Competition and demography rather than dispersal limitation slow down upward shifts of trees' upper elevation limits in the Alps

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This document is the accepted manuscript version of the following article:
Scherrer, D., Vitasse, Y., Guisan, A., Wohlgemuth, T., & Lischke, H. (2020). Competition and demography rather than dispersal limitation slow down upward shifts of trees' upper elevation limits in the Alps. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13451>

Abstract

1. Species range limits are expected to be dramatically altered under future climate change and many species are predicted to shift their distribution upslope to track their suitable conditions (i.e. based on their niche). However, there might be large discrepancies between the speed of the upward shift of the climatic niche and the actual migration velocity of the species, especially in long-lived organisms such as trees. In fact, most studies did not find any significant upward shift of the distributional limits of temperate forest trees over the last decades. It therefore beckons the questions why trees are moving upslope much slower than their bioclimatic envelope and what are the implications for ecosystem functioning.
2. Here, we compared the simulations of the upslope displacement of the bioclimatic envelope of 16 tree species inhabiting temperate mountain forests under ongoing and future climate change obtained by correlative species distribution models (SDMs) to those from a dynamic forest model accounting for dispersal, competition and demography. We then partitioned the discrepancy in upslope migration velocity between the SDMs and the dynamic forest model into different components by manipulating dispersal limitation, interspecific competition and demography.
3. Tree species in the dynamic forest model migrated only slowly upslope in contrast to the SDMs. Most of the difference in migration velocity can directly be attributed to tree's demography (long life cycle), followed by effects of competition and only a marginal contribution of dispersal limitation. Additionally, lower elevation species ("non-treeline") shifted slower upslope than high elevation species ("treeline") indicating a strong effect of inter-specific competition at their leading edge.
4. *Synthesis*. Forests have a high inertia to climate change because of their longevity and ability to acclimatise to high climatic fluctuations. Lower elevation tree species (deciduous) only slowly establish in stands at higher elevation where coniferous species dominate and likely profit from facilitation by disturbance events. Therefore, forest ecosystems seem to persist, even if climate becomes unfavourable, until they approach a tipping point at which an extreme event (e.g.,

40 drought, storm or insect attack) leads to a large dieback and resource change enabling new
41 suitable species to spread and establish.

42

43 Keywords: climate change, climate potential, dynamic forest models, mountain forest, *Picea abies*,
44 species distribution model, TreeMig

Introduction

Species range limits and abundance are expected to be dramatically altered under ongoing and future climate warming (Parmesan *et al.* 1999; Deutsch *et al.* 2008; Pereira *et al.* 2010; Lindner *et al.* 2014; Dyderski *et al.* 2018). One of the most iconic ecological limits is the treeline, i.e. the boundary beyond which trees are not able to thrive, which is generally determined by climatic factors putting constraints on the tree life-form (Körner 2012; Paulsen & Körner 2014). As a result, the treeline is expected to shift upward in elevation or latitude with the projected future climate (Dullinger, Dirnböck & Grabherr 2004; Gehrig-Fasel, Guisan & Zimmermann 2007; Körner 2012). However, only few tree species make the treeline (called hereafter “treeline” species) whereas numerous tree species have their upper elevation limits (UELs) below the treeline (called hereafter “non-treeline” species). The UEL of these “non-treeline” species seem also indirectly linked to temperature (e.g., by late spring frost tolerance and limitation in tissue and seed maturation; Körner *et al.* 2016; Lenz *et al.* 2016) but such limits are less visible and their dynamics have been much less studied than the treeline (but see Vitasse *et al.* 2012; Körner *et al.* 2016), especially in the context of climate change. In addition, the UEL may remain stable while the abundance peak or the rear edge limit may move upward (Lenoir *et al.* 2008; Freeman *et al.* 2018; Rumpf *et al.* 2018) or sometimes even downward (Lenoir *et al.* 2010b). Although many models predict a rapid upslope shift of the suitable climate conditions and thereby the potential UEL for most tree species in the next decades, only small shifts (Peñuelas & Boada 2003; Gehrig-Fasel, Guisan & Zimmermann 2007) or even no shifts at all have been observed during the last decades (Lenoir *et al.* 2008; Lenoir *et al.* 2010b; Bertrand *et al.* 2011; Küchler *et al.* 2015), especially for “non-treeline” species (Shi *et al.* 2020). This discrepancy between bioclimatic envelope based expectations and observations could be explained by three main factors: 1) long generation time, slow regeneration speed, high plasticity and rare mast fructification (e.g., Bertrand *et al.* 2011; Copenhaver-Parry *et al.* 2020), 2) limited dispersal capacities (e.g., Svenning & Skov 2007; Lenoir *et al.* 2010a) and 3) suppressed establishment due to competition and fluctuating resource availabilities (e.g., Bertrand *et al.* 2016; Shi *et al.* 2020).

71 While empirical data about past forest dynamic at the upper elevational limit exist (i.e., vegetation
72 surveys, dendrochronological series, old pictures, aerial images), we largely depend on model
73 projections to assess future trends especially under increasing rates of environmental change. One
74 often used type of model to predict distributional changes are correlative species distribution models
75 (SDMs) relating occurrence data to environmental variables to construct the realised niche of a species
76 (Peterson *et al.* 2011; Guisan, Thuiller & Zimmermann 2017). For each species, the fitted niche can
77 then be projected in space and time to estimate the potential distribution of a species based on the
78 selected environmental predictors (i.e., usually climate) without explicitly considering any population
79 dynamic processes (i.e., dispersal, succession, competition; but see Guisan, Thuiller & Zimmermann
80 2017 for arguments about implicit inclusion of those processes). In contrast to purely correlative
81 models, in particular SDMs, dynamic vegetation models (Snell *et al.* 2014) quantitatively integrate
82 biological processes (e.g., dispersal, succession and competition) which have been recognized to
83 largely influence UELs (Feuillet *et al.* 2019; Copenhaver-Parry *et al.* 2020; Shi *et al.* 2020), while still
84 accounting for climatic suitability. These models use species-specific growth and demographic
85 parameters adjusted by spatially explicit local climatic conditions to simulate dynamic processes
86 relevant for populations, e.g. mortality, dispersal, competition for light and recruitment. There are also
87 hybrid models that combine features of SDM and dynamic approaches (Dullinger *et al.* 2012).

88 While the role of dispersal limitation on the ability of a species to track conditions of their shifting
89 climatic niche in a warming world is often discussed and studied (e.g., Svenning & Skov 2007; Engler *et al.*
90 2009; Vacchiano *et al.* 2018), the role of competition is much less obvious (Scheller & Mladenoff
91 2008; Meier *et al.* 2012). However, competition (e.g., due to light availability and shade tolerance;
92 Nieto-Lugilde *et al.* 2014) might play an important role in limiting a species' ability to migrate upslope,
93 especially in long-lived and highly competitive ecosystems such as forests where seedling
94 establishment is often highly dependent on disturbance events (Wohlgemuth *et al.* 2018; Bugmann *et al.*
95 2019).

96 In this study, we compared correlative SDMs with a dynamic forest model (TreeMig; Lischke, Löffler &
97 Fischlin 1998; Lischke *et al.* 2006) regarding the occurrences of 16 tree species of the Western Swiss
98 Alps to answer the following questions: (1) How well do these models estimate the observed species-
99 specific UEL for different tree species? (2) How will the estimated future UELs based on the dynamic
100 forest model differ from the UELs estimated by correlative SDMs under different climate warming
101 scenarios? And (3) how much of the differences between the potential and dynamically modelled UELs
102 (i.e., time lag) is explained by dispersal limitation, competition, succession and demography?

Material and Methods

Study area

The study area is located in the western Swiss Alps (Canton de Vaud, 46°10' to 46°30'N; 6°50' to 7°10'E, Figure 1) and represents both a priority area for interdisciplinary research at the University of Lausanne (<http://rechalp.unil.ch>; Von Daniken, Guisan & Lane 2014) and for conservation at the European level (Lassen & Savoia 2005). It covers ca. 700 km², which encompass an elevation gradient ranging from 372 m to 3,210 m a.s.l. with forested areas up to ~2000 m. The annual mean temperature and total precipitation vary, respectively, from 8°C and 1,200 mm at 600 m a.s.l. to -5°C and 2,600 mm at 3,000 m a.s.l. (MeteoSwiss 2015). Since the beginning of systematic meteorological observations over 150 years ago, average temperatures in Switzerland have increased by 1.7°C (MeteoSwiss 2015). While until the 1970ies temperatures mainly fluctuated, the warming has strongly advanced since the late 1980ies and is projected to further accelerate during the 21st century (MeteoSwiss 2015). In contrast, annual precipitation sums have not significantly changed in Switzerland during the last few decades (MeteoSwiss 2015). While the study area has been influenced by anthropogenic land-use (Gago-Silva, Ray & Lehmann 2017), we here decided to consider the whole study area as potentially colonisable by forest (i.e., no land-use filter excluding forest). This clearly leads to an overestimation of simulated forest cover at the lowest elevations where urbanised and agriculturally used land predominates. Similarly, it might lead to an overestimation of the actual highest elevation of the treeline, which in part of the study region is currently suppressed by land use as alpine pastures (Pellissier *et al.* 2013) but could nevertheless be recolonized in a near future as a result of the increasing abandonment of this traditional though little profitable land use (Gellrich *et al.* 2007). However, as we are mainly interested in the UEL of tree species rather than the area and amount of forest, this simplification should not cause large errors but rather prevent noise potentially caused by including uncertain future land-use scenarios (Gago-Silva, Ray & Lehmann 2017).

Study species

We modelled the current and future distribution of 16 widely spread, so-called principal tree species in Switzerland that are abundantly growing in the forests of the study area: *Abies alba* Mill., *Acer campestre* L., *Acer platanooides* L., *Acer pseudoplatanus* L., *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Picea abies* (L.) H. Karst., *Quercus pubescens* Willd., *Quercus petraea* Liebl., *Quercus robur* L., *Sorbus aria* (L.) Crantz, *Sorbus aucuparia* L., *Tilia cordata* Mill., *Tilia platyphyllos* Scop. and *Ulmus glabra* Huds. These species were subdivided into two groups with either species having an observed UEL above 1800 m a.s.l. within the study area and being considered as “treeline” species or all other species termed as “non-treeline” (Table S1). To simulate inter-specific competition more realistically, in the forest model we also included 12 less abundant woody species as competitors in our simulations: *Alnus glutinosa* (L.) Gaertn., *Alnus incana* (L.) Moench, *Alnus viridis* (Chaix) DC., *Betula pendula* Roth, *Castanea sativa* Mill., *Corylus avellana* L., *Larix decidua* Mill., *Pinus cembra* L., *Pinus mugo* Turra, *Pinus sylvestris* L., *Populus nigra* L., *Populus tremula* L., *Salix alba* L. and *Taxus baccata* L. The distributional limits of these additional species were not analysed further, as we did not have enough observations in the study area to allow a confident estimation of distribution limits or their data did not produce meaningful SDMs (AUC < 0.7; Swets 1988). To account for competition by other, non-tree vegetation types such as small shrubs or dense grass, likely affecting tree regeneration particularly above the treeline, we included an additional general plant functional type called “shrubs and grasses”.

Occurrence records (presence data) for all species were available from three main data sources: The Swiss national forest inventory (LFI-1; EAFV 1988), the Swiss forest vegetation database (Wohlgemuth 2012) and the cantonal forest inventory of Canton de Vaud (Hartmann, Fouvy & Horisberger 2009). The occurrences were aggregated to a 200 m grid to match the environmental data used for modelling and analysis resulting in 57,653 records across the 16 tree species (Table S1). All data were collected within the period 1981–2010, matching the 30-year average of the climatic data used for SDM modelling (see below).

Correlative species distribution models

For our correlative SDMs, we selected the following seven topo-climatic predictors based on explanatory power (model selection by AIC) and ecological significance: mean annual temperature ($^{\circ}\text{C}$; Tyear), minimum temperature of the coldest month ($^{\circ}\text{C}$; Tmin), temperature of the driest quarter ($^{\circ}\text{C}$; Tsummer), annual sum of precipitation (mm; Pyear), sum of precipitation of the driest quarter (mm; Psummer), slope ($^{\circ}$) and topographic position (concave-convex, unitless; Topo). These variables were derived from national gridded climate data (i.e., temperature and precipitation) and digital elevation models (DEM; Federal Office of Topography: swisstopo.ch) as spatial layers at a resolution of 200 m, with climatic data based on both the current conditions (reference period of 1981–2010) and future scenarios (IPCC's SRES A1B, A2 and RCP3PD for periods 2045-2075 and 2070-2100; meteoswiss.ch; Zubler *et al.* 2014). The scenarios A2, A1B and RCP3PD represent an average temperature increase of 3.2 – 4.8 $^{\circ}\text{C}$, 2.7 – 4.1 $^{\circ}\text{C}$ and 1.2 – 1.8 $^{\circ}\text{C}$, respectively, until the end of the 21st century (for details on scenarios see CH2011 2011). While we acknowledge that other environmental variables than derivations of temperature and precipitation are important in determining the distribution of trees (in particular bedrock/substrate and light availability; Mod *et al.* 2016), we decided to limit our variables in the SDMs to these factors to match the information given to the dynamic forest model (i.e., allowing a more straightforward comparison) and to focus on the bioclimatic predictors of the tree distributions.

To guarantee an independent evaluation of our SDMs, we split the available data into two subsets. The calibration dataset contained all occurrences within Switzerland outside of the study area and the evaluation dataset all occurrences within the study area. While our dataset contains both presence and absence data (i.e., most occurrences stem from plot observations) they naturally are restricted to the forested areas of Switzerland. As a result, they do not appropriately cover the available climate of Switzerland (i.e., mainly omitting the area above the current treeline) leading to unreliable extrapolations into this non-analog climatic areas (Fitzpatrick & Hargrove 2009). We therefore decided to use presence-only data in combination with 100,000 background points randomly sampled across the whole of Switzerland to provide a representative signal of the available climatic conditions. All our

models were run with biomod2 (Thuiller *et al.* 2009; Thuiller *et al.* 2019) in R.3.4.3 (R Core Team 2019) using an ensemble modelling approach (Araujo & New 2007) employing generalised linear models (GLM), generalised additive models (GAM), boosted regression trees (BRT) and random forests (RF). All modelling techniques were run with the default settings of biomod2 and the background data (pseudo-absences) were weighted to equal the presences (prevalence = 0.5). We used these four modelling techniques as they provide a mix of regression-based and machine learning techniques and are among the most applied in SDM studies (Guisan, Thuiller & Zimmermann 2017). The models were evaluated on the independent data of our study area using the area under the ROC curve (AUC) and maximizations of the true skill statistics (maxTSS; see Guisan, Thuiller & Zimmermann 2017). Variable importance was estimated based on permutation tests (Thuiller *et al.* 2019). All probabilistic predictions were binarised using a threshold optimising TSS (Liu *et al.* 2005).

Dynamic forest model

We used the dynamic forest landscape model (Shifley *et al.* 2017) TreeMig (for details see Lischke, Löffler & Fischlin 1998; Lischke *et al.* 2006) on a spatial grid of 200 m resolution. Process functions and relationships in the model are species-specific. In details, the local annual dynamics of each species in each of 15 discrete tree height classes is determined by germination from available seeds, mortality and growth from the next lower and to the next higher height class. Trees compete for light i.e., trees in higher height classes shade lower height classes, which implies that shade tolerance, shading ability, maximum height and growth – the latter influenced by environment – affect competitiveness. These species-specific demographic processes depend on temporally changing and spatially-explicit bioclimatic variables: mean temperature of the coldest month, degree-days and a yearly drought stress calculated from monthly precipitation, temperature, slope, aspect and a site-specific field capacity. Browsing is accounted for by a constant pressure and species-specific decrease of seedling survival (Kienast 1987). Effects of random medium scale disturbances are included by increasing tree mortality in each grid cell with a given probability (set to 0.001) and amount (set to 0.8; i.e., killing 80% of all individuals). The trees of each species and height classes within tree species are assumed to be

randomly distributed over the grid cell, implicitly accounting for random small-scale disturbance and resulting in a heterogeneous distribution of the light conditions. Seed production starts from a certain species-specific height class (Lischke & Löffler 2006), determining the generation time, and increases up to a maximum value in the highest height class. The seeds are dispersed to other grid cells with a distance-dependent probability, which combines frequent short-distance dispersal events with rare long-distance dispersal events up to several kilometres. The seeds landing in a cell are accumulated in the seedbank. The species-specific parameters used in the TreeMig model are given in the Supplementary Material (Table S2-S3). TreeMig produces various output variables (biomass, tree numbers, LAI) per ha, time step, height class, and species. Here, we evaluated only the species-specific biomass/ha.

Simulation setup

We used six different model setups with varying amounts of dispersal limitation and inter-specific competition (see below). All our simulations had four distinct time periods: a spin-up phase (1500-1863), a historic time period (1864-2015; from first systematic daily meteorological information to present), future warming projections (2016-2100) and a stabilising period (2101–2500). The necessary bioclimatic variables per grid cell and year were calculated with monthly temperature and precipitation data for the period 1500–2500, slope, aspect and field capacity values derived from the Swiss Soil Fertility Map (EJPD, EVD & EDI 1980). While slope, aspect and field capacity were considered static across time, temperature and precipitation (and their deviates) varied across time. The spatial variation within the study area (i.e., temperature and precipitation difference between two points in space) and the range of inter-annual variation for all time periods were based on our reference period (1981–2010). The climate of the spin-up period (1500–1863) was based on the long-term average temperature of 1864 to 1900 with randomized inter-annual variations. This spin-up phase had the sole purpose to establish a baseline forest (i.e., realistic tree communities along the elevation gradient) to start our climate forcing with historic and future data. As we start (year 1500) from seeds of all species across the whole study area it takes several hundred years to establish these tree communities (i.e.,

tree growth and species succession). The climate for the historic period 1864 to 1980 were calculated based on anomalies compared to our reference period (1981-2010) provided by 14 long-term homogenized climate stations (Bader & Bantle 2004) and considered to be spatially homogenous (i.e., same spatial variation as reference period). The climate from 1981 to 2015 was directly based on available data for the study area. The climate of the future was based on the previously mentioned climate change scenarios and used linear interpolation across time for temperature and precipitation to generate climate variables based on the available projections for 2035, 2065 and 2085 with added random inter-annual variation. The stabilising period (2101–2500) had the constant average temperature predicted for 2100 with random inter-annual variation.

The first of our six different model setups simulated all 29 species together (full competition) with species-specific seed production and dispersal kernels (TM_Normal = TreeMig with normal settings; see Table S4 for all following model setups). Our second model setup also simulated all species, but in addition to the normal recruitment of the species there was a constant seed rain (120 seed per ha, year and species) eliminating dispersal limitations (TM_UD; unlimited dispersal). The third model setup was eliminating all forms of inter-specific competition by running each species alone and therefore only suffering from intra-specific competition of age cohorts (TM_NC; no competition). The fourth model setup combined the setups with no dispersal limitation and no competition (i.e., each species alone with seed rain; TM_UD_NC). The last two scenarios ran each species in combination with *Picea abies* (two-species setup), which resulted to be the most competitive species in our model either with species-specific (TM_PA) or unlimited dispersal (TM_UD_PA).

Determination of the species upper elevation limits (UEls)

To determine the UELs of the 16 tree principal species, we defined a set of rules applicable to both the SDM and the TreeMig models. The original output of the SDMs is a habitat suitability, which is then reclassified into presence/absence data by a threshold, while the output of TreeMig is biomass per ha.

256 In a first step, we classified the whole elevation gradient in the study area into 50 m elevation bands.
257 For each band, we then calculated the percentage of presences predicted by SDMs and the predicted
258 average biomass per ha (i.e., for TreeMig). In a second step, we identified the elevation band with the
259 highest values (i.e., percentage of presence and biomass). In a last step, we defined the upper elevation
260 limit (UEL) as the highest elevated band in which the percentage of presence/biomass was still above
261 5% of the maximum value. This definition of 5% instead of fixed value (i.e., biomass) was chosen to
262 account for the very different amounts of biomass produced by the 16 study species. This procedure
263 to determine the UEL of each species was repeated separately for each simulation setup and climate
264 change scenario.

265 To check if our 5% rule returns realistic elevation limits, we compared the scores to field observations
266 in the study area (EAFV 1988; Wohlgemuth 2012) as well as with literature about the species limits in
267 Switzerland (Vitasse *et al.* 2012; Randin *et al.* 2013; Kollas, Körner & Randin 2014). To calculate the
268 proportional contribution of the three main processes – demography, competition and dispersal
269 limitation – to the upslope migration velocity (m/y; v_{UEL}), we compared the UEL based on the different
270 modelling setups. The v_{UEL} between 2000 and 2085 was calculated for the bioclimatic envelope model
271 (SDM) and all setups of the dynamic forest model (TreeMig). We assumed that the $v_{UEL_{SDM}}$ (upslope
272 migration velocity of bioclimatic envelope) is prone to follow climatic change while $v_{UEL_{TM\_Normal}}$
273 provides the most realistic estimate of upslope migration. The difference between the two ($v_{UEL_{SDM}} -$
274 $v_{UEL_{TM\_Normal}}$) must therefore be explained by demography, competition and dispersal limitation as the
275 explicit inclusion of these processes represents the major discrepancy between the two model types.
276 By comparing $v_{UEL_{TM\_UD}}$, $v_{UEL_{TM\_NC}}$ and $v_{UEL_{TM\_UD\_NC}}$ to $v_{UEL_{TM\_Normal}}$ we can estimate the contribution
277 of dispersal limitation, interspecific competition and the combined effect. We then simply assumed
278 that the remaining difference between the bioclimatic envelope ($v_{UEL_{SDM}}$) and “unrestricted” dynamic
279 forest model ($v_{UEL_{TM\_UD\_NC}}$) is explained by demographic effects (i.e., slow growth and tree species
280 succession). To statistically compare the contribution to v_{UEL} between the different processes and if
281 there is a difference between “treeline” and “non-treeline” species we used a two-way ANOVA with a

282 TukeyHSD as posthoc-test. The influence of the different scenarios and modelling procedures were
283 analysed both at the ecosystem level (i.e. average across species) as well as at the individual species
284 level.

Results

Model performance

The SDMs for the 16 principal tree species performed well with mean values and standard deviations of AUC and maxTSS of 0.88 ± 0.06 and 0.62 ± 0.11 respectively when evaluated on independent data (i.e. the study area; Figure S1). Overall, the most influential variable was mean annual temperature followed by slope (Figure S2) with variable importance strongly varying among species (Figure S3).

The species-specific biomass predictions of the dynamic forest model (TM_Normal) were mostly in line with observation data based on the national forest inventory both in term of relative contribution to the total biomass (Figure S4) and absolute values of biomass (Figure S5). The most notable exception was *A. alba*, for which the majority of the biomass was predicted at lower elevations (< 1000 m) while most observations stem from higher elevation areas (>1000 m; Figure S4). This lack of *A. alba* at low elevation is most likely due to a long tradition of human land-use supressing the species in the lowlands (Tinner *et al.* 2013; Vitasse *et al.* 2019). Both the dynamic models and observations highlight that at lower elevations (< 1000 m) *F. sylvatica* and *P. abies* build the majority of the biomass while at the higher elevation sites *P. abies* accounts for the vast majority of the biomass, with some contribution of *A. alba* (Figure S4).

Observations vs models

Our simulated species-specific UELs based on SDMs (Spearman correlation = 0.82) and TreeMig (TM_Normal; 0.87) correlated well with field observations for the period 1981 - 2015 (Figure 2, for the other TreeMig setups see Figure S6). However, both the SDMs and TreeMig simulations drastically overestimated the UEL of *Q. pubescens* and underestimated the one of *A. alba* (Figure 2).

Time lag

The average elevation difference between the potential UELs of species based on correlative SDMs and dynamic TreeMig predictions (TM_Normal) was almost zero in the year 2000 (Figure 3). However,

for the year 2060 the SDMs predicted the average potential species-specific UEL to be 475 m, 493 m and 247 m higher than based on the dynamic forest model (TM_Normal) for the climate change scenarios A1B, A2 and RCP3PD, respectively. Consequently, for the three climate change scenarios, simulations from the dynamic forest model required 42, 34 and 377 additional years, respectively, to reach the potential UELs predicted by the SDM for 2060. This gap between potential bioclimatic UELs (SDMs) and dynamic forest simulations (TM_Normal) widened even more in 2085, with 565 m / 253 years, 758 m / 256 years and 222 m / 364 years for scenarios A1B, A2 and RCP3PD, respectively (Figure 3, Figure S7-S8). These time lags are the direct consequences of the difference in upslope migration velocity between the bioclimatic envelope (i.e., $vUEL_{SDM}$) and the simulated forest dynamics (i.e., $vUEL_{TM\_Normal}$). While, in the period 2000 - 2085, the bioclimatic envelope shifted upslope at an average velocity of 11.2 ± 1.1 m (mean $\pm$ 95% C.I.), 13.6 ± 1.3 m and 4.7 ± 0.6 m per year for the scenario A1B, A2 and RCP3PD, respectively, the values resulted from the dynamic forest ($vUEL_{TM\_Normal}$) amounted to only 5.3 ± 1.4 m, 5.4 ± 1.5 m and 2.5 ± 0.7 m upslope per year, respectively (Figure 4, Table S5-S7). The patterns across the three climate change scenarios were similar and simply scaled with the expected amount of warming (Figures 3-6 for scenario A1B; figures for scenario A2 and RCP3PD in Supplementary Materials).

The difference found in $vUEL$ does not seem to be the effect of dispersal limitation, as the scenarios with unlimited dispersal only slightly reduced the difference between the bioclimatic envelope (SDM) and dynamic forest predictions of the UELs (TM_Normal; Figure 4; Table S5). In contrast, removing the effects of competition and succession largely reduced the difference between bioclimatic envelope and dynamic forest predictions (Figure 4). In fact, without competition and succession the average species UEL was predicted to be more than 200 m higher in the year 2000 than currently observed or predicted by SDMs (Figure 3). However, even with unlimited dispersal and without competition, the upslope migration velocity ($vUEL_{TM\_UD\_NC}$) was still slower than the bioclimatic envelope estimated by SDMs (Figure 4, Table S7). This proportion of the time lag (50–70%) is therefore directly linked to the

simulated demography of the tree species and reflects the trees' long generation times and thus few regeneration opportunities delaying the stepwise upwards migration across generations.

While under the two climate warming scenarios (A2, A1B) demographic processes ($p < 0.05$) and competition ($p < 0.1$) had a strong effect on the vUEL, dispersal limitation ($p > 0.95$) did not (Table S8). Additionally, "treeline" and "non-treeline" species were affected differently by these processes ($p < 0.05$, Table S8). This difference between "treeline" and "non-treeline" trees was driven by the effect of competition, which was almost zero for "treeline" species but significantly higher for "non-treeline" species (Table S5).

This very strong effect of competition/succession was largely due to the removal of *Picea abies* as competing species in our simulations, the latter being the dominant species of the mid to high elevation sites in the region. Results from the simulations that run each species in combination with *P. abies* (TM_PA and TM_UD_PA) were almost identical to the ones obtained from simulations with all species (TM_Normal), indicating that mainly *P. abies* is hindering the advancement of most species (Figure 3). The competition effect (especially by *P. abies*) hindering the upward migration of lower elevation species is further highlighted by the changes in the slope of the SDMs vs. TreeMig predictions across time (Figure 5, Figure S9-S10). While the simulations without competition (TM_NC and TM_UD_NC) showed a synchronised upwards migration across species (i.e., no change in slope across time), all the other simulations including competition (TM_Normal, TM_UD, TM_PA, TM_UD_PA) showed a reduction in slope across time, suggesting a slower upwards migration of "non-treeline" compared to "treeline" species (Figure 5, Figure S9-S10).

However, the effects of dispersal limitation and competition/succession were very species-specific (Figure 6, Figure S11-S12). In our TreeMig simulations, *P. abies* was clearly the dominant species at mid and high elevation and was neither limited by competition nor by dispersal (i.e., different scenarios have no effect). In fact, the UEL of *P. abies* as predicted by TreeMig was even always higher than the potential UEL based on SDMs or observations for all points in time (Figure 6). Additionally, our

359 simulations showed that *S. aria*, *S. aucuparia* and *A. campestre* were also hardly affected by
360 competition or dispersal limitation. All other species were significantly affected by competition,
361 especially *A. alba*, *F. sylvatica*, *F. excelsior*, *Quercus* species and *Tilia* species (Figure 6). A strong effect
362 of dispersal limitation was only observed for the three *Quercus* species, most notably *Q. robur* (Figure
363 6). However, this stronger effect of dispersal limitation might simply reflect an underestimation of
364 zoochorie in oak species (Gómez 2003; Pesendorfer, Sillett & Morrison 2017). For most species, the
365 effect of competition/succession was mostly due to *P. abies* (i.e., TM_PA is identical to TM_Normal),
366 but the three *Quercus* species seem also to be limited by competition with other lowland species (i.e.,
367 *F. sylvatica*; Figure 6). All these factors influencing the species' UELs and migration velocity lead to a
368 predicted reshuffling of the species along elevation with climate warming (Figure S13-S22)

Discussion

Simulations from the two types of models successfully defined the upper elevation limits (UEL) of most tree species under current conditions. However, simulations of the bioclimatic envelope models (SDMs) and the dynamic forests models (TreeMig) diverged under future climate warming suggesting a growing gap between the upslope displacement of the bioclimatic envelope and the actual migration of tree species. This gap, which translates to a migration lag between the bioclimatic envelope and predictions of the dynamic forest model, is especially large for “non-treeline” species. Analyses showed that population dynamics and inter-specific competition are the main factors explaining the divergence between the two model types, suggesting that these factors will likely hamper upslope advancement in the future.

Upward migration: limited by competition rather than seed dispersal

Our study provides several important general insights. Firstly, we quantify the effects that limit the observed upslope migration of trees compared to their bioclimatic envelope. Simulations suggest that most of the discrepancy between potential and observed upslope migration (e.g., Lenoir *et al.* 2010a; Küchler *et al.* 2015) accounts for the species’ population dynamics (i.e., slow biomass increase and long generation time, $59.8 \pm 14.1\%$ [mean $\pm$ 95% C.I.]) followed by competition effects (especially at the leading edge of low elevation species, $33.0 \pm 14.3\%$), while dispersal limitation only showed marginal effects on most species ($8.2 \pm 5.9\%$). This is in line with findings of Lenoir *et al.* (2008) and Küchler *et al.* (2015) showing that short lived understorey species react much faster to climate change than long-lived organisms such as trees. Here, we only studied the upslope migration of trees in a mountain area with steep environmental gradients (i.e., slopes) resulting in relatively short lateral distances to be travelled per degree of warming. Therefore, when looking at latitudinal rather than elevation gradients we expected the influence of dispersal limitation to increase, as the distances to travel per degree of warming are much larger in latitude than elevation (Jump, Mátyás & Peñuelas 2009). In fact, similar simulations with TreeMig along latitudinal transects in Siberia comparing tree shifts by migration to

ubiquitous seeds showed a migrational lag of several millennia due to seed dispersal limitations (Epstein *et al.* 2007; Goetz *et al.* 2010). Such population dynamic effects on delayed range shifts were already documented for alpine plants across the Alps (Dullinger *et al.* 2012).

Second, our dynamic simulations suggest that especially “non-treeline” species are limited in their ability to track the shifting suitable climatic conditions due to competition at their leading edge. This hampering of shifts by competition at the leading edge seems surprising, as it is generally assumed that lower elevation species should be stronger competitors than higher elevation species (i.e., specialists of harsher environments). This assumption is related to two distinct theories: (i) the Species Interactions–Abiotic Stress Hypothesis (SIASH) that states that abiotic drivers define range limits at the most stressful end of species range, while competition sets range limits at the most benign range end (Normand *et al.* 2009; Louthan, Doak & Angert 2015); (ii) the stress- gradient hypothesis (Bertness & Callaway 1994; Chamberlain, Bronstein & Rudgers 2014), suggesting that as environmental stress increases the competitive effects decrease and facilitation might increase (Callaway & Walker 1997; Choler, Michalet & Callaway 2001). Following these hypotheses, one would expect that the assumed stronger competitors would quickly outcompete the treeline species when shifting upwards. In particular, while the lower elevation species *F. sylvatica* and *A. alba* might ultimately be the stronger competitors, according to the simulations they are very slow to invade established stands of higher elevation species (mostly *P. abies*). Therefore, the abiotic and demographic processes responsible for the limitations at the leading and the trailing edge of a species distribution likely differ considerably leading to complex interactions among species (Kunstler *et al.* 2019; Shi *et al.* 2020). At higher elevations, environmental harshness can repeatedly reduce growth of “non-treeline” species such as *F. sylvatica* (synthesized by Packham *et al.* 2012), which reduces their competitiveness (e.g., Vanoni *et al.* 2016). Apart from the environmental gradient, also the succession gradient needs to be considered, which ranges from pioneer species being fast growing, shade-intolerant and often wind-dispersed over long distances, to stand-forming species eventually overgrowing pioneers, tolerating shade and often dispersing their seeds by animals over shorter distances. This successional gradient might be a further

explanation for why the two late successional species *F. sylvatica* and *A. alba* take so long (i.e., several 100 years in our simulations) to catch up with their climatic niche and eventually would replace *P. abies* and other higher elevation species.

Models reproduce observations variably

Our results demonstrate that, based on our “5% of maximum value” threshold, both the correlative and dynamic models predicted the UELs well for most species under current conditions (Spearman correlation > 0.8). This is a good additional validation for the usability of the presented approach comparing climate suitability with dynamic forest models. Nevertheless, there were some noteworthy species-specific differences between models and observations. Firstly, both the SDMs and TreeMig simulations overestimated the UEL of *Quercus pubescens* in the study area. This likely results from the strong competition with *F. sylvatica*. *Q. pubescens* only occurs on dry and calcareous sites where *F. sylvatica* cannot survive on such sites due to water shortage. In our study area, *F. sylvatica* dominates the comparably humid low elevation forest stands, suppressing oaks in general and *Q. pubescens* in particular (Rohner *et al.* 2012). As a consequence, *Q. pubescens* only rarely thrives in the study area (7 observations) and the estimation of the UEL was therefore uncertain. In fact, most of the calibration data for *Q. pubescens* stem from habitats in a drier region of Switzerland (i.e., Valais) where *F. sylvatica* is widely absent, and might therefore have introduced a climatic sampling bias to our models, leading to imprecise predictions (Mette *et al.* 2013). Additionally, the overall low biomass and frequency of *Q. pubescens* within the study area likely results in an overestimation of the UEL based on our 5% threshold method (i.e. “flat” density distribution) while observations might underestimate the UEL by missing some of the rare higher elevation populations (highest observation in the Valais at 1750 m a.s.l.; <https://www.lfi.ch/resultate/meldungen/>). Secondly, the current UELs of two very important tree species, *F. sylvatica* and *A. alba*, were underestimated by the TreeMig models. This seems to be related to competition with *P. abies*, as in our TreeMig models both *F. sylvatica* and *A. alba* are suppressed by *P. abies* at mid to high elevation. In fact, when the competition effect of *P. abies* was removed, the UELs of *F. sylvatica* and *A. alba* were overestimated toward higher elevations than

actually observed. This indicates that at least in some parts of the study area the suppression effect of *P. abies* seems to be lower than parameterised in the dynamic forest models, possibly because either forest management or specific environmental conditions may have hindered the competitive strength/growth of *P. abies*. Thirdly, our dynamic forest model overestimated the UEL of *P. abies*. This could be a direct effect of local land-use, more specifically the anthropogenic suppression of the treeline (in particular *P. abies* and *A. alba*) by a century-long use of this zone as alpine meadows and pastures (i.e., grazing/browsing; Gehrig-Fasel, Guisan & Zimmermann 2007; Pellissier *et al.* 2013), which is, however, not implemented in the models used here.

Interestingly, when competitive effects were removed from the dynamic forest model, most species had a current UEL about 200 m higher than in the observations. This discrepancy indicates that most species might not be in equilibrium with the current climate but already lag behind their physiological limit as a result of inter-specific competition that occurs at their leading edge, which is often set by competition (Species Interactions–Abiotic Stress Hypothesis, SIASH; Normand *et al.* 2009; Louthan, Doak & Angert 2015), most notably competition with *P. abies*.

It is important to keep in mind that the mostly good agreement between observation and model simulations does not indicate that climate and the distribution of the species are in an equilibrium state, but the SDMs simply approximate the current (possibly disequilibrium) state and assume this state to be conserved across time and space. Similarly, the species-specific parameters for environmental dependences used in the TreeMig model were partly based on estimates from these current observational data sources (Lischke *et al.* 2006).

Potential edge shifts under changing climate

In the projections regarding future climatic scenarios, almost all species lag behind their bioclimatic envelope computed by SDM predictions. However, the discrepancy between the two type of models is not uniform but highly species-specific, with “treeline” species being able to follow their potential limit much closer than “non-treeline” species. This might again be linked to different forest dynamics

at the trailing and leading edges of migrating tree species (Zhu, Woodall & Clark 2012). In our dynamic forest model, trees growing at the leading edge of the “treeline” species can migrate more or less unhindered into the newly available space empty of trees/forest (i.e., the alpine belt), despite the potential competition of tree seedlings with dwarf shrubs, tall herbs or alpine grasses accounted for in the simulations. In contrast, “non-treeline” species at their leading edge have to establish in sites already occupied by forest (i.e., the trailing edge of the “treeline” species) – a process that only works if prevailing trees die, e.g. by disturbances such as windthrow, pests and other extreme events and create open patches (Moser *et al.* 2010; Wohlgemuth *et al.* 2018; Bugmann *et al.* 2019). This is accounted for in TreeMig by random disturbances on the patch and stand scale, but not over larger areas. Because trees are long-lived organisms and thus are rather resilient to environmental fluctuations, and large-scale disturbances are not simulated, populations may be able to endure/persist for long times despite decreasing climatic suitability. This seems to hinder the upslope migration of lower elevation species, especially if they encounter the trailing edge of a very competitive, i.e. stand-forming, species. In our simulations, this is the case for most species trying to invade almost pure *P. abies* stands and for the oak species invading beech-dominated forests.

Our simulations showed that if these elements of competition at the leading edge of “non-treeline” species are removed, the migration velocity does increase substantially. Our dynamic forest model predicts that “treeline” species will move upslope considerably faster than lowland species even if they still fall behind their bioclimatic envelope. While we most likely overestimate the potential of this “treeline” species to invade the alpine areas, the advancement of the treeline might still drastically reduce the alpine areas (Pellissier *et al.* 2013), especially in productive and sheltered sites. In many places of the study area the treeline is currently suppressed and slowed in its advancement by land-use (i.e., alpine pastures). As more and more of these alpine pastures become unprofitable and get abandoned the advancement of the treeline might speed up considerably (Gellrich *et al.* 2007; Dubuis *et al.* 2013; Pellissier *et al.* 2013; Schwörer *et al.* 2014).

However, it is important to note here that the fast upslope migration of the “treeline” species is partially influenced by some model assumptions. For instance, alpine areas are considered ready for colonisation as soon as they become climatically suitable. Although competition with dwarf shrubs and grasses is implemented in the model, the potential of this competition might still be underestimated (Dullinger, Dirnböck & Grabherr 2004). Additionally, the suppression of seedlings by grazing and browsing, problems with soil formation, lack of mycorrhiza, snow mold (Cunningham *et al.* 2006), and wind and micro-topography effects (Barbeito *et al.* 2012) in the upper zones that are forest free were also not considered in our current simulations.

Conclusions

Implied by forest’s inertia under the absence of disturbance, climate change effects on tree distribution limits might be delayed by several decades, likely reflecting a high resilience of these ecosystems to environmental change. In particular, competition by prevailing trees rather than spread by seeds is likely to slow down upward shifts. Forest might be able to persist in unfavourable climatic conditions for an extended amount of time, thus slowly becoming more vulnerable to disturbances or extreme events and approaching a tipping point. Sufficiently large perturbation by extreme events such as drought, storms, fire, insect infestation or interactions of these agents might lead to a large-scale dieback of the prevailing but now “maladapted” tree species. This delayed dieback (in analogy to the local extinction debt; Dullinger *et al.* 2012; Rumpf *et al.* 2019) might have severe economic (e.g., loss of timber) and ecosystem service implications (e.g., loss of protection function; Thrippleton, Lüscher & Bugmann 2020). However, such a break-down (e.g., Schuldt *et al.* 2020) might be essential to provide the opportunity for new species (i.e., lower elevation species) to establish by natural regeneration and transition the forest ecosystem into a new “equilibrium” state (Beisner, Haydon & Cuddington 2003).

Acknowledgements

DS acknowledges funding from the Swiss National Forest Inventory run by the Swiss Federal Office for the Environment FOEN and the Swiss Federal Research Institute WSL. AG benefitted from support of

521 the Swiss National Science Foundation, EcoGeoINTEGRALP project (grant nr CR23I2_162754). The
522 study was supported by the SwissForestLab.

523 **Authors' contribution**

524 DS, AG, HL, and TW designed the study. DS and HL ran the models and analysis. DF and YV lead the
525 writing with significant contributions from all co-authors.

526 **Data availability**

527 All the species and climate data used for the bioclimatic envelope models and dynamic forest models
528 are available on EnviDat (doi: 10.16904/envidat.154; Scherrer *et al.* 2020).

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783 **Figure 1**

784

785 Figure 1: Study area in the Western Swiss Alps. Green shades indicate areas that were covered by
786 forest in the year 2000.

787

788 **Figure 2**

789
790 Figure 2: Correlation of the observed species-specific UEL with predictions based on SDMs (cor =
791 0.82) or TreeMig simulations (TM_Normal; cor = 0.87). Each point represents one of the 16 modelled
792 principal tree species. Aa = *Abies alba*, Ac = *Acer campestre*, Ap = *Acer platanoides*, As = *Acer*
793 *pseudoplatanus*, Cp = *Carpinus betulus*, Fs = *Fagus sylvatica*, Fe = *Fraxinus excelsior*, Pa = *Picea abies*,
794 Qp = *Quercus petraea*, Qu = *Quercus pubescens*, Qr = *Quercus robur*, So = *Sorbus aria*, Sr = *Sorbus*
795 *aucuparia*, Tc = *Tilia cordata*, Tp = *Tilia platyphyllos*, Ug = *Ulmus glabra*.

796

797 **Figure 3**

798

799 Figure 3: The mean elevation difference between the SDM and TreeMig predictions across the 16

800 principal tree species for the year 2000, 2060 and 2085 based on the climate change scenario A1B.

801 The lines represent the difference between the upper limit estimated by the dynamic forest model

802 (TreeMig) and the bioclimatic envelope (SDM prediction) of a given year (colours) across time. The

803 numbers indicated the average elevation difference at a given point in time and the years the

804 TreeMig models are ahead or behind the SDM predictions (time lag).

805

806

807 Figure 4: Density of the distribution of upslope migration velocity (v_{UEL}) for the time period 2000–

808 2085 for the 16 principal tree species based on different climate change scenarios and model setup.

809 The dashed lines represent the mean values. SDM represents the migration velocity (v_{UEL}) of the

810 bioclimatic envelope while dynamic forest model is displayed either with realistic dispersal and

811 competition (TM_Normal), without dispersal limitation (TM_UD), without intra-specific competition

812 (TM_NC) or a combination of both (TM_UD_NC).

813

814 **Figure 5**

815

816 Figure 5: Correlation of species UEL (dots) based on predictions of the dynamic forest model (TreeMig)

817 and the bioclimatic envelope (SDM prediction) for the different TreeMig setups and time steps based

818 on the climate change scenario A1B. Normal = TreeMig – Normal, UD = TreeMig – Unlimited dispersal,

819 NC = TreeMig – No competition, UD & NC = TreeMig – Unlimited dispersal & no competition, PA =

820 Competition with *P. abies* only, UD & PA = Unlimited dispersal & competition with *P. abies* only.

821 **Figure 6**

822

823 Figure 6: Species-specific UELs across time based on observations (2000), SDM predictions (2000,

824 2060, 2085) and TreeMig simulations (1950 to 2300, 25 year intervals). For the future climate, the

825 scenario A1B was used. Observation = Highest observation within study area, SDM = Correlative

826 species distribution model, TM_Normal = TreeMig simulation, TM_UD = TreeMig simulation with

827 unlimited dispersal, TM_NC = TreeMig simulation without competition, TM_UD_NC = TreeMig

828 simulation with unlimited dispersal and no competition, TM_PA = TreeMig simulation with *P. abies* as

829 sole competitor, TM_PA_UD = TreeMig simulation with *P. abies* as sole competitor and unlimited

830 dispersal.