Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality

P. Fons van Der, S. Ratcliffe, P. Ruiz-Benito, Michael Scherer-Lorenzen, Kris Verheyen, C. Wirth, M.A. Zavala, E. Ampoorter, L. Baeten, Luc Barbaro, et al.

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AUTHORS:

Fons van der Plas[1,2,3,*], Sophia Ratcliffe[3], Paloma Ruiz-Benito[4,5], Michael Scherer-Lorenzen[6], Kris Verheyen[7], Christian Wirth[3,8], Miguel A. Zavala[5], Evy Ampoorter[7], Lander Baeten[7], Luc Barbaro[9,10], Cristina C. Bastias[11], Jürgen Bauhus[12], Raquel Benavides[6], Adam Benneter[12], Damien Bonal[13], Olivier Bouriaud[14], Helge Bruelheide[8,15], Filippo Bussotti[16], Monique Carnol[17], Bastien Castagneyrol[9], Yohan Charbonnier[9], Johannes H. C. Cornelissen[18], Jonas Dahlgren[19], Ewa Checko[20], Andrea Coppi[21], Seid Muhie Dawud[22], Marc Deconchat[9,10], Pallieter De Smedt[7], Hans De Wandeler[23], Timo Domisch[24], Leena Finér[24], Mariangela Fotelli[25], Arthur Gessler[26], André Granier[13], Charlotte Grossiord[27], Virginie Guyot[9,10], Josephine Haase[6,28], Stephan Hättenschwiler[29], Hervé Jactel[9], Bogdan Jaroszewicz[20], François-Xavier Joly[29], Tommaso Jucker[30], Stephan Kambach[15,31], Gerald Kaendler[32], Jens Kattge[8,33], Julia Koricheva[34], Georges Kunstler[35], Aleksi Lehtonen[36], Mario Liebergesell[3,8], Peter Manning[1,2], Harriet Milligan[34],

23 Sandra Müller[6], Bart Muys[23], Diem Nguyen[37], Charles Nock[6], Bettina Ohse[3], Alain Paquette[38],

24 Josep Peñuelas[39,40], Martina Pollastrini[16], Kalliopi Radoglou[41], Karsten Raulund-Rasmussen[22],

25 Fabian Roger[42], Rupert Seidl[43], Federico Selvi[16], Jan Stenlid[37], Fernando Valladares[11], Johan van

26 Keer[44], Lars Vesterdal[22], Markus Fischer[1,2], Lars Gamfeldt[42], Eric Allan[1].

27

28 **AUTHOR AFFILIATIONS**

29 [1]Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland.

30 [2]Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Centre, Senckenberganlage 25,

31 60325 Frankfurt, Germany.

32 [3]Department of Systematic Botany and Functional Biodiversity, University of Leipzig, Johannisallee 21-23, 04103

33 Leipzig, Germany.

34 [4]Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, FK9 4LA, Stirling,

35 United Kingdom.

36 [5]Grupo de Ecología y Restauración Forestal, Departamento de Ciencias de la Vida, Universidad de Alcalá, Edificio

37 de Ciencias, Campus Universitario, 28805 Alcalá de Henares, Madrid, Spain.

38 [6]University of Freiburg, Faculty of Biology, Geobotany, Schänzlestr. 1, 79104 Freiburg, Germany.

39 [7]Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode, Belgium.

40 [8]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5E, 04103

41 Leipzig, Germany.

42 [9]BIOGECO, INRA, Univ. Bordeaux, 33610 Cestas, France.

43 [10]Dynafor, INPT-EI Purpan, INRA, Univ. Toulouse, 31320, Auzeville, France

44 [11]MNCN-CSIC, Serrano 115 bis 28006 Madrid, Spain.

45 [12]Faculty of Environment and Natural Resources, Chair of Silviculture, University of Freiburg, Fahnenbergplatz,

46 79085 Freiburg, Germany.

47 [13]INRA, UMR EEF, 54280 Champenoux, France.

48 [14]Faculty of Forestry, Stefan cel Mare University of Suceava, Universitatii Street 13, Suceava 720229, Romania.

49   [15]Institute of Biology / Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor

50   1, 06108 Halle (Saale), Germany.

51   [16]Department of Agrifood Production and Environmental Sciences, Laboratory of Applied and Environmental

52   Botany, University of Firenze, P.le Cascine 28, 50144 Firenze, Italy.

53   [17]Laboratory of Plant and Microbial Ecology, University of Liege, Botany B22, Chemin de la Vallee 4, 4000 Liege,

54   Belgium.

55   [18]Systems Ecology, Department of Ecological Science, Faculty of Earth and Life Sciences, Vrije Universiteit

56   Amsterdam, De Boelelaan 1085, 1081 HV, Amsterdam, The Netherlands.

57   [19]Swedish University of Agricultural Sciences, Skogsmarksgränd, 90183 Umeå, Sweden.

58   [20]Bialowieza Geobotanical Station, Faculty of Biology, University of Warsaw, 17-230 Białowieża, Poland.

59   [21]University of Firenze, Department of Biology, Botanical Laboratories, Via G. La Pira 4, 50121 Firenze, Italy.

60   [22]Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958

61   Frederiksberg C, Denmark.

62   [23]Department of Earth and Environmental Sciences, KU Leuven, University of Leuven, Celestijnenlaan 200E Box

63   2411, BE-3001 Leuven, Belgium.

64   [24]Natural Resources Institute Finland (Luke), Yliopistokatu 6, FI-80100 Joensuu, Finland.

65   [25]Forest Research Institute of Thessaloniki, Greek Agricultural Organization-Dimitra, 57006 Vassilika,

66   Thessaloniki, Greece.

67   [26]Swiss Federal Research Institute WSL, Research Unit Forest Dynamics, Zuercherstr, 111, 8903 Birmensdorf,

68   Switzerland.

69   [27]Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA.

70   [28]Institute for Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zurich,

71   Universitaetsstrasse 16, 8092 Zurich, Switzerland.

72   [29]Centre of Evolutionary and Functional Ecology (CEFE UMR 5175, CNRS – University of Montpellier –

73   University Paul-Valery Montpellier – EPHE), 1919 route de Mende, 34293 Montpellier, France.

74   [30]Forest Ecology and Conservation, Department of Plant Sciences, University of Cambridge, Downing Street,

75   Cambridge CB2 3EA, UK.

76   [31]UFZ – Helmholtz Centre for Environmental Research, Department Community Ecology, 06120 Halle (Saale),

77   Germany.

78   [32]Forest Research Institute Baden-Wurttemberg, Wonnhaldestrase 4, 79100 Freiburg, Germany.

79   [33]Max Planck Institute for Biogeochemistry, Hans-Knöll-Straβe 10, 07745 Jena, Germany.

80   [34]School of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK.

81   [35]Univ. Grenoble Alpes, Irstea, UR EMGR, Centre de Grenoble, 2 rue de la Papeterie-BP 76, F-38402 Saint-Martin-

82   d'Hères, France.

83   [36]Natural Resources Institute Finland (Luke), Jokiniemenkuja 1, FI-01370 Vantaa, Finland.

84   [37]Department of Forest Mycology and Plant Pathology, Swedish University of Agricultural Sciences, PO Box 7026,

85   SE-750 07 Uppsala, Sweden.

86   [38]Centre for Forest Research (CFR), Université du Québec à Montréal, Montréal (Québec), Canada.

87   [39]CREAF, Cerdanyola del Vallès, 08913 Catalonia, Spain.

88   [40]CSIC, Global Ecology Unit CREAF-CSIC-UB-UAB, Bellaterra, 08913 Catalonia, Spain.

89   [41]Democritus University of Thrace (DUTH), Department of Forestry and Management of the Environment and

90   Natural Resources, Pantazidou 193, 68200, Nea Orestiada, Greece.

91   [42]Department of Marine Sciences, University of Gothenburg, Carl Skottsbergs gata 22B, 41319 Göteborg, Sweden.

92   [43]University of Natural Resources and Life Sciences (BOKU), Institute of Silviculture, Vienna, Austria.

93   [44]Bormstraat 204 bus 3, 1880 Kapelle-op-den-Bos, Belgium.

94

95   [*]corresponding author: Fonsvanderplas@gmail.com; Senckenberganlage 25, D-60325 Frankfurt am Main, Germany;

96   Tel.: +49 69 7542 1820; Fax: + 49 69 7542 7904

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98   **AUTHOR CONTRIBUTIONS**

99   FvdP, EA, LG, MF, SR, PRB, MSL, CW, LB, RB, HB, TJ, SK, GK, CN, BO, AP and FR

100   developed the ideas of this study at a workshop organized by EA and LG. FvdP, SR and PRB

101   analysed the data. All authors, except FvdP, EA, MF, SKa, PM, BO, AP and FR contributed to

102   the data collection. FvdP wrote the manuscript. All authors contributed in editing the manuscript.

103

DATA ACCESSIBILITY STATEMENT

Should the manuscript be accepted, the data supporting the results will be published in Dryad

and the data DOI will be included at the end of the article.

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109

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123   **ABSTRACT**

124   Humans require multiple services from ecosystems, but it is largely unknown whether

125   trade-offs between ecosystem functions prevent the realization of high ecosystem

126   multifunctionality across spatial scales. Here, we combined a comprehensive dataset (28

127   ecosystem functions measured on 209 forest plots) with a forest inventory dataset (105,316 plots)

128   to extrapolate and map relationships between various ecosystem multifunctionality measures

129   across Europe. These multifunctionality measures reflected different management objectives,

130   related to timber production, climate regulation and biodiversity conservation/recreation. We

131   found that trade-offs among them were rare across Europe, at both local and continental scales.

132   This suggests a high potential for "win-win" forest management strategies, where overall

133   multifunctionality is maximized. However, across sites, multifunctionality was on average 45.8-

134   49.8% below maximum levels and not necessarily highest in protected areas. Therefore, using

135   one of the most comprehensive assessments so far, our study suggests a high but largely

136   unrealized potential for management to promote multifunctional forests.

137

INTRODUCTION

138

139   One of the greatest challenges in ecology is to understand the effects of global change

140   and nature management on the multiple ecosystem functions on which humans depend (MEA

141   2005). Such an understanding would help predicting the circumstances under which trade-offs

142   between different ecosystem functions are minimal and therefore when their simultaneous

143   provisioning, i.e. ecosystem multifunctionality (Hector & Bagchi 2007; Gamfeldt *et al.* 2008), is

144   maximised. Previous studies have identified conditions promoting local-scale ecosystem

145   multifunctionality, e.g. through the maximization of biodiversity (Lefcheck *et al.* 2015).

146   However, whether such relationships also exist at large spatial scales, and how they vary in

147   space, is less clear (Isbell *et al.* 2017). Understanding this is essential if ecosystem-functioning

148   studies are to provide policy-relevant advice, because most policy focuses on large scales.

149   Forests provide a number of functions related to key services such as timber production,

150   climate regulation and recreation (Gamfeldt *et al.* 2013), and are important for the conservation

151   of many plant and animal species (FAO 2015). Understanding large-scale relationships between

152   different functions is therefore important if we are to find "win-win" management scenarios,

153   which meet different forest management objectives and promote forest multifunctionality.

154   Quantifying many ecosystem functions at large scales has so far proven challenging.

155   Studies have used exhaustive remote sensing or ground-based measurements (e.g. Prince &

156   Goward 1995; Ratcliffe *et al.* 2016), mechanistic models (e.g. McGuire *et al.* 2001), indirect

157   measures (e.g. where certain habitat types are assumed to promote certain functions; Maskell *et*

158   *al.* 2013) or a combination of these (Maes *et al.* 2012; Mouchet *et al.* 2017) to quantify single or

159   multiple functions at large spatial extents. However, for some important functions, such as

160   biological pest control or timber quality, large scale maps have not yet been developed, limiting

161   our understanding of ecosystem functioning synergies and trade-offs. In contrast, many local-

162   scale studies, such as biodiversity experiments (e.g. Hector & Bagchi 2007; Zavaleta *et al.* 2009)

163   or comparative studies (Lavorel *et al.* 2011), have accurately quantified a large number of

164   functions. Extrapolating these small-scale observations to larger scales could increase our

165   understanding of the drivers of ecosystem functioning trade-offs and the resulting provision of

166   ecosystem multifunctionality.

167   Forests are often managed for a particular subset of functions related to certain ecosystem

168   services (e.g. timber production, climate regulation or nature conservation) that are prioritized by

169   a specific stakeholder group. We aimed to identify areas where functions of all these different

170   sets are high and where trade-offs are weakest. To this end, we combined a multi-site dataset,

171   containing accurate measures of multiple ecosystem functions, with a continental-scale

172   inventory-based dataset with high spatial plot coverage. We extrapolated regional scale

173   relationships between ecosystem functions and their drivers (e.g. forest community composition

174   and climate) to larger spatial scales (Fig. S1) to map both individual ecosystem functions and

175   ecosystem multifunctionality across Europe, in forests without recent intensive management. We

176   then tested for potential trade-offs between sets of functions, at scales relevant for policymakers.

177   To do this, we developed different measures of multifunctionality corresponding to

178   different management scenarios (Fig. 1). In these, functions related to (sustainable) timber

179   production, climate regulation or biodiversity conservation/recreation were prioritized (Fig. 1).

180   We also considered a scenario where all functions were valued equally. Our objectives were

181   firstly, to identify "multifunctionality hotspots", i.e. areas with highest multifunctionality.

182   Secondly, we investigated whether there are synergies (allowing for win-win management) or

183   trade-offs between different multifunctionality measures at both continental and local scales, and

184   how these varied in space. Finally, we investigated whether forest protection status is associated

185   with high multifunctionality, and thus whether potential win-win policies are realized in

186   (protected) forests.

187

188   **MATERIALS AND METHODS**

189   Our approach to extrapolate ecosystem functioning relationships from regional to

190   continental scales consisted of two main steps (Fig. S1). Firstly, statistical models were fitted to a

191   comprehensive (many ecosystem functions), multi-site dataset ('fitting dataset'). Secondly, these

192   models were extrapolated to a continental-scale dataset containing forest plots distributed across

193   Western Europe ('inventory dataset'). These two datasets share variables related to climate, soils

194   and tree composition, all potential drivers of ecosystem functioning. For three ecosystem

195   functions which were independently measured in the inventory dataset, we cross-validated

196   predicted ecosystem function values. Our approach allowed testing for trade-offs and synergies

197   between individual ecosystem functions and between different multifunctionality measures, at

198   different scales: 1) using all plots (thus including both local and large-scale variation in

199   functions) and 2) within 20×20km localities.

200

201   *Fitting dataset: design*

202   As part of the EU-FP7 FunDivEUROPE project (www.fundiveurope.eu), which

203   investigates how tree species composition and diversity drive forest ecosystem functioning, 209

204   30×30 meter plots (Fig. S2) were established. The plots covered six major regions/countries,

205   representing different forest types: 28 boreal forest (Finland), 43 temperate mixed forest

206   (Poland), 38 temperate deciduous forest (Germany), 28 mountainous deciduous forest

207   (Romania), 36 thermophilous deciduous forest (Italy) and 36 Mediterranean mixed forest plots

208   (Spain). These plots covered a broad climatic gradient: mean annual precipitation ranged from

209   484 to 819mm, mean annual temperature from 1.4 to 14.1°C (WorldClim; Hijmans *et al.* 2005)

210   and altitude from 87 to 1404m. Within regions, plots differed in the composition and diversity of

211   regionally common tree species, while site-related factors were similar. Management was either

212   at low intensity or absent (Baeten *et al.* 2013).

213

214   *Measurement and collation of fitting data*

215   In all plots, we measured 28 different ecosystem characteristics/processes ('ecosystem

216   functions' hereafter) linked to various ecosystem services (see overview in Fig. 1 and

217   methodology in Supplementary Material). For each plot we compiled data on tree species

218   composition (to derive measures of functional and phylogenetic diversity), stand structure, soil

219   pH, altitude and 18 climatic variables. Previous studies demonstrated that climate (Cramer *et al.*

220   2001), soil pH (Foy 1992), functional community composition (Diaz *et al.* 2004) and tree

221   diversity (van der Plas *et al.* 2016; Liang *et al.* 2016) can all drive (forest) functioning.

222   In each plot, we identified all tree stems ≥7.5cm in diameter at breast height (dbh) to

223   species level. With these data, we calculated total and average tree basal area. In addition, by

224   combining these observations with (1) published trait data (Kattge *et al.* 2011; Royal Botanic

225   Gardens Kew 2015; see Table S1) representing key life-history strategies (Westoby *et al.* 2002),

226   and (2) a phylogeny (Zanne *et al.* 2014), we calculated several metrics describing the functional

227   identity, functional diversity and phylogenetic diversity of the tree communities. Firstly, we

228   calculated Community Weighted Means (Garnier *et al.* 2004), reflecting functional identities of

229   communities, based on species values for specific leaf area ($cm^2\ g^{-1}$), maximum life span (log-

230 transformed; yrs), maximum height (m), wood density (g cm^{-3}), seed mass (mg), conifer

231 (proportion) and evergreen (proportion). Secondly, we calculated the functional (trait) diversity

232 within communities as Rao's Quadratic Entropy (Botta-Dukát 2005), for each trait separately

233 and for all traits combined. Finally, we calculated several phylogenetic diversity metrics:

234 Phylogenetic Species Variability, Phylogenetic Species Evenness (Helmus *et al.* 2007), Faith's

235 Phylogenetic Diversity (Faith 1992) and (abundance-weighted) Mean Phylogenetic Distance

236 (Webb *et al*. 2002). As inventory plots differed in size, tree species richness was not

237 investigated, and we selected functional and phylogenetic diversity metrics uncorrelated with

238 species richness.

239   To represent soil conditions we used pH (methods in Supplementary Materials), as it

240 drives many functions and was the only soil variable available for the inventory dataset. Eighteen

241 variables (see Table S2) related to climate (worldclim data; Hijmans *et al.* 2005) were collated at

242 a 30 seconds spatial resolution. Altitude data were collated from srtm.csi.cgiar.org.

243

244 *Analysis of the drivers of ecosystem functioning*

245   We used the Random Forest (Breiman 2001) algorithm to explain ecosystem function

246 variation in the fitting dataset. Random Forest is a machine-learning algorithm, powerful for

247 making predictions (but less suitable in explaining mechanisms) and incorporating both linear

248 and non-linear relationships, as well as interaction effects (Strobl *et al*. 2007). It is relatively

249 insensitive to multicollinearity and overfitting (Hastie *et al*. 2008), allowing for the inclusion of

250 many predictors. Initially, we included the 42 predictor variables described above (see also Table

251 S2), describing abiotic conditions, climate, stand structure, functional identity, and functional

252 and phylogenetic diversity. Random Forests were run in R (R Core Team 2013) with the

253   'randomForest' library (Liaw & Wiener 2012). Following Seidl *et al.* (2011), we iteratively

254   removed those variables not reducing the mean square error over random permutations of the

255   same variable. For final Random Forests, we identified, using the 'importance' function, the

256   degree to which the inclusion of each predictor decreases residual model variance.

257

258   *Forest inventory data*

259   We combined data from 163,451 plots of the National Forest Inventories (NFIs) of Spain

260   (59,048 plots), France (40,844), Wallonia (Belgium, 1,238), Germany (47,832), Sweden (11,212)

261   and Finland (2,456). NFIs contained data on individual trees in each plot, including species

262   identity, dbh and basal area. Furthermore, estimates of timber production (increase in tree basal

263   area per hectare per year), tree biomass and tree recruitment (tree saplings per hectare) were

264   available for many plots. To ensure that data from different NFIs were comparable to the fitting

265   dataset plots, we only included trees with dbh $\geq$7.5cm. Furthermore, we only included the

266   105,316 plots that were at low to mid-altitudes (<1500m), without indication of recent logging,

267   and dominated by one of the 'target' species of the fitting dataset (Baeten *et al.* 2013).

268   We calculated the same climate, functional identity and functional and phylogenetic

269   diversity variables for the NFI dataset as for the fitting dataset. Soil pH, calculated for the top

270   10cm of the soil at 1km^2 resolution, was obtained from the ESDAC database (Panagos *et al.*

271   2012). These variables had similar ranges as in the fitting dataset (Table S3).

272

273   *Extrapolating and mapping ecosystem functions across Europe*

274   We used the 'predict' function in R to predict values of each ecosystem function in

275   inventory plots, based on the Random Forests (built using the fitting dataset with independently

276   collected FunDivEUROPE data; Baeten et al. 2013) and the climate, functional identity,

277   diversity (of the most recent survey) and abiotic conditions in the inventory plots. To determine

278   the accuracy of our predictions, we correlated the three ecosystem functions (timber production,

279   tree biomass and tree recruitment) that were measured in inventory plots with the values

280   predicted by the Random Forests. We did the validations across all plots at continental scale

281   (local and large scale variation) and within (only local variation) and among (only large-scale

282   variation) 20×20km grid cells ('localities') containing ≥20 plots. In addition, we compared

283   observed correlations between ecosystem functions with extrapolated ones. We also compared

284   the average values for tree biomass and recruitment between fitting and inventory datasets

285   (productivity was not comparable as it was measured in different units). To investigate how

286   mapped functions changed across latitude, we fitted linear models with linear and quadratic

287   effects of latitude as predictors.

288

289   *Calculating multifunctionality and quantifying trade-offs*

290   We used the 'threshold-approach' (Gamfeldt *et al.* 2008) to calculate ecosystem

291   multifunctionality for each inventory plot, based on the predicted values of individual ecosystem

292   functions. Ecosystem multifunctionality was measured at both local and continental scales and

293   defined as the number of functions exceeding a threshold. The threshold was defined as the

294   proportion (25%, 50% (default threshold reported in main results), 75% or 90%) of the

295   'maximum' value observed for that function, either within a 20×20km locality (local scale) or

296   across Europe (continental scale). The maximum was defined as the 97.5[th] percentile of

297   observed functioning across plots, thus removing extreme outliers. For a concrete example on

298   quantifying multifunctionality, we refer to Fig. S3. We excluded ecosystem functions that (a) had

299   poor Ranfom Forest fit, with R^2 (correlation between observed and predicted) values <0.20

300   (default analysis; Fig. 1C) and (b), as a sensitivity analysis, also those which had a low validation

301   R^2 (see results: tree recruitment and the related function of seedling growth). As a further

302   sensitivity analysis, we calculated ecosystem multifunctionality using Random Forest R^2 values

303   as weights.

304   We also calculated multifunctionality according to various management objectives,

305   following Allan *et al.* (2015). In these measures, we gave different weightings to the various

306   ecosystem functions, according to their presumed importance (based on a consensus of expert

307   opinions of all authors) for delivering the ecosystem services required for the given objective

308   (Fig. 1). The equal weights measure described above corresponds with most previous studies

309   (e.g. Lefcheck *et al.* 2015). In the measures representing management objectives, functions were

310   weighted with loadings ranging from 0 (unimportant) to 1 (high importance). Functions directly

311   related to the objective received a weight of 1, i.e. timber production and quality for 'timber

312   production multifunctionality', carbon sequestration-related functions for 'climate regulation'

313   and functions directly measuring biodiversity (e.g. bird/understory diversity) for 'biodiversity

314   conservation/recreation'. Other functions were weighted 0.25; 0.50 or 0.75, depending on their

315   relevance (Fig. 1). We also quantified a 'narrow-sense' biodiversity conservation measure,

316   where only functions directly measuring biodiversity were included, with weights of 1 (Fig. 1).

317   Relationships between multifunctionality measures can either be caused by large-scale

318   climatic/biogeographical factors (e.g. temperature gradients) or local-scale factors (e.g.

319   management, soil conditions). Therefore, using Pearson correlations, we tested for trade-offs and

320   synergies, at both continental (all plots) and local scales (within localities with >10 plots). With

321   *t*-tests we investigated whether local-scale correlations, differed from zero.

322 Several functions had high weights in multiple multifunctionality measures, reflecting their

323 relevance for different ecosystem services (Fig. 1B). Raw correlation coefficients between

324 multifunctionality measures are therefore inflated by this overlap. To remove this effect, we

325 calculated a null expectation for the correlation-coefficients by reshuffling ecosystem function

326 values, without replacement, across plots 100 times. This eliminated any correlations among

327 functions, while maintaining the original distribution of values. With these resampled ecosystem

328 functions, we again calculated the different multifunctionality measures, and the average and

329 95% confidence intervals of the correlations between them. We calculated correlation-

330 coefficients corrected for overlap in functions by subtracting expected values (in the absence of

331 correlations among functions) from observed ones. As a sensitivity analysis, we repeated these

332 analyses only including plots located within those 150 localities in which validations of both

333 timber production and tree biomass were adequate (both $r>0.1$).

334

335 *Comparing multifunctionality between protected versus non-protected forests*

336 In total, 11.8% of the inventory plots were within protected areas which, depending on

337 the NFI, indicated either that forestry activities were restricted (Germany, Sweden) or that the

338 plot was in a National Park or nature reserve (Finland, France, Spain, Wallonia), see

339 Supplementary Material for more detailed information. Within each country, we investigated, for

340 each measure, whether local-scale multifunctionality was higher inside versus outside protected

341 areas, using Welch's *t*-tests.

342

343 **RESULTS**

344 *Explaining variation in ecosystem functioning*

345   On average, across the different ecosystem functions in our fitting dataset, Random

346   Forests explained 40.7% of the total variation. The explained variation in ecosystem functions

347   ranged from high (timber production: 72.5%; resistance to insect herbivory: 67.6%) to low

348   (browsing resistance: 2.4%, Fig. 1C). The single most important explanatory factor (i.e. with

349   lowest residual variance) varied between the functions. For sixteen functions it was a climate

350   variable, for six a functional identity variable, for two altitude, for two a functional diversity

351   variable and soil pH and average stem diameter for one each (Fig. 1C; Table S4).

352   Three ecosystem functions allowed for validation of predicted values in inventory plots.

353   For timber production and tree biomass, across all plots, predicted values correlated reasonably

354   well with observed values, with 'extrapolation' R^2 values (correlation between predicted and

355   observed values in inventory plots) of 0.219 and 0.280, respectively. For tree recruitment the R^2

356   was only 0.040; Fig. S4. Validations generally worked best at large spatial scales and less well at

357   local scales. Correlations between predicted and observed values of timber production, tree

358   biomass and tree recruitment were, respectively, 0.390; 0.472 and 0.027 *across* 20×20km

359   localities, and on average 0.127 (range: 0-0.976); 0.124 (range: 0-0.971) and 0.091 (range: 0-

360   0.967) *within* localities. Absolute values of tree biomass were similar between NFI observations

361   and Random Forest predictions, but for tree recruitment the values differed (Fig. S5). For more

362   information on model validations, see Supplementary Material (S3).

363

364   *Levels of ecosystem functioning and multifunctionality throughout Western Europe*

365   After removing ecosystem functions poorly explained by the Random Forests ($R^2<0.2$;

366   see Fig. 1C), we predicted levels of 22 ecosystem functions for the inventory plots (Fig. S6).

367   Many of the mapped functions showed clear continental trends. For example, some (e.g. timber

368   production) had highest levels in central Western Europe, while others had highest values in

369   boreal (e.g. timber quality) or Mediterranean (e.g. bat diversity) regions (Fig. S6; Table S5).

370   Most functions tended to be highest at mid-latitudes. Consequently, most continental-scale

371   multifunctionality measures were highest in central Western Europe (multifunctionality hotspots)

372   and lowest in southern Europe (Fig. 2). When only diversity measures were considered (narrow-

373   sense biodiversity conservation), multifunctionality was also high in southern/central Spain and

374   parts of Scandinavia. These patterns were broadly similar when functions with a high proportion

375   of explained variance were weighted more heavily (Fig. S7). As expected, local-scale

376   multifunctionality values did not show any large-scale spatial patterns (Fig. S8). Local

377   multifunctionality scores were on average 45.8%, 47.1%, 49.2%, 49.8% and 47.8% below their

378   maximum possible score (i.e. all functions above the 50% threshold) in the timber production,

379   climate regulation, broad-sense and narrow-sense biodiversity conservation and overall

380   multifunctionality scenario, respectively, and higher than 90% of the maximum possible score in

381   97, 49, 49 and 11,625 plots (out of 105,316 plots) in the timber production, climate regulation,

382   broad-sense and narrow-sense biodiversity conservation scenario, respectively, whereas it

383   exceeded 90% and 80% of maximum overall multifunctionality in only 3 and 446 plots

384   respectively (Fig. 2B). Importantly, while ecosystem functions varied strongly at the continental

385   scale (with 97.5 percentile values being on average 42.8% higher than mean values), there was

386   also substantial variation within localities, with 97.5 percentile values being on average 12.6%

387   higher than mean values (Table S6).

388

389   *Trade-offs and synergies*

390   Pairwise correlations between individual functions were positive on average at both

391   scales, although correlations were weaker at local ($\bar{r} = 0.012$) than at continental scales ($\bar{r} =$

392   0.021), probably due to lower variation in functioning within localities (Table S6). Moderately to

393   strongly positive correlations ($r > 0.3$; $n = 57$ (continental-scale) and 22 (local scale))

394   outnumbered negative ($r < -0.3$; $n = 45$ (continental-scale) and 14 (local-scale)) correlations

395   (Table S7,8). At the continental scale, correlations between timber production and tree biomass

396   were similar for observed ($r = 0.55$) and extrapolated ($r = 0.65$) values. However, within

397   localities this match was weaker ($\bar{r} = 0.63$ observed and 0.24 predicted), with fits generally best

398   in France and central/southern Spain, and weaker in Germany and northeast Spain (Fig. S9).

399   As different multifunctionality variables had similar continental-scale patterns (Fig. 2),

400   continental-scale correlations between most measures were positive (Table 1). Only correlations

401   between narrow-sense biodiversity conservation and both timber production ($r = -0.13$) and

402   climate regulation multifunctionality ($r = 0.01$) were not. These correlations became more

403   positive at more extreme (25 and 90%) multifunctionality thresholds (Table S9-S11).

404   Within localities, similar patterns were found. Relationships between timber production,

405   climate regulation and broad-sense biodiversity conservation/recreation were positive, whereas

406   relationships between narrow-sense biodiversity conservation and other multifunctionalty

407   variables were close to zero, or negative, on average (Fig. 3, Table 1). Negative relationships

408   largely disappeared when multifunctionality was based on 25% or 90% thresholds (Table S9-

409   S11). Importantly, positive relationships between timber production and climate regulation

410   multifunctionality, and to a lesser extent between timber production/climate regulation

411   multifunctionality and broad-sense biodiversity conservation/recreation multifunctionality, were

412   very widespread across Europe (Fig. 3).

413   We used null models to investigate whether observed correlations between

414   multifunctionality variables were larger than expected. Relationships between multifunctionality

415   variables were to a large extent driven by functions contributing to multiple multifunctionality

416   variables, as observed minus expected correlation-coefficients were often close to zero (Fig. 3,

417   Table 1). Nevertheless, at a continental scale, relationships between timber production, climate

418   regulation and broad-sense biodiversity conservation multifunctionality remained significantly

419   positive (all $P<0.05$). At the local scale, relationships between timber production and climate

420   regulation multifunctionality also remained significantly (although weakly) positive, whereas

421   relationships between timber production and the biodiversity conservation measures became

422   significantly, weakly, negative. In sensitivity analyses these patterns hardly changed when (i)

423   recruitment-related functions were omitted from multifunctionality measures, (ii) ecosystem

424   functions with a high Random Forest fit had proportionally higher loadings in multifunctionality

425   measures, or (iii) only plots from localities with high validation R^2 values of Random Forests

426   explaining timber production and tree biomass were included (Table 1). Negative relationships

427   largely disappeared when multifunctionality was quantified based on 25% or 90% thresholds

428   (Table S9-S11). Importantly, functional overlap-corrected correlation-coefficients between

429   different ecosystem multifunctionality scenarios varied greatly, from positive to negative,

430   throughout localities (Fig. 3).

431

432   *Multifunctionality inside versus outside protected areas*

433   Local-scale associations between values of multifunctionality and protection status

434   differed widely between countries and scenarios (Fig. 4). In Spain and Germany, timber

435   production and climate regulation multifunctionality were lower inside protected areas, whereas

436 the opposite was observed in France. In Germany, biodiversity conservation-related

437 multifunctionality was highest inside protected areas, whereas in France the opposite was found.

438 These results were largely insensitive to the way in which multifunctionality was quantified

439 (Table S12).

440

441 **DISCUSSION**

442 In our study trade-offs between groups of functions were rare in European forests, at both

443 continental and local scales. We found synergies between individual ecosystem functions and

444 few trade-offs between multifunctionality measures focused on timber production, climate

445 regulation and biodiversity conservation/recreation. When corrected for overlap in functions

446 among scenarios, some relationships were weakly positive throughout most of Europe (timber

447 production versus climate regulation), some were weakly negative (timber production versus

448 biodiversity conservation/recreation) and some were close to zero (climate regulation versus

449 biodiversity conservation/recreation).The lack of strong trade-offs indicates that functions related

450 to (sustainable) timber production can go hand in hand with functions related to services such as

451 biodiversity conservation. Mapping local trade-offs and synergies across Europe revealed

452 substantial variation in these relationships, showing that strong synergies are realized in a few

453 environments. While biodiversity and timber production are currently maximised in some

454 forests, suggesting a "win-win" for conservation and commercial forestry, across plots, average

455 multifunctionality values were almost 50% below maximum possible levels, and the proportion

456 of forest plots providing high levels of 'overall multifunctionality' (where timber production,

457 climate regulation and biodiversity conservation are all maximized) was very small. Hence,

458 while forest management has the potential to realize high multifunctionality, this is currently not

20

459   common. Most multifunctionality measures had many ecosystem functions in common, as some

460   ecosystem functions are valued under a range of different management objectives (e.g. Chan *et*

461   *al.* 2006; Allan *et al.* 2015). Relationships between different multifunctionality measures were

462   generally much more strongly positive if not corrected for this functional overlap. While these

463   raw correlations are statistically spurious (as the different measures partly contain the same data),

464   they can be highly relevant for management. For instance, tree growth is important for both

465   timber production and climate regulation, which suggests that forest management promoting tree

466   growth will maximize both services. Our results therefore suggest many possibilities for win-win

467   forest management strategies.

468   Our multifunctionality variables were intended to represent the bundle of functions

469   needed to meet certain forest management objectives (following Allan *et al.* 2015). They should

470   therefore be more useful to managers than traditional multifunctionality metrics that assume

471   equal importance of each ecosystem function. However, they could be further improved to

472   consider how multiple functions are related to final ecosystem services, using production

473   functions, and then services can be valued in monetary or other units to calculate the overall

474   benefits supplied by different management scenarios (e.g. Nelson et al. 2009; Bateman *et al.*

475   2013). Ultimately, sustainable ecosystem management needs to minimize trade-offs between

476   ecosystem benefits for different stakeholders (Díaz *et al.* 2015) and our targeted

477   multifunctionality metrics represent a step towards quantifying and mapping these trade-offs at

478   large scales.

479   Other studies, performed in grasslands (e.g. Lavorel *et al.* 2011) or across different

480   ecosystems or land-use types (Chan *et al.* 2006) have documented strong trade-offs between

481   ecosystem functions and services, especially between productivity-related functions and those

482 associated with biodiversity conservation or recreation. However, in forests, relationships

483 between tree biomass and the biodiversity of associated taxa often show more mixed patterns

484 (Jukes *et al*. 2007). For example, the positive relationship between tree productivity and bird

485 diversity in our data could be due to the strong dependence of specialist species on forests with

486 many old trees (Gil-Tena *et al.* 2007), while the trade-off between productivity and understorey

487 biomass may be driven by light competition between trees and understorey plants. When

488 biodiversity conservation multifunctionality was quantified using only the four direct measures

489 of biodiversity, weakly negative relationships with timber production and climate regulation

490 multifunctionality were found. Their approximately equal strength at continental and local scales

491 (Table 1) suggests that the relationship was primarily driven by local-scale factors, such as stand

492 composition. The negative response of understorey plants to tree growth is likely responsible for

493 this trade-off, as it is difficult to maximize timber production whilst maintaining an open canopy.

494   We also found that protected forests were not necessarily associated with high local-scale

495 ecosystem multifunctionality. In Spain, several multifunctionality measures were in fact lower

496 inside protected areas. In other countries, patterns were more mixed, but overall

497 multifunctionality was never highest inside protected areas. Importantly, associations between

498 forest protection status and multifunctionality were unlikely to be driven by climate, as local-

499 scale climatic variation is low within our 20×20km regions. Associations between local-scale

500 multifunctionality and protection status seem therefore to be driven by local factors, such as tree

501 diversity or composition. However, it is uncertain whether these observed relationships are

502 causal, as forests were likely not designated to be protected at random. For example, they may

503 have had low productivity and particular tree compositions before they were protected.

504 Furthermore, services such as the conservation of forest specialist species were not quantified,

505   but these could be high inside protected areas. Many protected areas were only established

506   relatively recently (Paillet *et al.* 2015), so protected forests may still be recovering from past

507   management. Finally, we only investigated forests without evidence of recent logging activity,

508   which may have reduced the contrast between protected and non-protected areas. Regardless,

509   although our results suggest a high potential for win-win forest management scenarios, the

510   simultaneous maximization of timber production, climate regulation and biodiversity has not yet

511   been realized within protected areas.

512   Our results also provide evidence that climate drives large-scale variation in many

513   ecosystem functions and the synergies between them. Many functions, such as tree biomass or

514   litter production, had highest levels in central Western Europe (Fig. S6) and some synergies

515   between multifunctionality scenarios were stronger at continental than at local scales. A strong

516   continental-scale synergy between earthworm biomass and litter decomposition (Table S7) may

517   have arisen because they were both strongly associated with climate (Table S4). The correlation

518   was also present at the local scale (Table S8), suggesting additional direct links between them.

519   While earlier studies have already shown the importance of climate for functions such as primary

520   production and carbon sequestration (e.g. Cramer *et al.* 2001), our more comprehensive study

521   shows that climate may be a driver of many more ecosystem functions, such as earthworm or

522   microbial biomass. The fact that so many functions appear related to climate, especially to wet

523   season precipitation (Table S4), may have important implications. For example, timber

524   production multifunctionality was lower in dry climates, suggesting detrimental effects of

525   projected future decreases in precipitation (IPCC 2014). However, while our approach is

526   powerful in describing patterns, it is not suited to identify underlying processes. Therefore, more

527 research on the causality of climate-ecosystem functioning relationships (e.g. De Boeck *et al.*

528 2008; Šímová & Storch 2017) is needed to predict ecosystem responses to climate change.

529   Extrapolations are still relatively rare in ecosystem functioning studies (but see Lee *et al.*

530 2000; Isbell *et al.* 2014; Manning *et al.* 2015), although other subtopics of ecology, such as

531 species distribution research (Elith & Leathwick 2009), have a much stronger tradition in this

532 respect. Three ecosystem functions could be validated with independent observations, which

533 showed that: (1) validations were generally adequate for timber production and tree biomass, but

534 not for tree recruitment, (2) validations worked best at large spatial scales, whereas at local

535 scales there was large variation in their accuracy but (3) relationships between different

536 multifunctionality variables were insensitive to the inclusion of localities where the validation

537 was less well supported. Our approach is therefore promising, but we emphasize that validations

538 could only be carried out for those three ecosystem functions for which independent inventory

539 data was available, so future validations of other functions are needed. Local-scale data related to

540 soil fertility or management could thus further improve the accuracy of ecosystem function

541 predictions.

542   Our study presents a new approach to quantify ecosystem functioning at scales relevant

543 for policy makers. The increasing availability of large datasets on ecosystem functioning from

544 integrated projects means our approach may become increasingly feasible for other systems and

545 regions. A further possibility would be to combine local-scale ecosystem functioning datasets

546 with remote sensing data to map services at large scales. Remote sensing approaches have

547 successfully predicted some ecosystem functions, but have difficulties with other functions, such

548 as soil processes (de Araujo *et al.* 2015). By combining data on forest and climate attributes with

549 remotely sensed parameters, we could map ecosystem functions even more accurately in the

550   future. Our study is a first step in reaching the ultimate goal of predicting how future ecosystem

551   functioning and service provision will be altered by ongoing global trends, such as climate

552   change (IPCC 2014), eutrophication and acidification (Galloway *et al.* 2008) or land-use change

553   (Newbold *et al.* 2015). Future studies could combine our approach with models on climate

554   change (e.g. IPCC scenarios), biodiversity change (e.g. Isbell *et al.* 2014) or management

555   scenarios to investigate the impacts of these global trends for the future functioning and service

556   provisioning of forests and other ecosystems.

557   In conclusion, our study, among most comprehensive overviews of forest ecosystem

558   functioning to date, showed that different measures of forest multifunctionality tend not to trade-

559   off with each other, at both local and continental scales. Within some areas there were strong

560   synergies between different multifunctionality measures, indicating that even though they are

561   currently uncommon, "win-win" forest management strategies are possible and could be

562   promoted in the future. However, we also found that multifunctionality is often not higher inside

563   than outside protected areas. Our study therefore suggests a high but unrealized potential for

564   multifunctionality in European forests.

565

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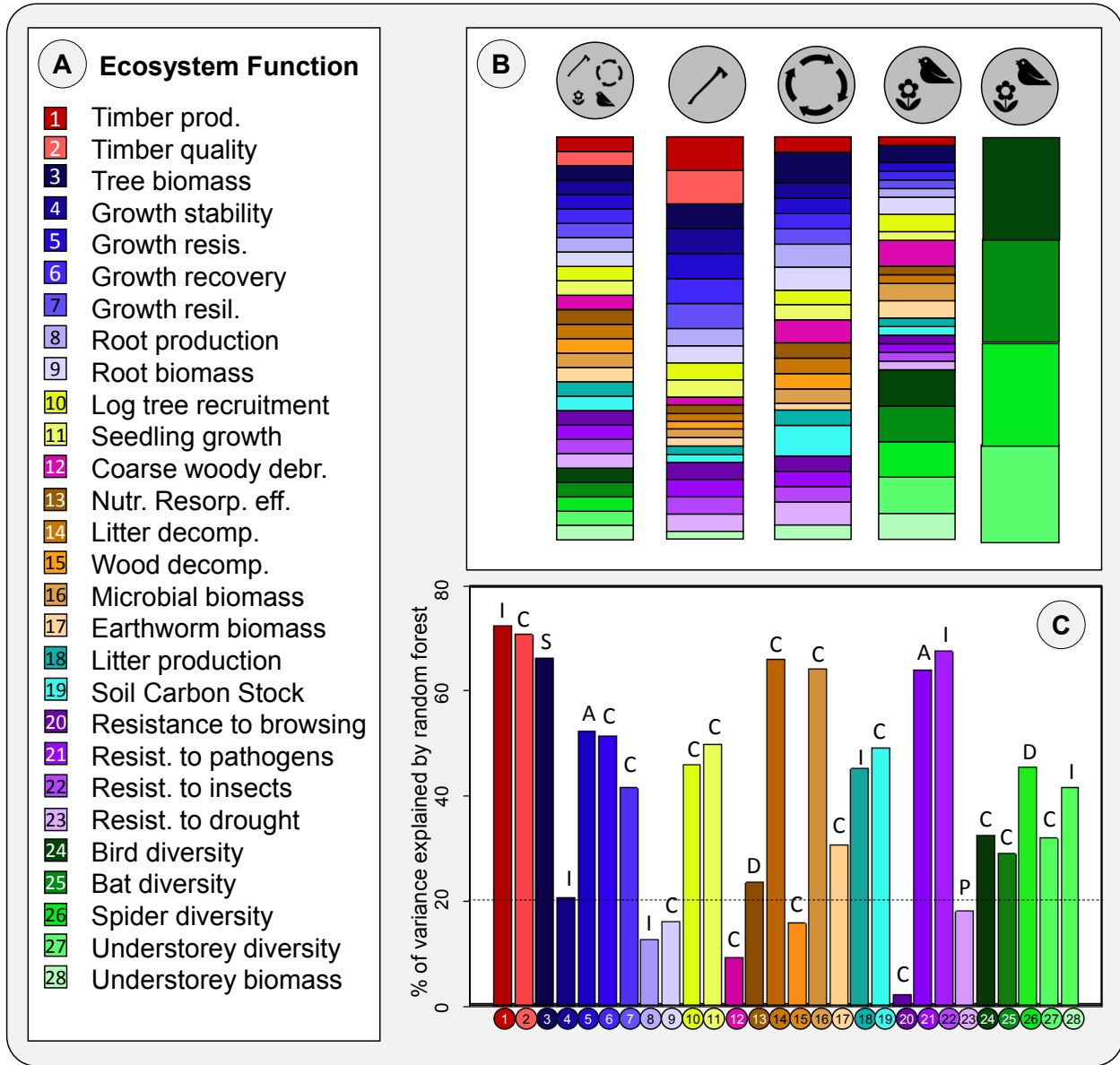
Figure 1. A: Ecosystem functions included in this study, with the colours and numbers referring

to the bars/circles representing them in B and C. B: Weightings used to produce five ecosystem

multifunctionality measures, reflecting different management scenarios. From left to right, the

'equal-weights', 'timber production', 'climate regulation', the 'broad-sense biodiversity

conservation/recreation' and the 'strict-sense biodiversity conservation' measure. In the equal

weights measure, all ecosystem functions are valued equally. In other measures, function

720   weightings reflect their importance for the management objective. Note that in the climate

721   regulation scenario, loadings of the decomposition variables are negative. C: Proportion of

722   variance of ecosystem functions explained by Random Forests. Letters above the bars indicate

723   which type of predictor was most important in explaining variation: C = climate-related; I =

724   functional identity-related; P = pH; A = altitude; D = biodiversity-related; S = stand structure

725   related. In further analyses, only those functions with R^2 values above 0.2 (dashed horizontal

726   line) were included.
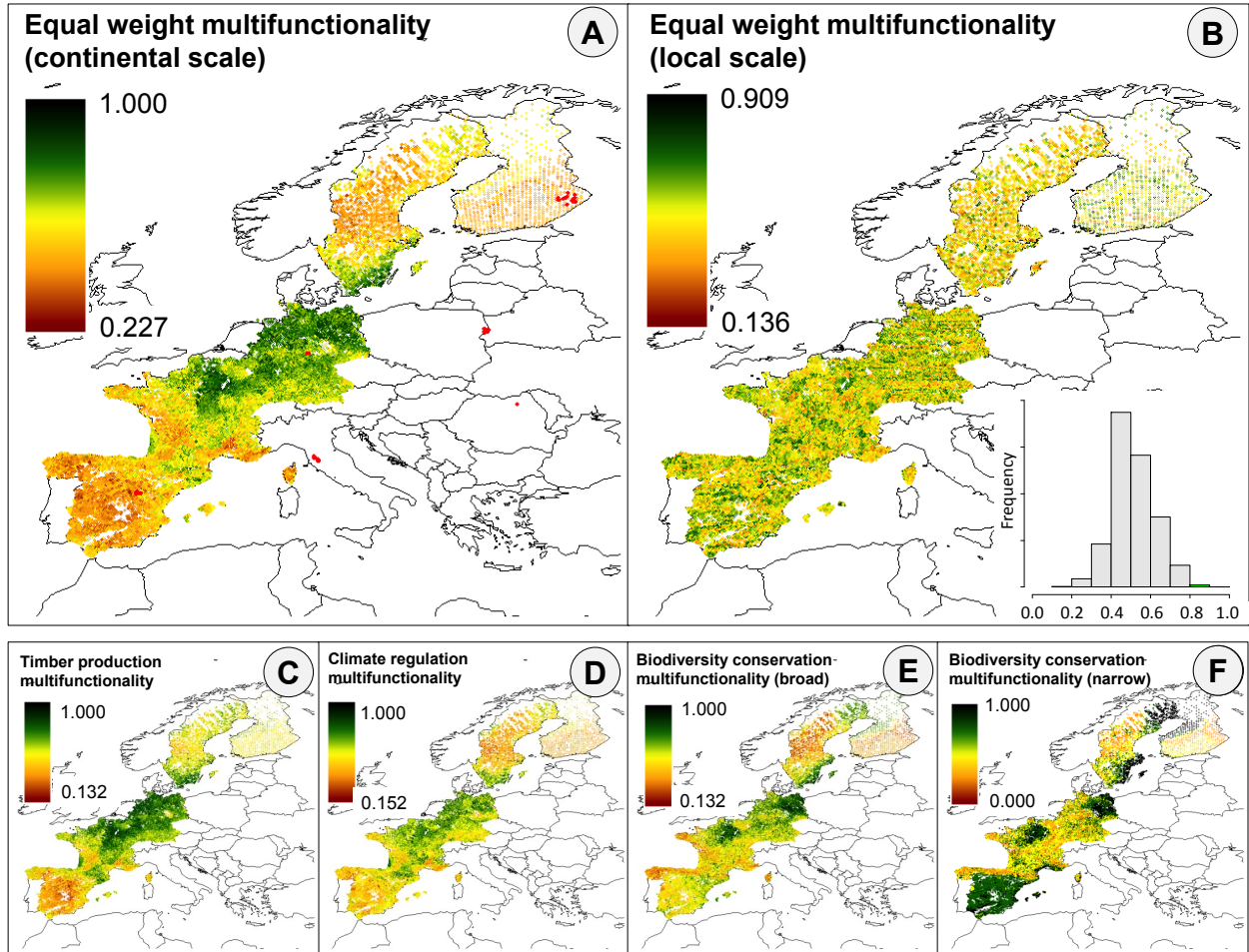
Figure 2. While high values of continental-scale multifunctionality (A, C-F) in central Europe across a range of scenarios indicate large scale synergies, at local scales (B) high overall multifunctionality is realized in only a few sites. Mapped levels of predicted large-scale multifunctionality are rescaled as the proportion of functions above a 50% threshold. Green values indicate relatively high functioning, while brown values indicate relatively low functioning. In A), locations of fitting dataset plot are shown in red. In B, where overall, local-scale multifunctionality is shown, the histogram indicates that in only a few plots, levels exceed 0.8.

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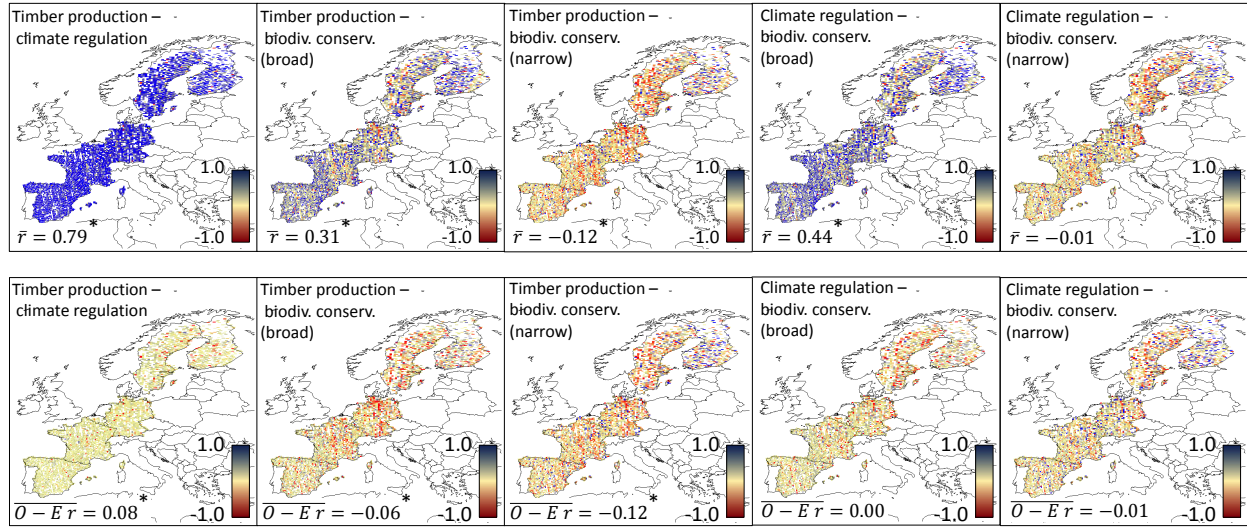
Figure 3. Substantial variation in the degree of local scale synergies and trade-offs exists across

Europe. Observed and observed minus expected correlation coefficients between

multifunctionality measures, within 20×20 km grid cells. Top: Values of all observed

multifunctionality measures, except for the narrow-sense biodiversity conservation measure,

correlate positively at local scales. Bottom: these correlations are largely driven by overlap in

ecosystem functions, as observed minus expected correlation-coefficients are close to zero.

Average correlations that deviate significantly from zero are indicated with an asterisk (*).

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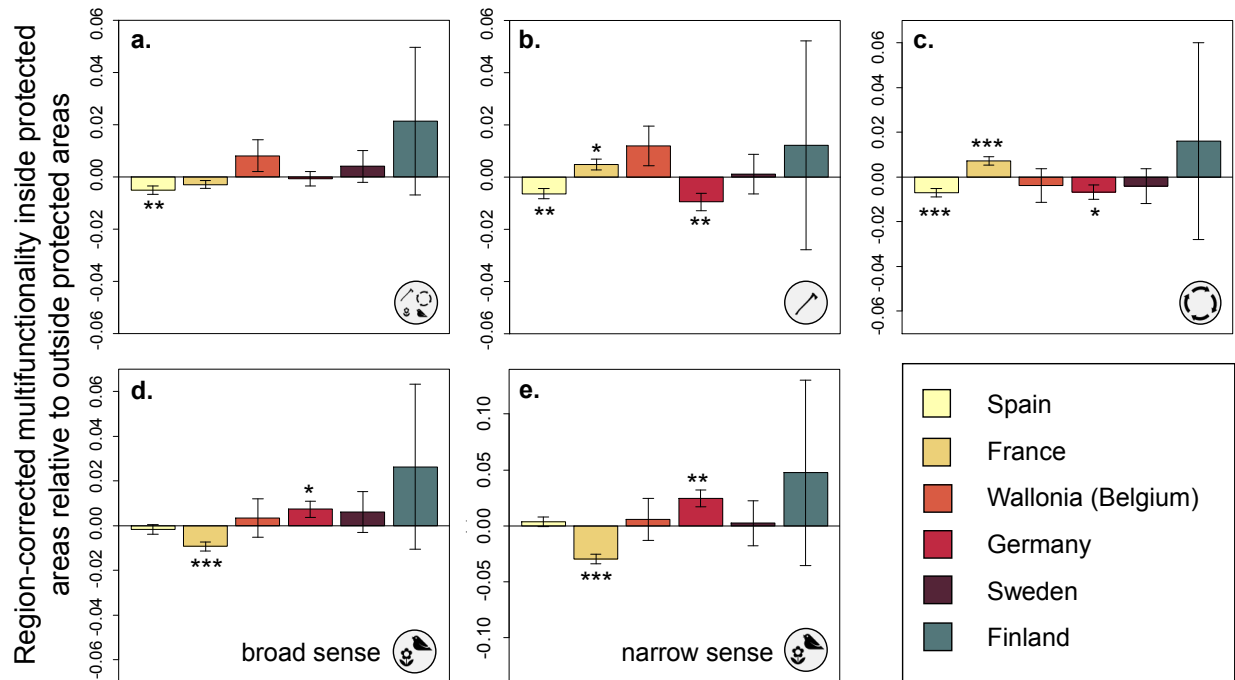
Figure 4. Local-scale ecosystem multifunctionality is generally not higher inside protected areas, for different multifunctionality measures and countries. Bars above zero indicate that multifunctionality is higher inside than outside protected areas, while bars below zero indicate the opposite. A: Equal-weight multifunctionality. B: timber production multifunctionality. C: climate regulation multifunctionality. D: broad-sense biodiversity conservation/recreation multifunctionality. E: narrow-sense biodiversity conservation/recreation multifunctionality.

753 Table 1. Correlations between values of different multifunctionality measures at both continental

754 and local scales and both across all plots and within countries. Here, multifunctionality was

755 based on a 50% threshold level. Correlations were also quantified after correcting for the overlap

756 in ecosystem functions between multifunctionality measures. This is indicated as 'no functional

757 overlap' or 'no FO' in the table. As sensitivity analyses, correlations were also calculated based

758 on (a) multifunctionality measures in which recruitment-related functions were excluded, (b)

759 multifunctionality measures in which loadings of ecosystem functions was proportional to

760 Random Forest R^2 values and (c) only those plots within 20x20 km grid cells with a high

761 validation R^2 (>0.10) for timber production and tree biomass. Significant correlations are shown

762 in bold. TP = timber production, CR = climate regulation, BCB = broad-sense biodiversity

763 conservation and BCN = narrow-sense biodiversity conservation.

	TP-CR	TP-BCB	TP-BCN	CR-BCB	CR-BCN
Continental scale, raw	**0.81**	**0.57**	**-0.13**	**0.63**	0.01
Continental scale, no FO	**0.06**	**0.15**	**-0.13**	**0.16**	0.01
Continental scale, no FO, no recruitment-related EFs	**0.07**	**0.16**	**-0.09**	0.20	**0.08**
Continental scale, no FO, corrected for EF R^2 values	**0.10**	**0.18**	**-0.17**	0.12	**-0.10**
Continental scale, no FO, only plots with high validation	**0.05**	**0.12**	**-0.35**	0.11	**-0.17**
Local scale	**0.79**	**0.31**	**-0.12**	**0.44**	-0.01
Local scale, Spain only	**0.79**	**0.32**	**-0.11**	**0.46**	0.02
Local scale, France only	**0.80**	**0.30**	**-0.12**	**0.42**	**-0.03**
Local scale, Wallonia only	**0.78**	**0.12**	**-0.31**	**0.38**	**-0.07**
Local scale, Germany only	**0.80**	**0.31**	**-0.16**	**0.47**	-0.01
Local scale, Sweden only	**0.73**	**0.30**	-0.03	**0.33**	-0.03
Local scale, Finland only	**0.77**	**0.34**	-0.08	**0.44**	-0.02
Local scale, no FO	**0.01**	**-0.08**	**-0.13**	**0.03**	**-0.01**
Local scale, no FO, Spain only	**0.01**	**-0.08**	**-0.11**	**0.05**	**0.02**
Local scale, no FO, France only	**0.01**	**-0.09**	**-0.13**	**0.01**	**-0.03**
Local scale, no FO, Wallonia only	0.00	**-0.26**	**-0.31**	-0.03	**-0.07**
Local scale, no FO, Germany only	**0.02**	**-0.08**	**-0.16**	**0.06**	**-0.01**
Local scale, no FO, Sweden only	**-0.05**	**-0.09**	-0.03	**-0.08**	**-0.04**
Local scale, no FO, Finland only	**-0.01**	**-0.05**	**-0.08**	**0.03**	**-0.02**
Local scale, no FO, no recruitment-related EFs	**0.03**	**-0.12**	**-0.14**	-0.04	**-0.02**
Local scale, no FO, corrected for EF R^2 values	**0.09**	**-0.07**	**-0.17**	-0.04	**-0.08**
Local scale, no FO, only plots with high validation	**0.10**	**-0.15**	**-0.29**	-0.06	-0.13

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