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1 **Title: High rates of short-term dynamics of forest ecosystem services**

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21 **Abstract**

22 Currently, the main tools for assessing and managing ecosystem services at large scales are maps
23 providing snapshots of their potential supply. However, many ecosystems change over short
24 timescales, thus such maps soon become inaccurate. Here we show high rates of short-term
25 dynamics of three key forest ecosystem services: wood production, bilberry production, and topsoil
26 carbon storage. Almost 85% of the coldspots and 65% of the hotspots for these services had
27 changed into a different state over a ten-year period. Wood production showed higher rates of short-
28 term dynamics than bilberry production and carbon storage. The high rates of dynamics mean that
29 static snapshot ecosystem service maps provide limited information for assessing and managing
30 multifunctional, dynamic landscapes, such as forests. We advocate that dynamic, spatially explicit
31 tools to assess and manage ecosystem service dynamics are further developed and applied in post-
32 2020 biodiversity and ecosystem service policy supporting frameworks.

33

34

35 Assessments of ecosystem services (ES) are pivotal in policy and land-use planning for sustainable
36 use of resources ¹⁻⁷. The main tools for assessing and managing ES are maps providing snapshots of
37 their potential supply ^{8,9}. Such static maps may enable the identification of areas of high or low ES
38 supply ¹⁰, or suggest spatial trade-offs and synergies amongst them ⁴. Large resources are allocated
39 to mapping ecosystem service supply on different spatial scales ^{5,11-13}. However, a major limitation
40 in the current management of ES is our poor understanding of how their potential supply changes in
41 space or over short timescales. ES dynamics result from dynamics of the environment, of the
42 species underlying ES, or management actions regulating the ES levels. These dynamics further
43 lead to constantly changing trade-offs and synergies through time. Consequently, static maps of ES
44 may soon become inaccurate after being produced. Static snapshot quantification and mapping of
45 ES may therefore lead managers to make erroneous inferences about ES delivery through space and
46 time, and thus manage ecosystems inefficiently. To effectively manage ES in changing landscapes,
47 we must account for how, and at what rates, different ES change.

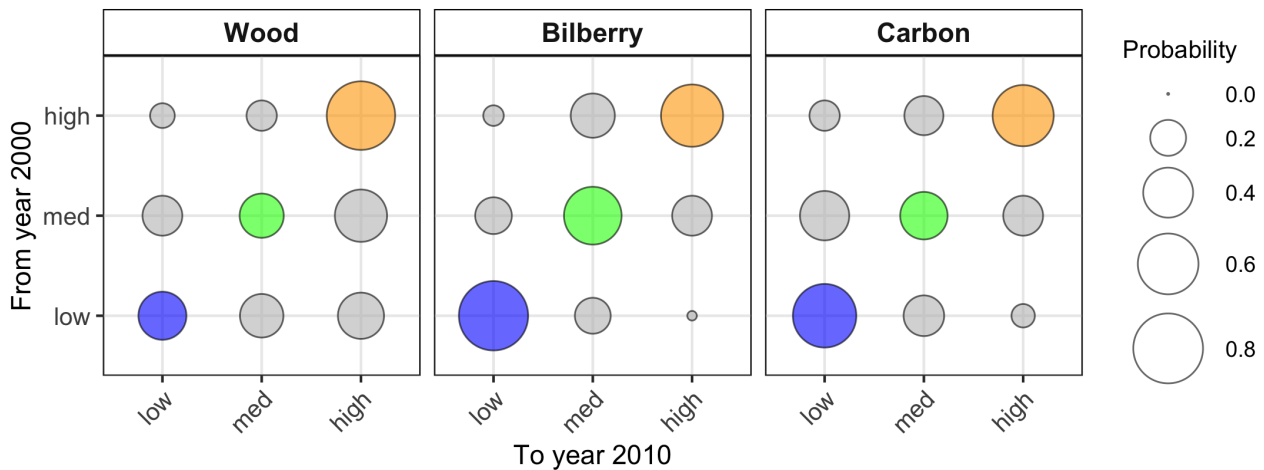
48 There is a paucity of studies that investigate how the short-term dynamics of ES affect our ability to
49 predict ES levels. An exception is the study of Holland et al. ¹⁴ that a decade ago inferred that
50 freshwater ES levels vary over the short term, based on samples of freshwater biodiversity
51 separated by five years. More recent studies have instead focused on gradual, long-term changes in
52 ES supply, mainly based on land cover maps or chronosequences ¹⁵⁻¹⁹. However, we are not aware
53 of any previous estimations of the *rates of short-term dynamics* in the levels of single or
54 combinations of ES based on measurements in the field. Thus, we need knowledge on these
55 potentially complex short-term ES dynamics, and how they may change over time. Knowledge on
56 these dynamics is needed to estimate the near future ES levels and also to understand the limitations
57 of static mapping of ES in assessing and managing ecosystems.

58 In this study, we use a nationwide Swedish forest dataset and present estimates of the short-term
59 dynamics of important boreal forest ES, including hot- and coldspots for these services. Boreal
60 forest is the largest terrestrial biome globally ²⁰; it constitutes 45% of the timber stock ²¹, and stores
61 one third of the forest carbon ^{22,23}. Moreover, the Nordic countries are large providers of wood to
62 the continuously growing global market ²⁴. In addition, other forest ES hold large values, for
63 instance, the estimated annual value of the harvested berries in Finland is 100 M€ ²⁵. Here, we ask if
64 there are differences in the rates of short-term dynamics between sites with high, medium, and low
65 levels of the ES wood production, bilberry production, and topsoil carbon storage (Supplementary

66 Table 1). We also examine whether there are differences in the rates of dynamics between single
67 services, and hot- and coldspots of all three services. This includes investigating whether the short-
68 term dynamics of ES change through succession, i.e. as the forest ages through time. Finally, we
69 test the importance of different environmental conditions in explaining the occurrence of hot- and
70 coldspots. We hypothesize that wood production in particular shows high rate of short-term
71 dynamics since this ES is intensively managed. We expect to observe the highest rate of ES
72 dynamics in young forest. Moreover, as hot- and coldspots summarize the levels of several ES, we
73 expect them to be even more dynamic than the individual ES of which they are composed. Finally,
74 we hypothesize that the occurrence of hot- and coldspots are explained by the most important
75 variables explaining the ES composing them, specifically tree species richness and biomass of tree
76 species ²⁶.

77 SHORT-TERM DYNAMICS OF SINGLE ES

78 Wood production showed higher rates of short-term dynamics than bilberry production and topsoil
79 carbon storage over the ten-year period, from 2000 to 2010 (Fig. 1). We categorized sites as having
80 ‘high’, ‘medium’ and ‘low’ levels of ES (see Fig. 1 caption for definition), and found that more
81 than half of the sites with low (63%) and medium (69%) wood production in 2000 had changed into
82 another wood production category by 2010. For high production sites, 23% had changed. Bilberry
83 production was the least dynamic ES with 21%, 46% and 37% of low, medium, and high sites,
84 respectively, changing into another category by 2010 (Supplementary Results 1 and Supplementary
85 Table 2). For carbon storage the corresponding changes were 34%, 64% and 39%. There are thus
86 substantial changes in the levels of forest ES when comparing one snapshot to another one,
87 separated by only ten years. For details on how these estimators were calculated, see Supplementary
88 Result 1 and Supplementary Table 2. Additionally, we found that the mean rate of short-term
89 dynamics of wood production was higher than that of bilberry and carbon storage dynamics, but
90 there was no difference in mean rates between the latter (Supplementary Table 3). The mean of all
91 ES increased at sites where the level was low in 2000 and decreased in two ES at sites where the
92 level was high (see Supplementary Fig. 1 for further details), reflecting the dynamics of the system.
93 Indeed, these changes in means did not result in also changes in category at more than 50% of these
94 sites (except that 63% of sites with low wood production changed category). This is possible as the
95 estimators of change in Fig. 1 and Supplementary Fig. 1 are different. Within and between the
96 bubbles in Fig. 1, changes take place, and the mean and distribution of all these changes are
97 presented in Supplementary Fig. 1.

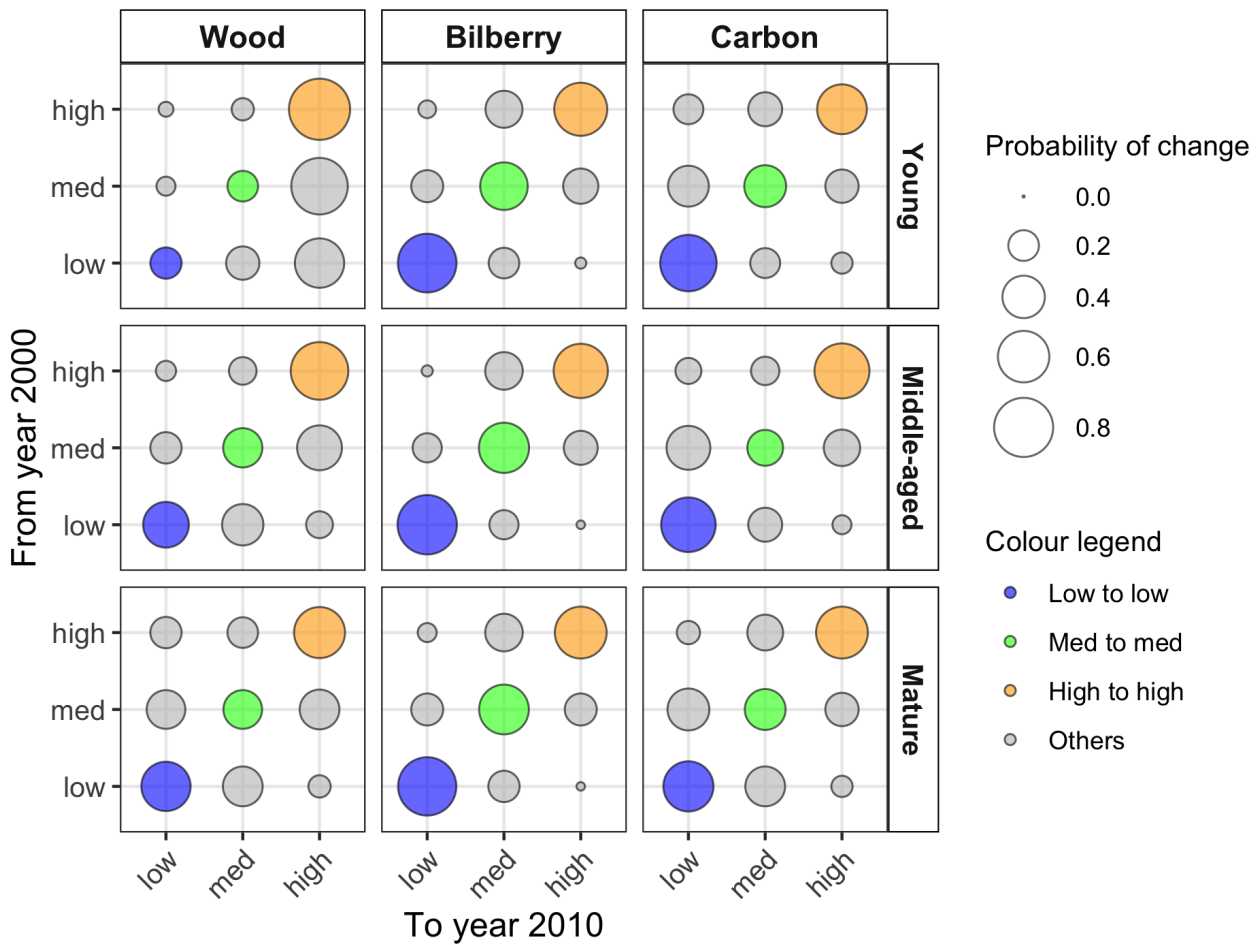


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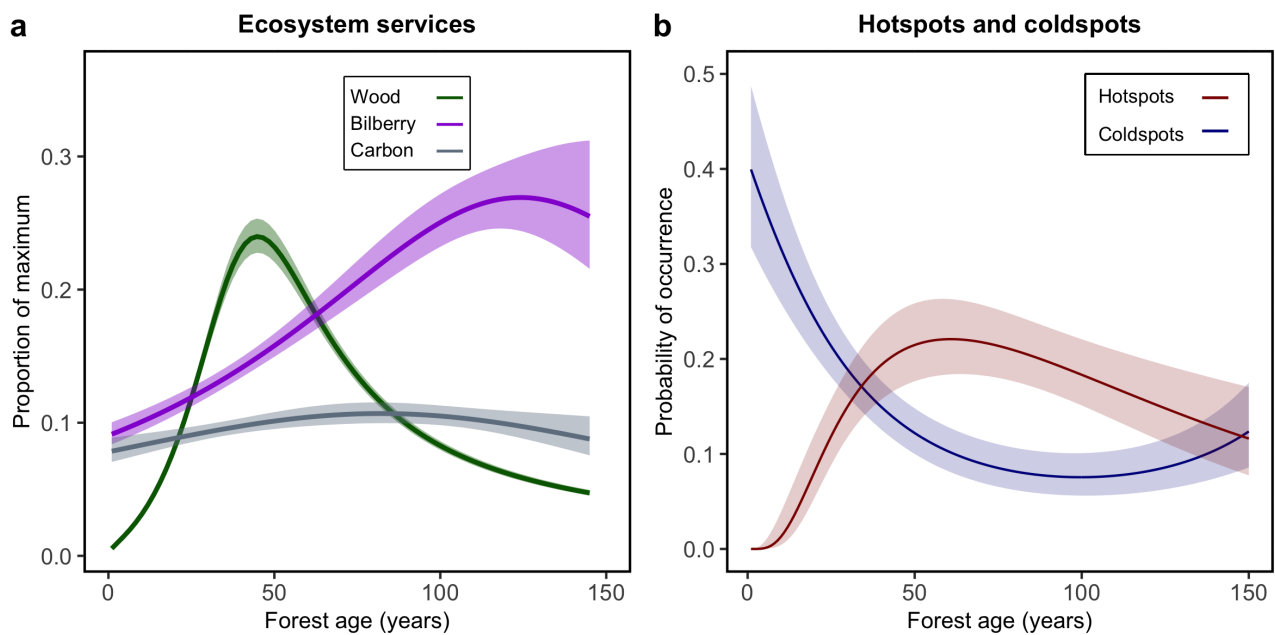
99 **Fig. 1 | Rates of short-term dynamics of single forest ES shown as probabilities of sites changing**
 100 **between categories over a 10-year period.** ‘High’ delivery is defined as the ES having a value higher than
 101 the 65th percentile of its maximum value observed, ‘low’ has a value lower than 35th percentile of its
 102 maximum, and ‘med’(medium) is in between (35th-65th percentiles). Changes into other categories are grey,
 103 while categories staying the same (i.e. no change) along the diagonals are blue for low staying low, green for
 104 medium staying medium, and orange for high staying high.

105 CHANGE IN SHORT-TERM DYNAMICS AS FOREST AGES

106 For wood production, the rates of short-term dynamics changed as the forest became older. Thus,
 107 the change in the levels of forest ES when comparing one snapshot to another separated by ten
 108 years varied with forest age. Specifically, the probability of sites changing from one ES category
 109 into another changed with age (Fig. 2). Sites were categorized into three age classes: young (<40
 110 years); middle-aged (40-70 years); and mature (>70 years). Sites delivering low levels of wood
 111 production were more dynamic in young forests (79% of the sites changing into another category)
 112 than in mature forests (45% changing into another category) (see Fig. 2 and Supplementary Result 2
 113 and Supplementary Table 4a for details). In contrast, sites with high wood production were more
 114 dynamic in mature forests (41% of the high sites changed to medium or low levels) than in young
 115 forests (14% changed). There was no clear change in the rates of dynamics of bilberry production or
 116 topsoil carbon storage as the forest aged (Fig. 2 and Supplementary material Table 4a). These
 117 results can be explained by changes in the mean rate of short-term dynamics in wood production as
 118 the forest ages (Supplementary Fig. 2). For bilberry, this relationship to age was weaker and for
 119 carbon storage it was detectable only at sites with low carbon storage.



132 Sites with high or low levels for all three of the ecosystem services considered, hereafter called
 133 hotspots and coldspots, respectively, are of particular interest for ES assessments. The probability
 134 of hotspot occurrence increased as the forest reached middle-age, and then decreased when the
 135 forest became older (Fig. 3b). This decrease in old forest was driven by decrease in wood
 136 production (Fig. 3a), in this study which included three ES. In contrast, the probability of coldspot
 137 occurrence decreased with age, being highest in young forests during the first decades after
 138 clearcutting.



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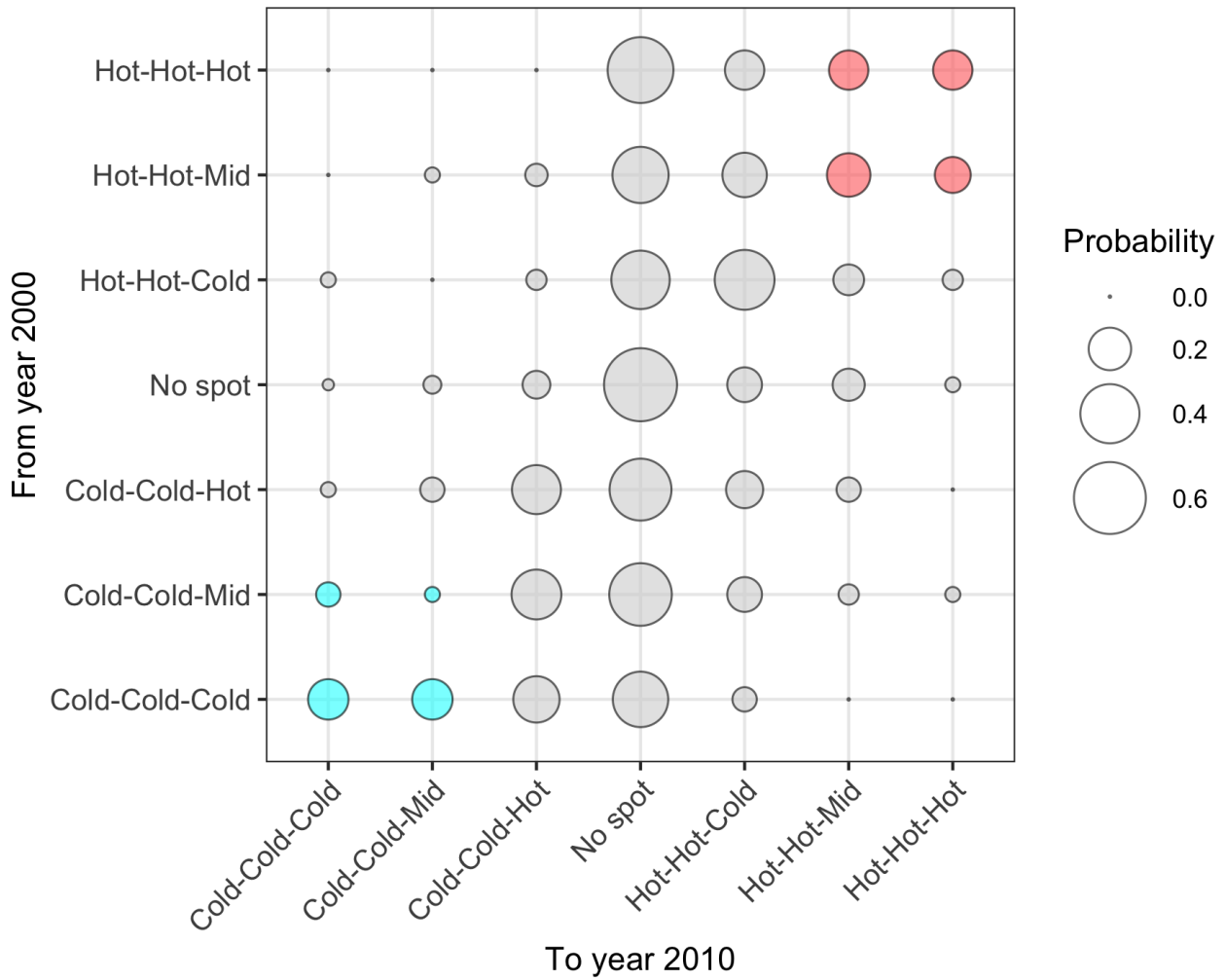
140 **Fig. 3 | Changes in single ES and hot- and coldspots through forest succession.** a,b, Predictions of single
 141 ES (proportion of the maximum value observed) (a) and probabilities of occurrence of hot- and coldspots (b)
 142 through forest succession based on generalized linear models (with 95% confidence bands). Hotspot is
 143 defined as at least two of the ES having a value higher than the 65th percentile of their maximum value and
 144 none having a value lower than the 35th percentile of their maximum, and coldspot as at least two of the ES
 145 having a value lower than the 35th percentile of their maximum and none having a value higher than the 65th
 146 percentile of its maximum.

147 The relationships between hot- and coldspots and forest age through succession were mainly driven
 148 by the development of the tree layer (Fig. 3b and Supplementary Tables 8-11 for model details), as
 149 indeed also shown earlier for single ES²⁶. This is confirmed by different relationships between hot-
 150 and coldspots and forest age when jointly accounting for all other variables in models with multiple
 151 variables (Supplementary Fig. 3). Thus, the relationships in Fig. 3 are driven by increasing biomass
 152 of the different tree species and species richness rather than by the increasing forest age *per se*.

153 More specifically, the probability of hotspot occurrence increased with increasing tree species
154 richness and the biomass of spruce, pine and birch (full model results in Supplementary Table 10).
155 In addition, the probability of hotspot occurrence decreased with pH and increased with soil
156 moisture, but was lower on peat soils. Finally, there was a non-linear relationship between hotspot
157 occurrence and temperature. The probability of coldspot occurrence correspondingly decreased with
158 increasing tree species richness and the biomass of trees, with an interaction effect between pine
159 and age (Supplementary Table 11). The probability further increased with pH and decreased with
160 soil moisture, temperature, and nitrogen deposition.

161 SUMMARY OF SHORT-TERM DYNAMICS OF COMBINED ES

162 The majority of the hotspots and coldspots changed into another category during the ten-year study
163 period (Fig. 4), and these changes were generally higher than for individual services (Fig. 1).
164 Specifically, 65% of the hotspots and 84% of the coldspots changed into another category (Fig 4,
165 Supplementary Table 12), as compared to 23-69% for individual services (Supplementary Table 2).
166 The hotspot sites were more likely to remain hotspots than the coldspot sites were to remain
167 coldspots ($Z = 2.4$, $N = 128$, $p = 0.016$, see details on transitions in Supplementary Table 12a). The
168 most stable category was No spot. This is not surprising as it is the biologically widest one covering
169 a wide range of ES levels, being based on 13 categories (see Supplementary Table 14). The
170 probability of hotspot becoming coldspot, and vice versa, was very low, whereas No spot sites
171 could end up in any category over the 10-year period.



172

173 **Fig. 4 | Joint short-term dynamics of combined ES quantified as the probabilities of sites changing to**
 174 **another category over a ten-year period.** The seven categories are based on the 27 possible combinations
 175 of the three levels ‘high’, ‘medium’ and ‘low’ for the three ecosystem services. These ranged from category
 176 Cold-Cold-Cold becoming increasingly warmer via No spot to category Hot-Hot-Hot. The levels concern
 177 any ES, so that in e.g. Hot-Hot-Cold, Cold represents low supply of any of the services. Hotspots are
 178 represented by red bubbles and coldspots by blue bubbles. See Methods and Supplementary Table 14 for a
 179 full description.

180

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182

183 **Discussion**

184 This study is the first to provide clear evidence for high rates of short-term dynamics in the supply
185 of both single ecosystem services, and of hot- and coldspots of multiple ES, in a production
186 ecosystem of large-scale societal importance. We used direct measures of the short-term dynamics
187 of the ES from field data from a whole country. Previous studies have instead inferred such
188 dynamics from biodiversity measures¹⁴ or presented gradual long-term changes using indicators of
189 ES^{18,19}. Observing such high rates of dynamics means that static maps of ES, as are used in present
190 ES assessments (e.g. in the European Union)^{5,27-31}, do not provide adequate information to make
191 well-informed management decisions³⁰⁻³². Static maps are snapshots and do not account for the
192 complex short-term dynamics of ecosystems. They may therefore lead managers to make erroneous
193 inferences about potential ES delivery through time, and consequently manage ecosystems
194 inefficiently. In addition to the forests studied here, this is also likely to be the case for other
195 production ecosystems in which dynamic ecosystem functions, natural conditions, or management
196 practices cause short-term dynamics in ecosystem service levels.

197 HOT- AND COLDSPOTS ARE MORE DYNAMIC THAN SINGLE ES

198 The reliance on static maps is particularly inappropriate for managing multifunctional landscapes,
199 i.e. for multiple ecosystem services instead of single services. This conclusion is supported by our
200 finding that combinations of high or low levels of several ES simultaneously, i.e. hotspots and
201 coldspots, showed high rates of short-term dynamics (Fig. 4), and somewhat higher rates than sites
202 delivering high or low levels of single services (Fig. 1). Almost 85% of the coldspots and 65% of
203 the hotspots changed over a 10-year period, and for single ES, 23-69% of the sites changed from
204 having high, medium, or low levels. The most likely explanation for the higher rates of dynamics of
205 hot- and coldspots compared to single services is that different individual services have different
206 spatio-temporal dynamics. The level of an ES is determined by a wide range of management actions
207 and environmental conditions, not least tree species richness and their biomass²⁶. Moreover, the
208 occurrence of hot- and coldspots were also largely determined by tree species richness and their
209 biomass (Supplementary Tables 10 and 11), in combination with soil moisture and chemistry, and
210 regional variation in temperature and nitrogen deposition. These actions and conditions also
211 manifest in different trajectories of ES levels through time, with our three example services
212 showing increasing, stable, or positively humped-shaped trajectories (Fig. 3). However, the

213 relationships are largely determined by the tree layer (see Gamfeldt et al. ²⁶ for individual services),
214 which is further determined by forest management.

215 Wood production showed the highest rate of short-term dynamics of our study services (Fig. 1).
216 There was a high probability of change for sites with high, medium and low levels over a 10-year
217 period. These dynamics differed between young and mature forests (Fig. 2). Likely explanations for
218 these dynamics are that wood production depends on a wide range of environmental conditions
219 ^{26,33,34} and that management efforts usually focus on this service, which is harvested approximately
220 when the ES is at a high level from an economic perspective. In contrast, bilberry production
221 showed the lowest rate of dynamics (Fig. 1-2). This is likely explained by its stability and
222 dominance in mature stands ³⁵. On the other hand, this is a proxy and actual berry counts may vary
223 between years ³⁶. Topsoil carbon storage showed intermediate rates of dynamics (Fig. 1) and
224 remained quite stable as the forest aged (Fig. 2). A likely reason is that its level and dynamics are
225 largely determined by the slow rates of litter and root decomposition related to mean temperature
226 and soil moisture ³⁷.

227 DYNAMICS CHANGE THROUGH FOREST SUCCESSION

228 Hotspots were most frequent in middle-aged forests, whereas coldspots were most frequent in
229 young forests during the first decades after clearcutting (Fig. 3). These findings reflect the changes
230 in the supply of high and low levels of these particular three services through succession. The
231 decrease in hotspots in older forest was driven by decreasing wood production, while bilberry and
232 many other ecosystem services increase in old forests ³⁸. The changes through succession are not
233 driven by age *per se*, but by the developing tree layer (tree species richness, composition and tree
234 biomass, see Supplementary Tables 10-11, Supplementary Fig. 3). Wood production changed
235 unimodally with age. After clearcutting (the most common harvesting method in northern European
236 forests), wood production was low during the first 20 years, but then increased quickly and peaked
237 in middle-aged forest. Thereafter, wood production decreased in these production forests. However,
238 recent work has showed it to be stable 50-100 years beyond the recommended harvesting age ³⁹,
239 which in Sweden is around 70-100 years. Bilberry production showed a linear increase as the forest
240 aged, reaching its maximum in mature and old-growth forests of over 100 years old (Fig. 3).
241 Previous studies show that bilberry yields are highest in mature stands and decrease drastically after
242 clear-cutting as they are sensitive to soil disturbance and scarification ³⁵. Finally, topsoil carbon

243 storage remained quite stable as the forest aged (Fig. 3). This seemingly contrasts earlier studies
244 showing increasing carbon storage through time. However, most previous research has focused on
245 other organic matter components than topsoil carbon, such as above or belowground biomass^{40,41}.

246 The fact that different ES follow different paths through succession implies that if we increase the
247 number of ES under study, we may find even more types of dynamics. These findings imply that it
248 will be increasingly difficult to provide high levels of multiple ecosystem services at the stand level,
249 as the demand for different forest ES from various societal actors increases. This suggests that
250 innovative landscape level solutions that increase forest diversity in space and time may have to be
251 developed for future forests to provide multiple ES to society. These solutions could involve
252 landscape-scale optimization approaches.

253 FUTURE DIRECTIONS

254 In a time of intensive resource exploitation and climate change, the capacity of ecosystems to
255 sustain many services and goods to society is uncertain. The ultimate goal of managing ecosystems
256 should be to assure and maintain the supply of *multiple* ES across space and through time^{34,42}.
257 However, the high rate of short-term dynamics of the hotspots (Fig. 4) and single services (Fig. 1)
258 challenges this joint maximization. Earlier work has focused on explaining service levels at certain
259 sites or in the landscape, e.g.^{26,33}, but has not accounted for their short-term dynamics. The
260 provisioning of ES is spatially heterogeneous and few areas provide high levels for multiple
261 services through time^{28,43}. Structural heterogeneity of the forest may promote the supply of
262 multiple ES⁴⁴, and some of the ES develop in a predictable way as the tree layer develops. In fact,
263 the optimization approach used by the industry and research on forest is suitable to identify
264 management that provides high levels of multiple ES at the landscape scale, e.g.^{42,45}. The approach
265 starts with formulating objectives to be fulfilled for the study landscape over a specified time
266 horizon (objectives that actors and stakeholders ideally agree on). Next, a large number of
267 management alternatives for each stand and each time step into the future is simulated. Finally,
268 mathematical optimization is used to select, for each stand, the management that jointly fulfils the
269 objectives initially agreed upon for the landscape, e.g.^{42,46}. The ES of interest can be included in the
270 form of predictive regression models that are becoming increasingly available, e.g.³⁵.

271 Short-term dynamics of ES are likely to be important in other production ecosystems as well. For
272 example, in agricultural landscapes, short-term dynamics are inevitable consequences of various
273 crop rotation systems^{47,48}. Rotations may range from simple ones with one or two species to
274 complex rotations with 6-7 species of crops over a rotation⁴⁹. More complex rotations have the
275 potential to replace the current dominance of a few crops over large areas, which require
276 management using fertilizers and pesticides^{47,49}. Understanding ES delivery from crop rotation
277 systems thus requires a more dynamic perspective where different crop species, sequences and their
278 distribution in the landscape interact with ecosystem services, e.g., biological control, pollination,
279 or carbon sequestration having joint but partly independent dynamics. The optimization approach to
280 assess multiple ecosystem services over time discussed for forests above may also be useful here,
281 again assuming that farm economy and other societal goals are compatible. In marine systems, the
282 fish resource itself moves around on different spatiotemporal scales and the short-term population
283 dynamics of fish have formed the basis for jointly managing this and other ES⁵⁰. Nevertheless,
284 Gissi et al.³⁰ recently proposed to incorporate temporal change in the spatial planning of marine
285 areas, and Maxwell et al.³¹ now criticize the developing agreement of the United Nations
286 Convention on the Law of the Sea for lack of focus on the fact that both catches and fisheries are
287 highly mobile. For certain ecosystems, such as forests, there is a fairly long tradition of planning
288 management using dynamic, spatially explicit decision support systems, e.g.⁵¹. Some of these
289 already include ES and incorporate optimization tools^{45,46}.

290 A limiting factor to adopting more dynamic and spatial approaches for ES management can be the
291 lack of predictive models for how ES of interest respond to changes in abiotic and biotic conditions
292 and management, e.g.³⁵. We therefore advocate allocating more resources to research on the
293 processes driving both the short-term and long-term dynamics of ES, where long-term in forestry
294 may be 30 years or more, and in agriculture at least one or several crop rotations, i.e. 7-15 years.
295 Moreover, we look forward to a transition from the current dominant use of static maps into more
296 frequent use of dynamic tools and perspectives in the EU and global post-2020 biodiversity and ES
297 policy supporting frameworks, such as the EU Biodiversity Strategy for 2030.

298

299

300 **Methods**

301 FOREST MANAGEMENT AND FOREST DATA

302 We studied Swedish boreal and boreo-nemoral forest composed of approximately 40% Scots pine
303 (*Pinus sylvestris*), 40% Norway spruce (*Picea abies*) and 20% broadleaved trees⁵². The low
304 proportion of broadleaved trees is due to the dominant clearcutting forestry that focuses on conifers.
305 After clear-cutting, there is often abundant natural regeneration of broadleaved trees, while conifers
306 are mainly planted. The rotation length is 70-150 years, and is shortest in the south⁵³. There are one
307 to three thinning events per rotation. The aim of thinning is typically to reduce broadleaved trees
308 but also to decrease competition from, and extract, naturally regenerated conifers.

309 We used a nation-wide forest dataset from the Swedish National Forest Inventory and the Survey of
310 Forest Soils and Vegetation, covering an area of 400,000 km² of land. Hereafter the inventories are
311 referred to as the NFI. The inventory uses a regular sampling grid with a randomly selected starting
312 point covering the whole country⁵⁴, with each tract being surveyed once every 5 years. The tracts,
313 which are rectangular in shape and are of different dimensions in different parts of the country,
314 consist of 8 (in the north) to 4 (in the south) circular sample plots. The circular plots have different
315 radii (5-20 meters) to ensure that the variables recorded characterize the short-term forest dynamics
316 and management. We used only plots on ‘productive forest’ (average production of standing
317 volume, stem volume over bark >1 m³ ha⁻¹ year⁻¹, 21 million hectares in Sweden). To be included
318 in our analyses, the plots had to be located on only forested land, i.e., not including any river, road,
319 grassland, etc. For the current study, we utilized data on the focal ES, forest age and other
320 environmental variables (Supplementary Table 15). The NFI sampling is designed for the data to be
321 representative of the common forest habitats, with a yearly budget for fieldwork and data
322 maintenance of 4.7 MEuro.

323 ECOSYSTEM SERVICES

324 The three ecosystem services studied can be classified according to the Common International
325 Classification of Ecosystem Services and Nature’s Contributions to People (Supplementary Table
326 1). Thus, they are of high economic, cultural and/or recreational importance.

327 *Wood production*

328 Wood production was estimated as the yearly change in tree biomass ($\text{kg m}^{-2} \text{ year}^{-1}$), calculated
329 over a period of 5 years for all tree individuals higher than 1.3 meters. For plots where biomass was
330 measured in 1999-2002, the baseline for wood production was thus measurements of biomass in the
331 years 1994-1997 (hereafter referred to as ‘2000’), and correspondingly, we used data from 2008-
332 2012 and 2003-2007 for what we hereafter refer to as year ‘2010’. We excluded plots that had been
333 harvested, cleared, or thinned within the two periods of measuring biomass for calculating
334 production, e.g. 2008-2012 to 2003-2007. Biomass was calculated using biomass functions^{55,56} and
335 was the sum of the biomass from the stem, twigs and branches, the stump and roots. For deciduous
336 tree species, there is only a function for *Betula spp.*, and this function was applied to all other
337 deciduous tree species. The *Pinus sylvestris* function was applied to *Larix decidua* and *Pinus*
338 *contorta*. Even though this creates a slight tree species bias, it has minor effects on our production
339 estimates since we calculated the difference in biomass between two points in time. This is a
340 provisioning service. The sample size for wood production was 4,444 plots.

341 *Bilberry production*

342 Bilberry production was measured as the percentage of the plot covered by bilberry (*Vaccinium*
343 *myrtillus*). The cover of bilberry is the main predictor of the annual bilberry production³⁵ and berry
344 production further varies between years³⁶. The cover of bilberry is strongly correlated with the
345 annual bilberry production^{35,57}. Bilberry is one of the most economically important wild berry
346 species in northern Europe³⁵. In addition to being a provisioning service, the recreational value of
347 picking bilberries also makes it a cultural service. We used data from 2,187 plots inventoried 1999-
348 2002 (hereafter ‘2000’), and 2009-2012 (hereafter ‘2010’).

349 *Topsoil carbon storage*

350 Soil carbon storage was measured as the amount of carbon (g m^{-2}) in the topsoil of the plot, which
351 consisted of either purely organic horizons, i.e. mor layers (63%) or peat layers (21%), or less
352 frequently of minerogenic A-horizons (16%). This is the part of the soil most affected by the current
353 above-ground biota. To compensate for the conceptual difference in topsoil types, mean soil carbon
354 stocks were set equal for purely organic soils (measured in the organic horizon down to a maximum
355 depth of 30 cm) and minerogenic topsoils (measured in the top 10 cm horizon). The soil fraction <2
356 mm was analysed. We used data on this regulating service from 2,001 plots inventoried 1999-2002
357 (hereafter ‘2000’), and 2009-2012 (hereafter ‘2010’).

358 CATEGORIES OF ES LEVELS, HOT- AND COLDSPOTS

359 For each of the three ES we defined three levels: high, medium, and low. ‘High’ level was defined
360 as plots with values higher than the 65th percentile of the maximum value observed when
361 combining the data from both snapshot inventories (2000 and 2010), ‘low’ level was defined as
362 plots with values lower than the 35th percentile of the maximum observed when combining both
363 datasets, while ‘medium’ level was defined as plots in between, i.e. higher or equal than the 35th
364 and lower or equal than the 65th percentiles of the maximum observed.

365 There is a wide range of methods to define hotspots and coldspots, and the most appropriate one
366 depends on the purpose of the study ⁵⁸. We used thresholds to define them ⁵⁹. Specifically, hot- and
367 coldspots are plots with high and low potential of ES supply. Hotspots were defined as at least two
368 of the ES having high level and the third having high or medium level. Coldspots were defined as at
369 least two of the ES having low level and the third having low or medium level (see Supplementary
370 Table 14). We also conducted a sensitivity analysis of the use of different sample sizes for different
371 ES, which did not change our conclusions, see Supplementary Fig. 4 and Supplementary Table 16
372 in Result 3. We further combined the levels ‘high’, ‘medium’ and ‘low’ for the three ES in 27 ways
373 (Supplementary Table 14). To summarize the findings for this large number of combinations, we
374 also aggregated them into seven coarser combinations according to Supplementary Table 14. These
375 ranged from the category Cold-Cold-Cold becoming increasingly warmer via No spot into the
376 category Hot-Hot-Hot.

377 To support our investigation of short-term dynamics of ES, we modelled and predicted the single
378 ES and hot- and coldspots as a function of forest age using data from 2000 (Fig. 3 and
379 Supplementary Tables 5-9). We also tested the importance of tree species richness, their biomass
380 and other environmental conditions in explaining the probability of hot- and coldspot occurrence
381 (Supplementary Tables 10-11). For corresponding tests for the individual ES using these data, see
382 the study by Gamfeldt et al. ²⁶. For modelling single ES (Fig. 3a), we used data from 2,001-4,444
383 plots (see above). Wood production was measured on all plots. Bilberry production was not
384 measured on all plots where topsoil carbon storage was measured, but there was a proportion of
385 plots where both were measured. In total, we had a sample of 996 plots where all three ES were
386 measured. This constitutes the sample for modelling hot- and coldspots in 2000 (Fig 3b).

388 We generally quantified the rates of short-term dynamics as the percent of plots that changed into
389 another category over a ten-year period, here 2000 to 2010. Ten years is the typical frequency of
390 updating forest management plans. Indeed, estimates of rates of dynamics are improved with
391 increasing number of surveys. However, our data from two nationwide surveys represent
392 approximately 21 million hectares of forest land and include a wide range of environmental
393 gradients. We expressed this rate as the probability (expressed as percentage) of a transition into
394 another category. In statistical terms, these probabilities (p) are the expected values of the Bernoulli
395 distribution, with variance $p(1-p)$, which we also presented. For bilberry, for example, the top left
396 bubble in Fig. 1 reflects the value 0.06 presented in Supplementary Table 2a. This value was
397 obtained by first determining the number of plots classified as having high cover in 2000 and being
398 resurveyed in 2010 (680) (No. plots in Supplementary Table 2a). Next, we determined which of
399 those plots were classified as having low cover in 2010 (41). Finally, we divided these values,
400 $41/680 = 0.06$. The variance was calculated as $0.06(1-0.06) = 0.056$ (Supplementary Table 2b). We
401 calculated these rates and probabilities both for single ES, and between seven aggregations of the
402 27 possible combinations (Supplementary Table 14) of coldspots, No spots, hotspots, etc. (results in
403 Fig. 4 and Supplementary Table 12). For a sensitivity analysis of these estimates of probabilities of
404 transitions, see Supplementary Figs. 3-4 and Supplementary Tables 16-17 in Result 3. We presented
405 these probabilities for the whole country and for three forest age classes: (i) young forests: less than
406 40 years, (ii) middle-aged forests: 40-70 years, and (iii) mature forests: older than 70 years, which
407 are ready to be harvested or are old-growth (more than approximately 130 years). To test whether
408 there was a difference in probabilities for hotspots remaining hotspots compared to coldspots remaining
409 coldspots, we fitted a generalized linear model. As these are binary response variables, we assumed
410 Bernoulli distributions.

411 To complement the estimates of short-term dynamics based on rates of transitions described above,
412 we also investigated both mean rates of ES dynamics and changes in mean levels. Specifically, we
413 tested whether there were differences in the mean rates of short-term dynamics of change between
414 the ES using pairwise t -tests (Supplementary Table 3). We also tested whether the mean levels of
415 each ES changed between 2000 and 2010 for sites categorized as either high, medium, or low, using
416 paired t -tests assuming equal variances in ES levels in the two years (Supplementary Figure 1).
417 Finally, we modelled the rate of short-term dynamics of each ES and forest age for sites categorized

418 as either high, medium, or low (Supplementary Figure 2). We selected these models, specifically
419 including (or excluding) age and age squared, based on Akaike's Information Criterion (AIC) ⁶⁰.

420 ES THROUGH SUCCESSION AND GIVEN THE ENVIRONMENT

421 We investigated whether levels of single ES (proportion of maximum observed) and probabilities of
422 occurrence of hot- and coldspots changed through forest succession. Thus, we used space for time
423 substitution in which the contemporary spatial pattern is used to approximate the unobserved 150
424 years process (Fig. 3). We also tested the effect of other environmental variables on probabilities of
425 hotspot and of coldspot occurrence (Supplementary Tables 10 and 11). Specifically, we applied
426 generalized linear modelling with forest age and other explanatory variables (see Supplementary
427 Table 15 for variables). We assumed gamma distributions for the single ES and Bernoulli
428 distributions for the hot- and coldspots (see Supplementary Tables 5-11 for modelling results). We
429 selected among models based on AIC, on parameter estimates associated with the variables and on
430 knowledge of the biological system studied. This included testing different transformations and
431 squared terms of the variables. We first assessed the predictive power of each explanatory variable
432 based on AIC and on the parameter estimates. Next, we fitted a multiple model containing the
433 retained explanatory variables. Finally, we simplified this complex model by excluding and again
434 including earlier excluded variables in a stepwise procedure. All analyses were carried out using the
435 R software environment ⁶¹. We used the R packages ggpubr (v.0.3.0) and ggplot2 (v. 3.3.0) to
436 produce figures.

437 **Data availability**

438 The data used for this study are archived and openly available from the University of Jyväskylä
439 Dataverse Network (http://dvn.jyu.fi/dvn/dv/Boreal_forest).

440 **Code availability**

441 The code used to analyse the data and produce the figures is available from the corresponding
442 author upon request.

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451 **Author contributions**

452 T.S. conceived and obtained financial support for the study, and discussed the design with J.B., J.M.
453 and L.M.; M.T., L.M. and T.S. analysed the data; M.T. designed and produced the figures with the
454 input of all authors; T.S. and M.T. wrote the first draft of the manuscript. All authors interpreted the
455 results and provided input on the manuscript.

456 **Competing interests**

457 The authors declare no competing interests.

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