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1 Dynamics of forage production in pasture-woodlands of the Swiss Jura Mountains
2 under projected climate change scenarios
3

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25

26 ABSTRACT

27
28 Silvopastoral systems of the Swiss Jura Mountains serve as a traditional source of forage and timber
29 in the subalpine vegetation belt, but their vulnerability to land-use and climate change puts their
30 future sustainability at stake. In this paper we couple experimental and modelling approaches to
31 assess the impacts of climate change on the pasture-woodland landscape. We draw conclusions on
32 the resistance potential of wooded pastures with different management intensities by sampling
33 along a canopy-cover gradient. This gradient spans from unwooded pastures associated with
34 intensive farming, to densely wooded pastures associated with extensive farming. Transplanted
35 mesocosms of these ecosystems placed at warmer and drier conditions provided experimental
36 evidence that climate change reduced herbaceous biomass production in unwooded pastures, but
37 had no effect in sparsely wooded pastures, and even stimulated productivity in densely wooded
38 pastures. Through modelling these results with a spatially explicit model of wooded pastures
39 (WoodPaM) modified for the current application, results were extrapolated to the local landscape
40 under two regionalised IPCC scenarios for climate change. This led to the suggestion that within the
41 Jura pasture-woodlands, forage production in the near future (2000-2050 AD) would be affected
42 disproportionately throughout the landscape. A stable forage supply in hot, dry years would be
43 provided only by extensive and moderate farming, which allows the development of an insulating
44 tree cover within grazed pastures. We conclude that such structural landscape diversity would grant
45 wood-pastures with a buffering potential in the face of climate change in the forthcoming decades.

46

47

48 KEYWORDS

49

50 Pasture; Woodland; Silvopastoral system; Subalpine; Grassland; Ecotone; Aboveground biomass;
51 Drought; Transplantation

52

53 INTRODUCTION

54

55 **History and importance of pasture-woodlands**

56

57 Pasture-woodlands are a traditional man-made landscape in European mountains (Etienne 1996)
58 and cover a major part of the Swiss Jura Mountains. They consist of a mosaic of open grassland,
59 closed forest, and semi-forested pastureland with scattered or clumped trees and owe their shape to
60 a long history of multifunctional land use, mainly pasturing and forestry (Buttler et al. 2009).

61 Wood-pastures are true ecotones between closed forests and open grassland and thus more than just
62 a simple interface between those two vegetation types. In such silvopastoral ecosystems, grasslands
63 and woodlands are intimately associated in space and time as the result of a balance between
64 counteracting ecological processes (Gillet et al. 2002, Gillet 2008). Forest encroachment and its
65 suppression by browsing of livestock and extensive pasture management leads to a spatio-temporal
66 heterogeneity of the landscape, defined by disturbance regimes, microclimate, and topography, and
67 provides favourable conditions for high biodiversity (Gillet et al. 1999, Dufour et al. 2006).

68

69 At present, pasture-woodlands vary substantially in the amount and quality of ecosystem services
70 they provide. Economically important factors such as forage supply are maintained higher through
71 intensively managed treeless pastures than through extensive wood-pastures with free grazing
72 livestock. This is important for local farmers who, from a socio-economic view, are the main users
73 of wooded pastures and, as such, may deliberately shape the landscape into an unwooded one. Apart
74 from farmin, in some regions revenues generated from forestry activities may be substantial (Gillet
75 and Gallandat 1996). The significance of this landscape for the tourist economy has also been
76 acknowledged, though it remains difficult to measure (Miéville-Ott and Barbezat 2005).

77

78 The coexistence of pastureland and woodland in a single and diverse silvopastoral ecosystem is not
79 easy to preserve and calls for integrated management schemes (Barbezat and Boquet 2008). Both
80 intensification and extensification of the current land use may lead to a breakdown of this
81 precarious association, resulting in a segregation of woodland and grassland (Buttler et al. 2009).
82 Even though anthropogenic land use change has been considered a major threat for mountain
83 ecosystems worldwide (Körner et al. 2006), little is known about its interaction with climate change
84 in the future.

85

86

87 **Climate change in the European mountains**

88

89 Global warming and associated environmental changes are predicted to have a strong impact on
90 mountain ecosystems this century (IPCC 2007). The observed trend in Swiss mountains during the
91 20th century for a 1.5 K rise in mean annual air temperature (Beniston et al. 1997) is paralleled by
92 increased instances of extreme summer temperature maxima and prolonged droughts (Schär et al.
93 2004, Beniston 2009). Throughout the current century these tendencies are predicted to become
94 more pronounced and northern hemisphere temperate mountains will experience the most intensive
95 temperature rise with a rate of warming typically two-to-three times higher (range +2.8 K to +5.3
96 K) than that recorded over the 20th century (Nogues-Bravo et al. 2007). Alongside, predicted hot
97 spells and a 30 % diminishing precipitation will intensify the dry periods in Central Europe
98 (Beniston et al. 2007, CH2011). These will bring about changes in summer soil moisture

99 availability, plant phenology and growing season length, which would ultimately have
100 repercussions on ecosystem distribution and function (Parry 2000, FOEN/FSO 2011).

101

102

103 **Response of plant communities to climate change**

104

105 Episodic extreme climate events, such as summer heat waves, have strong and distinct impacts at
106 the landscape scale (Ciais et al. 2005, Reichstein et al. 2007, Teuling et al. 2010). A mechanistic
107 understanding of primary ecological processes occurring in a heterogeneous landscape such as
108 pasture-woodlands is therefore essential for an efficient management. To date, a wealth of literature,
109 encompassing various experimental methodologies, exists about the effects of warmer and drier
110 climate on pristine cold-adapted vegetation. Transplantation experiments along natural climatic
111 gradients, offer a powerful method for testing hypotheses about how species and communities are
112 affected by future climatic changes. Although there are relatively few published studies using this
113 technique, some successful attempts have been carried out in contrasting terrestrial environments: in
114 peatlands (Wieder and Yavitt 1994, Breeuwer et al. 2010), in boreal forests (Hobbie and Chapin
115 1998), in montane meadows (Bruehlheide 2003), in subalpine grasslands (Sebastian 2007), and in
116 alpine vegetation (Scheepens et al. 2010). The results from those, however, outline idiosyncratic
117 patterns for plant community responses to environmental change. Concerning plant aboveground
118 biomass, recent studies have reported an increase in annual herbaceous biomass production with
119 warmer and drier climate (Bruehlheide 2003, Sebastian 2007). Others (Harte and Shaw 1995, Zhang
120 and Welker 1996), to the contrary, have observed no cumulative change in aboveground biomass.
121 Drought alone has been found to exert a negative effect on plant biomass (Johnson et al. 2011). At
122 the level of plant community composition, these studies fail to give a holistic picture on shifts in
123 diversity resulting from a climate manipulation. Either graminoids or forbs have been shown to
124 successfully dominate after a climatic perturbation. Opportunistic plants may be granted
125 competitive advantage through advanced phenological development (Dunne et al. 2003, Körner
126 2003, Inouye 2008), or through utilization of newly available nutrient resources (Bowman et al.
127 2006, Soudzilovskaia et al. 2007). Others may benefit from their inherent tolerance to specific
128 environmental stress (Buchner and Neuner 2003, Brock and Galen 2005). Overall, more fertile
129 early-successional grassland communities have been shown as more responsive to climate warming
130 and drought, compared to late successional ones, typically found in areas of low intensity
131 management (Grime et al. 2000). Drought resistance and recovery potential of plant communities
132 have also been attributed to high species richness (van Ruijven and Berendse 2010), whereas
133 grazing of highland pastures has been shown to both promote herbaceous richness and decrease
134 evapotranspiration loss and thus water consumption (Körner et al. 2006). In comparison to
135 grasslands, forests exhibit a more conservative water use and hence cope better with long-lasting
136 heat and drought stress (Teuling et al. 2010).

137

138 In light of these findings, and given the heterogeneous landscape structure and high biodiversity of
139 pasture-woodlands, we suspect that the productivity of such a mosaic of forest and extensively
140 grazed diverse mountain grassland communities could be robust to the effects of heat and drought.

141

142

143 **Upscaling from experimental plots to landscape level**

144

145 Inspired by the work of Dunne et al. (2004), which demonstrates the challenging but beneficial task
146 of extrapolating experimental results on ecosystem response to climate change from the scale of
147 plots to that of landscapes, in this study we couple an experimental with a modelling approach. We
148 believe that such combinations of observational, manipulative and modelling techniques are highly
149 adapted to assess ecosystem vulnerability or resilience to environmental change (Spiegelberger et
150 al. 2012).

151
152 To this aim, we established a transplantation experiment along an altitudinal gradient, to derive the
153 response of plant communities of open grassland, semi-wooded pastures and grazed forests to
154 climate manipulation (warming of up to +4 K). We built the results on biomass production into a
155 dynamic simulation model of wood-pasture ecosystems, in order to assess the impact of drought
156 events on forage provision for livestock at landscape level and in the proximate timeframe of
157 climate change projections (until 2050 AD).

158
159

160 **Hypotheses**

161
162 We hypothesised that (1) herbaceous aboveground biomass (AGB) production in characteristic
163 plant communities from wood-pastures would be more stable under climate change than in those
164 from treeless grasslands. Based on this hypothesis at plot level, we predicted (2) that at landscape
165 scale forage production in wood-pastures would be more stable during projected heat wave periods,
166 than that in intensively-managed unwooded pastures. At last, (3) we put forward the hypothesis that
167 wooded pastures represent a more robust land use form than conventional treeless pastures
168 considering future climate change impacts.

169
170

171 **METHODS**

172

173 **Study area and design of the warming experiment**

174

175 The Combe des Amburnex in the Swiss Jura Mountains is a characteristic subalpine area of pasture-
176 woodlands, situated within the boundaries of the Park Jurasien Vaudois. The climate is
177 predominantly oceanic with a mean annual rainfall of *ca.* 1750 mm at 1350 m a.s.l. (including more
178 than 450 mm snow precipitation) and a mean annual temperature of 4.5 °C. The ground is generally
179 covered with snow from November to May.

180

181 In August 2009 three wooded pastures of similar area lying along the Combe des Amburnex at 1350
182 m were chosen according to their tree canopy cover resulting from different intensity of land use.
183 These were, in increasing order of management intensity – a densely wooded pasture, a sparsely
184 wooded pasture and an unwooded pasture. The pastures were situated within a 1 km distance from
185 each other, measured each about 2 ha, and shared the same geomorphology, microtopography and
186 exposition. Within each of the three pasture types, fifteen plots were randomly selected to represent
187 the characteristic herbaceous vegetation of the respective area. To allow for a transplantation of soil
188 turfs, plots were severed into 12 separate 20 cm × 20 cm and 30 cm deep soil cores and assembled
189 back into rectangular PVC boxes of 60 × 80 cm² size and of 30 cm height. Chunks of intersected
190 tree roots (diameter > 1 cm) were removed from the soil cores and the remaining gaps were filled in

191 with adjacent soil from the same horizon. The resulting 45 mesocosms were left in place to recover
192 from the excavation until the end of the vegetation season and then transported to their receptor
193 sites in October 2009. In total, three transplantation sites were established along an altitudinal
194 transect: Combe des Amburnex (1350 m a.s.l., N 46°54', E 6°23'), Saint-George (1010 m a.s.l., N
195 46°52', E 6°26'), and Arboretum d'Aubonne (570 m a.s.l., N 46°51', E 6°37'). The first site at 1350
196 m a.s.l. served as a control site with unchanged climate, and the other two were chosen to represent
197 a combination of annual temperature increase of +2 K and a precipitation decrease of -20 % at 1010
198 m a.s.l., and of +4 K and -40 % at 570 m a.s.l., respectively. These preliminary approximations
199 were derived from interpolated data from nearby weather stations. At each site fifteen mesocosms,
200 representing five replicates of each pasture type and all originating from the Combe des Amburnex,
201 were transplanted following a completely randomised design. The boxes were dug down to surface
202 level into previously prepared trenches thus preventing lateral heat exchange with the atmosphere.
203 Mesocosms with turfs from sparsely wooded pastures and densely wooded pastures were shaded
204 using two types of UV resistant nylon mesh, which reduced PAR by 40% and 80% respectively,
205 simulating field-measured light conditions in the corresponding habitats during the 2009 growing
206 season (*unpublished data*). The mesh fabric was suspended on wooden frames 50 cm above the
207 ground surface and did not intercept rain precipitation. Those remained in the field only during the
208 snow free period of the year, as to avoid interference with snowpack. As a means of keeping the
209 grazing pressure on the plots and to avoid a confounding effect of “abandonment” and accumulation
210 of standing litter, plots were clipped close to ground level at the end of the vegetation season.

211
212 Herbaceous biomass was harvested at the end of July 2010 during the first year following turf
213 transplantation, and served as an estimate of the annual AGB production. At each plot a fixed area
214 of 35 cm by 35 cm was cut down to *ca.* 1 cm above the soil surface, determined to species level,
215 dried at 70 °C for 48 h and weighed.

216
217 Climate parameters were monitored continuously throughout the experiment by means of one
218 automated weather station (Sensor Scope Sàrl, Switzerland) per experimental site measuring at a
219 one minute interval air temperature and humidity 2 m above the ground surface, as well as rain
220 precipitation. Decagon Devices Em50 data-loggers coupled to Decagon ECH₂O sensor probes
221 recorded soil temperature and volumetric water content at top soil horizon (0 to -3 cm) every minute
222 and data were averaged over one hour intervals. Data presented here are given for the months of the
223 2010 growing season – April, May, June, July, August, and September (AMJJAS).

224
225

226 **Statistical analysis of experimental data**

227
228 The experimental design allows for the explanation of annual variation of herbaceous biomass
229 during the first year after transplantation by four factors: two categorical ones - initial pasture type
230 and climate of the transplantation site; and two continuous physical ones – soil temperature and soil
231 moisture. Each of the two edaphic variables was averaged per plot over the growing season
232 (between respective soil thaw and day of harvest), thus integrating the microclimate conditions
233 experienced by the plants. An ANCOVA model was fit through the raw data, testing the
234 significance of single factors and their two-way interactions.

235
236 In order to extrapolate from experimental plot data, obtained under a distinct set of environmental
237 conditions, to continuous site gradients in real landscapes, we built a linear regression model

238 predicting the seasonal AGB production from the two continuous variables tree cover percentage
239 and degree of temperature change. The experimental shading of the plots was related to tree cover
240 as follows: 0 % shading (light extinction under the canopy) for unwooded pasture with 0 % tree
241 cover, 40 % shading for sparsely wooded pasture with 50 % tree cover, and 80 % shading for
242 densely wooded pasture with 100 % tree cover. Temperature increase (ΔT) was calculated as the
243 difference between local plant growing season temperature and that at the control site at 1350 m
244 a.s.l. during the experimental year 2010. The parameter estimates for those factors retained in the
245 optimal model fit were implemented into the landscape model of wooded pastures WoodPaM.

247 All statistical analyses were performed using R version 2.13.1. (R Development Core Team 2012).

250 **Spatially-explicit simulation model of wood-pasture ecosystems WoodPaM**

251
252 The dynamic simulation model of wooded pastures WoodPaM was developed by Gillet et al. (2002)
253 and Gillet (2008) to investigate the successional dynamics of wooded pastures in the Swiss Jura
254 Mountains. WoodPaM is a spatially explicit ecosystem model. As such, it is able to simulate the
255 emergence of a semi-open landscape structure from selective grazing of large herbivores (cattle) by
256 explicitly considering the foodchain from primary productivity to forage consumption by livestock.
257 During simulations, selective foraging of cattle causes local impacts on vegetation (i.e., grazing,
258 browsing, dunging, and trampling). Those, in turn, and together with geomorphologic and climatic
259 conditions, promote or hinder forest development, and by this means drive the development of the
260 landscape structure.

261
262 In WoodPaM, a pasture is represented by an arrangement of quadratic, 25 m wide, grid cells (as in
263 Figure 1). In each cell the vegetation is represented by a herb, a shrub, and a tree submodel.
264 Succession in the herb layer is driven by the intensity of grazing and dunging, as well as by tree
265 cover. As such, it is categorised in the following four vegetation types – eutrophic pasture,
266 oligotrophic pasture, fallow, and understory, which differ in pastoral value (PV) (see Table 1). A
267 first estimate of yearly forage production P in a grid cell is computed based on a new regression
268 model (in comparison to Gillet (2008)), which relates empirical data on productivity from the same
269 set of vegetation surveys from the Jura Mountains and the Alps as used in Gillet (2008) to the
270 pastoral value PV and the length of the vegetation period $vegdays$, with:

271
272 P = yearly forage production (t DM ha⁻¹ a⁻¹)

273 PV = average pastoral value of the herb layer in the grid cell, weighted by the relative cover of
274 vegetation types

275 $vegdays$ = length of the vegetation period (days)

276 fpm = maximal production (20 t DM ha⁻¹ a⁻¹)

277 fpi = “initial” production for $PV = 0$ (8.5 t DM ha⁻¹ a⁻¹)

278 ra = altitude effect on the growth coefficient ($2.152 \cdot 10^{-5}$)

279 rm = maximal growth coefficient for $A = 0$ (0.05)

280
281 During simulations, the first estimate of yearly forage production is calculated from the current
282 pastoral value of the vegetation types of each grid cell and the average length of the vegetation
283 period during the last 50 simulation years. By this means, we take into account that the productivity
284 of grassland plant communities increases slowly following the general trend of temperature rise (see

285 Figure 2), rather than spontaneously in single warm years. In the second case, a drought effect has
286 to be expected, which we address separately (see next paragraph).

287
288 As a further innovation in comparison to former versions of WoodPaM (see Gillet 2008, Peringer
289 et al. *this issue*), we modify the first estimate of forage production by applying a multiplier D for the
290 drought effect of high average temperatures in the vegetation period during hot years. This modifier
291 is calculated from the regression model of AGB response to transplantation along the climate
292 warming gradient (see section “Statistical analysis of experimental data” and “Effects of increased
293 temperature on aboveground biomass production at plot level”). No modifier is applied in cooler
294 years, because the transplantation experiment did not deliver data for climate cooling. The
295 temperature anomaly ΔT is the difference between the average temperature of the current vegetation
296 period to the long-term mean temperature of the vegetation periods during years 1961 to 2010 (the
297 experiment took place in year 2010, thus plant communities are adapted to recent past climate). As
298 the regression function also expresses the dependency of productivity on tree cover (low forage
299 production of understory in comparison to grassland), the pastoral value of understory is set equal to
300 the value of grassland (see Table 1). The combined impact of drought and tree cover is computed
301 according to Equation 1:

302
303 <eqn1>

304
305 Thus, the final yearly forage production in each cell, taking into account the slow prolongation of
306 the vegetation period and yearly positive anomalies in the average temperature of the vegetation
307 period, is computed as the product of P and D .

308
309 This model modification assumes that (1) the productivity of mountain grassland communities
310 slowly increases with the increasing length of the vegetation period experienced during the last 50
311 years (community adaptation), however (2) their productivity in extraordinary hot years is
312 consistently reduced by drought. We set the current climate (see Figure 2) as a baseline for the
313 estimation of the drought impact, because we do not expect the development of new (drought
314 resistant) genotypes, especially not, because grasslands are dominated by perennial species and
315 species immigration is slow.

316
317 Consequently, simulated forage production per grid cell is a function of the successional state of the
318 herb layer (pastoral value of vegetation types), the average length of the vegetation period during
319 the last 50 years, and a drought impact in single hot years. Local grazing impacts at grid cell level
320 depend on selective habitat use of cattle. In turn, the attractiveness of grid cells for cattle grazing
321 depends on their forage provision and local site characteristics (i.e., steepness of terrain, rock
322 outcrops). By this means, the feedback loop between grazing impacts and vegetation succession is
323 closed, from which the spatio-temporal distribution of productivity of herb layer vegetation types
324 emerges during simulations.

325
326 The ratio of consumed forage and forage production in a grid cell is expressed as local utilization
327 rate (LUR) and based on a daily forage consumption of 18 kg DM per livestock unit. The same ratio
328 calculated at pasture level is termed global utilization rate (GUR).

329

330 For a further and detailed description of the model structure and the implementation of herb layer
331 and tree layer dynamics, as well as that of rules for selective grazing, refer to Gillet (2008). Recent
332 model refinements beyond this model description are given in Peringer et al. (*this issue*).
333

334

335 **Design of simulations**

336

337 We simulate forage production under observed and projected climate in three separate wooded
338 pastures in the region of Bullet, Switzerland, which lie in the same landscape of the Swiss Jura
339 Mountains as the experimental site, *ca.* 40 km NE along the mountain crest. These pastures are
340 adjacent (Figure 1), hence share identical climate, but differ in grazing intensity and consequently in
341 their vegetation structure. *Les Planets Ouest* (1200 m a.s.l., N 46°83', E 6°55') is an intensively
342 used commonage with 46 LU (livestock units) on 25.6 ha, resulting in 1.79 LU/ha for 170 days/year
343 (see also Chételat et al. *this issue*). It is practically treeless, and for the purpose of this study it is
344 referred to as Intensive Wooded Pasture (IWP). *Les Planets Milieu Est* (1200 m a.s.l., N 46°84', E
345 6°55') is mostly open grassland but features some sparsely wooded pasture far in the Northwest. It
346 has a moderate stocking density with 22 LU on 14.1 ha, resulting in 1.56 LU/ha for 135 days/year,
347 and from here-on is referred to as Moderate Wooded Pasture (MWP). *Les Cluds Sud* (1200 m a.s.l.,
348 N 46°84', E 6°56') is a mosaic pasture with several patches of woodland and is extensively grazed
349 with 23 LU on 23.3 ha, resulting in 0.99 LU/ha for 153 days/year. It is referred to as Extensive
350 Wooded Pasture (EWP). Although ongoing socio-economic developments will likely lead to
351 reduced stocking of wooded-pastures (Huber et al. *this issue-a*), for the purpose of this study, we
352 simulate constant stocking densities.
353

354

355 Time series of temperature and precipitation are derived from the regionalisation of observed
356 climate in the period 1950-2000 AD and two climate change scenarios of the IPCC-SRES report
357 (2000) for the period 2000-2100 AD, as provided by the Climatic Research Unit CRU of the
358 University of East Anglia, Norwich, UK and the Tyndall Centre for Climate Change Research
359 (regionalization by Schmatz *personal communication*). We select the moderate scenario B2 with +4
360 K warming and the extreme scenario A1FI with +8 K warming, assuming that a realistic future
361 development will lie within the range between the two scenarios. The corresponding yearly mean
362 temperatures are displayed in Figure 2, together with the yearly mean temperatures of the
363 vegetation period. The latter drive drought impact during simulations, whereas the average
364 temperature of the last 50 years drives productivity increase. We initialized the model from aerial
365 photographs taken in 2000 AD and applied a 50-years spin-up period 1950-2000 AD. Simulations
366 run from 2000 on for a period of 50 years.
367

368

369

368 **RESULTS**

369

370 **Effects of increased temperature on aboveground biomass production at plot level**

371

372 Transplantation downslope exposed the plant communities in the experimental plots to an
373 (expected) increase in ambient air temperature and reduced precipitation during the vegetation
374 period (Table 1). Following this treatment, soil temperature generally increased, while soil moisture
375 decreased (Table 1). Along the gradient in simulated tree cover, at each site soil temperature
376 decreased almost linearly with approximately 1 K for each level of canopy shading (0 %, 40 %, and

377 80 %). Shading prevented also soil water evaporation at lower altitudes compared to the control
378 site. In the case of densely wooded pastures, soils kept up to 70 % of their moisture content at 570
379 m a.s.l. and 96 % at 1010 m a.s.l.

380
381 Results from the ANCOVA model indicated that AGB production along the transplantation gradient
382 was significantly affected by pasture type ($P_{2,25} < 0.001$), and its interaction with the altitude of the
383 transplantation site ($P_{4,25} < 0.001$). Significant effect exerted also soil temperature ($P_{1,25} = 0.016$)
384 and soil moisture ($P_{1,25} = 0.008$). AGB quantity decreased significantly along the land-use intensity
385 gradient in the order unwooded > sparsely wooded > densely wooded pastures (Figure 2). These
386 differences were most evident at the control site at 1350 m a.s.l., but were weakened at warmer
387 climate where AGB production was stimulated in densely wooded pastures, reduced in unwooded
388 pastures, and remained unchanged in sparsely wooded pastures (see Figure 2, and the statistically
389 significant interaction between pasture type and altitude). The transplantation altitude alone had no
390 consistent effect on AGB across the pasture types.

391
392 Fitting a linear regression model through the biomass data allowed us to estimate the influence of
393 landuse and climate parameters on pasture productivity. The resulting model ($R^2 = 0.85$, $P_{3,41} <$
394 0.001) is given in Equation 2:

395
396 <eqn2>

397
398 It expresses the production of herbaceous biomass *AGB* as a function of tree cover percentage
399 *TreeCover*, air temperature anomaly ΔT and their interaction. All parameter estimates, including the
400 model's intercept were highly significant ($P_{1,41} < 0.001$) and were hence implemented into the
401 WoodPaM model in the form of a factor applied to the first estimate of forage production in the
402 grassland-forest mosaic (see section "Spatially-explicit simulation model of wood-pasture
403 ecosystems WoodPaM").

404
405

406 **Effects of temperature anomalies on forage production at landscape level**

407
408 Simulated time series of global forage utilization rates (GUR) followed distinct trajectories
409 according to the management intensity within each of the studied pastures (Figure 4). Most obvious
410 was the trivial effect of a higher utilization rate with higher stocking density, which led to well-
411 separated curves for each pasture. The spin-up period ended around year 1980 and realistic
412 utilization rates were simulated for extensive (EWP, ~70 %), moderate (MWP, ~80 %) and intense
413 pastures (IWP, ~100 %). An utilization rate of 100 % means an optimal stocking density in an
414 economic sense, because all available forage is consumed. An utilization rate below 100 %
415 indicates undergrazed patches, which are typical in extensively grazed pastures, and provide niches
416 where shrubs and woods can develop and form the specific landscape mosaic of pasture-woodlands.

417
418 From year 2000 onwards, utilization rates did not decrease, as one would expect from the increase
419 in productivity following the prologation of the vegetation period with climate change (see Figure
420 2). The rapid temperature rise and subsequent increase in simulated drought due to an increasing
421 number of years with hot summers compensated for this effect. In the course of time, the utilization
422 rates of IWP and MWP started to fluctuate with increasing amplitude and peaks far above the
423 threshold of 100 %. To the contrary, the utilization rate of EWP remained always below 100 % and

424 fluctuations were far smaller. For the drastic warming scenario A1FI (+8K) such effects were even
425 more pronounced, especially in the projected heatwave in simulation years 2042-2047.

426
427 Overall, for current stocking densities, simulations of extensive pastures showed a continuous
428 provision of sufficient forage, while in intense pastures scarcity of forage was indicated. The stable
429 forage provision in EWP (i.e., low amplitude of projected GUR in Figure 4) might appear trivial
430 due to intrinsically low stocking densities in this pasture. Nevertheless the stimulated AGB
431 production in its forested landscape patches did provide a quantitative buffering capacity against
432 heatwaves. Such a contribution of landscape heterogeneity to ecosystem process resilience is
433 exemplified (Table 3) though the comparison of a pair of simulated years with hot (2021) and
434 ambient (2022) temperatures from the simulation continuum of IPCC-SRES climate change
435 scenario B2 (Figure 2). We chose two consecutive years in order to compare a quasi identical
436 landscape structure. Within the treeless IWP in the hot year 2021, forage production decreased with
437 drought causing an increase of 12.5 % in GUR (Table 3 and Figure 5). Similar drought impacts on
438 forage production were also recognisable within the grasslands of MWP and EWP (Figure 5),
439 however, the utilization rate in EWP, which is a true forest-grassland mosaic, increased only with
440 6.7% in GUR (Table 3). An additional mathematical correction for the potential bias of extensive
441 pastures being less prone to overshooting GUR levels in response to forage scarcity was
442 implemented by dividing GUR values for a given year by the longterm average GUR. As seen in
443 Table 3, the corrected differences in GUR values between the two years remained higher in IWP
444 and MWP (11.9 and 12.4, respectively) compared to those in EWP (9.5), which indicated the
445 simulated buffering potential of wood-pastures.

446
447
448 DISCUSSION

449
450
451 **Distinct effects of climate change on herbaceous production across land-cover types**

452
453 Our experimental study was novel for directly comparing climate change impacts on several
454 neighbouring grasslands experiencing different intensities of management, which were manifested
455 by a gradient of forest canopy cover and herbaceous species composition. The results unequivocally
456 displayed the decline in herbaceous productivity in open pastures in contrast to a stable and even
457 increasing one in forested pastures. This pattern became apparent after only one year of
458 experimental treatment, which emphasises the importance of stochastic heat waves for the
459 functioning of pasture-woodland ecosystems. As a result of the transplantation treatment, open
460 pastures experienced disproportionately stronger drought effects than the two wood-pasture types
461 and this was driven mainly by decreased soil moisture availability. Even though our simplistic
462 design for shading of the mesocosms did certainly not encompass all the microclimate effects of a
463 real tree canopy (i.e., ambient humidity, wind interception, canopy leachate and litter deposition, or
464 underground competition for resources), we believe our results on herbaceous production are robust
465 due to the appropriate use of control plots and the overall short time span of the treatment, which
466 prevented accumulation of confounding carry-over effects.

467
468 One of the most prominent factors driving the reduction in AGB was the decrease in soil moisture
469 availability during the plant growing season. Whereas soil temperature increased linearly with
470 warmer climate for all pasture types, we found that soil humidity was mainly affected in the

471 unwooded pasture plots paralleled by a decrease in standing plant AGB. Moreover most of this
472 AGB had already senesced at peak growing season due to drought (NDVI measurements,
473 *unpublished data*). This phenomenon arose from an intensified evapotranspiration in open-canopy
474 plots in comparison to the shaded ones, where the mesh covers have adequately served their “forest-
475 like” purpose in limiting energy exchange with the atmosphere during the hot summer months (see
476 Teuling et al. 2010).

477
478 An alternative explanation could be that intensive farming (Körner et al. 2006) coupled to high
479 fertilization levels and impeded successional development (Grime et al. 2000) played itself a role in
480 rendering intensively managed open pastures more vulnerable to climate change. One could
481 speculate that those grassland communities, composed of fast-growing species with access to high
482 nutrient availability, are more responsive to environmental change. This scenario, however, was not
483 explicitly tested in our experimental design (no fertilisation manipulations) and remains only
484 hypothetical.

485
486

487 **Landscape patterns of forage provision under climate change**

488
489 Our approach to implement experimental results into a process-based simulation model of wooded
490 pastures merits more than a simple extrapolation across spatial scales (from plot to landscape
491 levels). Since biomass production of grasslands forms represents the base of WoodPaM simulations,
492 climate change impacts on primary production mechanistically determine forage availability for
493 cattle, which in turn shapes landscape structure via selective grazing behaviour (Kohler et al. 2006).
494 Regardless of the limitations of our experimental design, which did not account for plausible
495 interaction between precipitation and temperature, we do not expect a qualitative bias in our
496 interpretations. Our confidence comes from the locally observed and predicted strong negative
497 correlation between these two climatic factors, hence we included only temperature in our
498 predictive model for AGB production. Even though we based our choice of transplantation gradient
499 on both current weather observations and climate predictions, we could not account for ecosystem
500 responses to future warm and wet, or cold and dry plant growing seasons.

501
502 While other studies of climate-change impacts on wooded pastures rely mainly on the climate
503 sensitivity of tree species (Peringer et al. *this issue*), ours focused on the functioning of grasslands.
504 The design of simulations encompassed a much shorter timeframe from 2000 to 2050 AD – a period
505 short enough to detect climatic stress while assuming no plant species adaptation (development of
506 drought adapted ecotypes), or significant community change through immigration. Even though this
507 assumption may appear unrealistic for the last decades of simulation, we considered three reasons
508 for it: (1) there is no simple way to implement evolutionary and dispersal processes for grassland
509 species in the model; (2) species shift from lowland following climate change is probably very slow
510 in this area, due to forest barriers to the dispersal of herbaceous species; (3) phenotypic plasticity
511 and genetic polymorphism of established plant populations is likely to allow yet some adaptation to
512 drought stress due to the long history (ecological continuity) of these mountain pastures.
513 Furthermore, this period is too short to produce any substantial shift in the tree layer and thus the
514 landscape structure; see Peringer et al. (*this issue*) for long term dynamics of climate change.
515 Nevertheless, one should bear in mind that, in the long run, impacts of climate change on grassland
516 productivity could feedback on landscape structure due to adaptive grazing behaviour of cattle
517 (Smit et al. 2007, Vandenberghe et al. 2007, Vandenberghe et al. 2009). In hot years, depleted

518 forage resources in open pastures would provoke cattle grazing in the forest understory, where
519 drought impacts were found to be smaller and forage would still be available. Forest regeneration
520 would be hence put at stake and landscape structural dynamics could be expected to shift towards a
521 more open landscape. Such a development would counteract projected forest encroachment and
522 canopy thickening (Peringer et al. *this issue*) rendering a stable forage provision in the far future.
523

524 Our simulations showed that in extensive grazing systems it was not only the generally lower
525 stocking density, but also the resulting grassland-forest mosaic, which contributed to the robust
526 provision of forage. The observed stable AGB production in sparsely wooded pastures, and
527 increasing production in densely wooded pastures in the face of warming and drought, were in
528 sharp contrast with the decreased AGB in unwooded pastures. Consequently, the apparent
529 advantage in terms of productivity of unwooded pasture diminished with drought and wooded
530 pastures became a forage source of similar importance. In sight of the relatively large area sparsely
531 and densely wooded pastures cover in extensively stocked pastures, such formerly unproductive
532 patches showed a clear potential to compensate the breakdown of productivity within open
533 grasslands.
534

535 Given that mosaic emergence is a process over centuries (Gillet 2008, Peringer et al. *this issue*),
536 such kind of resilience of the system is a precious good, because it is rapidly destroyed but slowly
537 reestablished. Chételat et al. (*this issue*) have shown that landscape transformations of such great
538 magnitude could result, for example, from higher wood and food demands (e.g. during wartime)
539 and from natural events (storms, droughts, bark beetle outbursts). Similar conclusions about the
540 beneficial role of tree canopy on understory microclimate during drought has been found for
541 agroforestry systems (Powell and Bork 2006). Across the landscape, spatial variation itself
542 stimulates ecosystem resilience and resistance to drought. Godfree et al. (2011) show that naturally
543 occurring extreme climatic events such as drought can be mitigated through the protective role of
544 heterogeneous environments. This concept is shared by Foley et al. (2005) who advocate the
545 maintenance of a diverse portfolio of ecosystem services by a single ecosystem, such that
546 sustainable land use strategies could be implemented for both short- and long-term needs. Here we
547 show that in the case of subalpine wooded pastures this can be accomplished through the
548 preservation of the mosaic landscape. It is, nevertheless, acknowledged that decisions about the
549 future of cultural landscapes (i.e. wood-pastures) come from stakeholders rather than scientists, and
550 that such a stability requires both maintenance of historically established agricultural practices
551 (Küster 2004) and adaptive management, including change in policies (Huber et al. *this issue-b*).
552 Either courses of intensification or abandonment would place the ecosystem's stability at stake and
553 disrupt the delivery of its prime ecosystems services.
554

554

555

556 CONCLUSION

557

558 In summary, different grassland types within the pasture-woodland landscape of the Swiss Jura
559 Mountains were shown to exhibit a strictly non-uniform response to climate change in terms of
560 herbaceous forage provision. The mosaic patchiness of the landscape would be a valuable asset in
561 the face of climate warming and its inherent diversity may hold the key to sustainable land use
562 management. Presented were empirical and modelling evidence, that wood-pastures may provide
563 forage for livestock in a robust way by buffering impacts of climate change for the next decades.

564 We believe that this property of the landscape should hence be credited in order to avoid any future
565 landscape segregation and associated economic and cultural impacts.

566
567

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- 732

733 Figure 1. Grassland-forest mosaic in year 2000 of the simulated pastures as estimated by aerial
734 photograph interpretation by M. Kalbermatten (see Chételat et al. this issue): The almost treeless
735 intensively grazed pasture *Les Planets Ouest* (IWP), the moderately grazed pasture *Planets Milieu*
736 *Est* (MWP), and the extensively grazed true mosaic pasture *Les Cluds Sud* (EWP).

737 Figure 2. Regionalised observed (1950-2000 AD) and simulated (2000-2050 AD) annual (thin solid
738 lines) and vegetation growing season (thick solid lines) temperatures for the two IPCC-SRES
739 scenarios (see text): B2 (dark grey) and A1FI (light grey). The average temperature of the
740 vegetation periods from 1961 to 2010 is presented as a reference threshold (thick dashed black line).
741 The difference between simulated yearly temperatures of vegetation periods and this reference
742 threshold is implemented as a parameter ΔT driving drought stress in simulations. The average
743 temperature of the last 50 years (thin dashed line) is used to simulate the increase of productivity
744 due to the prolongation of the vegetation period.

745 Figure 3. Change of above-ground biomass (AGB) production in relation to (a) soil moisture, and
746 (b) soil temperature in unwooded pastures (circles), sparsely wooded pastures (squares) and densely
747 wooded pastures (triangles). Altitudes of experimental plots are 570 m a.s.l. (black symbols), 1010
748 m a.s.l. (grey symbols) and 1350 m a.s.l. (empty symbols).

749 Figures 4. Global utilization rates (GUR) of produced forage for the three pastures and the two
750 IPCC-SRES climate change scenarios: (a) B2 and (b) A1FI. Pastures are *Les Cluds Sud* - EWP
751 (light grey curve), *Les Planets Milieu Est* – MWP (dark grey curve) and *Les Planets Ouest* IWP
752 (black curve).

753 Figure 5. Output maps of forage production and local utilization rate (percentage consumed forage)
754 in two arbitrarily chosen years – a hot one (2021) and a cool one (2022), based the moderate climate
755 change scenario B2 with contrasting average temperatures in the vegetation period ($\Delta 1.5$ K).
756 Darker tones indicate higher values of the respective parameters.

757
758

759 Table 1. Vegetation types of the herb layer and simulated environmental factors under which they
760 emerge, as well as their pastoral value, from which a first estimate of biomass production is
761 calculated.

762 Table 2. Microclimate data overview for the plant growing season (AMJJAS) of 2010. Presented
763 are mean parameter values for each altitude and pasture type.

764 Table 3. Simulated impact of drought on global utilization rates (GUR) in the three studied wood-
765 pastures. An arbitrarily comparison of a hot year (2021, growing season mean air temperature 11.3
766 °C) to a normal year (2022, growing season mean air temperature 9.6 °C) under the B2 IPCC-SRES
767 scenario. Long-term (1961-2010) average of the growing season temperature is 9.0°C.

768

769 Table 1

	<u>Dunging intensity</u>	<u>Dunging intensity</u>	<u>Tree cover</u>	<u>Pastoral value PV¹</u>
Eutrophic pasture	High	High	Low	40
Oligotrophic pasture	High	Low	Low	20
Fallow	Low	Low	Low	10
Understory	Low	Low	High	40

¹ The pastoral value is based on vegetation surveys (Gillet & Gallandat 1996, Gillet 2002, 2008), except for understory. Here PV is artificially set to the value of eutrophic pasture, because the lower productivity of understory is expressed by a combined influence of drought and tree cover (see text).

770

771 Table 2

Altitude [m a.s.l.]	1350			1010			570	
Air temperature [°C]	10.0			12.3			15.0	
Air humidity [%]	67.3			77.1			71.0	
Precipitation [mm]	707.6			599.7			520	
Pasture type ¹	<u>P</u>	<u>WP</u>	<u>F</u>	<u>P</u>	<u>WP</u>	<u>F</u>	<u>P</u>	<u>W</u>
Soil temperature [°C] ²	11.2 ± 0.2	10.4 ± 0.1	9.7 ± 0.1	14.8 ± 0.1	13.3 ± 0.1	12.4 ± 0.1	17.5 ± 0.2	16.2
Soil moisture [%] ³	42.9 ± 2.8	41.3 ± 2.3	33.0 ± 2.7	28.9 ± 1.1	31.8 ± 3.6	31.8 ± 0.5	25.6 ± 0.5	25.7

¹ Pasture type codes, where P refers to unwooded pasture with 0% canopy shading, WP – sparsely wooded pasture with 40% and F – densely wooded pasture with 80% canopy shading.

^{2,3} Reported values for soil temperature and moisture are means and standard errors for five replicate plots.

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773 Table 3

	<u>GUR of EWP (Les Cluds Sud) [%]</u>	<u>GUR of MWP (Les Planets Milieu Est) [%]</u>	<u>GUR of IWP (Les Planets Ouest) [%]</u>
Simulation year 2021	74.4	89.1	110.1
Simulation year 2022	67.8	78.7	97.6
Δ GUR between years 2021 and 2022	6.7	10.4	12.5
Average GUR in the period 1980-2000	70.0	83.8	104.4
Δ GUR between years 2021 and 2022 corrected ¹ for average GUR	9.5	12.4	11.9

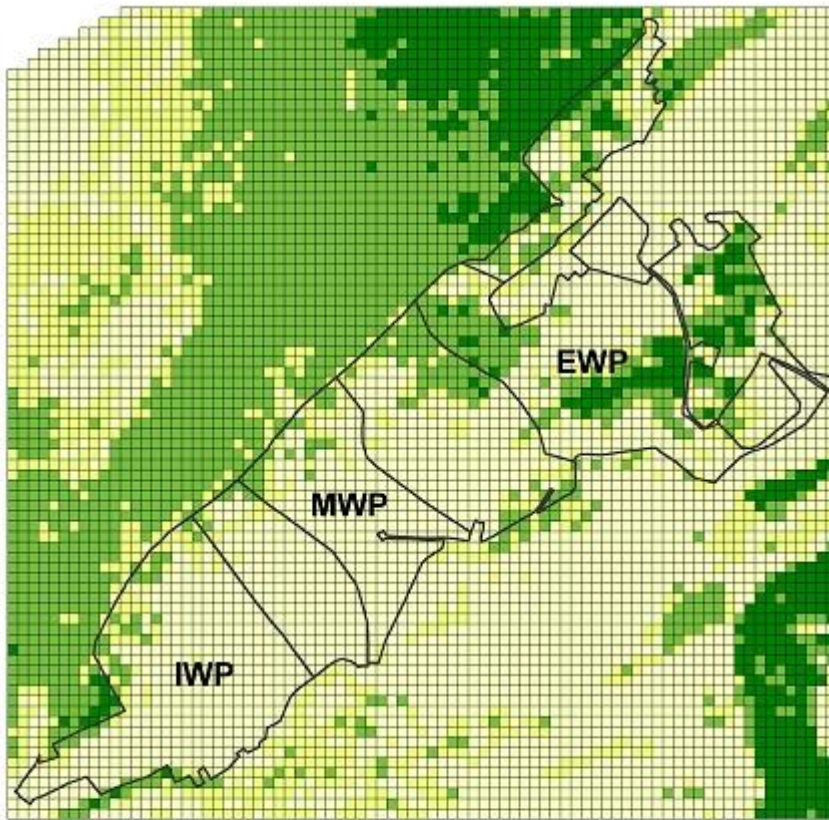
¹ Dividing the simulated GUR by the average GUR corrects for the trivial effect of lower drought impacts in extensive pastures.

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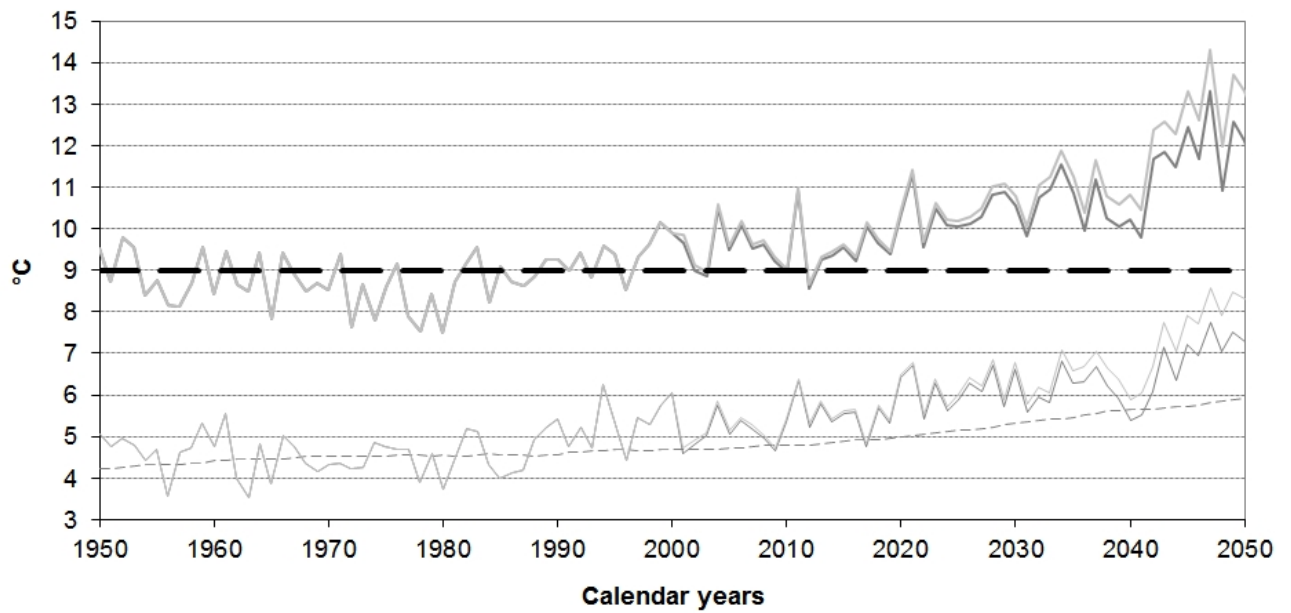
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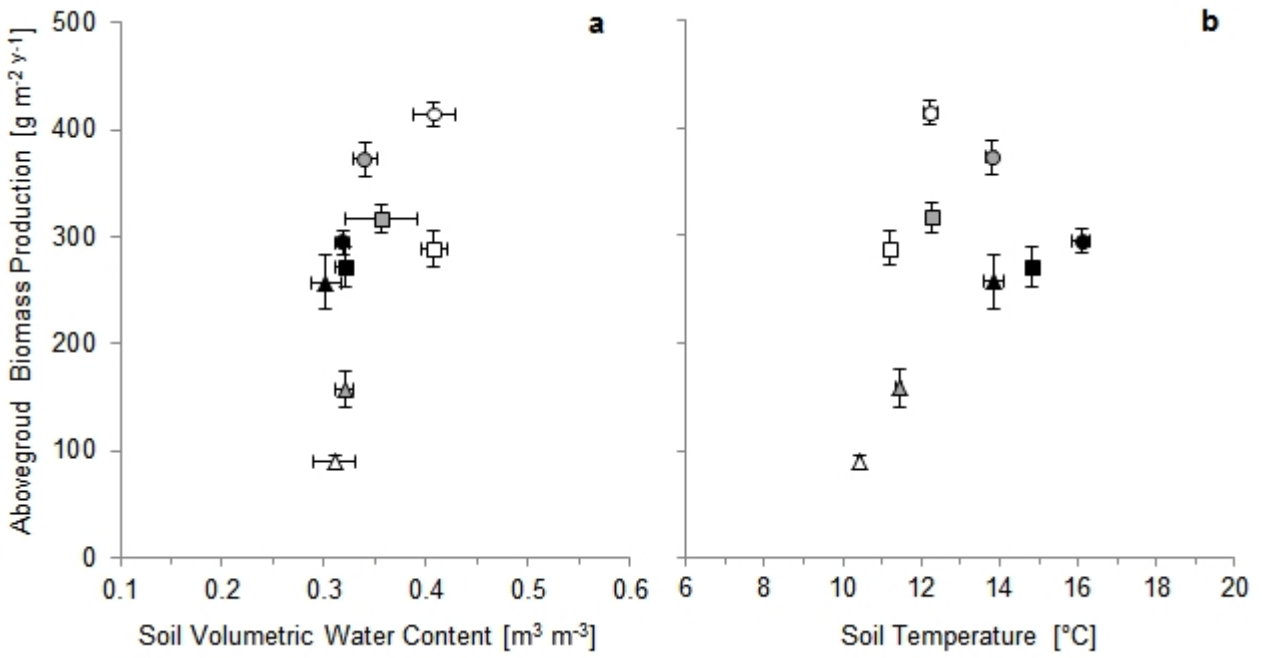
777 Figure 1



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779 Figure 2

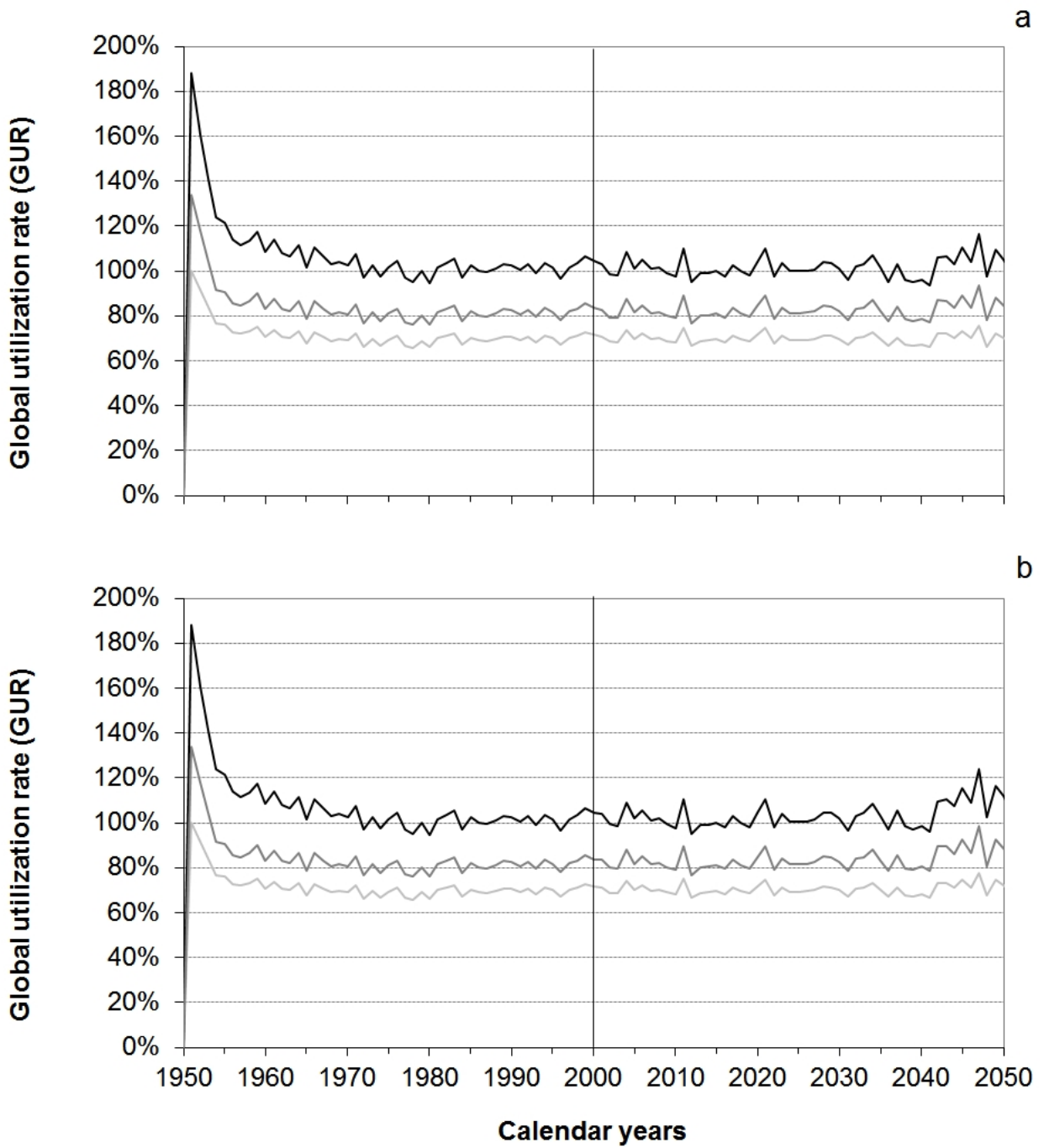


781 Figure 3



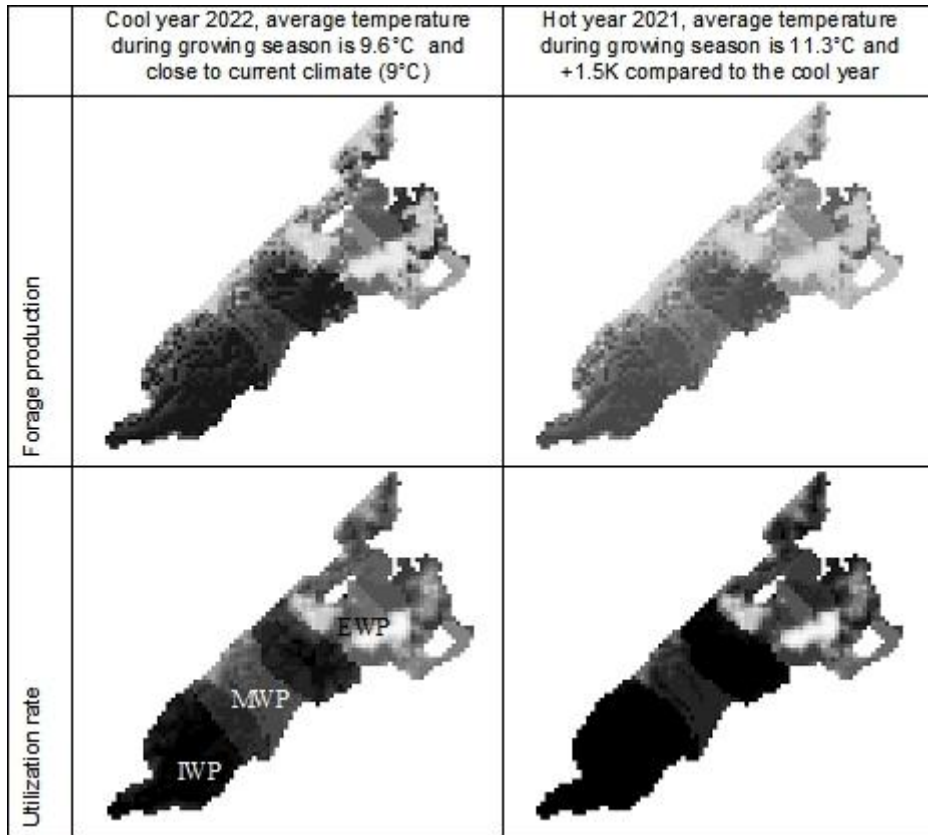
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785 Figure 4



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789 Figure 5
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