glaucinum* | *Moehringia trinervia* | *Moehringia trinervia* | *Prunella vulgaris* | *Stachys officinalis* |
| *Aconitum napellus aggr.* | *Campanula trachelium* | *Dryopteris carthusiana* | *Hieracium prenanthoides* | *Molinia litoralis* | *Molinia litoralis* | *Prunus avium* | *Stachys sylvatica* |
| *Aconitum paniculatum* | *Cardamine heptaphylla* | *Dryopteris dilatata* | *Hieracium vogesiacum* | *Monotropa hypopitys* | *Monotropa hypopitys* | *Prunus spinosa* | *Stellaria nemorum* |
| *Actaea spicata* | *Cardamine impatiens* | *Dryopteris filix mas* | *Hippocrepis emerus* | *Mycelis muralis* | *Mycelis muralis* | *Pteridium aquilinum* | *Streptopus amplexifolius* |
| *Adenostyles alliariae* | *Cardamine pentaphyllos* | *Dryopteris oreades* | *Homogyne alpina* | *Myosotis scorpioides* | *Myosotis scorpioides* | *Pulmonaria officinalis* | *Tamus communis* |
| *Adenostyles glabra* | *Cardamine pratensis* | *Elymus caninus* | *Hordelymus europaeus* | *Myosotis sylvatica* | *Myosotis sylvatica* | *Pulsatilla alpina* | *Taraxacum officinale* |
| *Adoxa moschatellina* | *Carduus defloratus* | *Epilobium alpestre* | *Hypericum maculatum* | *Myrrhis odorata* | *Myrrhis odorata* | *Quercus petraea* | *Taxus baccata* |
| *Aegopodium podagraria* | *Carduus personata* | *Epilobium angustifolium* | *Hypericum montanum* | *Nardus stricta* | *Nardus stricta* | *Quercus robur* | *Teucrium chamaedrys* |
| *Agrostis capillaris* | *Carex acutiformis* | *Epilobium montanum* | *Ilex aquifolium* | *Neottia nidus avis* | *Neottia nidus avis* | *Ranunculus aconitifolius* | *Teucrium montanum* |
| *Ajuga reptans* | *Carex alba* | *Epipactis atrorubens* | *Impatiens noli tangere* | *Orchis mascula* | *Orchis mascula* | *Ranunculus auricomus aggr.* | *Thalictrum aquilegiifolium* |
| *Alliaria petiolata* | *Carex digitata* | *Epipactis helleborine* | *Juglans regia* | *Oreopteris limbosperma* | *Oreopteris limbosperma* | *Ranunculus lanuginosus* | *Thesium alpinum* |
| *Allium ursinum* | *Carex ferruginea* | *Epipactis purpurata* | *Juniperus communis* | *Origanum vulgare* | *Origanum vulgare* | *Ranunculus platanifolius* | *Thymus pulegioides* |
| *Alnus incana* | *Carex flacca* | *Equisetum arvense* | *Juniperus nana* | *Orthilia secunda* | *Orthilia secunda* | *Ranunculus repens* | *Tilia cordata* |
| *Alnus viridis* | *Carex humilis* | *Equisetum sylvaticum* | *Knautia dipsacifolia* | *Oxalis acetosella* | *Oxalis acetosella* | *Rhamnus alpina* | *Tilia platyphyllos* |
| *Amelanchier embergeri* | *Carex montana* | *Equisetum telmateia* | *Laburnum alpinum* | *Paris quadrifolia* | *Paris quadrifolia* | *Rhamnus cathartica* | *Tofieldia calyculata* |
| *Anemone nemorosa* | *Carex ornithopoda* | *Erica carnea* | *Lamium montanum* | *Parnassia palustris* | *Parnassia palustris* | *Rhododendron ferrugineum* | *Tozzia alpina* |
| *Angelica sylvestris* | *Carex pallescens* | *Euonymus europaeus* | *Lamium purpureum* | *Petasites albus* | *Petasites albus* | *Ribes alpinum* | *Trifolium medium* |
| *Anthericum ramosum* | *Carex paniculata* | *Eupatorium cannabinum* | *Larix decidua* | *Petasites hybridus* | *Petasites hybridus* | *Ribes petraeum* | *Trifolium pratense* |
| *Anthriscus nitida* | *Carex sylvatica* | *Euphorbia amygdaloides* | *Laserpitium latifolium* | *Peucedanum ostruthium* | *Peucedanum ostruthium* | *Ribes rubrum* | *Trollius europaeus* |
| *Anthriscus sylvestris* | *Carlina simplex* | *Euphorbia cyparissias* | *Laserpitium siler* | *Phegopteris connectilis* | *Phegopteris connectilis* | *Rosa arvensis* | *Tussilago farfara* |
| *Anthyllis vulneraria aggr.* | *Carpinus betulus* | *Euphorbia dulcis* | *Lathyrus niger* | *Phragmites australis* | *Phragmites australis* | *Rosa corymbifera* | *Ulmus glabra* |
| *Aposeris foetida* | *Castanea sativa* | *Fagus sylvatica* | *Lathyrus pratensis* | *Phyllitis scolopendrium* | *Phyllitis scolopendrium* | *Rosa pendulina* | *Urtica dioica aggr.* |
| *Aquilegia atrata* | *Centaurea montana* | *Festuca altissima* | *Lathyrus vernus* | *Phyteuma betonicifolium* | *Phyteuma betonicifolium* | *Rubus caesius* | *Vaccinium gaultherioides* |
| *Aquilegia vulgaris* | *Cephalanthera damasonium* | *Festuca heterophylla* | *Leucanthemum vulgare aggr.* | *Phyteuma orbiculare* | *Phyteuma orbiculare* | *Rubus idaeus* | *Vaccinium myrtillus* |
| *Arabis hirsuta* | *Cephalanthera longifolia* | *Filipendula ulmaria* | *Ligusticum mutellina* | *Phyteuma spicatum* | *Phyteuma spicatum* | *Rubus saxatilis* | *Vaccinium vitis idaea aggr.* |
| *Arabis turrita* | *Cephalanthera rubra* | *Fragaria vesca* | *Ligustrum vulgare* | *Picea abies* | *Picea abies* | *Rumex alpestris* | *Valeriana dioica* |
| *Arnica montana* | *Chrysosplenium alternifolium* | *Fraxinus excelsior* | *Lilium martagon* | *Pimpinella major aggr.* | *Pimpinella major aggr.* | *Salix appendiculata* | *Valeriana montana* |
| *Arum maculatum* | *Cicerbita alpina* | *Galeopsis tetrahit* | *Listera cordata* | *Pinus cembra* | *Pinus cembra* | *Salix caprea* | *Valeriana tripteris* |
| *Aruncus dioicus* | *Cicerbita plumieri* | *Galium aparine* | *Listera ovata* | *Pinus sylvestris aggr.* | *Pinus sylvestris aggr.* | *Salvia glutinosa* | *Veratrum lobelianum* |
| *Asplenium fontanum* | *Circaea lutetiana* | *Galium mollugo* | *Lonicera alpigena* | *Pinus uncinata* | *Pinus uncinata* | *Sambucus nigra* | *Veronica chamaedrys* |
| *Asplenium ruta muraria* | *Cirsium oleraceum* | *Galium odoratum* | *Lonicera caerulea* | *Platanthera bifolia* | *Platanthera bifolia* | *Sambucus racemosa* | *Veronica officinalis* |
| *Asplenium trichomanes* | *Cirsium palustre* | *Galium pumilum* | *Lonicera nigra* | *Poa alpina* | *Poa alpina* | *Sanicula europaea* | *Veronica urticifolia* |
| *Asplenium viride* | *Clematis vitalba* | *Galium rotundifolium* | *Lonicera xylosteum* | *Poa nemoralis* | *Poa nemoralis* | *Saxifraga cuneifolia* | *Viburnum lantana* |
| *Aster bellidiastrum* | *Clinopodium vulgare* | *Gentiana asclepiadea* | *Lotus corniculatus* | *Poa trivialis* | *Poa trivialis* | *Saxifraga paniculata* | *Viburnum opulus* |
| *Astrantia major* | *Colchicum autumnale* | *Gentiana lutea* | *Lunaria rediviva* | *Polygala chamaebuxus* | *Polygala chamaebuxus* | *Saxifraga rotundifolia* | *Vicia sepium aggr.* |
| *Astrantia minor* | *Convallaria majalis* | *Gentiana purpurea* | *Luzula luzulina* | *Polygonatum multiflorum* | *Polygonatum multiflorum* | *Scabiosa columbaria* | *Vicia sylvatica* |
| *Athyrium filix femina* | *Cornus mas* | *Geranium sanguineum* | *Luzula nivea* | *Polygonatum odoratum* | *Polygonatum odoratum* | *Scrophularia nodosa* | *Vincetoxicum hirundinaria* |
| *Bartsia alpina* | *Cornus sanguinea* | *Geranium sylvaticum* | *Luzula pilosa* | *Polygonatum verticillatum* | *Polygonatum verticillatum* | *Sedum album* | *Viola biflora* |
| *Berberis vulgaris* | *Coronilla vaginalis* | *Geum rivale* | *Luzula sylvatica* | *Polygonum bistorta* | *Polygonum bistorta* | *Sedum maximum* | *Viola hirta* |
| *Betula pendula* | *Corylus avellana* | *Geum urbanum* | *Lycopodium annotinum* | *Polygonum viviparum* | *Polygonum viviparum* | *Senecio alpinus* | *Viola reichenbachiana* |
| *Blechnum spicant* | *Cotoneaster integerrimus* | *Glechoma hederacea* | *Lysimachia nemorum* | *Polypodium vulgare* | *Polypodium vulgare* | *Senecio ovatus* | |
| *Brachypodium pinnatum* | *Cotoneaster tomentosus* | *Globularia nudicaulis* | *Maianthemum bifolium* | *Polystichum aculeatum* | *Polystichum aculeatum* | *Sesleria caerulea* | |
| *Briza media* | *Crepis paludosa* | *Goodyera repens* | *Malus sylvestris* | *Polystichum lonchitis* | *Polystichum lonchitis* | *Silene dioica* | |

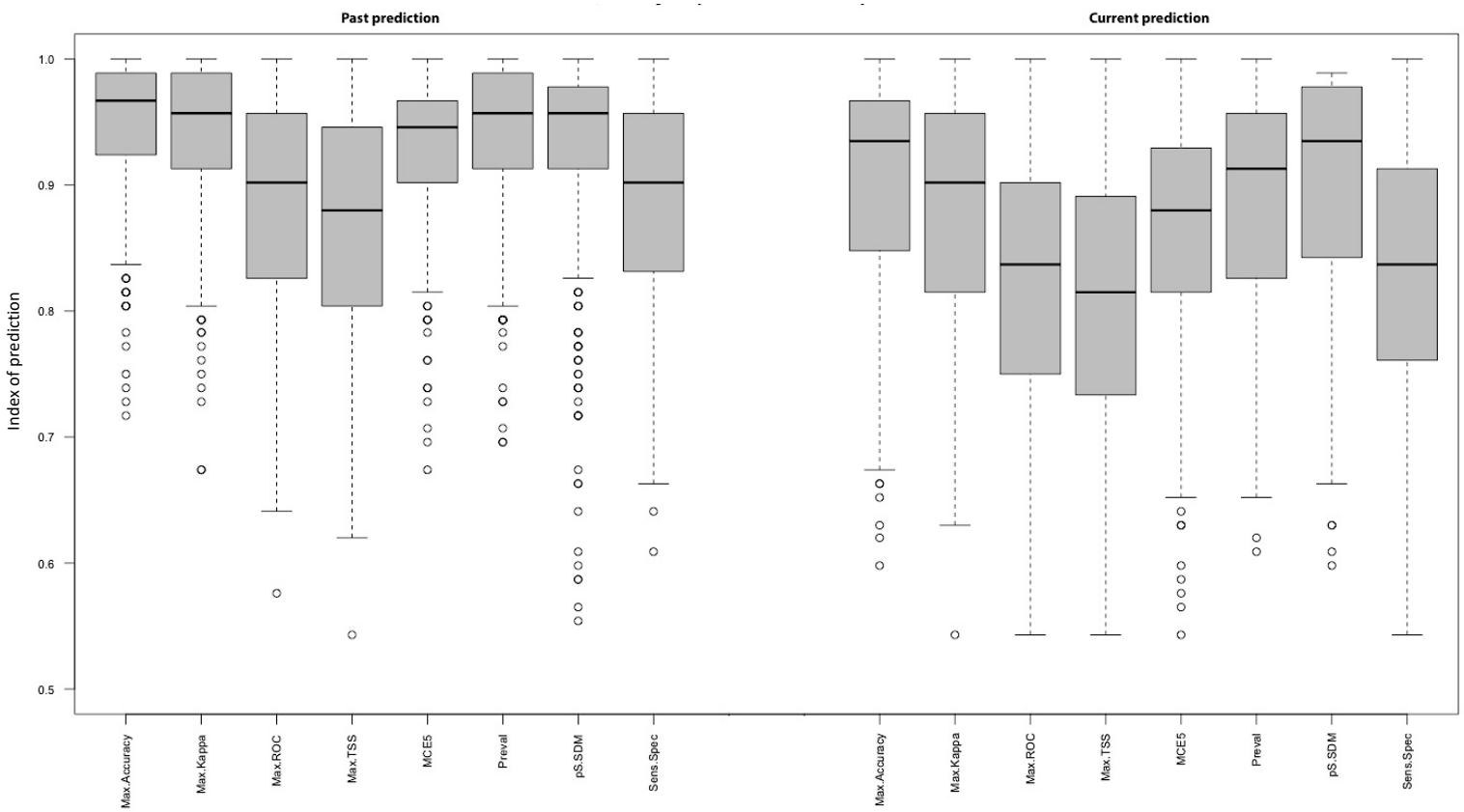
***Appendix 1*** *– List of forest species present in the 3076 inventories in the western Swiss Alps.*

## Species list N° 2

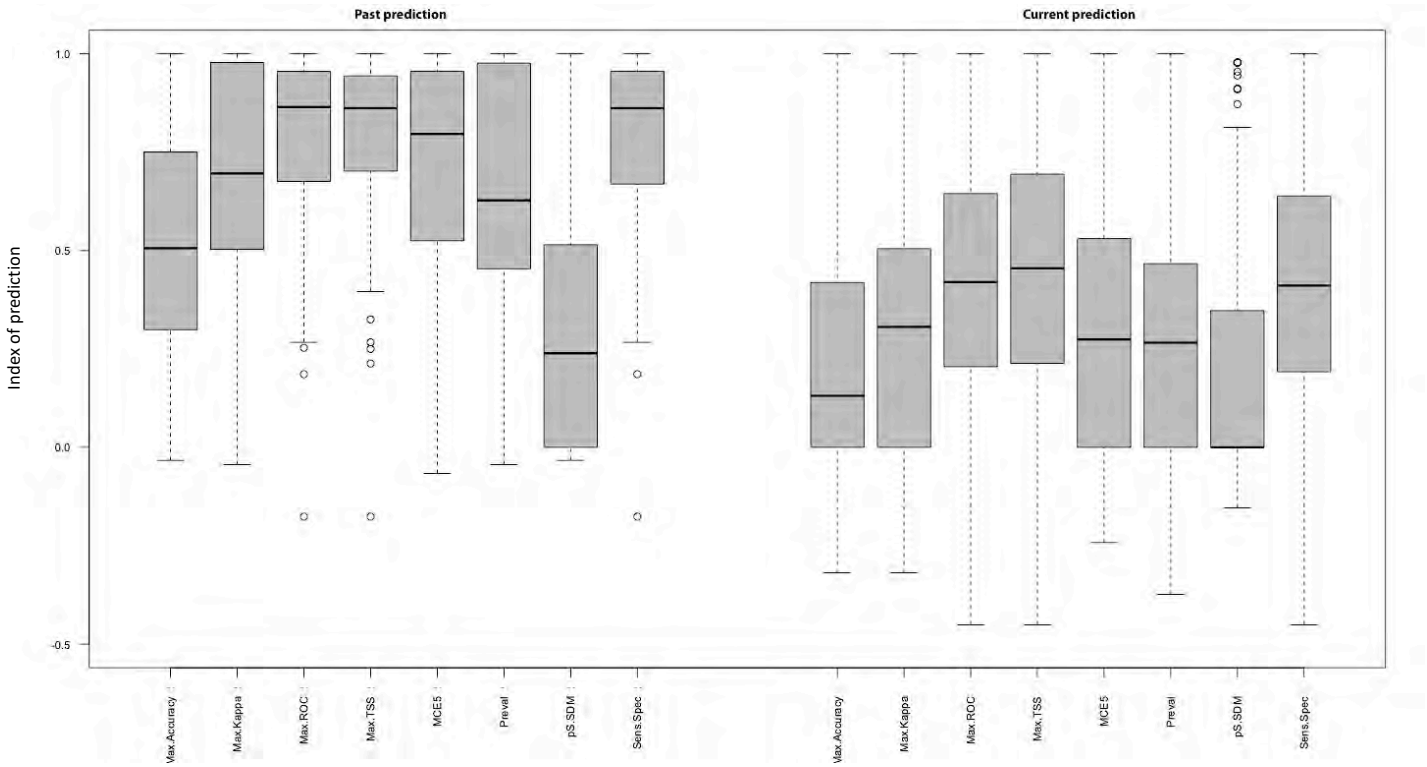
| Available species for modelling purpose | | | | | |
|---|---|---|---|---|---|
| *Abies alba* | *Cardamine impatiens* | *Equisetum sylvaticum* | *Lathyrus vernus* | *Polygonatum multiflorum* | *Sesleria caerulea* |
| *Acer campestre* | *Cardamine pentaphyllos* | *Erica carnea* | *Leucanthemum vulgare aggr.* | *Polygonatum odoratum* | *Silene dioica* |
| *Acer opalus* | *Cardamine pratensis* | *Euonymus europaeus* | *Ligusticum mutellina* | *Polygonatum verticillatum* | *Soldanella alpina* |
| *Acer platanoides* | *Carduus defloratus* | *Eupatorium cannabinum* | *Ligustrum vulgare* | *Polygonum bistorta* | *Sorbus aria* |
| *Acer pseudoplatanus* | *Carex acutiformis* | *Euphorbia amygdaloides* | *Lilium martagon* | *Polypodium vulgare* | *Sorbus aucuparia* |
| *Achillea macrophylla* | *Carex alba* | *Euphorbia cyparissias* | *Listera cordata* | *Polystichum aculeatum* | *Sorbus chamaemespilus* |
| *Aconitum lycoctonum* | *Carex digitata* | *Euphorbia dulcis* | *Listera ovata* | *Polystichum lonchitis* | *Sorbus mougeotii* |
| *Aconitum napellus* | *Carex ferruginea* | *Fagus sylvatica* | *Lonicera alpigena* | *Potentilla erecta* | *Stachys alpina* |
| *Actaea spicata* | *Carex flacca* | *Festuca altissima* | *Lonicera caerulea* | *Potentilla sterilis* | *Stachys sylvatica* |
| *Adenostyles alliariae* | *Carex humilis* | *Festuca heterophylla* | *Lonicera nigra* | *Prenanthes purpurea* | *Stellaria nemorum* |
| *Adoxa moschatellina* | *Carex montana* | *Filipendula ulmaria* | *Lonicera xylosteum* | *Primula acaulis* | *Streptopus amplexifolius* |
| *Aegopodium podagraria* | *Carex ornithopoda* | *Fragaria vesca* | *Lotus corniculatus* | *Primula elatior* | *Tamus communis* |
| *Agrostis capillaris* | *Carex pallescens* | *Fraxinus excelsior* | *Lunaria rediviva* | *Prunella vulgaris* | *Taxus baccata* |
| *Ajuga reptans* | *Carex paniculata* | *Galeopsis tetrahit* | *Luzula luzulina* | *Prunus avium* | *Teucrium montanum* |
| *Allium ursinum* | *Carex sylvatica* | *Galium aparine* | *Luzula nivea* | *Prunus spinosa* | *Thalictrum aquilegiifolium* |
| *Alnus incana* | *Carpinus betulus* | *Galium mollugo* | *Luzula pilosa* | *Pteridium aquilinum* | *Thesium alpinum* |
| *Alnus viridis* | *Castanea sativa* | *Galium odoratum* | *Luzula sylvatica* | *Pulmonaria officinalis* | *Tilia cordata* |
| *Anemone nemorosa* | *Centaurea montana* | *Galium pumilum* | *Lysimachia nemorum* | *Pulsatilla alpina* | *Tilia platyphyllos* |
| *Angelica sylvestris* | *Cephalanthera damasonium* | *Galium rotundifolium* | *Maianthemum bifolium* | *Quercus petraea* | *Trifolium medium* |
| *Anthericum ramosum* | *Cephalanthera longifolia* | *Gentiana asclepiadea* | *Malus sylvestris* | *Quercus robur* | *Trifolium pratense* |
| *Anthriscus nitida* | *Chrysosplenium alternifolium* | *Gentiana lutea* | *Melampyrum sylvaticum* | *Ranunculus aconitifolius* | *Trollius europaeus* |
| *Anthriscus sylvestris* | *Cicerbita alpina* | *Gentiana purpurea* | *Melica nutans* | *Ranunculus auricomus aggr.* | *Tussilago farfara* |
| *Aposeris foetida* | *Circaea lutetiana* | *Geranium sylvaticum* | *Melica uniflora* | *Ranunculus lanuginosus* | *Ulmus glabra* |
| *Aquilegia atrata* | *Cirsium oleraceum* | *Geum rivale* | *Melittis melissophyllum* | *Ranunculus platanifolius* | *Urtica dioica* |
| *Aquilegia vulgaris* | *Clematis vitalba* | *Geum urbanum* | *Mercurialis perennis* | *Ranunculus repens* | *Vaccinium myrtillus* |
| *Arnica montana* | *Clinopodium vulgare* | *Globularia nudicaulis* | *Milium effusum* | *Rhamnus alpina* | *Vaccinium vitis idaea* |
| *Arum maculatum* | *Colchicum autumnale* | *Goodyera repens* | *Monotropa hypopitys* | *Rhododendron ferrugineum* | *Valeriana dioica* |
| *Aruncus dioicus* | *Convallaria majalis* | *Gymnadenia conopsea* | *Mycelis muralis* | *Ribes alpinum* | *Valeriana tripteris* |
| *Asplenium fontanum* | *Cornus mas* | *Gymnocarpium dryopteris* | *Myosotis scorpioides* | *Ribes petraeum* | *Veratrum album* |
| *Asplenium ruta muraria* | *Cornus sanguinea* | *Gymnocarpium robertianum* | *Myosotis sylvatica* | *Ribes rubrum* | *Veronica chamaedrys* |
| *Asplenium trichomanes* | *Corylus avellana* | *Hedera helix* | *Myrrhis odorata* | *Rosa arvensis* | *Veronica officinalis* |
| *Asplenium viride* | *Cotoneaster tomentosus* | *Helleborus foetidus* | *Neottia nidus avis* | *Rosa corymbifera* | *Veronica urticifolia* |
| *Aster bellidiastrum* | *Crepis paludosa* | *Hepatica nobilis* | *Oreopteris limbosperma* | *Rosa pendulina* | *Viburnum lantana* |
| *Astrantia major* | *Crepis pyrenaica* | *Heracleum sphondylium* | *Origanum vulgare* | *Rubus caesius* | *Viburnum opulus* |
| *Astrantia minor* | *Cystopteris fragilis* | *Hieracium prenanthoides* | *Orthilia secunda* | *Rubus idaeus* | *Vicia sepium* |
| *Athyrium filix femina* | *Dactylis glomerata* | *Hieracium vogesiacum* | *Oxalis acetosella* | *Rubus saxatilis* | *Vicia sylvatica* |
| *Berberis vulgaris* | *Dactylorhiza maculata* | *Hippocrepis emerus* | *Paris quadrifolia* | *Rumex alpestris* | *Vincetoxicum hirundinaria* |
| *Betula pendula* | *Daphne laureola* | *Homogyne alpina* | *Parnassia palustris* | *Salix appendiculata* | *Viola biflora* |
| *Blechnum spicant* | *Daphne mezereum* | *Hordelymus europaeus* | *Petasites albus* | *Salix caprea* | *Viola hirta* |
| *Brachypodium pinnatum* | *Deschampsia cespitosa* | *Hypericum maculatum* | *Peucedanum ostruthium* | *Salvia glutinosa* | *Viola reichenbachiana* |
| *Bromus benekenii* | *Dryopteris carthusiana* | *Ilex aquifolium* | *Phragmites australis* | *Sambucus nigra* | |
| *Calamagrostis varia* | *Dryopteris dilatata* | *Impatiens noli tangere* | *Phyllitis scolopendrium* | *Sambucus racemosa* | |
| *Calamagrostis villosa* | *Dryopteris filix mas* | *Juglans regia* | *Phyteuma orbiculare* | *Sanicula europaea* | |
| *Caltha palustris* | *Elymus caninus* | *Juniperus communis* | *Phyteuma spicatum* | *Saxifraga cuneifolia* | |
| *Campanula barbata* | *Epilobium alpestre* | *Knautia dipsacifolia* | *Picea abies* | *Saxifraga paniculata* | |
| *Campanula cochleariifolia* | *Epilobium angustifolium* | *Laburnum alpinum* | *Pinus sylvestris* | *Saxifraga rotundifolia* | |
| *Campanula rhomboidalis* | *Epilobium montanum* | *Lamium montanum* | *Platanthera bifolia* | *Scrophularia nodosa* | |
| *Campanula rotundifolia* | *Epipactis atrorubens* | *Larix decidua* | *Poa nemoralis* | *Sedum album* | |
| *Campanula trachelium* | *Epipactis helleborine* | *Laserpitium latifolium* | *Poa trivialis* | *Senecio alpinus* | |
| *Cardamine heptaphylla* | *Equisetum arvense* | *Laserpitium siler* | *Polygala chamaebuxus* | *Senecio ovatus* | |

***Appendix 2*** *– List of species used for modelling.*

## Accuracy values of past and current predictions

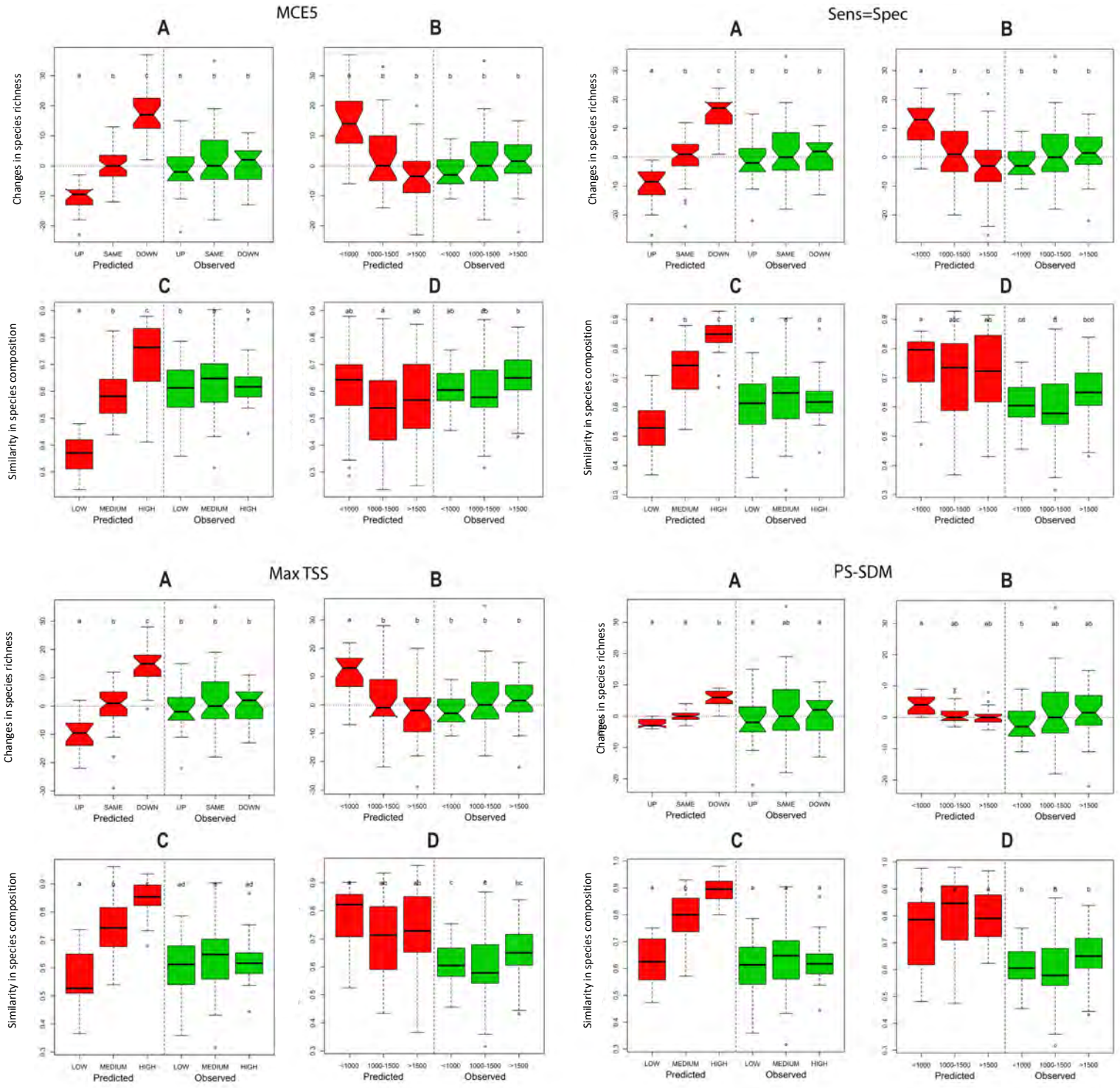



**TSS values of past and current predictions**




**Appendix 3** – *Boxplots illustrating past and current predictions for accuracy and TSS values according to threshold methods.*

## Species richness and similarity in plants composition




**Appendix 4** – *Graphics illustrating species richness changes and similarity in species composition between past and current conditions depending on the division selected for the random stratified (graphics A and C) and elevation belts (graphics B and D) for MCE5, Sens=Spec, max TSS and Ps-SDM threshold methods. When they are different, small letters on top of boxplots illustrate significant differences between groups.*

## Species frequency

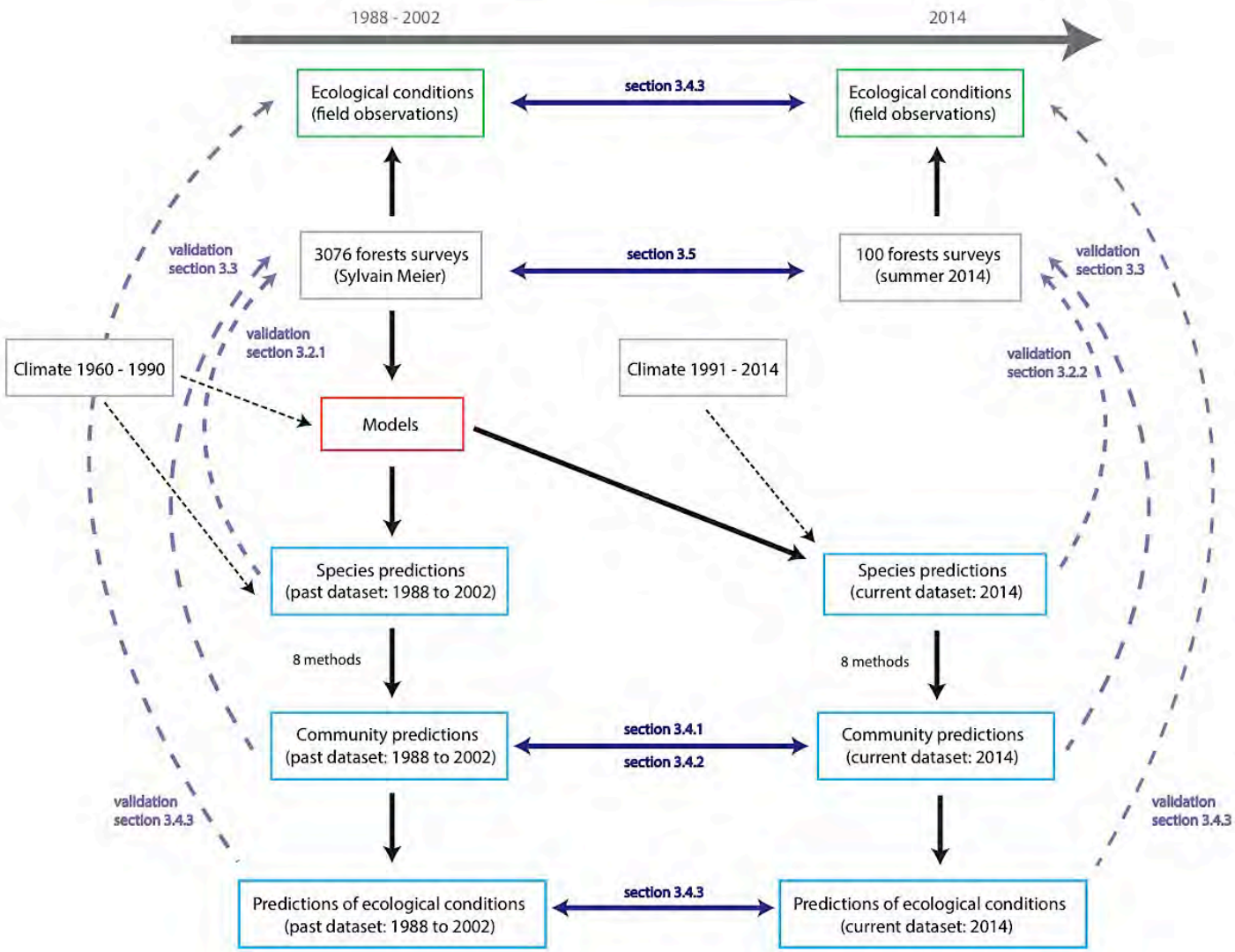
| Low elevation (<1000 m) | | | | | | Medium elevation (1000-1500 m) | | | | | | High elevation (>1500 m) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Past conditions | | | Current conditions | | | Past conditions | | | Current conditions | | | Past conditions | | | Current conditions | | |
| Species | Frecency | [%] | Species | Frecency | [%] | Species | Frecency | [%] | Species | Frecency | [%] | Species | Frecency | [%] | Species | Frecency | [%] |
| *Fagus sylvatica (A)* | 18 | 75 | *Hedera helix (H)* | 22 | 92 | *Picea abies (A)* | 29 | 91 | *Picea abies (A)* | 27 | 84 | *Picea abies (A)* | 31 | 86 | *Picea abies (A)* | 36 | 100 |
| *Fagus sylvatica (B)* | 15 | 63 | *Fagus sylvatica (A)* | 20 | 83 | *Picea abies (B)* | 23 | 72 | *Lamium galeobdolon (H)* | 25 | 78 | *Athyrium filix femina (H)* | 28 | 78 | *Sorbus aucuparia (H)* | 35 | 97 |
| *Fraxinus excelsior (H)* | 13 | 54 | *Fagus sylvatica (H)* | 20 | 83 | *Abies alba (A)* | 18 | 56 | *Acer pseudoplatanus (H)* | 23 | 72 | *Adenostyles alliariae (H)* | 27 | 75 | *Adenostyles alliariae (H)* | 30 | 83 |
| *Fagus sylvatica (H)* | 11 | 46 | *Fraxinus excelsior (H)* | 20 | 83 | *Athyrium filix femina (H)* | 17 | 53 | *Oxalis acetosella (H)* | 23 | 72 | *Sorbus aucuparia (B)* | 27 | 75 | *Athyrium filix femina (H)* | 30 | 83 |
| *Galium odoratum (H)* | 11 | 46 | *Acer pseudoplatanus (H)* | 15 | 63 | *Acer pseudoplatanus (A)* | 16 | 50 | *Picea abies (H)* | 23 | 72 | *Picea abies (B)* | 26 | 72 | *Hieracium murorum (H)* | 30 | 83 |
| *Hedera helix (H)* | 11 | 46 | *Fagus sylvatica (B)* | 15 | 63 | *Galium odoratum (H)* | 16 | 50 | *Athyrium filix femina (H)* | 22 | 69 | *Prenanthes purpurea (H)* | 26 | 72 | *Oxalis acetosella (H)* | 30 | 83 |
| *Mercurialis perennis (H)* | 11 | 46 | *Galium odoratum (H)* | 13 | 54 | *Hieracium murorum (H)* | 16 | 50 | *Sorbus aucuparia (H)* | 22 | 69 | *Vaccinium myrtillus (H)* | 26 | 72 | *Phyteuma spicatum (H)* | 29 | 81 |
| *Picea abies (A)* | 11 | 46 | *Lamium galeobdolon (H)* | 12 | 50 | *Lamium galeobdolon (H)* | 16 | 50 | *Dryopteris filix mas (H)* | 21 | 66 | *Aposeris foetida (H)* | 25 | 69 | *Picea abies (B)* | 29 | 81 |
| *Viola reichenbachiana (H)* | 11 | 46 | *Mercurialis perennis (H)* | 12 | 50 | *Dryopteris filix mas (H)* | 15 | 47 | *Hieracium murorum (H)* | 20 | 63 | *Picea abies (H)* | 24 | 67 | *Vaccinium myrtillus (H)* | 29 | 81 |
| *Lamium galeobdolon (H)* | 9 | 38 | *Fraxinus excelsior (A)* | 11 | 46 | *Prenanthes purpurea (H)* | 15 | 47 | *Picea abies (B)* | 20 | 63 | *Veronica urticifolia (H)* | 24 | 67 | *Prenanthes purpurea (H)* | 28 | 78 |
| *Abies alba (A)* | 8 | 33 | *Hedera helix (A)* | 11 | 46 | *Oxalis acetosella (H)* | 14 | 44 | *Prenanthes purpurea (H)* | 20 | 63 | *Hieracium murorum (H)* | 20 | 56 | *Aposeris foetida (H)* | 27 | 75 |
| *Acer pseudoplatanus (B)* | 8 | 33 | *Corylus avellana (B)* | 10 | 42 | *Acer pseudoplatanus (B)* | 13 | 41 | *Galium odoratum (H)* | 19 | 59 | *Ranunculus nemorosus (H)* | 19 | 53 | *Sorbus aucuparia (B)* | 26 | 72 |
| *Corylus avellana (B)* | 8 | 33 | *Hedera helix (B)* | 10 | 42 | *Fagus sylvatica (A)* | 13 | 41 | *Fagus sylvatica (H)* | 18 | 56 | *Abies alba (A)* | 18 | 50 | *Veronica urticifolia (H)* | 26 | 72 |
| *Dryopteris filix mas (H)* | 8 | 33 | *Picea abies (A)* | 10 | 42 | *Heracleum sphondylium (H)* | 13 | 41 | *Abies alba (A)* | 17 | 53 | *Luzula sylvatica (H)* | 18 | 50 | *Picea abies (H)* | 25 | 69 |
| *Fraxinus excelsior (A)* | 8 | 33 | *Acer pseudoplatanus (B)* | 9 | 38 | *Paris quadrifolia (H)* | 13 | 41 | *Acer pseudoplatanus (A)* | 17 | 53 | *Phyteuma spicatum (H)* | 18 | 50 | *Ranunculus nemorosus (H)* | 25 | 69 |
| *Hedera helix (A)* | 8 | 33 | *Corylus avellana (H)* | 9 | 38 | *Polygonatum verticillatum (H)* | 13 | 41 | *Fragaria vesca (H)* | 17 | 53 | *Sorbus aucuparia (H)* | 18 | 50 | *Rubus idaeus (H)* | 25 | 69 |
| *Oxalis acetosella (H)* | 8 | 33 | *Picea abies (B)* | 9 | 38 | *Geranium robertianum (H)* | 12 | 38 | *Paris quadrifolia (H)* | 17 | 53 | *Oxalis acetosella (H)* | 17 | 47 | *Petasites albus (H)* | 22 | 61 |
| *Phyteuma spicatum (H)* | 8 | 33 | *Viola reichenbachiana (H)* | 9 | 38 | *Petasites albus (H)* | 12 | 38 | *Polygonatum verticillatum (H)* | 17 | 53 | *Knautia dipsacifolia (H)* | 16 | 44 | *Homogyne alpina (H)* | 21 | 58 |
| *Picea abies (B)* | 8 | 33 | *Abies alba (A)* | 8 | 33 | *Picea abies (H)* | 12 | 38 | *Abies alba (H)* | 16 | 50 | *Solidago virgaurea (H)* | 16 | 44 | *Knautia dipsacifolia (H)* | 21 | 58 |
| *Acer pseudoplatanus (A)* | 7 | 29 | *Abies alba (H)* | 8 | 33 | *Veronica urticifolia (H)* | 12 | 38 | *Fagus sylvatica (A)* | 16 | 50 | *Chaerophyllum hirsutum (H)* | 15 | 42 | *Solidago virgaurea (H)* | 20 | 56 |
| *Cardamine heptaphylla (H)* | 7 | 29 | *Abies alba (B)* | 7 | 29 | *Fragaria vesca (H)* | 11 | 34 | *Acer pseudoplatanus (B)* | 15 | 47 | *Cicerbita alpina (H)* | 15 | 42 | *Abies alba (H)* | 19 | 53 |
| *Ilex aquifolium (B)* | 7 | 29 | *Acer pseudoplatanus (A)* | 7 | 29 | *Knautia dipsacifolia (H)* | 11 | 34 | *Fraxinus excelsior (H)* | 15 | 47 | *Petasites albus (H)* | 15 | 42 | *Fragaria vesca (H)* | 19 | 53 |
| *Rubus fruticosus aggr (H)* | 7 | 29 | *Dryopteris filix mas (H)* | 7 | 29 | *Mercurialis perennis (H)* | 11 | 34 | *Geranium robertianum (H)* | 15 | 47 | *Viola biflora (H)* | 15 | 42 | *Acer pseudoplatanus (H)* | 17 | 47 |
| *Abies alba (B)* | 6 | 25 | *Fraxinus excelsior (B)* | 7 | 29 | *Abies alba (H)* | 10 | 31 | *Petasites albus (H)* | 15 | 47 | *Dryopteris filix mas (H)* | 14 | 39 | *Chaerophyllum hirsutum (H)* | 16 | 44 |
| *Acer opalus (A)* | 6 | 25 | *Ilex aquifolium (H)* | 7 | 29 | *Acer pseudoplatanus (H)* | 10 | 31 | *Carex sylvatica (H)* | 14 | 44 | *Geranium sylvaticum (H)* | 14 | 39 | *Dryopteris filix mas (H)* | 16 | 44 |
| *Carex digitata (H)* | 6 | 25 | *Picea abies (H)* | 7 | 29 | *Epilobium montanum (H)* | 10 | 31 | *Fagus sylvatica (B)* | 14 | 44 | *Homogyne alpina (H)* | 13 | 36 | *Luzula sylvatica (H)* | 16 | 44 |
| *Fraxinus excelsior (B)* | 6 | 25 | *Rubus fruticosus aggr (H)* | 7 | 29 | *Fagus sylvatica (B)* | 10 | 31 | *Rubus idaeus (H)* | 14 | 44 | *Ranunculus aconitifolius (H)* | 13 | 36 | *Sorbus aucuparia (A)* | 16 | 44 |
| *Hedera helix (B)* | 6 | 25 | *Fragaria vesca (H)* | 6 | 25 | *Phyteuma spicatum (H)* | 10 | 31 | *Veronica urticifolia (H)* | 14 | 44 | *Rubus idaeus (H)* | 13 | 36 | *Ajuga reptans (H)* | 15 | 42 |
| *Paris quadrifolia (H)* | 6 | 25 | *Ilex aquifolium (B)* | 6 | 25 | *Abies alba (B)* | 9 | 28 | *Abies alba (B)* | 13 | 41 | *Sorbus aucuparia (A)* | 13 | 36 | *Cicerbita alpina (H)* | 15 | 42 |
| *Prenanthes purpurea (H)* | 6 | 25 | *Neottia nidus avis (H)* | 6 | 25 | *Aposeris foetida (H)* | 9 | 28 | *Phyteuma spicatum (H)* | 13 | 41 | *Dactylorhiza maculata (H)* | 12 | 33 | *Abies alba (A)* | 14 | 39 |
| *Abies alba (H)* | 5 | 21 | *Prenanthes purpurea (H)* | 6 | 25 | *Carex sylvatica (H)* | 9 | 28 | *Aposeris foetida (H)* | 12 | 38 | *Dryopteris dilatata (H)* | 12 | 33 | *Carex sylvatica (H)* | 14 | 39 |
| *Acer pseudoplatanus (H)* | 5 | 21 | *Sorbus aria (A)* | 6 | 25 | *Fraxinus excelsior (A)* | 9 | 28 | *Solidago virgaurea (H)* | 12 | 38 | *Rubus idaeus (B)* | 12 | 33 | *Lonicera nigra (H)* | 14 | 39 |
| *Athyrium filix femina (H)* | 5 | 21 | *Acer opalus (A)* | 5 | 21 | *Solidago virgaurea (H)* | 9 | 28 | *Adenostyles alliariae (H)* | 11 | 34 | *Valeriana tripteris (H)* | 12 | 33 | *Valeriana tripteris (H)* | 14 | 39 |
| *Ilex aquifolium (H)* | 5 | 21 | *Athyrium filix femina (H)* | 5 | 21 | *Sorbus aucuparia (H)* | 9 | 28 | *Ajuga reptans (H)* | 11 | 34 | *Abies alba (H)* | 11 | 31 | *Campanula rhomboidalis (H)* | 13 | 36 |
| *Picea abies (H)* | 5 | 21 | *Carex digitata (H)* | 5 | 21 | *Valeriana officinalis (H)* | 9 | 28 | *Mercurialis perennis (H)* | 11 | 34 | *Alnus viridis (B)* | 11 | 31 | *Dactylorhiza maculata (H)* | 13 | 36 |
| *Polygonatum verticillatum (H)* | 5 | 21 | *Carex sylvatica (H)* | 5 | 21 | *Adenostyles alliariae (H)* | 8 | 25 | *Ranunculus nemorosus (H)* | 11 | 34 | *Heracleum sphondylium (H)* | 11 | 31 | *Viola biflora (H)* | 13 | 36 |
| *Rosa arvensis (H)* | 5 | 21 | *Hepatica nobilis (H)* | 5 | 21 | *Carex montana (H)* | 8 | 25 | *Viola reichenbachiana (H)* | 11 | 34 | *Veratrum album (H)* | 11 | 31 | *Veratrum album (H)* | 12 | 33 |
| *Viburnum opulus (H)* | 5 | 21 | *Lonicera xylosteum (B)* | 5 | 21 | *Corylus avellana (B)* | 8 | 25 | *Aconitum lycoctonum (H)* | 10 | 31 | *Abies alba (B)* | 10 | 28 | *Aconitum lycoctonum (H)* | 11 | 31 |
| *Acer opalus (B)* | 4 | 17 | *Oxalis acetosella (H)* | 5 | 21 | *Dryopteris dilatata (H)* | 8 | 25 | *Corylus avellana (H)* | 10 | 31 | *Acer pseudoplatanus (B)* | 10 | 28 | *Blechnum spicant (H)* | 11 | 31 |
| *Arum maculatum (H)* | 4 | 17 | *Sorbus aucuparia (H)* | 5 | 21 | *Lonicera nigra (B)* | 8 | 25 | *Fraxinus excelsior (B)* | 10 | 31 | *Aconitum lycoctonum (H)* | 10 | 28 | *Geranium sylvaticum (H)* | 11 | 31 |
| *Carex sylvatica (H)* | 4 | 17 | *Taxus baccata (A)* | 5 | 21 | *Sorbus aucuparia (B)* | 8 | 25 | *Galeopsis tetrahit (H)* | 10 | 31 | *Ajuga reptans (H)* | 10 | 28 | *Lamium galeobdolon (H)* | 11 | 31 |
| *Cornus sanguinea (B)* | 4 | 17 | *Tilia platyphyllos (A)* | 5 | 21 | *Vaccinium myrtillus (H)* | 8 | 25 | *Heracleum sphondylium (H)* | 10 | 31 | *Hieracium prenanthoides (H)* | 10 | 28 | *Saxifraga rotundifolia (H)* | 11 | 31 |
| *Corylus avellana (H)* | 4 | 17 | *Acer opalus (H)* | 4 | 17 | *Aconitum lycoctonum (H)* | 7 | 22 | *Hordelymus europaeus (H)* | 10 | 31 | *Lamium galeobdolon (H)* | 10 | 28 | *Lonicera nigra (B)* | 10 | 28 |
| *Euphorbia dulcis (H)* | 4 | 17 | *Cardamine heptaphylla (H)* | 4 | 17 | *Centaurea montana (H)* | 7 | 22 | *Knautia dipsacifolia (H)* | 10 | 31 | *Rosa pendulina (H)* | 10 | 28 | *Acer pseudoplatanus (B)* | 9 | 25 |
| *Fragaria vesca (H)* | 4 | 17 | *Galeopsis tetrahit (H)* | 4 | 17 | *Lonicera xylosteum (B)* | 7 | 22 | *Lonicera nigra (H)* | 10 | 31 | *Acer pseudoplatanus (A)* | 9 | 25 | *Deschampsia cespitosa (H)* | 9 | 25 |
| *Lonicera xylosteum (B)* | 4 | 17 | *Hieracium murorum (H)* | 4 | 17 | *Maianthemum bifolium (H)* | 7 | 22 | *Neottia nidus avis (H)* | 10 | 31 | *Aster bellidiastrum (H)* | 9 | 25 | *Dryopteris dilatata (H)* | 9 | 25 |
| *Polystichum aculeatum (H)* | 4 | 17 | *Lonicera xylosteum (H)* | 4 | 17 | *Primula elatior (H)* | 7 | 22 | *Epilobium montanum (H)* | 9 | 28 | *Carex ferruginea (H)* | 9 | 25 | *Ranunculus aconitifolius (H)* | 9 | 25 |
| *Primula acaulis (H)* | 4 | 17 | *Paris quadrifolia (H)* | 4 | 17 | *Ranunculus nemorosus (H)* | 7 | 22 | *Helleborus foetidus (H)* | 9 | 28 | *Centaurea montana (H)* | 9 | 25 | *Abies alba (B)* | 8 | 22 |
| *Acer opalus (H)* | 3 | 13 | *Sorbus aria (H)* | 4 | 17 | *Rubus idaeus (H)* | 7 | 22 | *Lonicera xylosteum (H)* | 9 | 28 | *Deschampsia cespitosa (H)* | 9 | 25 | *Alnus viridis (B)* | 8 | 22 |
| *Allium ursinum (H)* | 3 | 13 | *Tilia platyphyllos (B)* | 4 | 17 | *Ajuga reptans (H)* | 6 | 19 | *Sorbus aucuparia (B)* | 9 | 28 | *Primula elatior (H)* | 9 | 25 | *Astrantia major (H)* | 8 | 22 |
| *Carex flacca (H)* | 3 | 13 | *Tilia platyphyllos (H)* | 4 | 17 | *Campanula rhomboidalis (H)* | 6 | 19 | *Fraxinus excelsior (A)* | 8 | 25 | *Rosa pendulina (B)* | 9 | 25 | *Heracleum sphondylium (H)* | 8 | 22 |
| *Carex humilis (H)* | 3 | 13 | *Acer campestre (H)* | 3 | 13 | *Carex flacca (H)* | 6 | 19 | *Lonicera nigra (B)* | 8 | 25 | *Epilobium angustifolium (H)* | 8 | 22 | *Hieracium lachenalii (H)* | 8 | 22 |
| *Corylus avellana (A)* | 3 | 13 | *Cardamine pentaphyllos (H)* | 3 | 13 | *Corylus avellana (H)* | 6 | 19 | *Ranunculus platanifolius (H)* | 8 | 25 | *Epilobium montanum (H)* | 8 | 22 | *Paris quadrifolia (H)* | 8 | 22 |
| *Daphne laureola (H)* | 3 | 13 | *Carex alba (H)* | 3 | 13 | *Fagus sylvatica (H)* | 6 | 19 | *Valeriana officinalis (H)* | 8 | 25 | *Lonicera nigra (B)* | 8 | 22 | *Rosa pendulina (H)* | 8 | 22 |
| *Epipactis helleborine (H)* | 3 | 13 | *Corylus avellana (A)* | 3 | 13 | *Fraxinus excelsior (H)* | 6 | 19 | *Viola biflora (H)* | 8 | 25 | *Polygonatum verticillatum (H)* | 8 | 22 | *Acer pseudoplatanus (A)* | 7 | 19 |
| *Hepatica nobilis (H)* | 3 | 13 | *Crataegus monogyna (B)* | 3 | 13 | *Ranunculus platanifolius (H)* | 6 | 19 | *Actaea spicata (H)* | 7 | 22 | *Salix appendiculata (B)* | 8 | 22 | *Centaurea montana (H)* | 7 | 19 |
| *Hieracium murorum (H)* | 3 | 13 | *Daphne laureola (H)* | 3 | 13 | *Rosa pendulina (H)* | 6 | 19 | *Carex digitata (H)* | 7 | 22 | *Anthoxanthum odoratum (H)* | 7 | 19 | *Dactylis glomerata (H)* | 7 | 19 |
| *Juglans regia (B)* | 3 | 13 | *Epipactis helleborine (H)* | 3 | 13 | *Rubus saxatilis (H)* | 6 | 19 | *Chaerophyllum hirsutum (H)* | 7 | 22 | *Blechnum spicant (H)* | 7 | 19 | *Epilobium montanum (H)* | 7 | 19 |
| *Larix decidua (A)* | 3 | 13 | *Helleborus foetidus (H)* | 3 | 13 | *Sorbus aucuparia (A)* | 6 | 19 | *Dryopteris dilatata (H)* | 7 | 22 | *Carex sylvatica (H)* | 7 | 19 | *Galium odoratum (H)* | 7 | 19 |
| *Ligustrum vulgare (B)* | 3 | 13 | *Hordelymus europaeus (H)* | 3 | 13 | *Viola biflora (H)* | 6 | 19 | *Epipactis helleborine (H)* | 7 | 22 | *Equisetum sylvaticum (H)* | 7 | 19 | *Lonicera alpigena (B)* | 7 | 19 |
| *Luzula nivea (H)* | 3 | 13 | *Ilex aquifolium (A)* | 3 | 13 | *Aegopodium podagraria (H)* | 5 | 16 | *Polystichum aculeatum (H)* | 7 | 22 | *Fragaria vesca (H)* | 7 | 19 | *Primula elatior (H)* | 7 | 19 |
| *Polygonatum multiflorum (H)* | 3 | 13 | *Larix decidua (A)* | 3 | 13 | *Astrantia major (H)* | 5 | 16 | *Rubus fruticosus aggr. (H)* | 7 | 22 | *Luzula luzulina (H)* | 7 | 19 | *Ranunculus platanifolius (H)* | 7 | 19 |
| *Rubus caesius (B)* | 3 | 13 | *Polygonatum multiflorum (H)* | 3 | 13 | *Cardamine heptaphylla (H)* | 5 | 16 | *Lonicera xylosteum (B)* | 6 | 19 | *Paris quadrifolia (H)* | 7 | 19 | *Veronica officinalis (H)* | 7 | 19 |
| *Rubus caesius (H)* | 3 | 13 | *Polygonatum verticillatum (H)* | 3 | 13 | *Chaerophyllum hirsutum (H)* | 5 | 16 | *Primula elatior (H)* | 6 | 19 | *Peucedanum ostruthium (H)* | 7 | 19 | *Alnus viridis (H)* | 6 | 17 |
| *Sambucus nigra (B)* | 3 | 13 | *Polystichum aculeatum (H)* | 3 | 13 | *Fraxinus excelsior (B)* | 5 | 16 | *Rubus saxatilis (H)* | 6 | 19 | *Ranunculus platanifolius (H)* | 7 | 19 | *Calamagrostis varia (H)* | 6 | 17 |
| *Sesleria caerulea (H)* | 3 | 13 | *Prunus avium (H)* | 3 | 13 | *Lonicera alpigena (B)* | 5 | 16 | *Sanicula europaea (H)* | 6 | 19 | *Sambucus racemosa (B)* | 7 | 19 | *Hepatica nobilis (H)* | 6 | 17 |
| *Sorbus aria (A)* | 3 | 13 | *Rubus idaeus (H)* | 3 | 13 | *Luzula sylvatica (H)* | 5 | 16 | *Vaccinium myrtillus (H)* | 6 | 19 | *Saxifraga rotundifolia (H)* | 7 | 19 | *Milium effusum (H)* | 6 | 17 |
| *Stachys sylvatica (H)* | 3 | 13 | *Ulmus glabra (A)* | 3 | 13 | *Lysimachia nemorum (H)* | 5 | 16 | *Vicia sepium (H)* | 6 | 19 | *Campanula rhomboidalis (H)* | 6 | 17 | *Peucedanum ostruthium (H)* | 6 | 17 |
| *Taxus baccata (A)* | 3 | 13 | *Veronica urticifolia (H)* | 3 | 13 | *Melica nutans (H)* | 5 | 16 | *Astrantia major (H)* | 5 | 16 | *Dactylis glomerata (H)* | 6 | 17 | *Polygonatum verticillatum (H)* | 6 | 17 |
| *Taxus baccata (B)* | 3 | 13 | *Viburnum opulus (B)* | 3 | 13 | *Milium effusum (H)* | 5 | 16 | *Calamagrostis varia (H)* | 5 | 16 | *Gymnocarpium dryopteris (H)* | 6 | 17 | *Rosa pendulina (B)* | 6 | 17 |
| *Tilia platyphyllos (A)* | 3 | 13 | *Viburnum opulus (H)* | 3 | 13 | *Polystichum aculeatum (H)* | 5 | 16 | *Cardamine heptaphylla (H)* | 5 | 16 | *Lonicera alpigena (B)* | 6 | 17 | *Rubus idaeus (B)* | 6 | 17 |
| *Ulmus glabra (A)* | 3 | 13 | *Acer opalus (B)* | 2 | 8 | *Saxifraga rotundifolia (H)* | 5 | 16 | *Carex flacca (H)* | 5 | 16 | *Polystichum lonchitis (H)* | 6 | 17 | *Campanula rotundifolia (H)* | 5 | 14 |
| *Ulmus glabra (B)* | 3 | 13 | *Acer platanoides (A)* | 2 | 8 | *Silene dioica (H)* | 5 | 16 | *Lysimachia nemorum (H)* | 5 | 16 | *Silene dioica (H)* | 6 | 17 | *Epilobium angustifolium (H)* | 5 | 14 |
| *Viburnum lantana (B)* | 3 | 13 | *Acer platanoides (H)* | 2 | 8 | *Sorbus aria (B)* | 5 | 16 | *Maianthemum bifolium (H)* | 5 | 16 | *Soldanella alpina (H)* | 6 | 17 | *Equisetum sylvaticum (H)* | 5 | 14 |
| *Viburnum lantana (H)* | 3 | 13 | *Actaea spicata (H)* | 2 | 8 | *Ulmus glabra (A)* | 5 | 16 | *Silene dioica (H)* | 5 | 16 | *Asplenium viride (H)* | 5 | 14 | *Gentiana lutea (H)* | 5 | 14 |
| *Acer campestre (B)* | 2 | 8 | *Ajuga reptans (H)* | 2 | 8 | *Veratrum album (H)* | 5 | 16 | *Valeriana tripteris (H)* | 5 | 16 | *Caltha palustris (H)* | 5 | 14 | *Hieracium prenanthoides (H)* | 5 | 14 |
| *Acer campestre (H)* | 2 | 8 | *Allium ursinum (H)* | 2 | 8 | *Actaea spicata (H)* | 4 | 13 | *Aruncus dioicus (H)* | 4 | 13 | *Campanula cochleariifolia (H)* | 5 | 14 | *Lathyrus vernus (H)* | 5 | 14 |
| *Acer platanoides (A)* | 2 | 8 | *Aquilegia atrata (H)* | 2 | 8 | *Aruncus dioicus (H)* | 4 | 13 | *Brachypodium pinnatum (H)* | 4 | 13 | *Crepis paludosa (H)* | 5 | 14 | *Luzula luzulina (H)* | 5 | 14 |
| *Acer platanoides (B)* | 2 | 8 | *Brachypodium sylvaticum (H)* | 2 | 8 | *Calamagrostis varia (H)* | 4 | 13 | *Hedera helix (H)* | 4 | 13 | *Galium odoratum (H)* | 5 | 14 | *Melampyrum sylvaticum (H)* | 5 | 14 |
| *Actaea spicata (H)* | 2 | 8 | *Carex humilis (H)* | 2 | 8 | *Crepis paludosa (H)* | 4 | 13 | *Homogyne alpina (H)* | 4 | 13 | *Melampyrum sylvaticum (H)* | 5 | 14 | *Polystichum lonchitis (H)* | 5 | 14 |
| *Aquilegia atrata (H)* | 2 | 8 | *Carpinus betulus (A)* | 2 | 8 | *Dactylis glomerata (H)* | 4 | 13 | *Melampyrum sylvaticum (H)* | 4 | 13 | *Polystichum aculeatum (H)* | 5 | 14 | *Saxifraga cuneifolia (H)* | 5 | 14 |
| *Carex alba (H)* | 2 | 8 | *Circaea lutetiana (H)* | 2 | 8 | *Epipactis helleborine (H)* | 4 | 13 | *Milium effusum (H)* | 4 | 13 | *Saxifraga cuneifolia (H)* | 5 | 14 | *Vaccinium vitis idaea (H)* | 5 | 14 |
| *Carex montana (H)* | 2 | 8 | *Clematis vitalba (A)* | 2 | 8 | *Geum rivale (H)* | 4 | 13 | *Mycelis muralis (H)* | 4 | 13 | *Acer pseudoplatanus (H)* | 4 | 11 | *Aconitum napellus (H)* | 4 | 11 |
| *Carpinus betulus (A)* | 2 | 8 | *Clematis vitalba (H)* | 2 | 8 | *Helleborus foetidus (H)* | 4 | 13 | *Sorbus aucuparia (A)* | 4 | 13 | *Aegopodium podagraria (H)* | 4 | 11 | *Alchemilla conjuncta (H)* | 4 | 11 |
| *Cephalanthera damasonium (H)* | 2 | 8 | *Cornus sanguinea (B)* | 2 | 8 | *Hordelymus europaeus (H)* | 4 | 13 | *Aegopodium podagraria (H)* | 3 | 9 | *Alnus viridis (H)* | 4 | 11 | *Alchemilla vulgaris (H)* | 4 | 11 |
| *Circaea lutetiana (H)* | 2 | 8 | *Cornus sanguinea (H)* | 2 | 8 | *Luzula luzulina (H)* | 4 | 13 | *Asplenium trichomanes (H)* | 3 | 9 | *Cystopteris fragilis (H)* | 4 | 11 | *Caltha palustris (H)* | 4 | 11 |
| *Clematis vitalba (A)* | 2 | 8 | *Daphne mezereum (B)* | 2 | 8 | *Melampyrum sylvaticum (H)* | 4 | 13 | *Bromus benekenii (H)* | 3 | 9 | *Dryopteris carthusiana (H)* | 4 | 11 | *Carex digitata (H)* | 4 | 11 |
| *Convallaria majalis (H)* | 2 | 8 | *Dryopteris dilatata (H)* | 2 | 8 | *Mycelis muralis (H)* | 4 | 13 | *Cardamine pentaphyllos (H)* | 3 | 9 | *Equisetum arvense (H)* | 4 | 11 | *Crepis paludosa (H)* | 4 | 11 |
| *Cornus mas (B)* | 2 | 8 | *Geranium robertianum (H)* | 2 | 8 | *Neottia nidus avis (H)* | 4 | 13 | *Cicerbita alpina (H)* | 3 | 9 | *Gentiana lutea (H)* | 4 | 11 | *Epipactis helleborine (H)* | 4 | 11 |
| *Cornus sanguinea (H)* | 2 | 8 | *Juglans regia (B)* | 2 | 8 | *Ranunculus lanuginosus (H)* | 4 | 13 | *Corylus avellana (B)* | 3 | 9 | *Geum rivale (H)* | 4 | 11 | *Equisetum arvense (H)* | 4 | 11 |
| *Crataegus laevigata (B)* | 2 | 8 | *Lathyrus vernus (H)* | 2 | 8 | *Rumex alpestris (H)* | 4 | 13 | *Dactylis glomerata (H)* | 3 | 9 | *Hypericum maculatum (H)* | 4 | 11 | *Euphorbia cyparissias (H)* | 4 | 11 |
| *Crataegus monogyna (B)* | 2 | 8 | *Ligustrum vulgare (B)* | 2 | 8 | *Sanicula europaea (H)* | 4 | 13 | *Daphne mezereum (H)* | 3 | 9 | *Larix decidua (A)* | 4 | 11 | *Galeopsis tetrahit (H)* | 4 | 11 |
| *Daphne mezereum (B)* | 2 | 8 | *Ligustrum vulgare (H)* | 2 | 8 | *Senecio ovatus (H)* | 4 | 13 | *Hieracium lachenalii (H)* | 3 | 9 | *Lonicera nigra (H)* | 4 | 11 | *Gentiana purpurea (H)* | 4 | 11 |
| *Daphne mezereum (H)* | 2 | 8 | *Luzula nivea (H)* | 2 | 8 | *Ulmus glabra (B)* | 4 | 13 | *Hieracium prenanthoides (H)* | 3 | 9 | *Lysimachia nemorum (H)* | 4 | 11 | *Geranium robertianum (H)* | 4 | 11 |
| *Deschampsia cespitosa (H)* | 2 | 8 | *Petasites albus (H)* | 2 | 8 | *Veronica chamaedrys (H)* | 4 | 13 | *Lonicera alpigena (H)* | 3 | 9 | *Mercurialis perennis (H)* | 4 | 11 | *Leucanthemum vulgare (H)* | 4 | 11 |
| *Dryopteris carthusiana (H)* | 2 | 8 | *Pinus sylvestris (A)* | 2 | 8 | *Viola reichenbachiana (H)* | 4 | 13 | *Luzula sylvatica (H)* | 3 | 9 | *Milium effusum (H)* | 4 | 11 | *Lonicera alpigena (H)* | 4 | 11 |
| *Dryopteris dilatata (H)* | 2 | 8 | *Pinus sylvestris (B)* | 2 | 8 | *Cardamine pentaphyllos (H)* | 3 | 9 | *Melica nutans (H)* | 3 | 9 | *Polygonum bistorta (H)* | 4 | 11 | *Lysimachia nemorum (H)* | 4 | 11 |
| *Geranium robertianum (H)* | 2 | 8 | *Polygala chamaebuxus (H)* | 2 | 8 | *Carex digitata (H)* | 3 | 9 | *Orthilia secunda (H)* | 3 | 9 | *Potentilla erecta (H)* | 4 | 11 | *Ranunculus lanuginosus (H)* | 4 | 11 |
| *Helleborus foetidus (H)* | 2 | 8 | *Primula acaulis (H)* | 2 | 8 | *Cirsium oleraceum (H)* | 3 | 9 | *Ranunculus lanuginosus (H)* | 3 | 9 | *Ranunculus lanuginosus (H)* | 4 | 11 | *Salix appendiculata (H)* | 4 | 11 |
| *Hippocrepis emerus (H)* | 2 | 8 | *Primula elatior (H)* | 2 | 8 | *Dactylorhiza maculata (H)* | 3 | 9 | *Rosa pendulina (H)* | 3 | 9 | *Rumex alpestris (H)* | 4 | 11 | *Silene dioica (H)* | 4 | 11 |
| *Lathyrus vernus (H)* | 2 | 8 | *Prunus avium (A)* | 2 | 8 | *Galeopsis tetrahit (H)* | 3 | 9 | *Saxifraga rotundifolia (H)* | 3 | 9 | *Silene vulgaris (H)* | 4 | 11 | *Silene vulgaris (H)* | 4 | 11 |

***Appendix 5*** *– Table containing species with the highest increase or decrease in frequency for past and current conditions. Letters in bracket correspond to the strata of plant height (A: tree >6 m, B: shrub 0.5-6 m and C: herbaceous <0.5 m).*

## Species cover

| Low elevation (<1000 m) | | | | Medium elevation (1000-1500 m) | | | | High elevation (>1500 m) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Past conditions | | Current conditions | | Past conditions | | Current conditions | | Past conditions | | Current conditions | |
| Species | Cover | Species | Cover | Species | Cover | Species | Cover | Species | Cover | Species | Cover |
| *Castanea sativa (A)* | 2.83 | *Carex acutiformis (H)* | 2.65 | *Sesleria caerulea (H)* | 2.45 | *Picea abies (A)* | 2.29 | *Alnus incana (H)* | 2.45 | *Calamagrostis villosa (H)* | 2.65 |
| *Sorbus hybrides (A)* | 2.83 | *Castanea sativa (A)* | 2.65 | *Picea abies (A)* | 2.28 | *Fagus sylvatica (A)* | 2.21 | *Calamagrostis villosa (H)* | 2.45 | *Picea abies (A)* | 2.45 |
| *Vinca minor (H)* | 2.83 | *Fagus sylvatica (A)* | 2.53 | *Allium ursinum (H)* | 2.28 | *Impatiens noli tangere (H)* | 2.19 | *Picea abies (A)* | 2.35 | *Alnus incana (B)* | 2.12 |
| *Fagus sylvatica (A)* | 2.51 | *Juglans regia (A)* | 2.45 | *Fagus sylvatica (A)* | 2.23 | *Melica uniflora (H)* | 2.12 | *Fagus sylvatica (A)* | 2.12 | *Fagus sylvatica (A)* | 2.12 |
| *Carex acutiformis (H)* | 2.45 | *Sorbus latifolia (A)* | 2.45 | *Melica uniflora (H)* | 2.12 | *Abies alba (A)* | 2.12 | *Calamagrostis varia (H)* | 2.09 | *Acer pseudoplatanus (A)* | 2.06 |

**Appendix 6** – *Table containing species with the highest increase or decrease in cover for past and current conditions. Letters in bracket correspond to the strata of plant height (A: tree >6 m, B: shrub 0.5-6 m and C: herbaceous <0.5 m).*




**Appendix 7** – *Figure illustrating stages of the project. Grey boxes present the initial climate and species data. Light blue boxes show the different predictions. Black arrows indicate steps of the methodology before analysis. Dark blue arrows show comparative analysis between past and current conditions with corresponding sections of the report. Light blue dotted arrows correspond to comparative analysis between predictions and field observations with linked sections of the report (Pascal Vittoz and Stéphanie Massy).*