

1 **Calibrating and testing FVS to simulate tree encroachment and control measures for heathland**
2 **restoration in southern Europe**

3

4 **Abstract**

5 We used the Forest Vegetation Simulator (FVS) to simulate tree encroachment and tree control measures in a
6 continental heathland in Southern Europe, where the goal is the conservation of *Calluna vulgaris* (L.) Hull.

7 We selected as management target a maximum basal area of $4.6 \text{ m}^2 \text{ ha}^{-1}$, corresponding to a minimum

8 *Calluna* cover of 25%, and modeled stand dynamics along a 50-year period under 3 management scenarios:

9 1) no management, 2) low-frequency prescribed burning, and 3) low-frequency prescribed burning followed

10 by annual grazing. We initialized and calibrated the Northeastern variant of FVS with data measured in the

11 field, and the Fire and Fuel Extension (FFE) with additional data from a prescribed burning experiment. We

12 carried out most of the calibration by multipliers, including a novel way to simulate the impact of grazing on

13 shoot height and survival. In order to simulate fire behavior, we designed a custom fire behavior fuel model

14 for heath fuels. Successful validation of simulated stand-scale attributes and post-fire mortality was carried

15 out using equivalence testing. Model projections showed that stand basal area would exceed the target

16 threshold under both the no-management and the prescribed burning scenario, 5 and 10 years into the

17 simulation respectively. Conversely, prescribed burning followed by yearly grazing successfully controlled

18 encroaching trees throughout the simulation, by keeping their basal area below the threshold associated to

19 the maintenance of the heathland cultural landscape.

20

21 **Keywords**

22 *Calluna vulgaris* (L.) Hull, Fire and Fuel Extension, Forest Vegetation Simulator, grazing, prescribed

23 burning

24

25

26

27 **Introduction**

28 Changes in the historical management of agricultural and pastoral areas impact biodiversity in several European
29 habitats (McDonald et al. 2000, Sitzia et al. 2010). Heathlands dominated by *Calluna vulgaris* (L.) Hull are
30 protected under the EU Habitat Directive (HD 92/43/ECC) (European Council 1992), and are being targeted
31 by efforts for the restoration of traditional management (Hobbs and Gimingham 1987, Davies et al. 2008).

32 In Southern Europe, changes in grazing management and pastoral fire use are among the main threats to
33 heathlands (Bartolomé et al. 2005, Ascoli and Bovio 2010, Cazau et al. 2011). After the introduction of
34 pastoral fire bans, shepherds have been burning surreptitiously in high fire danger seasons (Moreira et al.
35 2011). The resulting increase in burn size, frequency and severity has the potential to cause heathland losses
36 (Borghesio 2009, Lonati et al. 2009). The encroachment of pioneer tree species after fire accelerates
37 heathland loss (Ascoli and Bovio 2010), and may be facilitated in Southern Europe by the reduced *Calluna*
38 competitiveness (Gimingham 1972), the absence of a thick acidic organic layer which inhibits tree
39 establishment in other biogeographic areas (Rode 1999), a high tree resilience to fire (Ascoli and Bovio
40 2010) and heathland fragmentation (Bartolomé et al. 2005).

41 In order to maintain heathlands, a prescribed burning return interval of 10-20 years has been recommended
42 (Davies et al. 2008, Fernandes and Loureiro 2010). The objective is to regenerate *Calluna* before it reaches the
43 degenerate phase (*sensu* Watt 1955), to induce tree mortality (Borghesio 2009), and to produce a mosaic of
44 habitats that may support wildlife (Hobbs and Gimingham 1987, Davies et al. 2008). However, prescribed
45 burning alone seems to be insufficient to stop tree encroachment in southern heathlands, and additional tree
46 control measures such as domestic grazing have been recommended (Borghesio 2009, Cazau et al. 2011,
47 Ascoli et al. 2013).

48 The conservation of EU Habitats (HD 92/43/EEC) requires the assessment of alternative management options,
49 and the choice of performance indicators to monitor their long-term effects (Ferranti et al. 2010). However, the
50 potential for conservation experiments to inform heathland management is limited by the temporal constraints
51 of long-term monitoring. Simulation modeling has been widely used to address fire management for

52 biodiversity conservation (Driscoll et al. 2010), and could be helpful to provide insights on alternative
53 management options for heathland conservation at large spatial and temporal scales.

54 The Forest Vegetation Simulator (FVS) can model stand development following alternative silvicultural
55 treatments, including prescribed burning (Reinhardt and Crookston 2003 and subsequent updates). By relating
56 stand structural attributes to indices of habitat suitability (Crookston and Dixon 2005), FVS users may simulate
57 such indices through time and in response to alternative management scenarios (e.g., Fulé et al. 2004,
58 Vospernik et al. 2007, Zielinski et al. 2010). However, FVS has been rarely used to forecast tree encroachment
59 and its consequences on non-forested habitats, particularly in Europe (Crookston and Dixon 2005). Moreover,
60 the use of FVS out of its recommended range of application requires calibrating and validating all model
61 components (Sterba and Monserud 1997).

62 The goal of this study is to calibrate and use FVS to simulate the impacts of alternative tree control measures to
63 restore southern European heathlands invaded by early-seral tree species. We calibrated FVS for the species of
64 interest, modeled stand development using FVS, and fire effects using the Fire and Fuel Extension (FFE) under
65 the following scenarios: (1) no management, (2) low-frequency prescribed fire, (3) low-frequency prescribed
66 burning followed by yearly grazing as an additional tree control measure. We were able to assess heathland
67 habitat quality by computing a stand density threshold related to target *Calluna* cover, and monitoring the
68 simulated changes of stand density through time under each simulation scenario.

69

70 **Methods**

71 *Study site*

72 The study area is the Vauda Natural Reserve, established in 1993 to protect a continental heathland habitat
73 located on a fluvial terrace at the foot of the southern European Alps in Northwest Italy (45° 13' 13'' N,
74 7°41'17'' E) (Figure 1). The area is topographically homogenous (elevation: 240-480 m a.s.l., slope < 5°), and
75 is characterized by ancient and leached soils with low pH (4.8) and a thin organic layer (Borghesio 2009).
76 Mean annual temperature is 11.8°C, with monthly means ranging from 1.4°C in January to 22.1°C in July.
77 Annual precipitation is 1130 mm. Winter is the driest season, with 190 mm of rain from December to March
78 (Lonati et al. 2009).

79 Despite conservation policies, the heathland is rapidly converting to woodland (Regione Piemonte 2004).
80 Aspen (*Populus tremula* L.) and birch (*Betula pendula* Roth) are the primary encroaching tree species.
81 Mature birch and aspen stands are interspersed with late-seral species such as of oak (*Quercus robur* L.,
82 *Quercus petraea* L.) and hornbeam (*Carpinus betulus* L.) (Regione Piemonte 2004; Borghesio 2009).

83

84 *Initialization dataset*

85 We set up a long-term experiment in year 2005 to test the response of heathland to prescribed burning,
86 cutting and grazing (Ascoli et al. 2009). Experimental units 600 to 1250 m² in size were established in areas
87 where time since last fire was 8-10 years, as assessed from fire perimeters for the years 1994-2005 (data source:
88 Regione Piemonte) (Figure 1). We treated units according to 8 different combinations of prescribed burning,
89 cutting and grazing, plus an unmanaged control (Ascoli et al. 2009). Each treatment was replicated 4 times
90 and monitored for 5 years (Lonati et al. 2009; Ascoli et al. 2013).

91 We carried out prescribed burning in early winter 2005. Individual burns ranged between 1250 and 4000 m².
92 During burning operations, mean (\pm SE) air temperature, moisture and wind speed were 8°C (\pm 3), 47% (\pm 6) and
93 5.8 km h⁻¹ (\pm 0.4), respectively. Dead fine fuels moisture on a dry weight basis ranged from 10 to 30%. The
94 ignition technique was linear (strips of 25-50 m) and with the wind, as recommended for Atlantic heathlands
95 (Davies et al. 2008, Fernandes and Loureiro 2010). For each burn, we collected observations of rate of spread
96 (ROS) (N =94, excluding back-fire phases) and fuel samples before and after fire to estimate fuel consumption
97 Details of the sampling design and field protocols are in Ascoli et al. (2009), and short-term results in Lonati
98 et al. (2009) and Ascoli et al. (2013).

99 The post-fire grazing treatment was carried out by a herd of about 100 goats, stationed on experimental units
100 for 3.5 h day⁻¹ over a period of 4 weeks each year (between April and May), corresponding to a stocking
101 density of 20 Livestock Units (LU) ha⁻¹ day⁻¹ and a stocking rate of 135 LU ha⁻¹ (Lonati et al. 2009).

102 In each unit, we recorded the following variables before and after treatment, yearly until 2009: (1) *Calluna*
103 percent cover was assessed using the Vertical Point Quadrat (VPQ) method (Wilson 1963) along fixed line
104 transects (length =10 m; 2-4 transects per unit); (2) stand structure and composition were assessed on 2x10 m
105 plots superimposed on VPQ transects, by recording species, vitality (live or dead), presence of grazing
106 damage, diameter at breast height (DBH), height (HT), crown base height and crown radius of all trees with a

107 height ≥ 1.3 m, and species, vitality, grazing damage, height, and crown base height (h_c) of all trees < 1.3 m. We
108 measured or computed the following plot-scale variables for each unit and year: tree density (TPHa), basal area
109 (BA), age (A) of sprouts as the time since last fire, percent tree canopy cover, percent tree mortality (p_{mort})
110 following prescribed fire (for 1-cm wide DBH classes), trees per hectare (TPHa_{killed}) and basal area (BA_{killed})
111 killed by fire, and median height (HT₅₀) of grazed, ungrazed, and all sprouts.
112 Among the 36 experimental units, we selected those (N = 11) with the highest basal area (BA) in the last year
113 of monitoring, i.e., those experiencing ongoing tree encroachment, as initialization data for FVS. Tree and plot
114 data were converted to imperial units and entered into FVS treelist and stand list files by using the Database
115 extension (Crookston et al. 2003). Trees shorter than 1.3 m were added by using the NATURAL keyword
116 (from the Partial Establishment Model, Ferguson and Crookston 1991) for each species and plot. NATURAL
117 parameters were: seedling density and average height from initialization plot data; seedling survival = 100%;
118 shade code = 0 (seedlings occurring uniformly on plots). Initial plot age was set to 5 years.

119

120 *Habitat suitability metric and simulation design*

121 Previous research on vegetation classification in the study area (Regione Piemonte 2004) identified a minimum
122 *Calluna* cover of 25% in order to classify the vegetation as a heathland. *Calluna* cover is significantly affected
123 by tree density (Borghesio 2009, Ascoli and Bovio 2010). In order to assess heathland habitat suitability, we
124 fitted a linear regression model between pre-treatment BA and *Calluna* cover in all experimental units (N = 36),
125 and computed the maximum allowable BA to maintain a *Calluna* cover equal or greater than 25%.
126 Subsequently, we designed the following FVS simulation scenarios to test the effectiveness of alternative
127 management options in maintaining BA lower than the target value: (1) no management (2) prescribed burning
128 in winter every 15 years (3) prescribed burning in winter every 15 years followed by grazing every year in
129 spring. Initialization plots were run as individual stands in FVS without any management schedule. The
130 simulation period was 50 years, i.e. the timespan covered by at least 3 management series, with cycle length = 5
131 years (set by TIMEINT keyword). We did not simulate regeneration by seed in any scenario, since the main
132 regeneration strategy observed after initial encroachment is stump and root sprouting (Ascoli and Bovio 2010;
133 Ascoli et al. 2013).

134

135 *Calibration dataset*

136 Instead of programming new submodels, we parameterized one of the existing geographic variants of FVS,
137 assuming that model form could be left unchanged. We chose the Northeastern variant (FVS-NE) (Dixon and
138 Keyser 2008), because it includes both quaking aspen (*Populus tremuloides* Michx) and grey birch (*Betula*
139 *populifolia* Marshall), i.e., two vicariant species of those under study (Catling and Spicer 1988, Chantal et al.
140 2005, Suvanto and Latva-Karjanmaa 2005, Schenk et al. 2008).

141 In order to build a calibration dataset, we randomly established 32 plots (Basal Area Factor =1 m² ha⁻¹) in areas
142 where time since last fire was >15 years (Figure 1). Within each plot, we recorded species and DBH of all trees.
143 Additionally, we measured height, live crown height, average crown radius and extracted an increment core at
144 1.3 m height from 3 individuals per species and DBH class (0-15; 16-30; 31-45 cm), amounting to a maximum
145 of 18 intensively sampled trees per plot, augmented by 15 open-grown trees per species, located outside of the
146 plot network. In the lab, we computed tree- and stand-scale variables needed to calibrate FVS-NE submodels
147 (Dixon and Keyser 2008), i.e., crown width, percent crown ratio (CR), quadratic mean diameter (QMD), tree
148 density, stand density index (SDI), and basal area of trees one 5 cm diameter class below the subject tree and
149 larger (BAL). We prepared tree cores following standard dendrochronology procedures (Stokes and Smiley
150 1968), measured ring width to the nearest 0.01 mm, and computed mean annual basal area growth (ABAG) for
151 the last 5 years. For each core, we computed total tree age (A) by adding up rings counted at breast height, the
152 number of missing rings at the pith of each core (which we estimated by means of a pith locator), and a species-
153 specific average time to reach 1.3 m height, which we computed for both birch and aspen by fitting a linear
154 height-age model on data from the 11 initialization plots (Equation 1):

155

156 [1] $A = a_1 HT$,

157

158 where a_1 is a species-specific coefficient fitted by ordinary least-squares regression.

159

160 *Calibration of FVS submodels*

161 Most submodels were calibrated by keywords, except for the following, which were left to default FVS-NE
162 behavior, using aspen and grey birch as surrogate species: (1) bark ratio coefficients, which can not be

163 calibrated by keywords in FVS; (2) height dubbing, since FVS is able to perform self-calibration of the height-
164 diameter submodel, and all initialization plots had 3 or more measured heights per species; (3) height growth,
165 which could not be calibrated using one-time measurements, hence FVS-NE default equations and parameters
166 (Dixon and Keyser 2008) were left unchanged; (4) small tree diameter growth, which is driven by height
167 growth, and could not be calibrated as well. All statistical analyses were carried out at a significance of $p \leq 0.05$
168 using IBM SPSS 19 software (SPSS Inc., Chicago). All equations use metric units.

169 Under the assumption that all plots were growing in similar site conditions, we set aspen as the site species, and
170 fitted an available site index curve (Equation 2: Carmean et al. 1989) on height-age measurements in dominant
171 and codominant aspen trees (i.e., DBH rank <5) of the calibration dataset:

172

$$173 \quad [2] \quad HT = b_1 SI^{b_2} \left(1 - e^{-b_3 A}\right)^{b_4 SI^{b_5}},$$

174

175 where HT is tree height, SI is species site index at age 50 fitted by nonlinear regression, and b_1 - b_6 are aspen
176 coefficients from Carmean et al. (1989). Site index for birch was handled by FVS-NE default site index
177 conversions, using grey birch as a surrogate species.

178 We used the CRNMULT keyword to calibrate the equation used by FVS-NE to predict missing crown ratios
179 for both aspen and birch (Equation 3, Holdaway 1986):

180

$$181 \quad [3] \quad CR = CRNMULT * 10c_1 \left[1 + c_2 BA + c_3 \left(1 - e^{-c_4 DBH}\right)\right]^{-1},$$

182

183 where c_1 - c_4 are default FVS-NE coefficients for grey birch and aspen. Equation 2 was solved for CRNMULT
184 by nonlinear regression.

185 We used the CWEQN keyword to fit a new crown width model for missing crown width of aspen and birch
186 forest-grown trees (Equation 4):

187

$$188 \quad [4] \quad FCW = 1 + d_1 DBH^{d_2},$$

189

190 where FCW is observed crown width of forest grown trees, and d_1 - d_2 are species-specific coefficients computed
191 by nonlinear regression.

192 We used the READCORD keyword to calibrate the large tree (DBH >12.7 cm) diameter growth submodel
193 (Equation 5, Teck and Hilt 1991). This multiplier is designed to correct any consistent bias in the performance
194 of component models when FVS is applied to a specific set of stands, such as when extending the effective
195 range of the model (Hamilton 1994).

196

197 [5]
$$ABAG = READCORD * e^{-\beta_3 BAL} \beta_1 SI \left(1 - e^{-\beta_2 DBH}\right)^{0.7},$$

198

199 where β_1 - β_3 are default FVS-NE coefficients for grey birch and aspen. Equation 4 was solved for READCORD
200 by nonlinear regression.

201 We used the SDIMAX keyword to replace default maximum SDI for aspen and grey birch with maximum SDI
202 measured in monospecific stands (i.e., >75% basal area by either species). We used the MORTMSB across all
203 QMDs in order to force FVS mortality predictions to follow a calibrated self-thinning slope. The slope was
204 fitted by ordinary least-square regression of $\ln(TPHa) - \ln(QMD)$ pairs (Equation 6) in the calibration dataset,
205 after elimination of outliers (i.e., plots with TPHa <400):

206

207 [6]
$$\ln TPHa = a - b \ln QMD,$$

208

209 where a and b are the intercept and slope of the self-thinning line. The SDIMAX and MortMSB keywords help
210 identify the number of trees to kill; equations that distribute mortality to the individual trees were left
211 unchanged.

212

213 *Model validation*

214 Model predictions of QMD, TPHa and BA under the no management scenario were subset at a simulation time
215 of 15, 25 and 35 years, and validated against QMD, TPHa and BA observed in calibration plots by multiple two
216 one-sided (TOST) equivalence tests (Robinson and Froese 2004), as recommended by FVS validation

217 guidelines (Cawrse et al. 2009). The amplitude of the equivalence intervals was set to $\pm 20\%$, corresponding to
218 an intermediate choice between a strict and liberal test (Welleck 2003). We log-transformed all data in order to
219 normalize the error distributions. Subsequently, we grouped both the subset of simulated stands and the
220 observed in three QMD classes (<7.5 , $7.5-12$ and >12.5 cm), and carried out a TOST equivalence test ($p \leq 0.05$)
221 for each QMD class and variable, for a total of 9 tests. If the equivalence interval for each variable was within
222 the two one-sided confidence intervals, we could reject the null hypothesis of dissimilarity between the
223 simulated and observed populations.

224

225 *Simulation of prescribed burning*

226 In order to simulate fire behavior and effects by FFE, the following is needed: (a) input a fire behavior fuel
227 model; (b) parameterize fire weather and fuel moisture; (c) simulate fire occurrence; and (d) calibrate the
228 sprouting submodel.

229

230 (a) Fire behavior fuel model selection: we designed a custom fuel model (heath-FM) for fuel beds
231 constituted by the live crown of *Calluna* and cured herbs (Ascoli and Bovio 2010), following the
232 method by Burgan (1987). Custom fuel models have proven to improve Rothermel's (1972) fire spread
233 prediction in Atlantic heaths (Davies et al. 2006). Although *Calluna* fuels are live, they are particularly
234 flammable due to the low moisture content of the leaves (45-75%) during the dormant season in winter
235 (Davies et al. 2010). In addition, surface area-to-volume ratio (SAV) and high heat content exceed
236 ranges provided by the standard fuel models used by FFE (Scott and Burgan 2005). The heath-FM was
237 conceived as static, since prescribed fire was simulated only in winter, when herbs are fully cured.
238 SAV and high heat content for *Calluna* and herbs were set after Gillon et al. (1997) and Davies et al.
239 (2006). Fuel load and depth were measured in experimental units before prescribed burning (Ascoli et
240 al. 2009). Median fuel loads for cured herbs and *Calluna* were entered in the heath-FM as 1h and live
241 woody fuel, respectively. As Rothermel's model (1972) was found to underpredict rate of spread
242 (ROS) in *Calluna* fuels (Davies et al. 2006), and knowing that small reductions of bulk density can
243 increase simulated ROS (Burgan 1987), we used the 95th percentile of the observed fuel bed depth in
244 order to reduce bulk density estimates. The heath-FM was entered using the DEFULMOD keyword.

245 Fuel dynamics were not simulated by using default FFE fuel accumulation routines. The fuelbed
246 driving fire behavior in our study site is a mixed grass and shrub layer, while FFE routines simulate
247 accumulation of mainly litter and dead woody fuels (Reinhardt and Crookston 2003). In addition, FFE
248 assigns to live herbs and shrubs a constant loading (0.77 t ha^{-1} each: Chojnacky et. al. 2004), which
249 underestimates that of the study site. Therefore, additional DEFULMOD keywords were invoked by
250 setting Event Monitor conditions to let fuel models change with increasing stand basal area and
251 decreasing *Calluna* cover. The standard fuel model TU3 (Scott and Burgan 2005) was invoked in
252 advanced tree encroachment stages, where hardwood litter and herbs represent the main fuel bed. TU3
253 was partially customized by setting live woody fuel load to zero (i.e., *Calluna* is mostly absent), and
254 shifting the fuel load of live herbs to 1h fuels (i.e., a static model with fully cured herbs). The transition
255 between fuel models was smoothed by using the weighting function of the FUELMODL keyword. The
256 weights assigned to TU3 were 0, 0.75 and 1 at thresholds of BA associated to a *Calluna* cover of
257 $>25\%$, $1-25\%$ and $<1\%$ respectively.

258 (b) Fire weather and fuel moisture: we preliminarily set “moist” conditions for dead fine fuels (i.e., 12%
259 moisture of 1h fuels), and 45% moisture for woody fuels (values from field observations), by using
260 the MOISTURE keyword. In order to compute wind speed at 7.14 m (20 ft), as needed by
261 FIRECALC, we divided the average midflame wind speed observed in prescribed burn experiments
262 by the correction factor associated to pre-fire mean canopy cover of the 11 initialization plots (after
263 Reinhardt and Crookston 2003), so as to mimic average burning conditions.

264 (c) Fire occurrence: we simulated a prescribed fire every 15 years by invoking the FIRECALC keyword.
265 The first fire was set to occur 5 years after model initialization. Prescribed burning was simulated as
266 headfire, i.e., the ignition technique recommended for heathland conservation (Davies et al. 2006,
267 Fernandes and Loureiro 2010).

268 (d) Calibration of post-fire sprouting: FVS-NE logic assumes that the number of sprouts following a
269 disturbance is a function of $\text{TPHa}_{\text{killed}}$ in birch, and $\text{BA}_{\text{killed}}$ in aspen. We computed a calibration
270 factor for post-fire sprout density in birch (Equation 7) and aspen (Equation 8, rewritten in metric
271 units after Crouch 1981), using data from repeated measurements in experimental units treated by
272 prescribed burning ($N=12$). Since preliminary fitting of Equation 8 led to an overestimation of aspen

273 sprout density at higher pre-fire BA, we mitigated the aspen calibration factor (m_{aspen}) by a negative
274 exponential function of BA_{killed} (Equation 9):

275

276 [7] $TPHa_{\text{birch}} = 2TPHa_{\text{killed}}m_1$,

277 [8] $TPHa_{\text{aspen}} = \mu_1(\mu_2 + \mu_3A^2 + \mu_4A^3 + \mu_5A^5 + \mu_6A^7) \frac{0.404}{198} BA_{\text{killed}} m_{\text{aspen}}$,

278 [9] $m_{\text{aspen}} = m_2 e^{-m_3 BA_{\text{killed}}}$,

279

280 where μ_1 - μ_6 are model parameters after Crouch (1981), and m_1 - m_3 are species-specific calibration
281 factors fitted by nonlinear regression.

282 For both birch and aspen, we computed a calibration factor for post-fire sprout height as the ratio
283 between default FVS-NE sprout height and observed average height of sprouts in the first growing
284 season after prescribed fire. Both the density and the height calibration factors were used as multipliers
285 to parameterize a species-specific SPROUT keyword.

286

287 *Verification of prescribed burning simulations*

288 We verified simulated fire behavior and effects by (a) comparing predicted and observed flame length, and (b)
289 comparing predicted and observed mortality for each burn and DBH class.

290 Since flame length is difficult to measure accurately in the field, we first computed Byram's fireline intensity
291 using (i) heat of combustion from heath-FM, (ii) ROS observations for headfire phases (N=94), and (iii) fuel
292 consumption measured in each prescribed burning experiment, then used fireline intensity to compute flame
293 length in each burn according to Albini (1976). Observed flame length was compared to that simulated by
294 FFE (all stands and fires under heath-FM) by a t-test ($p \leq 0.05$).

295 In order to compare predicted and observed post-fire mortality, we first computed mortality probabilities
296 (p_{mort}) simulated by FVS (Equation 10, rewritten in metric units after Reinhardt and Crookston 2003):

297

298 [10]
$$P_{mort} = \frac{1}{1 + e^{\left[p_1 + p_2 \left(1 - e^{\frac{-vD}{2.54}} \right) + p_3 c^2 \right]}}$$

299

300 where D is the midpoint of 1-cm wide DBH classes, v is the default FFE species-specific bark
 301 thickness:DBH ratio, p_1 - p_3 are default FFE parameters (Reinhardt and Crookston 2003), and c is percent
 302 scorched crown volume, which we computed for each simulated fire using Equation 11 (Reinhardt and
 303 Crookston 2003):

304

305 [11]
$$c = 100(h_s - h_c) \frac{2l - (h_s - h_c)}{l^2},$$

306

307 where l is crown length, h_c is crown base height, and h_s is mean predicted crown scorch height of all FVS+FFE
 308 simulations under heath-FM. Crown length and crown base height were computed for the simulated stands at
 309 the time of each fire by entering the midpoints of 1-cm wide DBH classes in the calibrated crown ratio
 310 submodel (Equation 3) and in the uncalibrated height dubbing submodel (Wykoff et al. 1982).

311 Previous studies suggested the existence of differences in morphological traits at the base of the stem between
 312 European species and North American vicariants, especially for birch (Catling and Spicer 1988). In order to test
 313 whether the accuracy of mortality predictions (Equation 10) would increase by taking into account species-
 314 specific stem base morphology, we measured bark thickness (Bt) of 74 aspen and 60 birch trees from the
 315 calibration dataset at a height of 0.2 and 1.3 m the stem. We computed modified bark ratios (v_{20} and v_{130}) by
 316 ordinary least square regression between DBH and bark thickness at 0.2 and 1.3 m (Equation 12). To obtain the
 317 modified mortality predictions, we entered modified bark ratios in Equation 10, and reduced the resulting p_{mort}
 318 by 20%, in order to replicate how FFE behaves when simulating fire in hardwoods before greenup (i.e.,
 319 during the dormant season).

320

321 [12]
$$Bt_i = v_i DBH,$$

322

323 where i is the sampling height (i.e., 0.2 and 1.3 m), and v_i is the species- and height-specific slope of an
324 ordinary least-square regression model.

325 Observed tree mortality was measured after both prescribed burning and pastoral fires in the study area. As
326 few aspen individuals with DBH >10 cm were available in prescribed burning units, we measured tree
327 vitality (live or dead) and DBH from an additional 262 birch and 378 aspen trees in adjacent areas affected
328 by headfire in winter 2008 under comparable fuel, weather and fire behavior conditions (Ascoli and Bovio
329 2010). DBH range was 1-30 cm and 1-24 cm for birch and aspen, respectively. Finally, we assessed the
330 accuracy of mortality estimates (all fires pooled) for each 1-cm DBH class (N =24) from the three simulation
331 approaches (i.e., FVS default output and 2 mortality equations refitted with custom Bt) against observed data
332 by multiple regression-based TOST (Robinson et al. 2005). Since the models failed to exhibit a normal error
333 distribution, we used non-parametric bootstrap (N =10000) to construct confidence intervals that did not
334 depend on such assumption. The amplitude of the equivalence intervals was set to $\pm 25\%$. Bootstrapped
335 equivalence tests were carried out by using the function `equiv.boot()` of the R package `equivalence`
336 (<http://cran.r-project.org/web/packages/equivalence/index.html>, retrieved November 2012). If the equivalence
337 interval for the mortality variable was within the two one-sided confidence intervals, we could reject the null
338 hypothesis of dissimilarity between the simulated and observed populations.

339

340 *Simulation of grazing*

341 This scenario included prescribed burning every 15 years, starting 5 years into the simulation, and grazing
342 every year after the first fire. FVS-NE does not include any explicit option to simulate grazing. Therefore, the
343 impact of grazing on sprout height and survival was simulated as follows: (i) we set cycle length = 1 year by
344 the `TIMEINT` keyword; (ii) we simulated grazing-induced mortality by invoking the `FIXMORT` keyword
345 every year after the first prescribed burning. `FIXMORT` was parameterized for aspen and birch with the
346 average percent mortality and maximum affected DBH observed in experimental units treated by goat grazing
347 (N =16). We set `FIXMORT` to trigger mortality additionally to that already occurring due to self-thinning, and
348 to kill trees starting from the smallest DBH; (iii) we simulated bud damage by using the `HTGSTOP` keyword.
349 Parameters of `HTGSTOP` were: affected height ≤ 1.5 m (i.e., maximum goat grazing height according to Bailey
350 1985); probability of damage for the current stocking density (i.e., 135 LU ha⁻¹) =60% (after Mayer et al.

351 2006); mean proportion of height growth retained (HTG_{ret}) computed as the ratio of median heights of grazed to
352 ungrazed shoots in experimental units treated by grazing. We modeled HTG_{ret} as a function of stand median
353 height (Equation 13):

354

355 [13] $HTG_{ret} = h_1 + h_2 \ln H_{50}$,

356

357 where h_1 and h_2 are parameters fitted by nonlinear regression. FIXMORT and HTGSTOP were invoked each
358 year following the first winter prescribed burning. Grazing simulations were limited to 40 cycles due to internal
359 FVS constraints (maximum number of cycles reached).

360 For all calibrated submodels (Equations 1-13), we computed the following goodness-of-fit statistics: R-squared
361 (pseudo- R^2 in nonlinear regressions), root mean square error (RMSE), percent RMSE and mean absolute bias.

362

363 **Results**

364 The linear model of *Calluna* cover vs. BA (Figure 2, $p < 0.001$, $R^2 = 0.69$) suggested a maximum allowable BA
365 of $4.6 \text{ m}^2 \text{ ha}^{-1}$ for a *Calluna* cover of 25%. We selected this level as the management target against which to
366 assess simulation results.

367 In the initialization plots (Table 1), mean (\pm SE) density and BA were $4273 \pm 1069 \text{ stems ha}^{-1}$ (17409 ± 2312
368 when including trees of all heights) and $1.5 \pm 0.35 \text{ m}^2 \text{ ha}^{-1}$, respectively. BA was therefore lower than the
369 habitat suitability metric. Aspen dominated the stands, contributing 91% of total BA on average with a DBH
370 range of 0.5 to 3.6 cm (Table 2). Mean height was 1.8 m for birch, and 1.2 m for aspen. Mean *Calluna* cover
371 was $52\% \pm 4$. In the calibration dataset, tree density ranged from 301 to 15076 trees ha^{-1} , and decreased with
372 increasing QMD (i.e., 7649, 1996, and 831 trees ha^{-1} on average in the three QMD classes). BA followed a
373 less clear trend, and ranged between 1.5 and $29.0 \text{ m}^2 \text{ ha}^{-1}$. Average species composition (relative BA) was
374 46% birch, 48% aspen and 6% late successional species, but both pure birch and pure aspen stands were
375 included. Maximum recorded DBH and height were 52 cm and 22.3 m for birch, and 35.5 cm and 22 m for
376 aspen, respectively. Tree age ranged between 10 and 53 years for birch ($N = 165$) and between 11 and 51
377 years for aspen ($N = 175$).

378 Most calibrated submodels had a reasonable fit ($R^2 > 0.6$), except for site index, large tree diameter growth,
379 aspen sprouting ($R^2 < 0.6$), and crown ratio doubling ($R^2 < 0.3$) (Table 3). All parameters were significant (p
380 ≤ 0.05). Percent RMSE was always lower than 33%, except in the large tree growth (birch), bark thickness
381 (aspen) and age at breast height (aspen) submodels.
382 Mean age at breast height was 3.44 and 3.25 years for aspen and birch respectively, computed from Equation
383 1. Site index for aspen was 21.6 m; FVS-NE computed a site index for birch of 19.8 m (by model default,
384 birch grows slower than aspen). SDI maxima for monospecific stands (>75% basal area of one species) used
385 to parameterize the SDIMAX keyword were 300 and 260 for aspen (N = 20) and birch (N = 8), respectively.
386 The self-thinning slope used to parameterize MORTMSB (i.e., parameter b in Equation 6) was -1.82 across
387 all QMDs.

388

389 *No-management scenario*

390 No management simulations produced realistic stand dynamics across all 50 years of simulation time, i.e.,
391 increasing mean diameter, asymptotically increasing basal area, and decreasing stand density following the
392 initial ingrowth peak. BA exceeded the selected threshold at simulation time = 5 years (Figure 3a). Simulated
393 BA, QMD, and TPHa were successfully validated against the observations by equivalence testing (Table 4),
394 except for QMD at earlier stand development stages.

395

396 *Prescribed burning scenario*

397 BA thresholds to set the transition between the heath-FM and the customized TU3 fuel model (Table 5) were
398 based on the relationship between tree BA and *Calluna* cover (Figure 2): (i) $BA < 4.6 \text{ m}^2 \text{ ha}^{-1}$ (i.e., *Calluna*
399 cover >25%): 100% heath-FM; (ii) $BA 4.6\text{-}8.6 \text{ m}^2 \text{ ha}^{-1}$ (i.e., *Calluna* cover 1-25%): 25% heath-FM, 75% TU3;
400 (iii) $BA > 8.6 \text{ m}^2 \text{ ha}^{-1}$ (i.e., *Calluna* cover <1%): 100% TU3 fuel model. ROS and fireline intensity (mean \pm SE)
401 from the prescribed burning experiments in heath fuels were $4.39 \pm 0.25 \text{ m min}^{-1}$ and $1387 \pm 98 \text{ kW m}^{-1}$,
402 respectively. Calculated flame length was $2.00 \pm 0.07 \text{ m}$.

403 Mean canopy cover in the pre-treatment initialization dataset was 18%, producing a wind speed scale factor
404 of 0.3 (after Reinhardt and Crookston 2003) and thus a wind speed at 7.14 m (20 ft) of 32 km h^{-1} (12 mph).

405 Flame length simulated using heath-FM alone was $1.90 \pm 0.10 \text{ m}$ (N = 11), which was not statistically different

406 from flame length in experimental prescribed burning under heath fuels (two-sample t-test: $p=0.202$). Flame
407 length simulated under the 25% heath-FM and 75% TU3 fuel model was 1.90 ± 0.05 m ($N=5$), while flame
408 length under the TU3 fuel model was 1.7 ± 0.02 m ($N=17$).

409 Bark thickness at 1.3 m was higher than the FVS-NE default for both birch and aspen (i.e., $v_{130}=0.033$ and
410 0.044 , respectively), and further increased at 0.2 m (Table 2). Mean simulated scorch height (h_c) entered in
411 Equation 11 was 8.2 m. For both birch and aspen, the FVS-NE default model overpredicted tree mortality
412 (mean bias =21.1% and 11.0%, respectively). The agreement between predicted and observed mortality
413 increased in models with custom bark ratios, and was higher when the 0.2 m bark ratio was used. Tree
414 mortality estimates were more accurate for aspen under all simulation approaches (Table 6).

415 Following calibration, the sprouting submodel (i.e., density multipliers m_1 - m_3 set as in Table 3, height
416 multiplier for both aspen and birch set to 1.25), produced a persistent but reduced sprouting density following
417 fire, and consequent effects on QMD and BA. However, BA still exceeded the selected management threshold
418 (thick line in Figure 3b), even if 10 years later than in the no management scenario.

419

420 *Prescribed burning and grazing scenario*

421 Average yearly mortality rate in experimental units treated by prescribed burning and grazing was 15% for
422 aspen and 22% for birch. Maximum affected DBH was 2 cm for aspen and 3 cm for birch. 40-year simulations
423 (Figure 3c) produced post-fire pulses of vegetative regeneration that were later killed, or sustained reduced
424 height (and diameter) growth, due to the impact of grazing. Few trees escaped, but BA was maintained below
425 the habitat suitability threshold for the entire duration of the simulation.

426

427 **Discussion**

428 *FVS calibration*

429 In this research, we carried out one of the first calibrations of FVS in Europe. The modeled ecosystem is a
430 simple one, and the analysis was limited to early successional stages (i.e., 50 years of stand development) with
431 2 main forest species. The combinations of several datasets from the same study area allowed us to build a
432 calibration dataset comparable to what we wanted to simulate in terms of stand age, thus avoiding extrapolation
433 of short growth trends to an entire rotation.

434 Instead of programming a new local variant (as in Sterba and Monserud 1997), we decided to use available
435 calibration keywords, and associate the species to be modeled to vicariant species in the FVS variant of choice.
436 Hence, we left the model form of each FVS component unchanged, while rescaling submodel predictions by
437 using multipliers to better fit observed data. Crown ratio was the only submodel affected by a systematic bias
438 (i.e., overpredicted). However, root mean square errors of individual submodels were acceptable (<33%) even
439 when model fit (assessed by R^2 or pseudo- R^2) was poor (e.g., in the crown ratio submodel), and did not scale up
440 into stand-scale predictions, that were successfully validated against observations.

441 Submodels requiring more than one observation in time (e.g., large tree height growth) could not be calibrated
442 with our dataset. However, scaling of growth rates should be simulated by applying either a height increment,
443 or a basal area increment multiplier, and not both (Hamilton 1994).

444 During calibration attempts, we observed that small variations in the mortality adjustments (i.e., SDIMAX and
445 MORTMSB) could produce large changes in stand basal area and trees per hectare after a few decades. This is
446 consistent with evidences from previous calibration efforts (e.g., DeRose et al. 2008), and shows the high
447 leverage that characterizes the mortality submodel in FVS. However, a sensitivity analysis of the whole FVS
448 suite of models would be important in determining which components and variables have the greatest influence
449 on the outputs and deserve priority in calibration efforts.

450 This study also documents the first use of the Fire and Fuel Extension in Europe. Calibration of fuel
451 accumulation with FFE was not possible under a herb-shrub fuel type. However, since *Calluna* cover is directly
452 related to stand density, we were able to simulate fuel dynamics by invoking a transition in fuel models as a
453 function of basal area thresholds, similarly to western FVS variants (Reinhardt and Crookston 2003).

454 The customized fire behavior fuel model for heathland fuels provided predictions of fire behavior that were
455 verified by statistical testing against observed data, confirming the adequacy of Rothermel's (1972) model for
456 homogeneous and vertically oriented fuels, e.g. shrublands and grasslands (Cruz and Fernandes 2008).

457 The most important fire effect simulated by FFE is tree mortality. Our results showed an overestimation of
458 aspen and birch mortality using FFE default models for vicariant species. Discrepancies between the observed
459 and simulated mortality rates for each DBH class are not likely to depend on percent crown scorch. In fact,
460 scorch height (and scorch volume) in FVS directly relates to flame length (van Wagner 1973), which was
461 simulated in a credible way. Rather, results showed the importance of bark thickness ratio for predicting

462 mortality in the simulated species. Bark ratios measured at 130 cm were higher than default values provided by
463 FFE by 2% for birch and 48% for aspen. At 20 cm height, the difference was remarkably higher (i.e., 150% and
464 161% respectively). In literature, bark thickness of *Populus tremuloides* has already been shown to increase
465 closer to the stem base, e.g., by 74% according to Brown and DeByle (1987). In data observed for *Populus*
466 *tremula*, bark thickness at the stem base was more than double than at breast height (102% increase).
467 Concerning birch, bark thickness:DBH ratio at the stem base was measured to be 144% higher than at breast
468 height, which is consistent with previous literature (Bhat 1982) but not likely to happen in *Betula populifolia*
469 (Catling and Spicer 1988). When mortality was computed using v_{20} , accuracy of FFE predictions significantly
470 increased. This is ecologically sound: active combustion in heath fuels occurs within the *Calluna* layer, which
471 is limited to the base of the trees. For these reasons, we think that introducing the possibility to set user-defined
472 bark thickness coefficients in FFE would improve the accuracy of FFE simulations for species characterized by
473 such resistance trait. On the other hand, the instruction to decrease mortality by 20% when fires occur before
474 greenup resulted in a better simulation of the observed mortality.

475 Finally, simulation of yearly grazing was possible by reducing cycle length to 1 year and using keywords not
476 originally intended for this disturbance. 1-year cycles were made necessary because, in FVS, all regeneration
477 becoming established within a cycle is passed to the FVS tree list at the end of the projection cycle (Dixon
478 2002). This made it impossible to modify survival and height growth of grazed regeneration before cycle end. It
479 would be desirable to improve simulation of intra-cycle disturbances by both designing specific keywords, and
480 allowing for variable timesteps in simulating event occurrence. It was not possible to validate simulations of the
481 grazing treatment, due to lack of long-term data.

482

483 *Ecology and restoration of encroached heathlands*

484 Aspen and birch are circumboreal tree genera, with wide ecological amplitude both in Europe and in North
485 America (Chantal et al. 2005, Suvanto and Latva-Karjanmaa 2005, Schenk et al. 2008). This facilitated the
486 process of localizing a FVS variant by adopting models fitted for vicariant species.

487 Regarding response to fire, the species exhibited different resistance traits when compared to North American
488 equivalents, but similar resilience characteristics, i.e., a high sprouting ability. Due to the high resilience to fire
489 of the species analyzed, under a fire return interval of 15 years, tree basal area would exceed the threshold

490 associated with loss of significant *Calluna* cover in about 10 years, starting from an initial stage of
491 encroachment. Therefore, prescribed burning alone would not be sufficient to keep tree encroachment below
492 the desired threshold, unlike what would happen in ecosystems where the encroaching species are more fire
493 sensitive (DiTomaso et al. 2006).
494 Additional tree control by periodic grazing successfully maintained habitat suitability within the desired target
495 for all the length of the simulation. To this extent, the use of FVS allowed us to quantitatively test management
496 scenarios that were previously suggested only in a descriptive way (Borghesio 2009, Ascoli et al. 2013). Stands
497 after 40 years exhibited a two-layered structure, with few dominant trees of multiple ages able to escape all
498 disturbances that had occurred, and a dense regeneration layer, maintained at a low height by repeated animal
499 grazing. This is compatible with data from both permanently grazed stands in the same site (Istituto per le
500 Piante da Legno e l'Ambiente 1996, Ascoli and Bovio 2010), and the structure of grazed woodlands burned
501 periodically in different ecosystems (Madany and West 1983, Levick et al. 2009, Garbarino et al. 2011).

502

503 **Conclusions**

504 This research used FVS to simulate tree encroachment in a habitat where the species of conservation interest
505 were not trees. Non-tree vegetation can be represented by FVS only in a limited way, e.g., by using the Canopy
506 and Shrubs Extension, which is currently available only for northern Idaho and western Montana variants
507 (Moeur 1985). As a result, FVS is of limited use for evaluating habitat requirements associated to detailed
508 predictions of non-tree vegetation. In applications that require such estimates, FVS users rely on gross
509 relationships between tree canopy cover and the amount of non-tree vegetation expected on a given habitat
510 (Crookston and Dixon 2005). In this study, FVS was used to model tree and stand growth in order to monitor a
511 habitat suitability metric of choice, i.e., *Calluna* cover as a function of stand basal area.
512 Our approach to calibration, i.e., using mostly multipliers rather than refitting models entirely, produced
513 accurate predictions, and can make more efficient use of data, thus proving a prototype for similar efforts in
514 regions outside the FVS native boundaries. Despite some limitations, the calibrated FVS-NE produced
515 statistically validated and ecologically sound predictions, and could be used to inform restoration management
516 of heathlands in the study area, for example by testing the effect of different fire return intervals, grazing
517 regimes, and acting along a gradient of increasing tree encroachment.

518

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671

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676

677 **Figure captions**

678 Figure 1. Localization and perimeter of the study area (Managed Natural Reserve “Vauda” in Northern
679 Italy), wildfire perimeters (source: Regione Piemonte), and location of sampling units (experimental and
680 calibration datasets).

681 Figure 2. Ordinary least squares regression of *Calluna* cover (%) vs. tree basal area (BA; m² ha⁻¹). N = 36.

682 Figure 3. 50-year simulation of BA, TPHa and QMD in the initialization plots under the (a) no-management,
683 (b) prescribed burning, and (c) prescribed burning and grazing scenarios (mean of 11 stands). Vertical lines
684 mark the occurrence of a prescribed fire. Horizontal line: BA management threshold. Grazing simulations were
685 limited to 40 cycles due to internal FVS constraints (maximum number of cycles reached).

686

687 **Table captions**

688 Table 1 - Mean (\pm SE) stand characteristics of the initialization and calibration datasets, grouped by QMD class,
689 All data from for trees ≥ 130 cm height. Initialization plots measured on fixed 2x10m plots, calibration plots by
690 angle count sampling (BAF =1 m² ha⁻¹).

691 Table 2 - Mean (\pm SE) and range of tree-scale variables in the initialization and calibration datasets. All data
692 from trees ≥ 130 cm height.

693 Table 3 – Calibration statistics for Equations 1-13: predicted variable, number of observations, parameter
694 estimates and associated SE and p-values, R² (pseudo-R² in case of nonlinear models), root mean square error
695 (RMSE), RMSE% and mean bias (predicted – observed).

696 Table 4 – Summary of TOST equivalence tests for the validation of QMD, BA and TPHa simulated at time
697 15, 25 and 35 against variables observed in the calibration dataset. N_{sim}, N_{obs}: number of simulated and
698 observed stands, respectively, in each QMD class. $\pm t_{\text{conf}}$, $\pm t_{\text{equiv}}$: lower and upper t values for the 95%
699 confidence intervals and 20% equivalence intervals, respectively. Values in bold indicate that the null
700 hypothesis of dissimilarity has been rejected.

701 Table 5 – Parameters of heath-FM and customized TU3 used to simulate fire behavior in heathland fuels when
702 tree encroachment is at an initial stage. 1h = dead fine fuels < 6 mm; 10h = dead fine fuels > 6 mm and < 25
703 mm; 100h = dead fine fuels > 25 mm and < 75 mm; SAV: surface area to volume ratio.

704 Table 6 – Summary of equivalence-based regression test results, fire mortality model. Model: 1= mortality
705 predicted using default bark thickness; 2= mortality predicted using custom bark thickness at 1.3 m; 3=
706 mortality predicted using custom bark thickness at 0.2 m. n: sample size. $\beta_0 \subset I_0$ and $\beta_1 \subset I_1$: proportion of
707 bootstrapped samples that fall into intervals of equivalence for the slope and of the intercept, respectively.

708 The approximate joint two one-sided 95% confidence intervals for the slope and intercept are ($C_{\beta_0}^-$, $C_{\beta_0}^+$) and
709 ($C_{\beta_1}^-$, $C_{\beta_1}^+$), respectively. The former should fall within the intercept interval of equivalence ($I_{\beta_0}^-$, $I_{\beta_0}^+$) = $I \pm$
710 25%, and the latter by the slope interval of equivalence ($I_{\beta_1}^-$, $I_{\beta_1}^+$) = 1 ± 0.25 . Values in bold indicate that the
711 null hypothesis of dissimilarity has been rejected.

712

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714

715 **Tables**
716

717 Table 1

| Dataset | QMD (cm) | N | BA (m² ha⁻¹) | TPHa | Relative BA birch | Relative BA aspen |
|----------------|-----------------|----------|---|-------------|------------------------------|------------------------------|
| Initialization | < 3 | 11 | 1.5±0.35 | 4273±1069 | 0.09±0.03 | 0.91±0.03 |
| Calibration | 3 – 7.5 | 11 | 13.3±2.01 | 7649±1154 | 0.47±0.09 | 0.47±0.09 |
| Calibration | 7.5 – 12.5 | 13 | 17.2±1.14 | 1996±159 | 0.39±0.09 | 0.54±0.09 |
| Calibration | > 12.5 | 10 | 14.3±1.74 | 831±126 | 0.55±0.12 | 0.40±0.11 |

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720 Table 2

| Attribute | Initialization | | | | Calibration | | | |
|--------------------------|----------------|------|------|---------|-------------|------|------|-----------|
| | n | Mean | SE | Range | n | Mean | SE | Range |
| <i>Birch</i> | | | | | | | | |
| DBH (cm) | 36 | 2.7 | 0.24 | 0.8-5.3 | 281 | 14.9 | 0.46 | 2.0-52.0 |
| H (m) | 49 | 1.8 | 0.17 | 0.3-4.6 | 165 | 13.6 | 0.33 | 5.3-22.3 |
| Crown ratio (%) | - | - | - | - | 165 | 54.3 | 1.21 | 13.9-85.1 |
| Crown width (m) | - | - | - | - | 165 | 3.7 | 0.14 | 0.7-9.2 |
| Age (yrs) | 49 | 3.1 | 0.33 | 1.0-5.0 | 165 | 31.2 | 0.70 | 10.0-53.0 |
| 5yr radial growth (mm) | - | - | - | - | 68 | 19.5 | 1.20 | 1.5-100.4 |
| Bark thickness 0.2m (mm) | - | - | - | - | 40 | 18.1 | 1.58 | 2.1-46.0 |
| Bark thickness 1.3m (mm) | - | - | - | - | 51 | 7.3 | 0.57 | 1.3-18.0 |
| <i>Aspen</i> | | | | | | | | |
| DBH (cm) | 347 | 1.5 | 0.04 | 0.5-3.6 | 257 | 13.8 | 0.45 | 1.5-35.5 |
| H (m) | 494 | 1.2 | 0.04 | 0.1-4.1 | 175 | 12.6 | 0.32 | 3.2-22.0 |
| Crown ratio (%) | - | - | - | - | 175 | 55.9 | 1.01 | 26.2-87.3 |
| Crown width (m) | - | - | - | - | 175 | 4.2 | 0.15 | 0.8-11.6 |
| Age (yrs) | 494 | 2.3 | 0.09 | 1.0-5.0 | 175 | 28.6 | 0.68 | 10.6-51.1 |
| 5yr radial growth (mm) | - | - | - | - | 79 | 27.2 | 1.34 | 4.3-88.3 |
| Bark thickness 0.2m (mm) | - | - | - | - | 76 | 12.3 | 0.87 | 0.4-32.0 |
| Bark thickness 1.3m (mm) | - | - | - | - | 79 | 6.8 | 0.53 | 0.2-20.0 |

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723 Table 3

| Variable [Equation] | Species | n | Parameter | Estimate | SE | R ² | RMSE | RMSE % | Mean bias |
|--------------------------------|---------|-----|------------|----------|--------|----------------|---------------------------------------|--------|--|
| Age [1] | birch | 49 | a_1 | 0.021 | 0.001 | 0.61 | 1.46 years | 12.0% | -0.32 years |
| | aspen | 494 | a_1 | 0.025 | 0.0004 | 0.68 | 1.29 years | 42.2% | -0.28 years |
| HT [2] | aspen | 32 | SI | 21.6 | 0.63 | 0.44 | 1.38 m | 8.5% | +0.01 m |
| CR [3] | birch | 165 | $CRNMULT$ | 1.294 | 0.024 | 0.27 | 13.7 % | 21.4% | +11.8% |
| | aspen | 175 | | 1.343 | 0.020 | 0.17 | 11.4 % | 16.3% | +12.1% |
| FCW [4] | birch | 165 | d_1 | 2.654 | 0.240 | 0.75 | 0.85 m | 26.8% | -0.02 m |
| | | | d_2 | 0.801 | 0.042 | | | | |
| | aspen | 175 | d_1 | 2.990 | 0.263 | 0.75 | 0.97 m | 31.8% | +0.00 m |
| | | | d_2 | 0.837 | 0.042 | | | | |
| ABAG [5] | birch | 68 | $READCORD$ | 1.015 | 0.095 | 0.21 | 0.042 m ² ha ⁻¹ | 49.0% | +0.000 m ² ha ⁻¹ |
| | aspen | 79 | | 1.031 | 0.067 | 0.59 | 0.045 m ² ha ⁻¹ | 27.9% | +0.000 m ² ha ⁻¹ |
| ln TPHa [6] | pooled | 32 | a | 11.781 | 0.274 | 0.88 | 1278.7 ha ⁻¹ | 4.0% | 0.0 ha ⁻¹ |
| | | | b | 1.828 | 0.121 | | | | |
| TPHa _{birch} [7] | birch | 12 | m_1 | 1.503 | 0.076 | 0.71 | 445.1 ha ⁻¹ | 16.2% | +128.5 ha ⁻¹ |
| TPHa _{aspen} [8,9] | aspen | 57 | m_2 | 34.700 | 3.003 | 0.40 | 10093.5 ha ⁻¹ | 26.4% | -349.5 ha ⁻¹ |
| | | | m_3 | 0.52 | 0.005 | | | | |
| Bt _i [12] | birch | 40 | v_{20} | 0.115 | 0.005 | 0.93 | 0.53 cm | 30.2% | +0.59 cm |
| | | 51 | v_{130} | 0.045 | 0.002 | 0.94 | 0.20 cm | 32.8% | -0.13 cm |
| | aspen | 76 | v_{20} | 0.085 | 0.003 | 0.93 | 0.36 cm | 44.0% | -0.25 cm |
| | | 79 | v_{130} | 0.048 | 0.002 | 0.93 | 0.21 cm | 47.0% | -0.06 cm |
| HTG _{ret} [13] | pooled | 16 | h_1 | 9.158 | 1.119 | 0.65 | 1.35 % | 1.5% | +0.12% |
| | | | h_2 | 45.458 | 0.965 | | | | |

725
726

Table 4

| QMD class (cm) | | QMD | BA | TPHa |
|----------------|---------------------|---------------------|---------------------|---------------------|
| < 7.5 | N _{obs} | 9 | 9 | 9 |
| | N _{sim} | 11 | 11 | 11 |
| | ±t _{conf} | -0.91 – 1.41 | -10.24 – 10.81 | -8.49 – 8.05 |
| | ±t _{equiv} | -1.73 – 1.73 | -1.73 – 1.73 | -1.73 – 1.73 |
| 7.5 – 12.5 | N _{obs} | 13 | 13 | 13 |
| | N _{sim} | 11 | 11 | 11 |
| | ±t _{conf} | -5.16 – 3.89 | -15.6 – 12.03 | -10.97 – 11.32 |
| | ±t _{equiv} | -1.72 – 1.72 | -1.72 – 1.72 | -1.72 – 1.72 |
| > 12.5 | N _{obs} | 8 | 8 | 8 |
| | N _{sim} | 11 | 11 | 11 |
| | ±t _{conf} | -7.08 – 8.22 | -13.71 – 12.93 | -9.23 – 9.08 |
| | ±t _{equiv} | -1.74 – 1.74 | -1.74 – 1.74 | -1.74 – 1.74 |

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730 Table 5

| Fuel Model | Fuel load (t ha ⁻¹) | | Type | SAV ratio (m ² /m ³) | Fuel bed depth (cm) | Dead fuel extinction moisture (%) | Heat content | | | Dead | Live | | | |
|------------------|---------------------------------|------|------|---|---------------------|-----------------------------------|--------------|------------|------|-------------------|------|------|-------|--------------------|
| | 1h | 10h | 100h | Live herbs | Live woody | Dead 1h | Live herbs | Live woody | Dead | | | Live | | |
| Heath-FM | 3.10 | 0 | 0 | 0 | 0 | 6.7 | Static | 6240 | - | 8810 ^a | 42.6 | 30 | 18608 | 22940 ^b |
| TU3 ^c | 3.93 | 0.34 | 0.56 | 0 | 0 | 0 | Static | 5906 | - | - | 39.6 | 30 | 18608 | 18608 |

731 ^a after Davies et al. (2006); ^b after Gillon et al. (1997); ^c modified from Scott and Burgan (2005).

732

733

734 Table 6
735

| Species | Model | n | $\beta_0 \subset I_0$ | $\beta_1 \subset I_1$ | C_{60}^- | C_{60}^+ | I_{60}^- | I_{60}^+ | C_{61}^- | C_{61}^+ | I_{61}^- | I_{61}^+ |
|---------|-------|----|-----------------------|-----------------------|--------------|--------------|--------------|--------------|------------|------------|------------|------------|
| Birch | 1 | 24 | 0.037 | 0.000 | 0.353 | 0.467 | 0.461 | 0.769 | 1.706 | 2.795 | 0.75 | 1.25 |
| Birch | 2 | 24 | 0.481 | 0.000 | 0.345 | 0.480 | 0.410 | 0.683 | 1.466 | 2.533 | 0.75 | 1.25 |
| Birch | 3 | 24 | 0.982 | 0.886 | 0.362 | 0.451 | 0.274 | 0.456 | 0.981 | 1.354 | 0.75 | 1.25 |
| Aspen | 1 | 24 | 0.940 | 0.003 | 0.429 | 0.537 | 0.439 | 0.731 | 1.334 | 2.139 | 0.75 | 1.25 |
| Aspen | 2 | 24 | 0.993 | 0.027 | 0.419 | 0.561 | 0.403 | 0.672 | 1.246 | 2.551 | 0.75 | 1.25 |
| Aspen | 3 | 24 | 0.996 | 0.892 | 0.430 | 0.532 | 0.330 | 0.549 | 0.925 | 1.351 | 0.75 | 1.25 |

736

7 39'E

45 15'N

- Reserve of Vauda
-  Pastoral fires (1994-2012)
-  Exp. units (Ascoli et al. 2009)
-  Calibration dataset





