FOREST BIODIVERSITY AND ECOSYSTEM SERVICES

Extreme climate events counteract the effects of climate and land-use changes in Alpine tree lines

Ceres Barros[1,2]*, Maya Guéguen[1,2], Rolland Douzet[3], Marta Carboni[1,2], Isabelle Boulangeat[4], Niklaus E. Zimmermann[5,6], Tamara Münkemüller[1,2] and Wilfried Thuiller[1,2]

[1]Laboratoire d'Écologie Alpine (LECA), Université Grenoble Alpes, F-38000 Grenoble, France; [2]Laboratoire d'Écologie Alpine (LECA), CNRS, F-38000 Grenoble, France; [3]Station Alpine Joseph Fourier - UMS 3370, Université Grenoble Alpes, SAJF, F-38000 Grenoble, France; [4]Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Québec G5L 3A1, Canada; [5]Landscape Dynamics Unit, Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland; and [6]Department of Environmental Systems Science, Swiss Federal Institute of Technology ETH, CH-8092 Zürich, Switzerland

Summary

1. Climate change and extreme events, such as drought, threaten ecosystems world-wide and in particular mountain ecosystems, where species often live at their environmental tolerance limits. In the European Alps, plant communities are also influenced by land-use abandonment leading to woody encroachment of subalpine and alpine grasslands.

2. In this study, we explored how the forest–grassland ecotone of Alpine tree lines will respond to gradual climate warming, drought events and land-use change in terms of forest expansion rates, taxonomic diversity and functional composition. We used a previously validated dynamic vegetation model, FATE-HD, parameterized for plant communities in the Ecrins National Park in the French Alps.

3. Our results showed that intense drought counteracted the forest expansion at higher elevations driven by land-use abandonment and climate change, especially when combined with high drought frequency (occurring every 2 or less than 2 years).

4. Furthermore, intense and frequent drought accelerated the rates of taxonomic change and resulted in overall higher taxonomic spatial heterogeneity of the ecotone than would be expected under gradual climate and land-use changes only.

5. *Synthesis and applications*. The results from our model show that intense and frequent drought counteracts forest expansion driven by climate and land-use changes in the forest–grassland ecotone of Alpine tree lines. We argue that land-use planning must consider the effects of extreme events, such as drought, as well as climate and land-use changes, since extreme events might interfere with trends predicted under gradual climate warming and agricultural abandonment.

Key-words: agricultural abandonment, climate change, drought, dynamic vegetation model, forest–grassland ecotone, global change, land-use changes, mountain ecosystems, synergistic effects of disturbances, woody encroachment

Introduction

Many ecosystems around the globe are threatened by changes in climate and land use, which impact biodiversity at different levels. Mountain ecosystems, in particular, are especially vulnerable to the effects of climate change, as they harbour many species that are near their environmental tolerance limits. Changes in climate drive species range shifts and impact physiological processes, and might also impact the provisioning of ecosystem services (Bellard *et al.* 2012). Land-use changes, be it by conversion of natural habitats into agricultural or urban lands, or by abandonment of managed areas, could aggravate the effects of climate change, as well as contribute to large and sudden changes of available habitats and ecosystem

*Correspondence author.
E-mail: ceres.barros@univ-grenoble-alpes.fr

services (Asner *et al.* 2004). Climate, however, is not only predicted to change in its long-term average, but also with regard to extreme events (e.g. drought), expected to intensify in many regions (IPCC 2012).

Drought affects plant reproduction, growth and survival and can ultimately lead to changes in forest (Park Williams *et al.* 2013) and grassland (Gu *et al.* 2007) productivity, to changes in vegetation composition of landscapes (Clark *et al.* 2016), and result in significant forest dieback at the global scale (Allen *et al.* 2010). Forest dieback can have cascading effects on biodiversity, carbon, water and nutrient cycling, and ultimately on the provisioning of ecosystem services, such as carbon uptake and storage (Anderegg, Kane & Anderegg 2013). Such effects are likely very important in forest–grassland ecotones of mountain environments, where many tree species live close to their lower temperature limits and may reach their soil moisture limits in dry valleys (Goldblum & Rigg 2010). This is the case even in regions like the European Alps, where tree lines are further constrained by land use for farmlands, grazing and mowing (Carlson *et al.* 2014). In recent years, drought events have caused Swiss forests to suffer significant diebacks of Scots pine (*Pinus sylvestris* L.), favouring replacement colonization by pubescent oak (*Quercus pubescens* L.) and a turnover of forest composition (Rigling *et al.* 2013). Moreover, plant communities in mountainous areas are threatened by changes in land use that affect plant community structure and composition (Tasser & Tappeiner 2002). For example, simulations of vegetation dynamics in the European Alps predict that land-use abandonment and climate warming will interact and increase forest expansion towards higher elevations (Dirnböck, Dullinger & Grabherr 2003; Boulangeat *et al.* 2014).

Although forest–grassland ecotones in the European Alps are facing environmental changes originating from three fronts (i.e. gradual and extreme climate change, and land-use abandonment), so far no study has investigated their joint effects, especially from a forecasting perspective (Seidl *et al.* 2011). While climate change and land abandonment should lead to forest expansion and woody encroachment of subalpine and alpine pastures (Asner *et al.* 2004), drought stress increases tree mortality, causing forest dieback. Consequently, we can expect that drought might counter the effects of gradual climate change and land-use abandonment, but this is likely to depend on drought frequency and intensity, as well as on the identity of species within communities. Milder droughts may contribute to faster woody encroachment of subalpine and alpine pastures by favouring species adapted to drier environments. On the other hand, very severe and/or frequent droughts are likely to slow forest progression. Such effects may not be homogeneous in space, especially if certain areas are prone to more intense or more frequent drought (Dobbertin *et al.* 2005; Worrall *et al.* 2013).

Here, we study, in a spatially explicit manner, how drought frequency and intensity interact with climate and land-use practices and affect forest–grassland ecotones in the European Alps using the landscape dynamic vegetation model FATE-HD (Boulangeat, Georges & Thuiller 2014). Although FATE-HD does not simulate drought effects at the individual and physiological level, it can capture drought at the community level providing useful insights for management and conservation planning of complex ecosystems. For example, ecosystem management and conservation in the European Alps focuses on maintaining a bundle of ecosystem services (Grêt-Regamey, Walz & Bebi 2008; EC 2015), managing for a high diversity of habitats and on protecting biodiversity *per se*. Although this includes maintaining forest cover, there is also an important focus on avoiding woody encroachment of open habitats. FATE-HD provides information on these different conservation goals.

Specifically, we explored (i) under which conditions drought reversed the trend of forest expansion that is observed under climate change and land-use abandonment; (ii) whether forest–grassland ecotones suffered important changes in taxonomic and functional diversity when exposed to extreme events; and (iii) the possible spatio-temporal dynamics of these changes. Finally, (iv) we evaluated the consequences of drought regimes in the context of current land-use management and the provisioning of ecosystem services in the European Alps.

Materials and methods

STUDY AREA

We focused our study on the forest–grassland ecotone habitats of the Ecrins National Park (ENP), situated in south-east France in the French Alps. The park covers an area of 178 400 ha (elevation ranging from 669 to 4102 m a.s.l.), with a rich diversity of plant species (ca. 2000) and ecosystems, from mountainous to alpine habitats – the majority being open habitats (60% of the park surface). Land use consists mainly of agricultural activities (grazing, 48%; crop fields and mown grasslands, 9·8%; and forest management, 14%), which are accurately mapped (Esterni *et al.* 2006).

THE BASE MODEL: FATE-HD

FATE-HD has already been parameterized to explore the synergistic effects of land-use (LU) and climate changes (CC) on the vegetation of the ENP (Boulangeat *et al.* 2014), and we have now extended it to incorporate drought effects. We first give a brief description of the base model (further details in Appendix S1 in Supporting Information and in Boulangeat, Georges & Thuiller 2014) and then follow with a more detailed description of the new drought module.

FATE-HD models the spatio-temporal dynamics of plant functional groups (PFGs) by explicitly simulating their population dynamics and dispersal, interactions for light resources, and their responses to climate and different LU regimes. FATE-HD has been parameterized for 24 PFGs representative of both the taxonomic and functional diversity of the rich flora in the ENP (Boulangeat *et al.* 2012b). They consist of six chamaephyte groups (C1-6), 10 herbaceous groups (H1-10) and eight phanerophyte groups (P1-8), each occupying up to five height strata and passing through four ages (1–4) that have different responses to disturbances (see

Table S1 in Appendix S1). The abundance of a given stratum in a pixel determines the amount of light that reaches lower strata. Interactions for light resources are simulated by accounting for the amount of light reaching each PFG cohort in a stand and the PFG's light preferences. Responses to climate are simulated through habitat suitability (HS) maps (constructed *a priori* based on observed occurrences) for each PFG, and climate change is simulated by changing HS maps at regular intervals (Appendix S1). Land-use disturbances are modelled in a spatially explicit manner, by assigning mowing, grazing (with intensities low, medium or high) or no disturbance to each pixel (Appendix S1). Model output consists of yearly strata and PFG abundances per pixel.

SIMULATING DROUGHT EVENTS

Whether or not a PFG was affected by drought depended on the comparison of the PFG's past drought exposure to simulated yearly drought intensity values. To calculate each PFG's past drought exposure, we combined PFG occurrences (from the vegetation data base of the Conservatoire Botanique National Alpin; see Boulangeat *et al.* 2012a; and CBNA 2015) with monthly values of a moisture index (MI, Thornthwaite 1948) across the entire French Alps for 1961–1990 (Appendix S2). MI was calculated as the difference between precipitation and potential evapotranspiration (negative MI indicating drought; Appendix S2). For each PFG, we extracted the distribution of monthly MI values from each plot where it occurred (hereafter $MI_{1961-1990}$). We then defined drought intensity (*Din*) as the lowest MI value in a year for each occurrence plot. Finally, a PFG's past drought exposure was defined as the distribution of these experienced *Din* values (hereafter $Din_{1961-1990}$).

At each year, the PFGs' past drought exposure calculated above was compared with values of *Din* within each pixel (*Din* maps; Fig. 1). The comparison triggered, or not, consequences of drought events through two sequential modelling steps: (i) 'identifying drought effects' and (ii) 'modelling drought response'.

1. *Identifying drought effects under past and future conditions.* In the simulations, yearly *Din* values per pixel were obtained from past observations of MI values in the French Alps (validation runs) or from calculations of MI values using future climate predictions (future drought scenario runs). Drought was detected for a PFG in a given pixel, for a given simulation year, when the pixel *Din* was 'abnormally' low relative to the PFGs past drought exposure ($Din_{1961-1990}$ distribution, Fig. S1 in Appendix S2). The drought status was classified as 'no drought', 'moderate drought' or 'severe drought', depending on two 'drought detection thresholds', which were defined as deviations from mean values of PFGs' past drought exposure ($Din_{1961-1990}$ distribution). No drought was detected if the pixel *Din* value was greater than $\bar{x} - 1 \cdot 5 \times SD$ of $Din_{1961-1990}$ ($\bar{x}$ and SD being the mean and standard deviation, respectively; step 2.1 in Fig. 1). Moderate and severe drought occurred if the pixel *Din* was less than $\bar{x} - 1 \cdot 5 \times SD$ of $Din_{1961-1990}$ (step 2.2) and less than $\bar{x} - 2 \cdot 0 \times SD$ of $Din_{1961-1990}$, respectively (step 2.3; see PFG drought detection thresholds in Table S3).

Effects of severe drought depended on the accumulation of past drought events ('cumulative effect of drought'; steps 2.3.1 ii and 2.3.2). This cumulative effect of drought was meant to simulate the fact that after long periods of water stress, less intense droughts may also have severe effects on tree mortality (McDowell *et al.* 2008; Allen *et al.* 2010). Cumulative effects of drought were twofold and are regulated by two PFG-specific parameters: the PFG's sensitivity to a severe drought ('drought sensitivity'; Table S3 in Appendix S2) and the PFG's response to successive droughts ('cumulative drought response'; Table S3). Drought sensitivity expressed the number of droughts a PFG must experience before suffering severe effects due to a severe drought (step 2.3; see 'Modelling drought responses' below). For herbaceous groups, severe drought
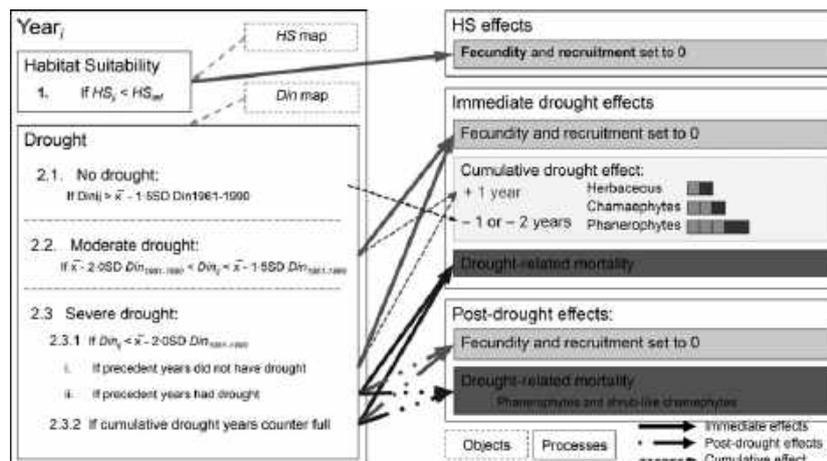

Fig. 1. Drought simulation scheme. For each year *i*, a PFG's habitat suitability (HS; step 1) and drought effects (step 2) are evaluated within a pixel *j*. If HS_{ij} or Din_{ij} are below reference values (HS_{ref} and $\bar{x} - 1 \cdot 5$ SD of $Din_{161-1990}$, respectively), PFG fecundity and recruitment are set to 0 (medium grey arrows and boxes). Additionally, if Din_{ij} crosses the reference value, one drought year is added to the PFG's cumulative drought effects counter (thin dashed arrows and light grey box). Severe drought effects occur if conditions 2.3.1 ii or 2.3.2 are met (dark grey arrows and boxes), consisting in immediate and post-drought effects (full and dash-dot arrows, respectively). Otherwise, only moderate drought effects are caused (2.1 and 2.3.1 i; medium grey full arrows). Drought recovery is simulated by subtracting one (phanerophytes and shrub chamaephytes, C4) or two drought events from the cumulative drought effects counter (thin, dark grey and dashed arrow). Small light grey squares indicate the 'drought sensitivity' parameter, and the total number of squares indicates the size of the counter ('cumulative drought response' parameter). See Table S3 in Appendix S2 for full parameter list and refer to main text for further details.

effects occurred during the first severe drought they experienced (drought sensitivity = 1). In contrast, chamaephytes and phanerophytes were less sensitive: chamaephytes only suffered severe effects during the second drought they experienced, while phanerophytes and shrubs (C4) were only affected severely during the third drought event (step 2.3.1 ii; years represented as light grey squares in Fig. 1). After a certain number of droughts experienced, the PFG's tolerance is weakened and all drought events (moderate or severe) have severe consequences. The cumulative drought response parameter expressed how many successive drought events were tolerated by a PFG before any subsequent drought events started having severe effects (step 2.3.2). Again, chamaephytes and phanerophytes (together with group C4) were more tolerant and only suffered severe effects from subsequent droughts after three and five drought events, respectively (total number of squares in Fig. 1). Herbaceous groups only needed two drought years to be severely affected by any subsequent drought.

Finally, to simulate drought recovery (and avoid accumulating drought years indefinitely), we removed one drought year (phanerophytes and shrub chamaephytes) or 2 years (herbaceous groups and most chamaephytes) from the PFGs' cumulative effect counters during each non-drought year (dark grey dashed arrow in Fig. 1).

2. *Modelling drought responses.* Drought effects were twofold, immediate and/or post-drought (occurring the year after drought), in order to simulate demographic responses during and after drought occurs (Allen *et al.* 2010). Drought immediately affected a PFG's recruitment and fecundity, which were set to 0 during the present drought year (moderate and severe droughts). A severe drought also increased PFGs mortality (0–60% depending on the PFG type, soil moisture preference and age) and caused PFGs to resprout (0–80% depending on PFG type, soil moisture preference and age). Post-drought effects were only modelled after a severe drought. To this end, PFG recruitment and fecundity were set to 0, PFG mortality was increased, and resprouting of PFGs was activated (although less than for immediate drought effects: 0–20% for mortality and 0–50% for resprouting). We calculated each PFG's soil moisture preference class (0 = drought tolerant to 3 = drought intolerant; see details in Appendix S2) considering both PFGs' past drought exposure (via their $MI_{1961-1990}$ distributions) and expert knowledge on the soil moisture requirements of the PFGs. Drought-intolerant PFGs responded with higher mortality rates, and, across PFGs, younger and older PFG (extremes of the size gradient) also suffered higher mortality rates (McDowell *et al.* 2008). Herbaceous and most chamaephyte PFGs never resprouted during drought, did not suffer post-drought mortality, but always resprouted after a severe drought. Younger individuals (age 1) were never capable of resprouting (see Appendix S2 for further details on parameterization and Table S3 for the full list of drought-related parameters).

Finally, we also simulated the protective effect of canopy cover as a buffer against drought effects. Canopy cover has been shown to increase seedling survival, by an amelioration of local microclimate conditions in terms of air and soil temperature, radiation and humidity (Gómez-Aparicio *et al.* 2005; Kane *et al.* 2011). Hence, in simulations, pixel *Din* values were increased by 25% in pixels where tree cover (strata > 1·5 m) was at least 40% (definition of semiclosed habitats according to the ENP park data base; Esterni *et al.* 2006) – recall that less negative *Din* values correspond to less severe drought.

SIMULATION EXPERIMENTS

Simulations started with an initialization phase of 850 years during which current climate and land-use regimes were modelled (Fig. 2). This phase allowed a stabilization of PFGs and achieving the current vegetation state before any future scenarios of climate, land-use or drought regime changes were applied (Boulangeat, Georges & Thuiller 2014). All scenario simulations started from the last year of the initialization phase, which will be referred to as year 0 hereafter.

We simulated one scenario of gradual CC, five scenarios of increasing drought frequency that were combined with three scenarios of increasing drought intensity (see below) and with two scenarios of LU change, totalling to 30 scenarios runs (Fig. 2). Since changes in drought regimes are thought to be a consequence of CC, we always changed background climate through its impact on habitat suitability for PFGs. Additionally, we ran two baseline simulations with only gradual CC (i.e. no drought), each with a scenario of LU.

Drought was implemented similarly to CC, by feeding maps of drought intensity (*Din*) values. Like maps of 'current' HS, 'current' *Din* maps were calculated by averaging past MI values across years 1961–1990. Since drought events are caused by extreme values of temperature and/or precipitation (IPCC 2012), we used the predicted temperature and precipitation maps for 2080 (following the A1B scenario described in Appendix S1) to calculate future maps of *Din* values. Current IPCC predictions indicate that drought frequency and intensity are to increase in the future (IPCC 2012); hence, we simulated three different drought intensities with linearly increasing drought frequencies and fixed periods without drought events to test our hypotheses. This allowed the vegetation to recover by avoiding long periods of continuous drought if frequency was high. Drought was then set to occur either every year or every 2, 4, 8 or 16 years (five drought frequency scenarios), with a 10-year no-drought period after each sequence of five drought events. Future and current *Din* maps were alternated to create drought and no-drought years, respectively. As for drought intensity, we calculated three levels of intensity ('low', 'medium' and 'high') that would not greatly deviate from climate predictions. Medium intensity corresponded to forecasted *Din* values for the year 2080, and low/high intensity corresponded to an increase/decrease of these values by 20%, respectively, (three intensity scenarios; see Fig. S1 in Appendix S2).

Land-use scenarios consisted of removing all grazing and mowing activities to simulate LU abandonment, or to continue current LU practices to simulate a 'business-as-usual' scenario (two LU scenarios). Land-use abandonment was applied at year 4 until the end of the simulation, whereas gradual CC was applied by changing PFG habitat suitability at regular 15-year intervals, starting at year 15 until year 90 (Appendix S1 and Boulangeat *et al.* 2014). The duration of drought regimes depended on the scenario of drought frequency, but covered at least the period of gradual CC (years 15–90) and finished before year 105. For all scenarios, simulations were run for a total of 200 years and replicated three times (Fig. 1).

We validated the drought module by running a simulation using observed data of drought events that occurred between 1961 and 1990 (Fig. 1). Model output was compared to vegetation plots from the ENP data base and the previous validation of FATE-HD (Boulangeat, Georges & Thuiller 2014). We found that the simulated vegetation represented the observed vegetation

Fig. 2. Simulation experiment workflow. An initialization phase (0–850 years) allowed reproducing the current vegetation state of the Ecrins National Park. The last 50 years of the initialization phase (800–850 years) were used to validate the drought module, while the last year (year 850) was the starting point of scenario simulations, which lasted 200 years. Climate change was implemented from years 15 to 90. Land-use changes were implemented at year 4, remaining unchanged until the end of the simulations. Drought regimes were initiated at year 15, lasting at least as long as climate change, up to year 105.
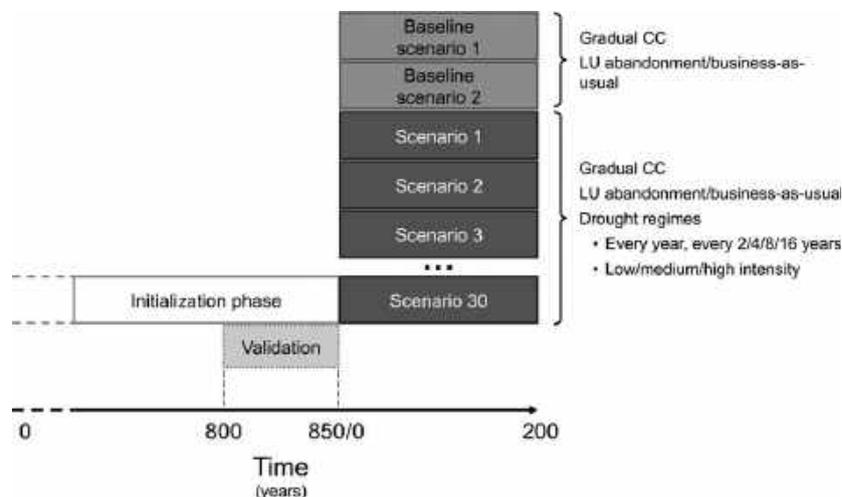
of the park well and concluded that the inclusion of drought effects led to good model performance (Appendix S3).

ANALYSIS OF RESULTS

To answer our first question regarding the effects of drought and LU on forest expansion, we analysed how different combinations of drought intensity, drought frequency and LU regimes influenced the speed at which forest and shrubland migrated towards higher elevations. Forest and shrubland pixels were identified based on the percentage of tree cover (strata > 1·5 m), which was larger than 60% for forest and between 10% and 60% for shrubland (Esterni *et al.* 2006). Rates of forest and shrubland expansion (RFE and RSE, respectively) were estimated independently for three different time frames. The first reflected the initial impacts of gradual CC, LU and drought disturbances (years 0–49). The second reflected responses to ongoing CC and drought events and medium-term responses after they ended (years 50–149). The last time frame reflected long-term responses to gradual climate and LU changes, as well as recovery from drought events and the eventual establishment of new equilibria (years 150–200). Hence, for each time frame (and each scenario), we regressed yearly maximum elevation obtained for forest and for shrubland pixels against time to obtain the rates of expansion (regression slopes). Responses of RFE and of RSE to drought and LU regimes, and their interactions, were analysed separately for each time frame using analyses of variance (ANOVAS). Four levels of drought intensity ('no drought', 'low', 'medium' and 'high') and six of drought frequency ('no drought', every year and every 2, 4, 8 and 16 years) were used as independent factors. Land use was used as a factor with two levels ('abandonment' and 'business-as-usual'). Model selection was based on Akaike Information Criterion (AIC) values, model parsimony and analyses of residuals.

Taxonomic response of the forest–grassland ecotone to simulated drought, CC and LU, was assessed by quantifying PFG turnover both spatially and temporally, using a measure of β-diversity. The ecotone was spatially delimited for each scenario at year 0, using a buffer distance around the upper tree line (1000 m above and 500 m below), tree line being defined at the third quartile of elevation values of forest pixels. Mean β-diversity was calculated using a multiplicative decomposition of γ- and α-diversity, calculated as the inverse Simpson concentration (Whittaker 1972):

$$\gamma/\alpha = \frac{1}{\sum p_{(i)}^2} \qquad \text{eqn 1}$$

$$\beta = \gamma \times \sum \left(\frac{1}{n} \times \frac{1}{\alpha_i} \right) \qquad \text{eqn 2}$$

where p is the relative abundance of each PFG across pixels (for γ-diversity), or in each pixel i (for α-diversity), and n the total number of communities. Alpha and γ-diversity are bounded between unity and the maximum number of PFGs; β-diversity is bounded between unity and the maximum number of communities (Tuomisto 2010). For temporal turnover, β-diversity was calculated per pixel (i.e. communities) with reference to year 0 at subsequent 5-year intervals (year five against year zero, year 10 against year zero, etc.), then averaged across all ecotone pixels to obtain a value per pair of years. Spatial turnover was calculated across all ecotone pixels (for a given year) every 5 years.

We also explored how community-averaged soil moisture preference changed spatially under different drought regimes and different LU practices. Focusing again on the ecotone, we calculated community-weighted mean values of soil moisture preference classes (CWM$_{SM}$) every 5 years, by weighing PFG soil moisture preference values (SM$_j$) by PFG relative abundances (abund$_j$, j being a PFG) for each pixel (Garnier *et al.* 2004; Violle *et al.* 2007):

$$CWM_{SM} = \sum SM_j \times abund_j \qquad \text{eqn 3}$$

Since we were interested in mapping increases or decreases of CWM$_{SM}$, rather than following its temporal evolution, we calculated changes in CWM$_{SM}$ per pixel, as the difference between CMW$_{SM}$ values of a given year and year 0. Negative values indicated shifts towards communities with preference for drier soils, while positive values indicated shifts to communities with higher moisture requirements. Resulting CWM$_{SM}$ changes were mapped for different scenarios of drought intensity/frequency and LU management to obtain a spatial image of functional community shifts. In addition, we assessed whether changes towards communities with higher or lower soil moisture preference were linked to elevation, by calculating Pearson product–moment correlation coefficients between values of change and elevation across ecotone pixels.

Results

When considering all scenarios of drought and land-use regimes, rates of forest expansion (RFE) towards higher elevations were not significantly different from the rates of shrubland expansion (RSE; Fig. S4). While RSE was always significantly affected by drought intensity and frequency, RFE only responded significantly to these factors during the early phases of the simulations (years 0–49 and 50–149 in Fig. 3a and Tables S5 and S6). Both RSE and RFE were more affected by different drought intensities, rather than frequencies (Table S6). Also, RSE and RFE responded differently to the interaction between drought intensity and frequency, which significantly affected RFE between years 0 and 149, but only had a significant effect on RSE during the last 50 years.

Between years 0 and 49, high drought intensity generally increased RSE and RFE, especially when associated with higher drought frequencies (RSE ~ -2.5 m year^{-1} and RFE between approximately -2.5 and -2 m year^{-1};

left panels in Fig. 3a,b). This pattern was then reversed between years 50–149, where medium and high drought intensities caused RSE to decrease (RSE almost always <1 m year^{-1}; middle panel in Fig. 3a), a pattern that could also be seen for forest expansion under land-use abandonment (middle panel in Fig. 3b) and for shrubland expansion during the last time frame (right panel in Fig. 3a). The effect of drought frequency on RSE was more evident during the first two time frames, where increasing frequencies led to larger departures from baseline expansion rates (left and middle panels in Fig. 3a). On the other hand, the effect of drought frequency on RFE (and on RSE during the last 50 years) was largely dependent on drought intensity. While increasing the frequency of low intensity drought events did not seem to impact forest expansion more than climate and land-use changes alone, it clearly aggravated the effects of high intensity drought events (left and middle panels in Fig. 3b, but see also right panel in Fig. 3a for a similar pattern). The effect of LU gained importance during the two last time frames, where land-use abandonment
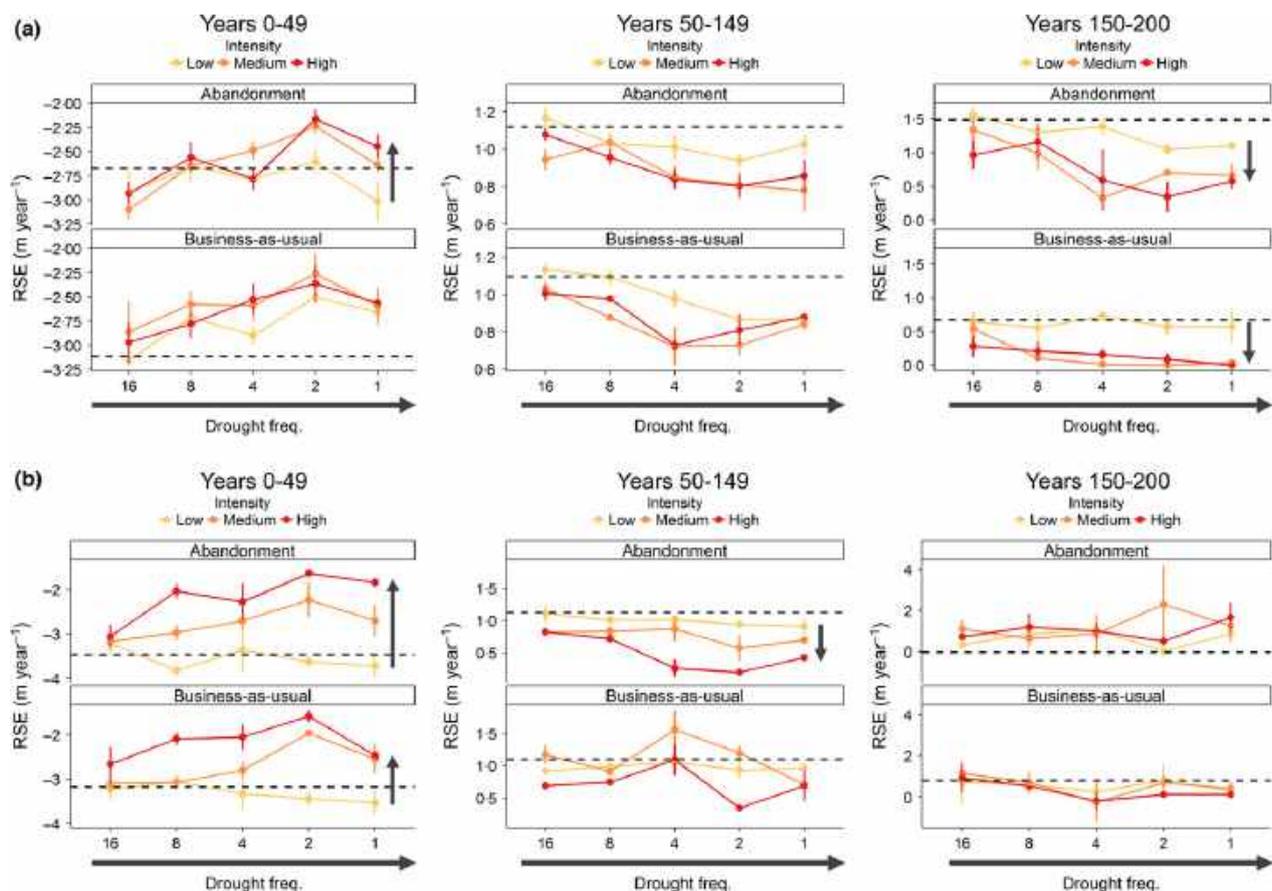

Fig. 3. Effects of drought intensity, drought frequency and land-use practices on (a) rates of shrubland expansion (RES) and on (b) rates of forest expansion (RFE) for the three simulation time frames. Plots show the rates of expansion of all forest and shrubland pixels averaged across the three simulation repetitions. Dashed lines show baseline levels. Vertical arrows indicate increasing drought intensities (colour-coded from low to high), while horizontal arrows along the *x*-axis indicate increasing frequency (from every 16 years, '16', to every year, '1'). Climate change and drought were implemented between years 15 and 90 (drought regimes up to year 105) and land-use abandonment started at year 4 onward. [Colour figure can be viewed at wileyonlinelibrary.com]

generally increased RSE and RFE across the different drought intensity and frequency levels (middle and right panels in Fig. 3a,b). In fact, during the last 50 years, the response of RFE was only significantly affected by LU, despite that there seems to be a negative effect of high drought intensity when current land-use practices were kept (see right panel in Fig. 3b).

Given that higher drought frequencies generally increased the effects of high intensity drought events, enhancing the differences between drought intensity levels, we analysed ecotone community responses by contrasting the two most extreme drought frequency scenarios (in terms of RSE and RFE) across LUs: (i) infrequent droughts (occurring every 16 years) and (ii) frequent droughts (occurring every 2 years). Drought regimes only seemed to affect PFG turnover (measured by β-diversity) when drought was frequent and their impact differed between LU scenarios (Fig. 4). In general, the ecotone became increasingly different from its initial state during the period of gradual CC, especially under a LU abandonment scenario (Fig. 4; see also Fig. S5). However, frequent drought events affected the rates at which these changes occurred. Temporal taxonomic turnover accelerated during periods of drought, but stabilized at lower levels towards the end of the simulations, especially if drought intensity was high (Fig. 4b). Similarly, more frequent drought events increased spatial taxonomic heterogeneity, especially in combination with high drought intensity (Fig. S5).

Since drought effects on forest and shrubland expansion were stronger during the first two simulation phases (years 0–149), we analysed functional changes in forest–grassland ecotone communities during this period. In general, soil moisture preference showed important changes across this time period (differences between years 145 and year 0 ranged from −2·17 to 1·55 CWM_{SM} units; Fig. 5). These changes were significantly correlated with elevation, although correlation values were relatively low due to higher variance at lower elevations (Fig. S6). Mapping the difference in soil moisture preference values between year 145 and year 0 revealed a tendency for communities to become more drought tolerant across the landscape, especially at higher elevations (see sign of correlations with elevation in Fig. 5). Although visual patterns are very similar with or without drought effects, the correlation between CWM_{SM} and elevation is weaker under highly intense and frequent drought. Land-use abandonment contributed to larger changes towards lower values of CWM_{SM} than did current LU activities and also decreased the strength of the correlation between CWM_{SM} and elevation (compare upper and lower panels in Fig. 5a–c).

Discussion

Despite the likelihood that drought frequency and intensity will increase in European mountainous areas (Calanca
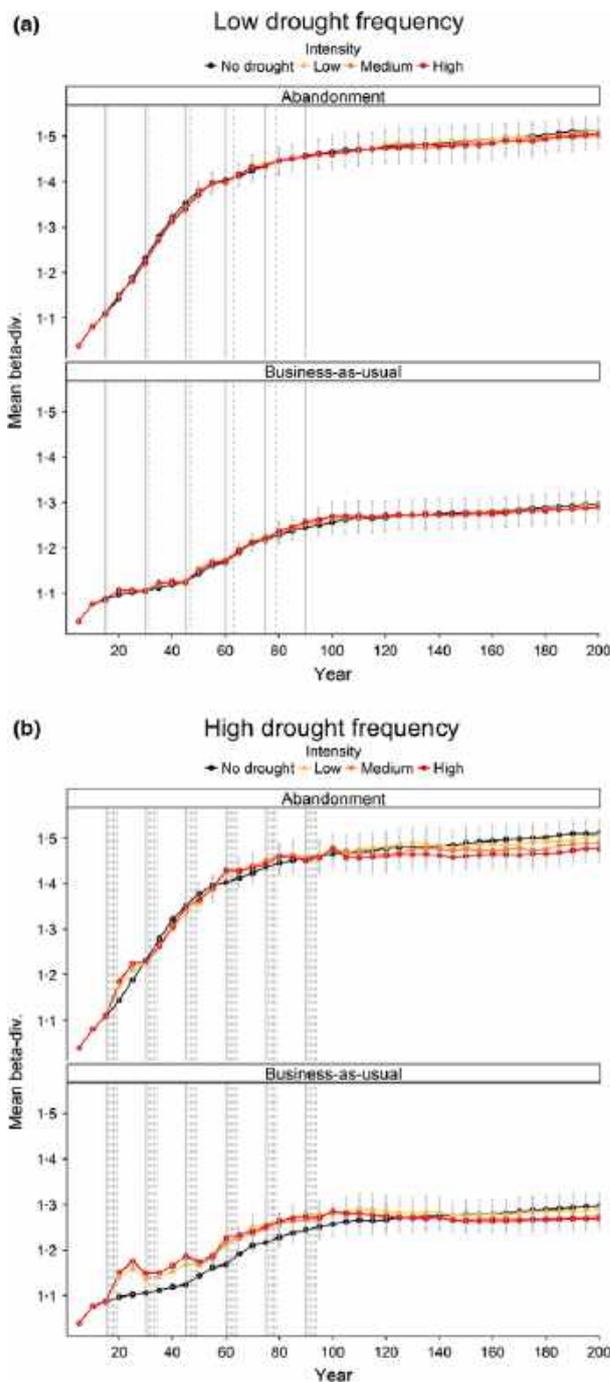

Fig. 4. Effects of drought intensity (colour-coded) and land-use practices on temporal β-diversity are shown for scenarios of (a) low drought frequency (every 16 years) and (b) high frequency (every 2 years). Temporal β-diversity was calculated every 5 years with respect to year 0 in each scenario, within forest–grassland ecotone boundaries defined at year 0 in each scenario, and averaged across simulation repetitions. Vertical lines indicate climate changes (full line) and drought events (dashed lines); land-use abandonment started at year 4 onward. Standard error bars are shown in grey for each point. [Colour figure can be viewed at wileyonlinelibrary.com]

2007), their impact has been largely understudied. Our simulations revealed that drought can have significant impacts on the dynamics of forest–grassland ecotones in
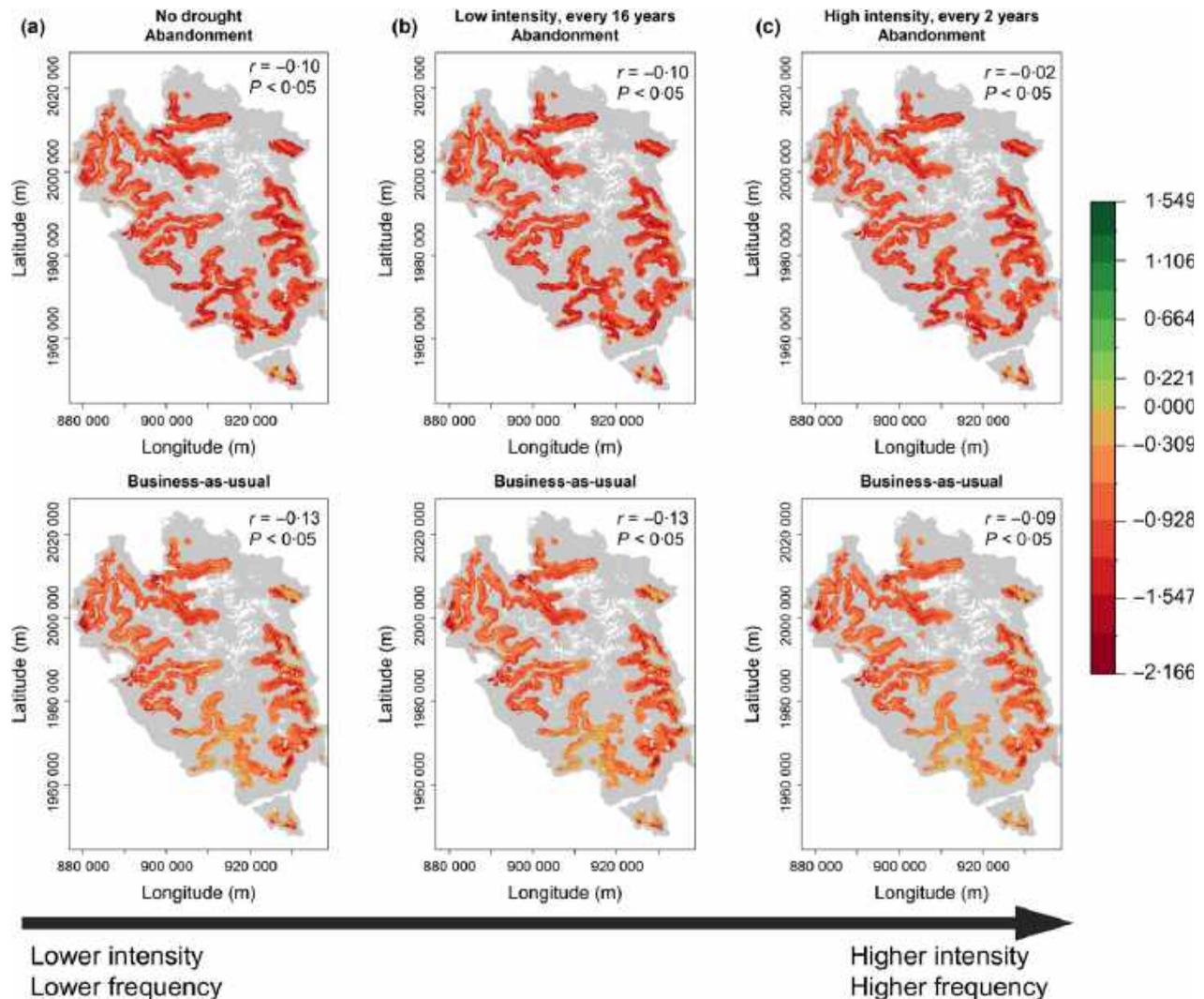
Fig. 5. Functional responses of the forest–grassland ecotone across land-use scenarios for (a) baseline simulations and for two extreme scenarios of drought: (b) low intensity drought events occurring every 16 years and (c) high intensity drought events occurring every 2 years. Maps show differences in community-weighted mean (CWM) soil moisture preference values calculated between year 145 and year 0 of the scenario simulations, averaged across simulation repetitions. Negative values indicate communities that became more drought tolerant. Pearson moment correlation values between CWM differences and elevation are shown in the top right corners. Also, see Fig. S6 for temporal evolution of CWM values.

the European Alps and that these impacts can partially change under different land-use scenarios.

We used a dynamic vegetation model to simulate drought effects on vegetation. Unlike physiological approaches that provide prediction of drought effects at the individual level, FATE-HD provides an overview at the landscape level bypassing the issues associated with simulating physiological processes. The validation of FATE-HD suggests that the model gives a realistic picture of the mechanisms driving vegetation dynamics in the park. Using a particular period (here 1961–1990) for parameterization may have biased our estimates of drought sensitivity and severity, since two important drought events have affected the ENP in the early 2000s (Bonet *et al.* 2016). Yet, this bias is equal among scenarios and should not affect their relative differences. Our approach might also suffer from the fact that it does not

include other important factors that may interact with drought, such as pests, insect outbreaks or atmospheric CO_2, which may influence vegetative growth. However, this would require a complex physiological model difficult to parameterize for such a rich and diverse region. Therefore, our aim was not to provide quantitative estimates of vegetation changes, but, instead provide a qualitative comparison of the possible effects of different drought regimes on landscape succession.

DROUGHT EFFECTS ON WOODY ENCROACHMENT

Drought events showed opposing effects compared to land-use abandonment and gradual climate change, by accelerating forest and shrubland expansion during the first years of drought and decelerating it in subsequent years, especially when drought frequency and intensity

were high. While effects of infrequent drought (occurring every 16 years) or of low intensity drought were not easily distinguishable from simply ignoring extreme events, an increase of drought frequency to every 1–2 years, or of drought intensity, changed forest and shrubland expansion rates (Fig. 3). Indeed, high drought frequencies have been shown to aggravate the effects of short drought events, causing similar levels of tree mortality as those observed during prolonged droughts (Adams *et al.* 2009). Similarly, our results showed that, when drought was frequent, low and medium drought intensities resulted in rates of shrubland expansion almost as low as those of high drought intensities (years 50–149 in Fig. 3a). On the other hand, mild drought events may increase forest expansion if they remain below species-specific tolerance thresholds (Bachelet *et al.* 2001), which could explain the higher forest and shrubland expansion rates during the first 50 years (Fig. 3a,b). In fact, in our simulations, herbaceous and most chamaephyte PFGs were more sensitive to drought than phanerophytes, meaning that these groups were more negatively affected by successive moderate droughts and competed less for light resources, eventually reducing forest retraction.

Obviously, quantitative expansion rates are related to the way drought effects were parameterized. We used a conservative approach when simulating drought-related mortality, which only occurred in response to severe drought. In addition, severe drought effects were only triggered if a minimum number of drought events were accumulated, with phanerophyte groups being the least affected by drought. Although this led to smaller effects of drought at low frequencies, our parameterization reflects the observed resistance of these groups to drought in the study area, relatively to the climate period of reference. Furthermore, decisions on cumulative effects for different PFG life forms were based on expert knowledge from botanists working within the ENP, which we believe is highly valuable. While our parameterization of drought effects might not reflect true quantitative estimates, it allows exploring how different drought frequencies affect the progression of tree line towards higher elevations in the Alps and how these effects are modulated by land uses.

DROUGHT EFFECTS ON ECOTONE BIODIVERSITY

Unlike woody encroachment, changes in tree line biodiversity were mainly impacted by gradual climate change and land-use regimes. Climate-induced changes in community composition invariably increased with time (Fig. 4). Land-use abandonment led to more homogeneous landscapes due to grassland conversion to forest, while current land-use practices led to higher heterogeneity, as grasslands were artificially kept open and forests colonized unmanaged areas (Fig. S5). However, drought regimes had important effects on the rate at which these changes occurred. Turnover rates increased during periods of frequent drought (Fig. 4b) and the ecotone became spatially more heterogeneous than under the effect of gradual climate change (Fig. S5). Under land-use abandonment, this was due to the fact that despite the conversion of large open areas to forest, which increased overall spatial homogeneity (upper panels in Figs 4b and 5b), higher PFG mortality caused by drought negatively affected the colonization of certain warm-adapted and/or drought-adapted PFGs, reducing the effects of gradual climate change (such as C1, C4, C5 and P7; see Tables S2 and S3 in Appendix S2). Oppositely, the business-as-usual scenario prevented forest colonization in managed areas but allowed it in other areas, maintaining a higher spatial β-diversity (as in Boulangeat *et al.* 2014); however, frequent drought selected against PFGs with lower drought resistance (such as H6, H7 and P2; Tables S2 and S3 in Appendix S2) and in favour of less sensitive herbaceous and chamaephyte groups (such as C5 and H5; Tables S2 and S3 in Appendix S2) increasing the speed at which the ecotone changed (see lower panel in Fig. 4b) and the heterogeneity between managed areas and those that became invaded (lower panel in Fig. S5b).

As with taxonomic turnover, changes in community soil moisture preference were also mainly driven by gradual climate change and land-use practices (Fig. 5). Community soil moisture preference generally decreased during, and sometime after, the period of simulated drought and climate change (years 0–145); yet, this varied not only between scenarios of land-use change, but also with elevation (see steeper curves at lower elevations in Fig. S6). This functional homogenization following gradual climate change, especially in combination with land-use abandonment, was due to the replacement of drought-intolerant ecotone communities by more drought-tolerant ones across the entire landscape. Furthermore, our results suggest that frequent and intense drought may cause functional shifts in communities that are not necessarily similar to those observed under gradual climate warming (Figs 5 and S6).

Changes in understorey communities may be the direct result of drought-related mortality, but also the indirect result of change in forest cover. Not only did we simulate changes in light interception at the canopy level, but also its buffering effect against drought stress, two factors that are at the origin of negative feedbacks of forest cover reduction on understorey communities (McDowell *et al.* 2008; Allen *et al.* 2010; Anderegg, Kane & Anderegg 2013). Therefore, the simulated loss of tree cover exposed understorey communities to stronger drought effects and changed their exposure to light, most likely leading to changes in community composition and structure that may be similar to what has been reported in previous studies (Anderegg *et al.* 2012). Future studies will be needed to evaluate these changes, whether community composition can revert back to pre-drought conditions and how long this takes to happen.

CONSEQUENCES FOR LAND-USE MANAGEMENT AND ECOSYSTEM SERVICES

Land-use abandonment did not significantly reduce the effects of high drought intensity and frequency on forest expansion, suggesting that it affected forest expansion less than drought or gradual climate change, at least at the analysed time scale (Fig. 3b and Table S6). Land-use abandonment increased forest expansion for high drought frequencies and intensities mostly during the first 50 years of simulations (Fig. 3b) and baseline rates of forest expansion were always similar between the two land-use scenarios. The effect of land-use practices seemed to gain importance in later years, with land-use practices being the only factor significantly affecting forest expansion during the last 50 years of the simulation (years 150–200 in Fig. 3b and Table S6). Although land use had impacts on the short term, changes to PFG colonization that greatly impact vegetation structure were more visible on the long term, since in FATE-HD there is a lagged response of PFG demography, dispersal and biotic conditions necessary to establish canopy cover (Boulangeat *et al.* 2014). On the other hand, the effects of land-use abandonment on the spatial and temporal turnover of taxonomic and functional composition were evident on the short term, but partially affected under frequent and intense drought.

These results have important implications for the way land-use planning should consider drought effects on vegetation. Current ecosystem management in the European Alps responds to recent trends of land-use abandonment and climate change, as both promote the loss of open habitats by woody encroachment (MacDonald *et al.* 2000; Gehrig-Fasel, Guisan & Zimmermann 2007). In the ENP, management focuses on maintaining biodiversity at different levels, from protecting diversity and ecosystems *per se*, to preserving multiple ecosystem services (Parc National des Ecrins 2015). Sustainable grazing and mowing practices prevent forest expansion, help protect subalpine and alpine grasslands and species of conservation concern (Andrello *et al.* 2012) and ensure the provision of fodder for cattle and the maintenance of open habitats for cultural and leisure activities (Parc National des Ecrins 2015). Our predictions indicate that frequent and intense drought will counteract the effects of gradual climate change, leading to lower forest expansion rates even under land-use abandonment (see also Lenoir *et al.* 2010). Projections under the IPCC SRES A2 scenario by Calanca (2007) predicted a 50% probability of drought occurrence between 2071 and 2100 in the European Alps, in comparison with 18% calculated for the period 1901–2004. Recent drought events have been reported to cause important forest dieback in the Swiss Alps (Rebetez & Dobbertin 2004; Rigling *et al.* 2013), and drought sensitivity has increased in the last century even for forest stands on mesic sites (Weber *et al.* 2013). If drought frequency and intensity increase and forests retract, we may not only expect losses of forest cover and biodiversity, but also habitat shifts and important changes in ecosystem service provisioning. Forests in the European Alps are important carbon sinks, but also exert control on avalanches, rock fall (Berger & Chauvin 1996; Weber *et al.* 2013) and flood regimes at lower elevations (Descroix & Gautier 2002; Marston, Bravard & Green 2003). If ecosystem management continues to prioritize the conservation of multiple ecosystems services and, thus, a mosaic of habitats (as is current practice in the ENP), land-use planning in the Alps needs to prevent woody encroachment (and the loss of open habitats), as well as to incorporate accurate and spatially explicit drought predictions to avoid loss of forest cover in areas where drought effects are expected to be very severe. This is not only valid in the European Alps, but also in other mountain ecosystems where tree line is actively managed and where land-use and climate changes will likely interact with changes in drought regimes. Besides delaying forest progression, drought might also compromise grassland communities by driving phenological, taxonomic and functional shifts (De Boeck *et al.* 2016), which could be different from those observed under gradual climate changes (Figs 4, 5, S5 and S6). These shifts can alter the ratios between more and less productive species, having repercussions on nutrient cycling and other ecosystem services, such as fodder production (Nandintsetseg & Shinoda 2013). Hence, conserving the taxonomic and functional biodiversity of forest–grassland ecotones in mountain areas is of great importance to ensure the provisioning of multiple ecosystem services. In a European context, management of these ecosystems must not only focus on tree line advancement driven by land-use abandonment and facilitated by warming, but also on eventual forest retraction and changes to grassland diversity caused by drought, which might impact the provisioning of ecosystem services.

Data accessibility

Rates of shrubland and forest expansion, taxonomic temporal and spatial turnover, changes in community-weighted mean soil moisture preferences at ecotone level and ʀ scripts for analysis of results are available from Dryad Digital Repository http://dx.doi.org/10.5061/dryad.s3015 (Barros *et al.* 2016).

References

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A. & Huxman, T.E. (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*, **106**, 7063–7066.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Anderegg, W.R., Anderegg, L.D., Sherman, C. & Karp, D.S. (2012) Effects of Widespread Drought-Induced Aspen Mortality on Understory Plants. *Conservation Biology*, **26**, 1082–1090.

Anderegg, W.R., Kane, J.M. & Anderegg, L.D. (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, **3**, 30–36.

Andrello, M., Bizoux, J.-P., Barbet-Massin, M., Gaudeul, M., Nicolè, F. & Till-Bottraud, I. (2012) Effects of management regimes and extreme climatic events on plant population viability in Eryngium alpinum. *Biological Conservation*, **147**, 99–106.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E. & Harris, A.T. (2004) Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, **29**, 261–299.

Bachelet, D., Neilson, R.P., Lenihan, J.M. & Drapek, R.J. (2001) Climate change effects on vegetation distribution and carbon budget in the Unisted States. *Ecosystems*, **4**, 164–185.

Barros, C., Guéguen, M., Douzet, R., Carboni, M., Boulangeat, I., Zimmermann, N.E., Münkemüller, T. & Thuiller, W. (2016) Data from: Extreme climate events counteract the effects of climate and land-use changes in Alpine treelines. *Dryad Digital Repository*, http://dx.doi.org/10.5061/dryad.s3015

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Berger, F. & Chauvin, C. (1996) Cartographie des fonctions de protection de la forêt de montagne: appréciation des potentialités d'avalanche sous couvert forestier. *Revue de Géographie de Lyon*, **71**, 137–145.

Bonet, R., Arnaud, F., Bodin, X., Bouche, M., Boulangeat, I., Bourdeau, P. *et al.* (2016) Indicators of climate: Ecrins National Park participates in long-term monitoring to help determine the effects of climate change. *eco. mont-Journal on Protected Mountain Areas Research*, **8**, 44–52.

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L. & Thuiller, W. (2012a) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal of Biogeography*, **39**, 204–214.

Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne, S. *et al.* (2012b) Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Global Change Biology*, **18**, 3464–3475.

Boulangeat, I., Georges, D. & Thuiller, W. (2014) FATE-HD: a spatially and temporally explicit integrated model for predicting vegetation structure and diversity at regional scale. *Global Change Biology*, **20**, 2368–2378.

Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Van Es, J., Abdulhak, S., Zimmermann, N.E. & Thuiller, W. (2014) Anticipating the spatio-temporal response of plant diversity and vegetation structure to climate and land use change in a protected area. *Ecography*, **37**, 1230–1239.

Calanca, P. (2007) Climate change and drought occurrence in the Alpine region: how severe are becoming the extremes? *Global and Planetary Change*, **57**, 151–160.

Carlson, B.Z., Renaud, J., Biron, P.E. & Choler, P. (2014) Long-term modeling of the forest-grassland ecotone in the French Alps: implications for land management and conservation. *Ecological Applications*, **24**, 1213–1225.

CBNA (2015) Conservatoire Botanique Nationale Alpin (ed. P. Segura).

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C. *et al.* (2016) The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology*, **22**, 2329–2352.

De Boeck, H.J., Bassin, S., Verlinden, M., Zeiter, M. & Hiltbrunner, E. (2016) Simulated heat waves affected alpine grassland only in combination with drought. *New Phytologist*, **209**, 531–541.

Descroix, L. & Gautier, E. (2002) Water erosion in the southern French Alps: climatic and human mechanisms. *Catena*, **50**, 53–85.

Dirnböck, T., Dullinger, S. & Grabherr, G. (2003) A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, **30**, 401–417.

Dobbertin, M., Mayer, P., Wohlgemuth, T., Feldmeyer-Christe, E., Graf, U., Zimmermann, N. & Rigling, A. (2005) The decline of Pinus sylvestris L. Forests in the Swiss Rhone Valley-a Result of Drought Stress? *Phyton (Horn)*, **45**, 153.

EC (2015) European Commission – Environment: Biodiversity strategy.

Esterni, M., Rovera, G., Bonet, R., Salomez, P., Cortot, H. & Guilloux, J. (2006) DELPHINE - Découpage de l'Espace en Liaison avec les Potentialités Humaines et en Interrelation avec la Nature. Parc National des Ecrins.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M. *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.

Gehrig-Fasel, J., Guisan, A. & Zimmermann, N.E. (2007) Tree line shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science*, **18**, 571–582.

Goldblum, D. & Rigg, L.S. (2010) The deciduous forest–boreal forest ecotone. *Geography Compass*, **4**, 701–717.

Gómez-Aparicio, L., Gómez, J.M., Zamora, R., Boettinger, J.L. & Ezcurra, E. (2005) Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *Journal of Vegetation Science*, **16**, 191–198.

Grêt-Regamey, A., Walz, A. & Bebi, P. (2008) Valuing ecosystem services for sustainable landscape planning in Alpine regions. *Mountain Research and Development*, **28**, 156–165.

Gu, Y., Brown, J.F., Verdin, J.P. & Wardlow, B. (2007) A five-year analysis of MODIS NDVI and NDWI for grassland drought assessment over the central Great Plains of the United States. *Geophysical Research Letters*, **34**, L06407.

IPCC (2012) Managing the risks of extreme events and disasters to advance climate change adaptation. *A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change* (eds C.B. Field, V. Barros, T.F. Stocker, D. Qin, D.J. Dokken, K.L. Ebi, M.D. Mastrandrea, K.J. Mach, G.-K. Plattner, S.K. Allen, M. Tignor & P.M. Midgley), pp. 582. Cambridge University Press, Cambridge, UK, and New York, NY, USA.

Kane, J., Meinhardt, K., Chang, T., Cardall, B., Michalet, R. & Whitham, T. (2011) Drought-induced mortality of a foundation species (Juniperus monosperma) promotes positive afterlife effects in understory vegetation. *Plant Ecology*, **212**, 733–741.

Lenoir, J., Gégout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E. *et al.* (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, **33**, 295–303.

MacDonald, D., Crabtree, J., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Lazpita, J.G. & Gibon, A. (2000) Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management*, **59**, 47–69.

Marston, R.A., Bravard, J.-P. & Green, T. (2003) Impacts of reforestation and gravel mining on the Malnant River, Haute-Savoie, French Alps. *Geomorphology*, **55**, 65–74.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T. *et al.* (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.

Nandintsetseg, B. & Shinoda, M. (2013) Assessment of drought frequency, duration, and severity and its impact on pasture production in Mongolia. *Natural Hazards*, **66**, 995–1008.

Parc National des Ecrins (2015) La charte en actions: programme 2014–2016.

Park Williams, A., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M. *et al.* (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, **3**, 292–297.

Rebetez, M. & Dobbertin, M. (2004) Climate change may already threaten Scots pine stands in the Swiss Alps. *Theoretical and Applied Climatology*, **79**, 1–9.

Rigling, A., Bigler, C., Eilmann, B., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C. *et al.* (2013) Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biology*, **19**, 229–240.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K. *et al.* (2011) Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling*, **222**, 903–924.

Tasser, E. & Tappeiner, U. (2002) Impact of land use changes on mountain vegetation. *Applied Vegetation Science*, **5**, 173–184.

Thornthwaite, C.W. (1948) An approach toward a rational classification of climate. *Geographical Review*, **38**, 55–94.

Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2–22.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Weber, P., Bugmann, H., Pluess, A.R., Walthert, L. & Rigling, A. (2013) Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees*, **27**, 171–181.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.

Worrall, J.J., Rehfeldt, G.E., Hamann, A., Hogg, E.H., Marchetti, S.B., Michaelian, M. & Gray, L.K. (2013) Recent declines of Populus tremuloides in North America linked to climate. *Forest Ecology and Management*, **299**, 35–51.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. FATE-HD model.

Table S1. Plant functional groups and their trait values.

Appendix S2. Parameterising and simulating drought effects.

Table S2. Description of the simulated plant functional groups (PFG) and their representative species.

Table S3. Drought-related parameters used in FATE-HD.

Fig. S1. Current and future drought intensity (*Din*) maps.

Appendix S3. Validation of drought module.

Table S4. Model accuracy after implementing drought effects.

Fig. S2. Observed vs. simulated tree cover in different habitats with and without drought effects.

Fig. S3. Observed vs. simulated strata abundances with and without drought effects.

Fig. S4. Rates of forest (RFE) and shrubland expansion (RSE) across all scenarios.

Fig. S5. Effects of drought intensity and land-use practices on ecotone spatial β-diversity.

Fig. S6. Temporal evolution of community-weighted mean (CWM) soil moisture preference.

Table S5. Models of the response of forest and shrubland expansion to drought and land-use factors.

Table S6. Effects of drought and land-use factors on forest and shrubland rates of expansion.