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

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10

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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

104 **DATA ACCESSIBILITY STATEMENT**

105 Should the manuscript be accepted, the data supporting the results will be published in Dryad
106 and the data DOI will be included at the end of the article.

107

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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

138 **INTRODUCTION**

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 ≥ 7.5 cm 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 ($\text{cm}^2 \text{g}^{-1}$), 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 ≥ 7.5 cm. 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 1km² 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 97.5th 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 Random 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 multifunctionality
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

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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584

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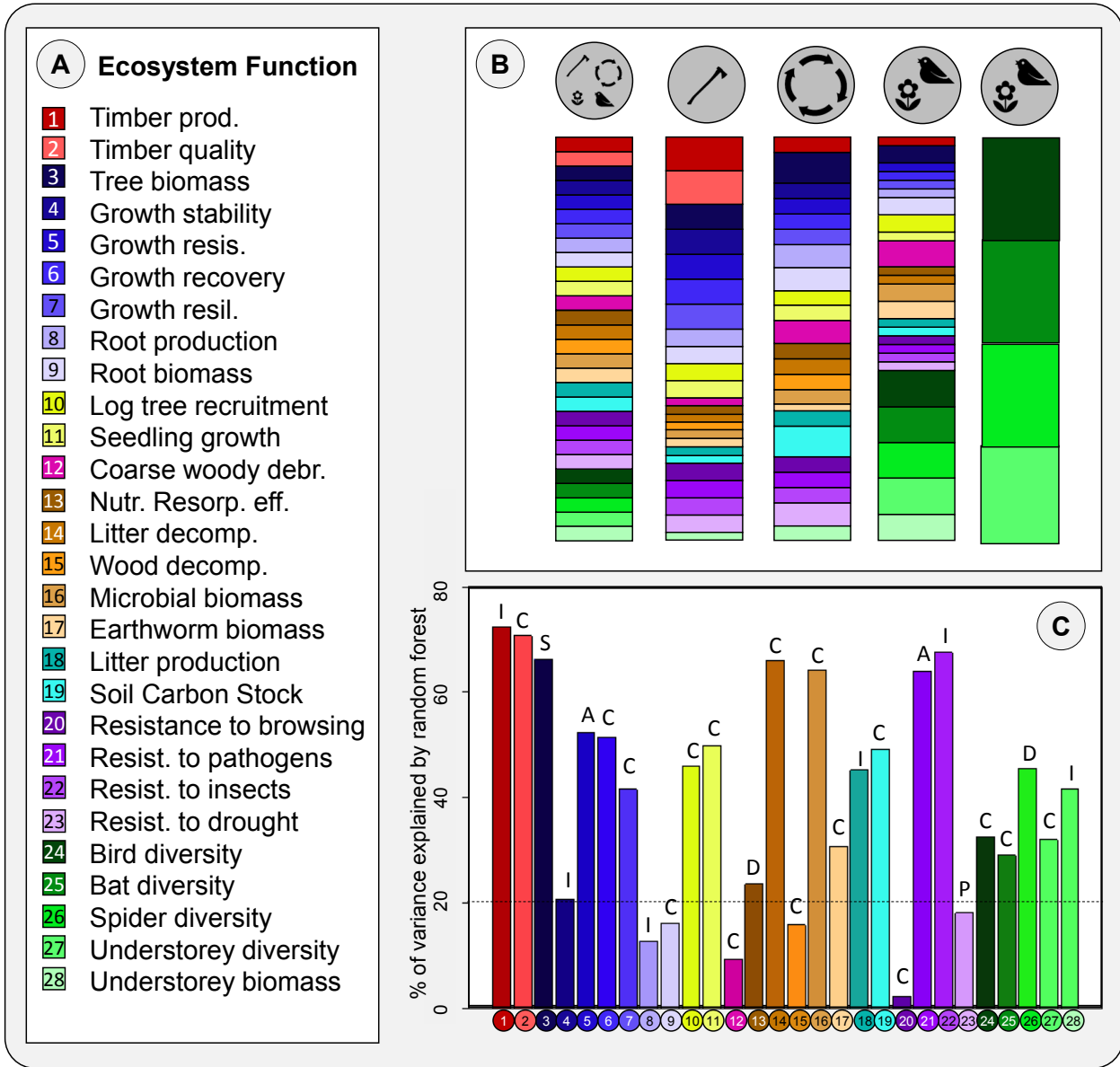
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713

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

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

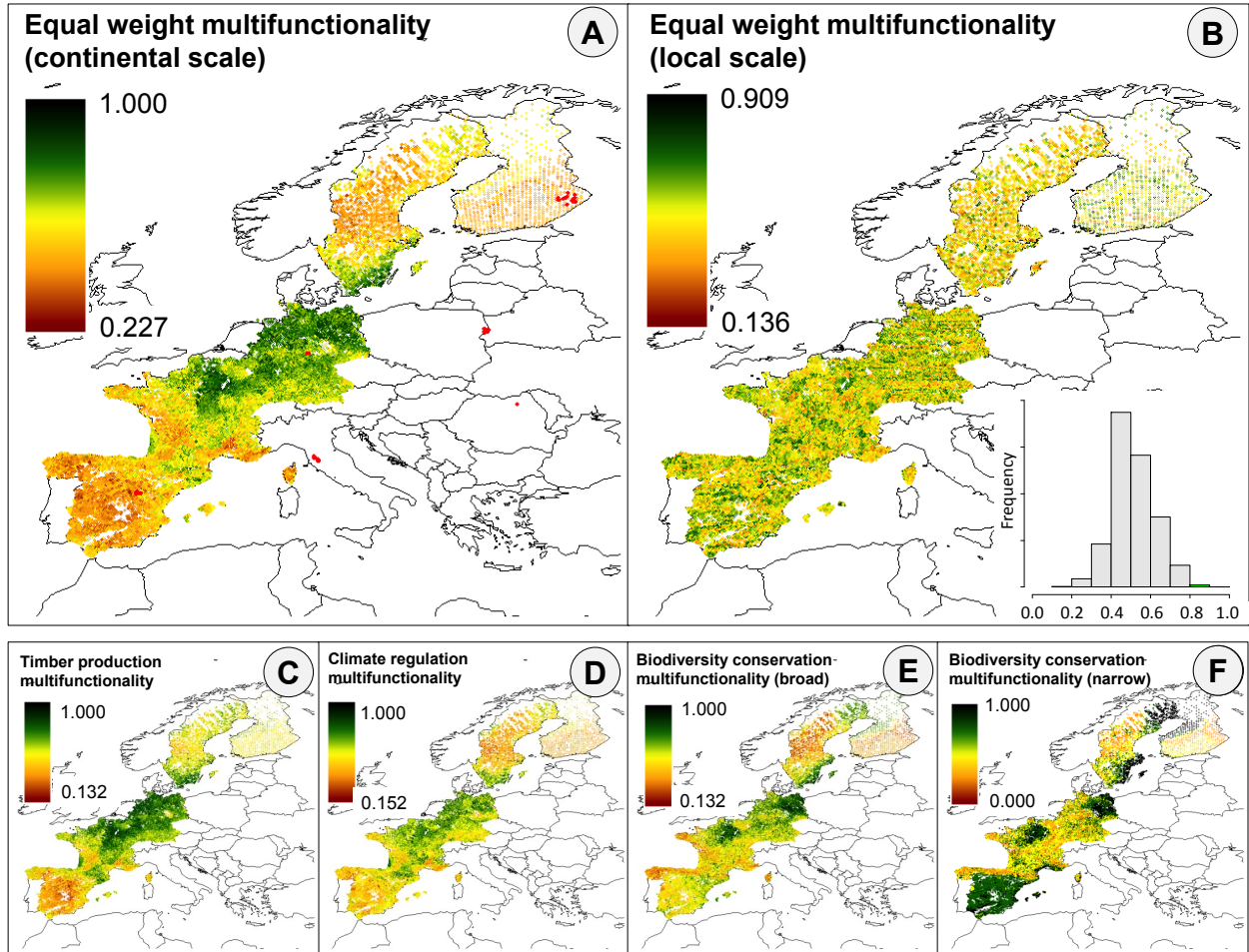
716 multifunctionality measures, reflecting different management scenarios. From left to right, the

717 ‘equal-weights’, ‘timber production’, ‘climate regulation’, the ‘broad-sense biodiversity

718 conservation/recreation’ and the ‘strict-sense biodiversity conservation’ measure. In the equal

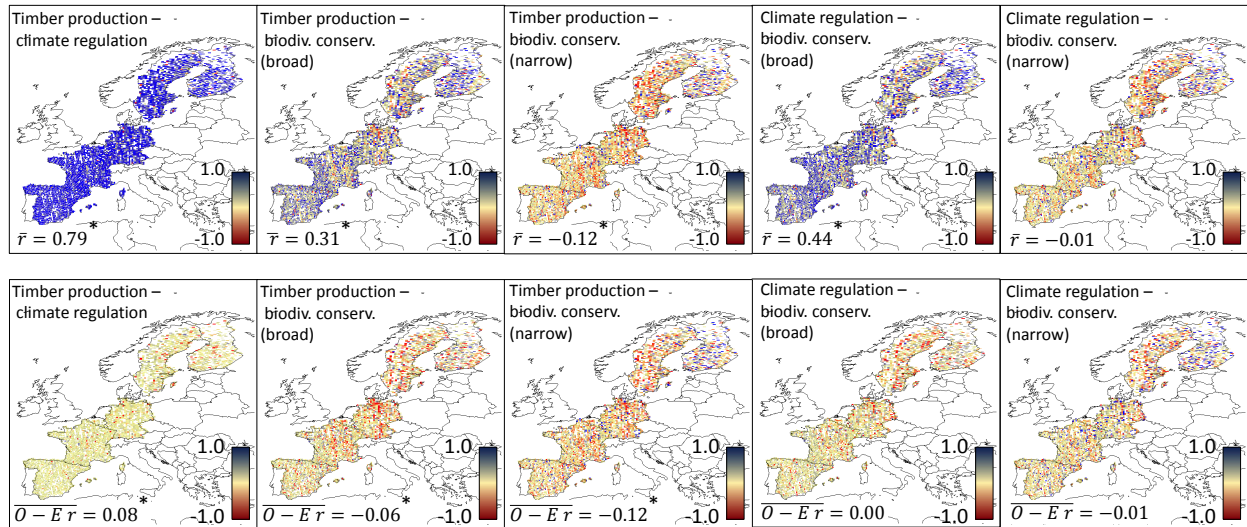
719 weights measure, all ecosystem functions are valued equally. In other measures, function

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.



727

728 Figure 2. While high values of continental-scale multifunctionality (A, C-F) in central Europe
 729 across a range of scenarios indicate large scale synergies, at local scales (B) high overall
 730 multifunctionality is realized in only a few sites. Mapped levels of predicted large-scale
 731 multifunctionality are rescaled as the proportion of functions above a 50% threshold. Green
 732 values indicate relatively high functioning, while brown values indicate relatively low
 733 functioning. In A), locations of fitting dataset plot are shown in red. In B, where overall, local-
 734 scale multifunctionality is shown, the histogram indicates that in only a few plots, levels exceed
 735 0.8.



736

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

738 Europe. Observed and observed minus expected correlation coefficients between

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

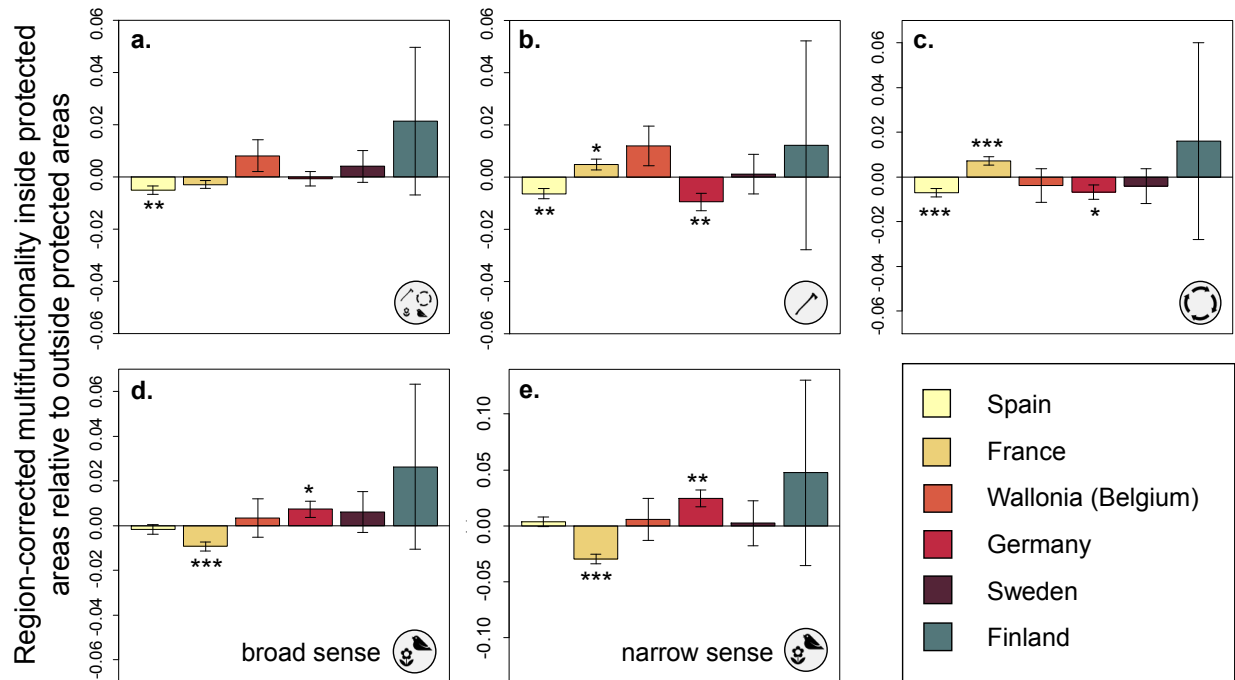
740 multifunctionality measures, except for the narrow-sense biodiversity conservation measure,

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

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

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

744



745

746 Figure 4. Local-scale ecosystem multifunctionality is generally not higher inside protected areas,

747 for different multifunctionality measures and countries. Bars above zero indicate that

748 multifunctionality is higher inside than outside protected areas, while bars below zero indicate

749 the opposite. A: Equal-weight multifunctionality. B: timber production multifunctionality. C:

750 climate regulation multifunctionality. D: broad-sense biodiversity conservation/recreation

751 multifunctionality. E: narrow-sense biodiversity conservation/recreation multifunctionality.

752

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 R² values and (c) only those plots within 20x20 km grid cells with a high
761 validation R² (>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

764